Assessing the effects of fishing on fish communities using South African case studies: empirical and theoretical approaches

Dawit Yemane Ghebrehiwet

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

UNIVERSITY OF CAPE TOWN

February 2007

Supervisors:	Prof. John G. Field
	Dr. Rob W. Leslie
	Dr. Yunne –J. Shin

DECLARATION

The outcomes presented in this thesis are my own except those acknowledged below and in the acknowledgement section of the thesis. Starting with theoretical section the OSMOSE model used was developed by Dr. Yunne –J. Shin in IRD, CRH. For the purposes of this thesis I added some methods to the model to enable generation of outputs by grid cells and the spatial implementation of fishing mortality. Initial conception and development of the project was greatly facilitated by Prof. John G. Field whom I thank greatly. All major support towards the successful completion of this thesis are either acknowledged in the acknowledgment section or cited in the text. Some of the work presented in this thesis is already published thus I acknowledge helpful comments from anonymous referees.

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

....

Dawit Yemane Ghebrehiwet

ACKNOWLEDGEMENTS

During the progress of this thesis many individual have helped me directly or indirectly. I summarise here the support and encouragement of those individuals or institution without whom the thesis would not have been completed. To begin with my deepest gratitude and appreciation goes to my three supervisors (Prof. John G. Field, Dr. Rob W. Leslie, and Dr. Yunne –J. Shin) for their understanding, patience, critical but positive comments on my work, and kind approach towards me. Prof. Field always believed I could improve and encouraged me from the beginning when I started my Masters thesis. He helped me to improve my English, though I still have more to learn. I also thank him for teaching me science and letting me teach myself. Dr. Leslie has been very helpful in improving my knowledge of the south coast demersal fishery. I would like to thank him for always picking up fisheries issues in my work which I either forgot or thought unimportant. I thank Dr. Shin for teaching me Java programming and encouraging me in understanding the IBM model OSMOSE and adding some methods to the model. I would like to thank Dr Marc Griffiths for his support for the works presented in Chapters 2 and 3. He has been helpful in increasing my understanding of the linefishery of South Africa and he kindly shared his expertise and data.

My appreciation and gratitude also goes to researchers from MCM: Dr. Lynne Shannon (data relevant for OSMOSE), Dr. Carl van der Lingen (information on spatial distribution of species in OSMOSE), Janet Coetze (information on spatial distribution of species in OSMOSE), Jean Glazer (effort information for the demersal hake directed trawl fishery), Phoeby Mullin (longline effort information),

Dr. Colin Attwood (suggesting possible area of the proposed MPAs). I thank Dr. Larry Hutching for his insight into anything in the southern Benguela whenever I had the chance to talk to him. I would like to thank all of them for their open and helpful discussions whenever I jumped into their offices without prior notice. In the department of Mathematics and Applied Mathematics: Rebeeca Rademayer for kindly providing me with hake catch data. From our lab: Margit Wilhelm, David Miller, Maya Pfaff, Elliot Weni, Nontsasa Tobi, Sergio Neira; I thank you all for my interactions which were usually fun. I always remember and thank Evie Wieters, Maya, Tore Johannesson, and Margit for the friendly and enjoyable coffee breaks and the wonderful coffee I had with them all. From our department: Dr. Coleen Moloney (for some discussion on chapter 3), Andrea Plos (technical issues), Gilly Smith (kind help for renewing my study permit). I would like to thank many individuals from IRD for their help and friendship during my stay in Sete, France. Dr. Laurent Drapeau for discussion about some spatial issues and lending me S-Plus software, and various shape files. Financial support for my study was kindly provided by: the National Research Foundation (NRF) of South Africa, the University of Cape Town, and IRD of France. My family back home in Eritrea though far far away but close enough to always encourage me and make me feel happy whenever I speak to them on the phone. I greatly appreciate my sister with her family overseas for her support.

ABSTRACT

Thesis title: Assessing the effects of fishing on fish communities using South African case studies: empirical and theoretical approaches

Name: Dawit Yemane Ghebrehiwet
Date: February 2007

Currently heavy fishing is recognized as one of the major threats to the structural and functional organization of marine ecosystems in many coastal nations. The threat is mainly the result of the inherent nature of the various fishing activities: size selectivity, habitat destruction, biomass removal, and uncertainty in resource status and management of the resource. Thus this thesis investigates structural changes that result from fishing. This thesis aims to answer whether there were changes in the structure of fish communities off the coast of South Africa using two case studies, to explore the response of fish communities to the proposed creation of Marine Protected Areas and to investigate the alternate application of spatially uniform and heterogeneous fishing mortalities. The research questions of the thesis are answered through empirical analysis of landing data for the line fishery and analysis of demersal trawl survey data from the south coast of South Africa, and analysis of output of the Individual Based Model OSMOSE applied to the southern Benguela. Structural changes in the landings from the line fishery and south coast survey data are assessed using a variety of ecosystem indicators believed to capture such changes: size-based indicators (mean size, slope and height of the size spectra, mean $L_{\max}$, proportion of size classes), species-based indicators (ordination by multidimensional scaling, and dendrograms, various diversity indices, dominance curves). Inferences are based on the reference directions of the indicators, according to the expected response of indicators to heavy fishing. Structural changes in the fish communities are observed, over the spatial and temporal bounds of the two case studies, to be the most likely cause of the observed changes is heavy fishing, although the influence of environmental factors cannot be ruled out. Investigation of alternative implementation fishing mortality using the simulation model OSMOSE showed that the system and species biomass do differ between the two implementations, but the variability in the system remains the same. The modelled response of fish communities to the introduction of Marine Protected Areas is an overall increase in relative biomass of large predatory fishes and a decline in the biomass of prey and competitor species.

Keywords: fishing effects, indicators, IBM, linefish, demersal community, South Africa

Thesis overview

Chapter 1 provides the introduction and context of the thesis and its objectives and main research questions. The rest of the Chapters contribute to the thesis by investigating the various structural changes to fish communities that may result from fishing, arranged as a series of papers. The final Chapter link outcomes from Chapters 2 to 8 and summarises how they answer the research questions outlined in Chapter 1.

Chapter 1 Background

This Chapter summarizes what the thesis attempts to address, the approach adopted in assessing the impact of fishing (reference points, reference direction), the material used (data, and the ecosystem considered), definition of terms used, and how the different sections complement each other and help achieve the final objectives of the thesis. As fishing activity generally affects marine ecosystems through its impact on the structural organization (size structure of populations or communities, relative abundance of various groups in an ecosystem). The thesis attempts to address these aspects of fishing effects, using various indicators of the effects of fishing computed from different types of data (commercial catch for the linefish species, survey data for demersal species) and from outputs of an Individual Based Model, OSMOSE.

Chapter 2 Effects of fishing on South African linefish species: changes in the size and dominance structure

This chapter assesses changes in the size structure of the linefish species using various size-based indicators (slope and height of the size spectra, mean length of species, mean length of the community in the catch) and dominance structure using *k*-dominance curves.

Chapter 3 Comparison of fish community size spectra based on length frequencies and mean lengths

The role of the kind of information used (mean length and length frequencies) in the construction of size spectra, and on the conclusions drawn regarding the size structure of a community is investigated. This chapter aims to answer whether the combined use of mean length and length frequency influences the conclusions drawn regarding the size structure of the community studied.

Chapter 4 The effects of fishing on the demersal fish community of the South African South coast: assessing changes in the size structure

The size structure of the demersal community is assessed based on information obtained from research surveys. Various size-based indicators are used to infer changes in the size structure of the community with time. This chapter aims to study weather expected changes in the size structure of the demersal community have occurred, in response to fishing.

Chapter 5 Spatio-temporal dynamics in the community structure of the South African South coast demersal fish community

The structure of the demersal community is investigated using multivariate techniques. The main emphasis in this Chapter is the temporal component of observed changes as its spatial component has been dealt with in a previous study (Smale *et al.* 1993).

Chapter 6 Patterns in the diversity of demersal fish communities of the South African South coast

Spatial and temporal patterns in the diversity of the demersal community are investigated using sets of diversity indices that summarise various aspects of diversity (richness, evenness, taxonomic relatedness). Furthermore, the influence of using various diversity indices on the conclusions drawn is investigated using multivariate technique.

Chapter 7 The effects of fishing on the demersal fish community: assessment using Abundance Biomass Comparison (ABC) curves

Abundance Biomass Comparison ABC curves are applied to the South coast demersal community and inference is drawn based on trends in the *W-statistic* (summary statistic of the ABC curve) relative the starting years, in the light of possible impacts of fishing. Though this method has been mainly used in benthic ecology this chapter and related works from other regions suggest it could also give useful insight into the structure of fish communities.

Chapter 8 Exploring the effects of a non-uniform distribution of fishing mortality on fish communities: an IBM approach using OSMOSE

An overview of various modelling approaches used in the context of modelling ecosystems is provided here with emphasis on individual based models and particularly OSMOSE (its structure, process flow and scheduling). This chapter attempted to address two aims: the first is the effect of introducing spatially variable mortality due to fishing, the second is the response of modelled fish communities to the introduction of "no-take" Marine Protected Areas (MPAs). The issue of spatially variable mortality is explored on the modelled system in two ways: first by imposing the distribution of commercial fishing effort as a weighting so that mortality due to fishing is distributed according to the distribution of fishing effort, second through the application of a management strategy that incorporate "no-take" zones.

Chapter 9 Synthesis: putting it all together

The outcomes of all the chapters are discussed in relation to the research questions outlined in Chapter 1. An overall discussion regarding the impacts of fishing on the studied fish communities and a general synthesis is given here. Different aspects of the study of the effects of fishing are discussed including: the issue of data, and the indices used to assess changes in community structure.

TABLE OF CONTENTS

Chapter 1: Introduction

Fishing is one of the ways in which human beings interact with the coastal and oceanic ecosystems and their associated biota. Wild capture fisheries have been carried out for a long time as sources of protein and employment. Jackson *et al.* (2001) grouped human impacts on the marine environment through exploitation, into three periods: aboriginal, colonial, and global; where aboriginal use represents subsistence exploitation of nearshore and coastal ecosystems using simple technologies that varied in magnitude and geographic extent. Colonial use encompasses the systematic exploitation and depletion of coastal and shelf seas by foreign and distant fleets incorporating the fishery into the developing market economy. The recent and geographically pervasive exploitation of coastal, shelf, and oceanic fisheries integrated into a global pattern of resource consumption, with more frequent overexploitation and substitution of fisheries is characterized as global use. The majority of catches globally come from smaller areas of the total marine environment: coastal upwelling areas and shelf seas.

Harvesting fishes from the marine environment has been increasing steadily since the turn of the century and dramatically increased after the 1950s with the commencement of industrial fisheries, from its historical low catches to its highest of around 80 - 85 million metric tons in the late 1980s, since then it has been declining (Pauly *et al.* 2003). The rapid rise in global landings was associated with an increase in the number of species targeted and expansion of the fisheries horizontally and vertically towards previously unfished areas (Jackson *et al.* 2001, Pauly *et al.* 2003). The substantial rise in global landings has left its imprints in many local and regional fisheries around the world, which has become apparent to fisheries scientists in two different ways: direct and indirect. The direct way is the marked decline in abundance of many fish stocks that are targeted by the fishery differentially, removing the larger size classes and most valuable species (Gislason *et al.* 2000), whereas the indirect effects, usually observed after the direct impact, comprise effects on the non-target species, phenotypic responses through changes in life history traits (Rochet 1998, Hutchings 2005), changes in community structure, size composition both at the population and community levels, and changes in trophic structure (Jennings *et al.* 2002).

Many of the direct local and regional effects of heavy fishing include overexploitation and the collapse or near-collapse of many fisheries around the world. There are many cases of overexploitation world-wide and some cases of collapses. For example, the collapse of the Canadian cod fishery off Newfoundland in 1992, the near collapse of Northeast Arctic cod in the late 1980s and for the second time around mid 1990s, North Sea herring twice once in the late-1960s and mid 1970s, and for the second time 20 years later in the 1990s, the major decline in the traditional ground fishery resource off New England (Hilborn *et al.* 2001): In South Africa several linefish species are overexploited, but only seventy four (*Polysteganus undulossus*) to a level of commercial extinction (Griffiths 2000). The history of fisheries management is also characterized by uncertainty in resource status, inherent variability in the resource that can mask the effects of overfishing, complex biotic interactions among the different components and with the physical environment, lack of controls and replicates also precludes scientific understanding and consensus among fisheries scientists (Ludwig *et al.* 1993).

The above reported examples of overexploitation and the inherent uncertainties in fisheries and difficulties in fisheries management led to a number of regional and international agreements and declarations calling for a more Precautionary Approach in the management of fisheries (Hilborn *et al.* 2001, Garcia and Cochrane 2005) for example:

The Bonn convention on Migratory species of wild animals, 1979

The Law of the sea convention, 1982

The convention on biological diversity, 1992

The Jakarta Mandate, 1992

The UN Food and Agricultural Organization, FAO, Code of Conduct for responsible fisheries, 1995

The Reykjavick Declaration, 2001

The Johannesburg World Summit on Sustainable Development (WSSD), 2002

All these international agreements resulted in what is currently termed as Ecosystem Approach to Fisheries EAF (Garcia and Cochrane 2005). Though there are few related acronyms: Ecosystem Based Fisheries Management EBFM (Link 2005, Pikitch *et al.* 2004), Ecosystem Approach to Fisheries Management EAFM (Jennings and Dulvy 2005), the overall message or objective is similar, viz. holistic consideration of all ecosystem components, recognizing complexity and diversity of ecosystems, and their interaction when managing fisheries. Although in its infancy in terms of practical application, many coastal nations have pledged, during the Johannesburg WSSD in 2002, to implement an EAF by the year 2012 (Garcia and Cochrane 2005). However its implementation does not come without prerequisites which can be grouped into three main aspects; (1) diagnosis, understanding ecosystem impact of harvesting (especially of over harvesting) and the impact of environmental forcing on harvesting and measuring such impacts, (2) prognosis, developing an understanding of future projection of the status of the ecosystem with respect to both fisheries and environmental impact, and (3) management systems, the ability of the management system to adopt and implement procedures suitable for an EAF. Each of these categories presents its own technical and conceptual problems and each could be the subject of a full study.

Over the past decade various studies have sought to understand the ecosystem impacts of heavy fishing, this required the development of new indicators or refining existing single species indicators that are mainly used in single species management procedures. Many ecosystem indicators have been proposed; each believed to capture different aspects of the ecosystem. The majority of the indicators can broadly be grouped into size-based, tropho-dynamic based, and species-based. To help towards their further use and development, ecosystem indicators are expected to satisfy some criteria, (Rochet and Trenkel 2003, Rice and Rochet 2005): they should be meaningful (relationship of the indicator to the state of the ecosystem or any of its components), reflect the expected effects of fishing (the response of the indicators to the increase in fishing), be exclusive (observed response of the indicators should exclusively be attributed to fishing impact) and measurable (the indicators should be easily computed).

Indicators can be calculated across the ecological hierarchy (population, community, ecosystem), and thus their interpretation pertains to the level of hierarchy they refer to. Furthermore, various indicators can be calculated from different data sources with variable information content (averages or detailed). The first data source is fishery dependent data, where commercial landings and size composition are obtained from catch log books. The second source of data is fishery independent where size and catch data are collected during routine fish surveys. Although research surveys are usually targeted towards providing information for the assessment and management of a few commercially important species, information on any aspect of the bycatch species collected during the course of the surveys is indispensable for the assessment of the status of these species and of the ecosystem. The third source of data is the output of various ecosystem models. Data from any of the above sources are also available to various degrees of detail, from crude averages over specified spatial and temporal bounds to detailed ones. This highlights the need to investigate the influence of the kind of information used on the final conclusions about the state of the ecological hierarchy concerned (population, community, and ecosystem). In addition the spatial and temporal dynamics of indicators have also been reported based on data obtained from various spatial (local to basin scale to global) and temporal scales (short term to decadal).

This calculation of indicators is followed by the assessment of the impact attributable to fishing. This presents another problem on how to decide on the impact of fishing. In this context there are some approaches, related to single species management such as the use of reference points which are needed to compare with the current and future projections of the ecosystem state. These approaches include the use of reference points reflecting the pristine state, target reference points where we would like certain aspect of the ecosystem or its components to be, limit reference points to indicate undesirable ecosystem states, and reference directions. Reference direction is believed to be more useful than arbitrary reference points for size-based indicators (Shin *et al.* 2005). Reference directions for any set of ecosystem indicators have also been advocated for situations in which the value of an indicator is not satisfactory or is close to the limit reference point, and a target reference point has not or cannot be defined (Trenkel and Rochet 2003, Jennings and Dulvy 2005).

As most of the empirical analyses of the impact of fishing on fish communities are based on data obtained from patchily distributed surveys or commercial landings, understanding the overall impact and future implications is limited, thus signifying the need for experimental or theoretical approaches through various modelling tools to aid understanding of the impact of fishing and possible future consequences of current strategies.

For the purpose of this thesis communities are generally referred to as a group of species occurring in the same place at the same time so that species included are not restricted by resource use or phylogeny (Chapman and Reis 1992, Fauth *et al.* 1996). Specifically the term "demersal fish communities" as used in Chapters 4, 5 and 6 is taken to include teleots, elasmobranchs, and cephalopods.

Communities are generally identified in two different ways: in terms of the type of the environment in which they reside (coral reef community, inshore community, offshore community) and by the dominant species in the community (Chapman and Reiss 1992).

This thesis attempts to address some aspects of the implementation of an EAF empirically based on two case studies: the line fish community of the west and south coast of South Africa and the demersal community of the south coast of South Africa. Theoretically, I adopt an Individual Based Modelling IBM approach using the OSMOSE model (Shin and Cury 2001). The majority of inferences drawn with respect to the trends from either the empirical analysis or modelling study will be based on reference directions for size-based indicators, whereas for species based indicators changes in any of the indices will be discussed in relation to what has been reported from related studies elsewhere and based on ecological interpretation of the changes. The first case study of 12 main line fish species covers a wide spatial domain and includes a long time series of landing data over 100 years (1896 – 1998) as snapshots over three periods. The study uses mean lengths of species for the historical period and length-frequency data for the contemporary period. The species included in this study are mainly targeted by the line fishery, and hence referred to as line fish species. As most of the fishing practices are size selective, this leads to exploitation of larger individuals of target species and generally larger species (Jennings *et al.* 1999), hence changes in the size and community structure are the most commonly expected and observed responses of fish communities, in addition to the decline in biomass. Two aspects of the line fish community are investigated: size and community structure using size-based indicators (mean population size, mean community size), and species-based indicators (dominance curves, cluster analysis and non metric multidimensional scaling). Furthermore, the effect of the kind of data used (mean length or length frequencies) in the construction of size spectra is investigated in this case study. The second case study covers part of the spatial domain (south coast only) of the line fish study. It is based on demersal fishes caught during routine 6-monthly demersal trawl surveys. It covers a temporal window of 18 years. The size structure, catch rate, and community structure of the demersal community is investigated using the relevant indicators. For the theoretical part, the IBM OSMOSE is used with some enhancement to the earlier version of the model giving spatially explicit outputs. The role of spatially variable fishing mortality is investigated by implementing an alternative fishing mortality procedure using a weighting mechanism based on the spatial distribution of the demersal trawl fishing effort and the pelagic purse-seine fishing effort. The impact of increasing fishing scenarios is investigated qualitatively and quantitatively. The role of spatially variable fishing mortality is also investigated by modelling three proposed Marine Protected Areas MPAs individually and simultaneously along the coast. This exercise presents a two-fold benefit; firstly in the context of the implication of spatially variable mortality due to fishing, second in the management context when the MPAs are used as part of fisheries management procedures to get an idea of the possible consequence of establishment of such areas alone or as a network. OSMOSE has almost the same spatial domain as the first case study.

The rationale behind this study can broadly be divided into two aspects. First this study is the first of its kind in that it attempts to assess changes in the demersal fish community of the south coast of South Africa, in the light of the effects of heavy fishing, across the spatial and temporal bounds and across taxa, target and non-target, caught by different gears. It will also complement previous studies on the assessment of long-term changes in line fish communities of the west and south coasts (Griffiths 2000). Furthermore, it combines empirical data analysis and a simulation modelling approach to understand the effects of fishing. Outputs of this study in synthesis, documentation, or in concept, are expected to contribute to the knowledge pool required for an Ecosystem Approach to Fisheries (EAF) in South Africa.

Research goal

This project is aimed at assessing the effects of fishing on the linefishery of the Cape region and demersal fishery of the Agulhas Bank using diverse ecosystem indicators (size-based and species-based) estimated empirically and from model output.

Research questions

- Are there spatio-temporal changes in the size structure, in the species composition, and in the community structure of the fish communities?
- How does fishing modify the structure of the fish communities and ecosystem?
- Has fishing effort increased?
- Are there signs of overfishing at either of the ecological hierarchy levels (population or community) assessed?

Chapter 2 Effects of fishing on the line fish species: changes in the size and dominance structure

Abstract

A data set of linefish landings, effort, and fish size-distribution records has been assembled from archives to cover three short periods over the past 100 years from 1897 – 1998 in four sub-regions of the former Cape Colony, South Africa. Both linefish landings and effort have increased several-fold over the past 100 years. The aggregate catch per unit effort (CPUE) has declined by more than 80% from what it used to be in the 1890's, but several species have declined much more. Multivariate analysis of CPUE shows that the 1897 – 1906 years cluster quite close to the 1927 – 1931 years, with a major gap to 1986-1998, showing a large change in abundances of linefish species between the 1930s and 1990s, which is also the period when fishing effort increased most. Analysis of historical mean size and modern length–frequency data shows that in eight out of 12 species considered, the mean length of fish has declined between the 1890s and 1990s with increased fishing pressure. Size spectra were constructed based on mean length and CPUE of the 12 species. Slopes become significantly more negative in the modern period, showing that the modern linefish catch has fewer large fish and relatively more small ones than previously. Changes in linefish community, implied by changes in catch composition, are different in the four sub-regions. The cool-temperate upwelling sub-regions differ from the warm-temperate ones, particularly with regard to the influence of the fast-growing, nomadic, pelagic snoek (*Thyrsites atun*). Inclusion of snoek gives the size spectrum of the cool-temperate sub regions a shallower slope than the warm-temperate regions. The cool Western Cape shows a trend towards increasing dominance with increased effort, whereas the warm-temperate sub-regions show decreased dominance with increased fishing pressure.

Key words: community structure, dominance curve, linefish, size spectrum, South Africa

2.1 Introduction

The linefishery of the present Western and Eastern Cape Provinces (the former Cape Province) has a long history that dates back to the turn of the 19th century. It is the biggest line fishery in South Africa, comprising some 2500 commercial vessels, which land around 15500 tons per annum or 95% of the nation's linefish landings, (Griffiths 2000). It is composed of commercial and recreational sectors, which target around 40 teleost species, 20 of which are economically important (S. Lamberth MCM, pers.comm). Competition for the same resource among user groups, a large number of species of contrasting life history strategies, diverse behavior patterns, and different habitat preferences make the management of the linefishery complex. Owing to its long history of fishing and failure of the regulatory schemes (Attwood and Bennett 1995, Brouwer *et al.* 1997), many of the Cape linefish species are overexploited (Griffiths 1997a, b). Recent work by Attwood and Farquhar (1999), which assessed the state of the linefishery between Cape Hangklip and Walker Bay in the Southwestern Cape (see Fig 1), has demonstrated the long-term over-exploitation of most species. One of the main targeted species even has disappeared from the catch completely (Seventy four *Polysteganus undulosus*). Griffiths (2000) further confirmed this trend for the whole Cape region. He showed that, according to long-term catch per unit effort (CPUE) and effort data, most of the linefish species are overfished, especially the large warm-temperate reef (dermersal) fishes (e.g. silver kob *Argyrosomus inodorus*, geelbek *Atractoscion aequidens*, and seventy four).

Long-term historical fisheries data (e.g. abundance and number of species, size composition, fishing ground, gear used and fishing effort) give insight into the status and structure and/or function of the fish community before heavy fishing pressure and are indispensable to evaluate the effects of fishing on the fish community. This study aims to confirm that changes in catch rate have occurred over time using multivariate analysis, and assess the long-term changes in the size composition (size spectra and changes in mean size), and dominance structure (k-dominance curves) of the linefish catch in the whole Cape region over a 100-year period (1897 – 1998).

2.2 Methods

2.2.1 Spatial and temporal coverage

The present study covers the entire Cape region previously known as the Cape Province. It extends from the Orange River on the West coast to the Kei River in the East (Fig. 1). The Cape region is subdivided into four coastal sub-regions (Western Cape, Southwestern Cape, Southern Cape, Southeastern Cape), each characterized by a different history of fishing (Griffiths 2000). The Cape region comprises two biogeographic zones (Branch and Branch 1981), the cool temperate Western Cape and the warm temperate Southern and Southeastern Cape. The Southwestern Cape is a transition sub-region where species common to both regions are present. The Western and Eastern parts of the Cape are distinct in terms of prevailing oceanographic conditions. The former is characterized by the cool Benguela current and coastal upwelling, which result in high productivity (Shannon and Nelson 1996). The warm southward flowing Agulhas current characterizes the Eastern Cape (Schumann 1987), which has limited inshore dynamical upwelling. Differences among the four sub-regions are also highlighted by the occurrence of some of the linefish species as discrete stocks. For example white stumpnose *Rhabdosargus globiceps* occurs as four discrete stocks in the four sub-regions (Griffiths *et al.* 2002) and silver kob as three discrete stocks (Griffiths 1997b). Geelbek, on the other hand, exists as three age-structured subpopulations in three sub-regions forming a single stock (Griffiths and Hecht 1995). The study covers three brief periods over the past 100 years, comprising two historical periods (1897 – 1906, 1927 – 1931) and the modern period (1986 – 1998).

The Cape line fishery has always used a range of hook sizes, depending upon the target species and their sizes. Simple J-hooks are used and hook design has not

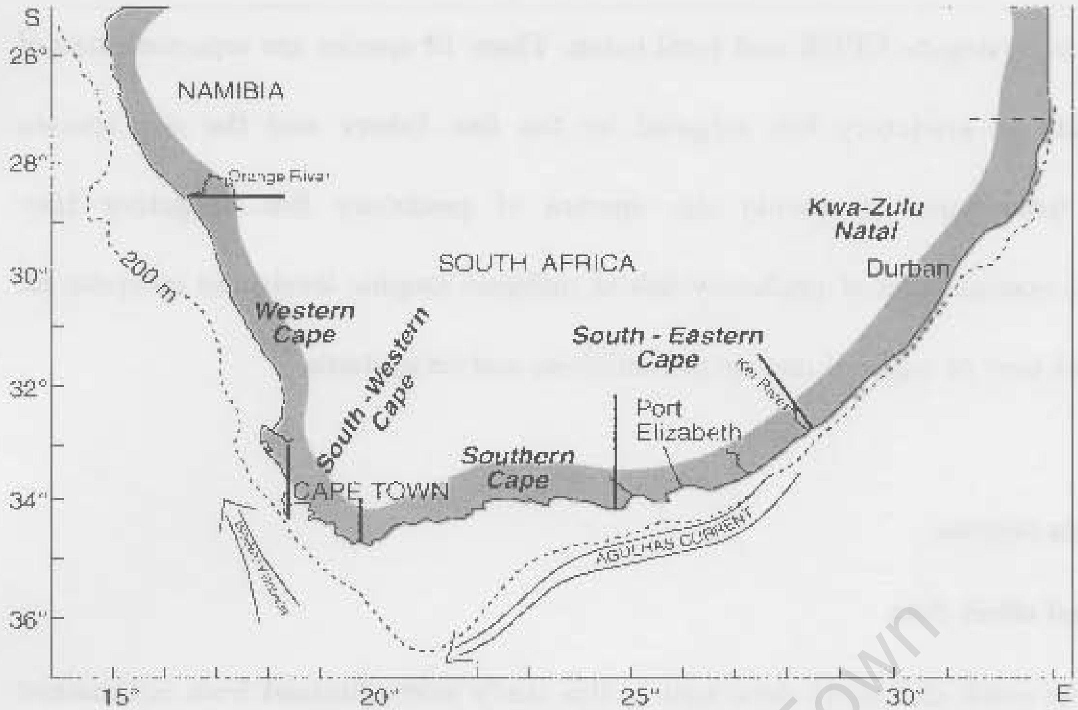


Figure 2.1. Map of South Africa showing the four sub-regions of the Cape.

changed significantly over the 100 year period. There are no indications that mean hook size has changed over time. When hooks decrease in size in a particular sector, it is usually done to compensate for declining catch rates resulting from the removal of larger fish. Thus there was no reason to believe that hook size has caused the patterns of changes reported in this chapter; on the contrary, fishers may have continued to use larger hooks because of minimum size regulations for the targeted species first introduced in 1940 and strengthened in 1985.

The study is based on only species for which consistent long-term data are available. These 12 main linefish species (see Table 2.1) ranging in mean length from 25 – 90 cm. The line fishery catch records for three of these species (panga, chub mackerel and hake) have historically been confounded with trawl and other fishery records. Therefore data from these three species have been omitted from the analysis of aggregate CPUE and total catch. These 12 species are representative of community of predatory fish targeted by the line fishery and the size spectra derived from them represents size spectra of predatory fish. Together they represent communities of predatory fish at different trophic levels and comprise an important part of regional marine communities and ecosystems.

2.2.2 Data sources

Catch and effort data

The catch and effort data used in this study were obtained from commercial line fisheries and consists of two historical and one modern data set:

1897 – 1906

The data for this period were obtained from the reports of John D. Gilchrist who was "Government Marine Biologist" during that period (Gilchrist 1898, 1899, 1900, 1901, 1902, 1903, 1904, 1906, 1907). The data were collected by observers at all major harbours in the four coastal regions of the Cape. They include information on the catch of each of the main linefish species and number of boats operating in each sub region.

1927 - 1931

Catch data for this period were obtained from unpublished monthly catch records that were collected by the Cape Provincial Administration. The numbers of boats operating at each fishing site were obtained from Fishing Harbour Reports of the Department of Mines and Industries (Mansergh *et* *al.* 1926, 1927, 1928) and from Report No. 180 of the Board of Trade and Industries (Fahey *et al.* 1934).

1986 – 1998

Catch and effort data for the modern data period were obtained from compulsory daily catch and effort returns submitted by owners of boats involved in commercial line fishing.

Size composition

Information on the size composition for the period 1897 – 1906 was obtained from Gilchrist's records mentioned above, in which the mean weight of each species caught in the 1897 – 1906 period is reported. The mean sizes for 1927 – 1931 are not available, thus those available for the closest period 1917 – 1919 were used. They were estimated from monthly number and catch weight data for each species obtained from the line fish section of Marine and Coastal Management (MCM). Because the data were not available for all sites in each region they were not used in CPUE analysis. The mean sizes of each species from 1917 – 1919 period were used directly in the comparison of mean sizes over three periods. In addition they were used as close approximates of mean sizes of each species in the construction of size spectra for 1927 – 1931. For the modern period, length frequencies of the linefishes were obtained from official observers at fishing harbours in the four regions of the Cape.

2.2.3 Analysis of catch and effort

The aggregate total catch (tons) for each sub-region was calculated as the sum of the catches of each linefish species included in this study. The annual aggregate CPUE (tons per boat-year) was calculated by dividing the total catch by the effort (number of boats per year). In the analysis of the catch and effort data shallow water hake *Merluccius capensis*, panga, *Pterogymnus laniarius* and chub mackerel *Scomber japonicus* were not included because the majority of the catches of these species is made by fisheries other than the linefishery. But these species were included in the analysis of community structure because they are still caught by the line fishery and they are not a new addition to the list of species caught by this fishery. They have been targeted by the fishery since the 1890s when the commercial landing log books were available. Details of possible sources of bias in available handline CPUE as indices of linefish abundance for each period are given in Griffiths (2000).

2.2.4 Cluster analysis and ordination

Multivariate analysis of the annual CPUE (tons per boat-year) of each species was carried out, using cluster analysis and ordination techniques, to assess overall changes in catch composition with time (Clarke and Warwick 1994). The CPUE data of each species in each year for the whole Cape was first *root-root* transformed, as the range of values was wide. This was done to prevent data from abundant species from swamping that from less abundant species, thereby affecting the similarity matrix and in turn the classification and ordination. The Bray-Curtis measure of similarity was used, as it avoids the problem of joint absences and gives more weight to abundant species than to rare ones (Field *et al.* 1982). Finally group-average linkage was used to produce the dendrogram of the time series. Clarke and Warwick (1994) and Field *et al.* (1982) suggest that cluster analysis and ordination techniques give better information when used together. Non-metric multidimensional scaling (MDS) was used to create the ordination plot. The ordination of the time series using CPUE of each species was computed from the Bray-Curtis similarity matrix. Details of clustering and ordination techniques, their advantages and drawbacks are given in Clarke and Warwick (1994).

2.2.5 Changes in mean size (length)

The average length of each species in the historical period was calculated from the mean weight using the length-weight relationship of each species (Mann 2000). The availability of individual length-weight relationships for each species reduces the error that may be introduced by applying a single theoretical length-weight relationship ($W = 0.01*L^3$) for all species as used by Bianchi *et al.* (2000, 2001).

In addition the mean-sizes (weight or length) of each species were considered to be consistent during the period 1897 - 1906 and among the four coastal regions. This may bias the estimates of the size spectrum. Nevertheless comparison with the modern data is expected to capture changes in size composition over the long term. The changes in mean length of each species were assessed by comparing weighted mean lengths in the three periods. The average lengths of each species in each period were weighted by the CPUE of each species in each region to get weighted mean lengths for the whole Cape region.

The mean length of the landed catch was calculated by weighting the length of each species by its corresponding CPUE in each year.

$$\overline{catchL} = \frac{\sum L_{ij} * C_{ij}}{\sum C_{ij}}$$

Where $\overline{catchL}$ is mean catch length, L_{ij} is length of $species_i$ in j^{th} year and C_{ij} is CPUE of $species_i$ in j^{th} year. In this way the mean landed catch length of each sub-region is calculated and then weighted by the aggregate CPUE of each sub-region to get the mean catch length for the whole Cape region.

2.2.6 Size spectra

An index of abundance for each species was estimated by dividing the catch (total number of individuals) in each year by the effort (boat-years), expressed as numbers per boat-year. Length frequencies of each species were used to estimate the mean length of each species for the modern period. The length frequency data for each species were not directly used for the comparative size spectra reported here, because such data were not available for the historical periods. Note that the analysis of size spectra in Chapter 3 has shown that slightly biased size spectrum statistics (slopes and heights) are obtained from mean size data for each species compared to size-frequency data for all species.

A size range of 25 – 89 cm was used in the size spectra. The size spectrum for each sub-region and period was then constructed by distributing the number of individuals of each species into the appropriate five-centimeter size classes (based on the mean length of that species) and then plotting the logarithm of overall abundance per size class against the logarithm of the class mark as applied by Bianchi *et al.* (2000, 2001). Slopes and intercepts (heights) were estimated using linear regression. Because slopes and heights are highly correlated with one another the trend in the height is partly the result of its correlation with the slope (Rice and Gislason 1996). Thus to make the slope and height of the size spectrum independent so that they provide different information the correlation should be removed. Daan *et al.* (2005) suggested a way of removing the correlation between the slope and height by estimating the height at the mean value of the independent variable ($\log_e$ class mark). By standardizing the independent variable to a mean of zero, the ordinate is moved systematically to the mid-point of the size-class giving the height at the mean size-class. Thus the height represents the (log) abundance of the mean size-class. Slope and height are then estimated by log-linear regression. The x-axis is expressed as log size-classes above and below a mean of zero. The significance of the trend in the slopes and heights of the size spectra over the 1897 - 1998 periods was tested using a Student t-test (Zar 1999).

2.2.7 *k*-dominance curves

The change with time in the dominance structure of the linefish catch was assessed graphically using *k*-dominance curves whereby cumulative dominance in biomass is plotted against species rank, or log species rank (Clarke 1990, Clarke and Gorley 2001). This approach is useful in that it picks up patterns of relative species abundance without reducing the information to a single summary statistic such as a diversity index (Clarke and Warwick 1994).

2.3 Results

2.3.1 Trends in catch, effort, and CPUE

The long-term trends in the aggregate total catch, effort, and catch per unit effort (CPUE) of the Cape linefishery are shown in Figures 2.2 and 2.3. The total catch for the whole Cape region has increased with time towards the contemporary period, with the increase in effort, while the CPUE declined substantially from around 93.94 tons.boat-year^{-1} in the 1890s to 12.25 tons.boat-year^{-1} in the 1990s (Fig. 2.2). The peak in CPUE in 1904 was caused by the exceptionally large catch of geelbek in the Southeastern Cape in that year. The majority of the region's landings come from the Western Cape. The total catch does not reflect the overall biomass removed by the linefishery because catches from several sites were excluded if they either lacked observers or the linefish catches were lumped with trawl catches. Thus abundance trends are mainly inferred from the trend in the CPUE. Similar trends of increase in the total catch and decline in the CPUE are found in the Western Cape (from 11.8 tons.boat-year^{-1} at the turn of the century to 5.63 tons.boat-year^{-1} in the 1990s, Fig.2.3a). The increase in the total catch in the Western Cape is mainly attributed to the dominant pelagic and nomadic snoek, which makes up 78% - 96% of the catch. In the Southwestern Cape the *CPUE* dropped from 25.8 tons.boat-year^{-1} to 2.31 tons.boat-year^{-1} between 1890s and

1990s (Fig. 2.3b).Snoek also contributes the largest proportion to the total catch of this region. In the Southern Cape the CPUE decreased from 12.8 tons.boat-year^{-1} in the 1890s to 2.36 tons.boat-year^{-1} in the 1990s (Fig. 2.3c) and Southeastern Cape's CPUE dropped considerably from 43.4 tons.boat-year^{-1} to 1.94 tons.boat-year^{-1} between 1890s and 1990s (Fig. 2.3d). Carpenter *Argyrozona argyrozona* and silverkob comprise the biggest proportion of the catch in the Southern and Southeastern Cape.

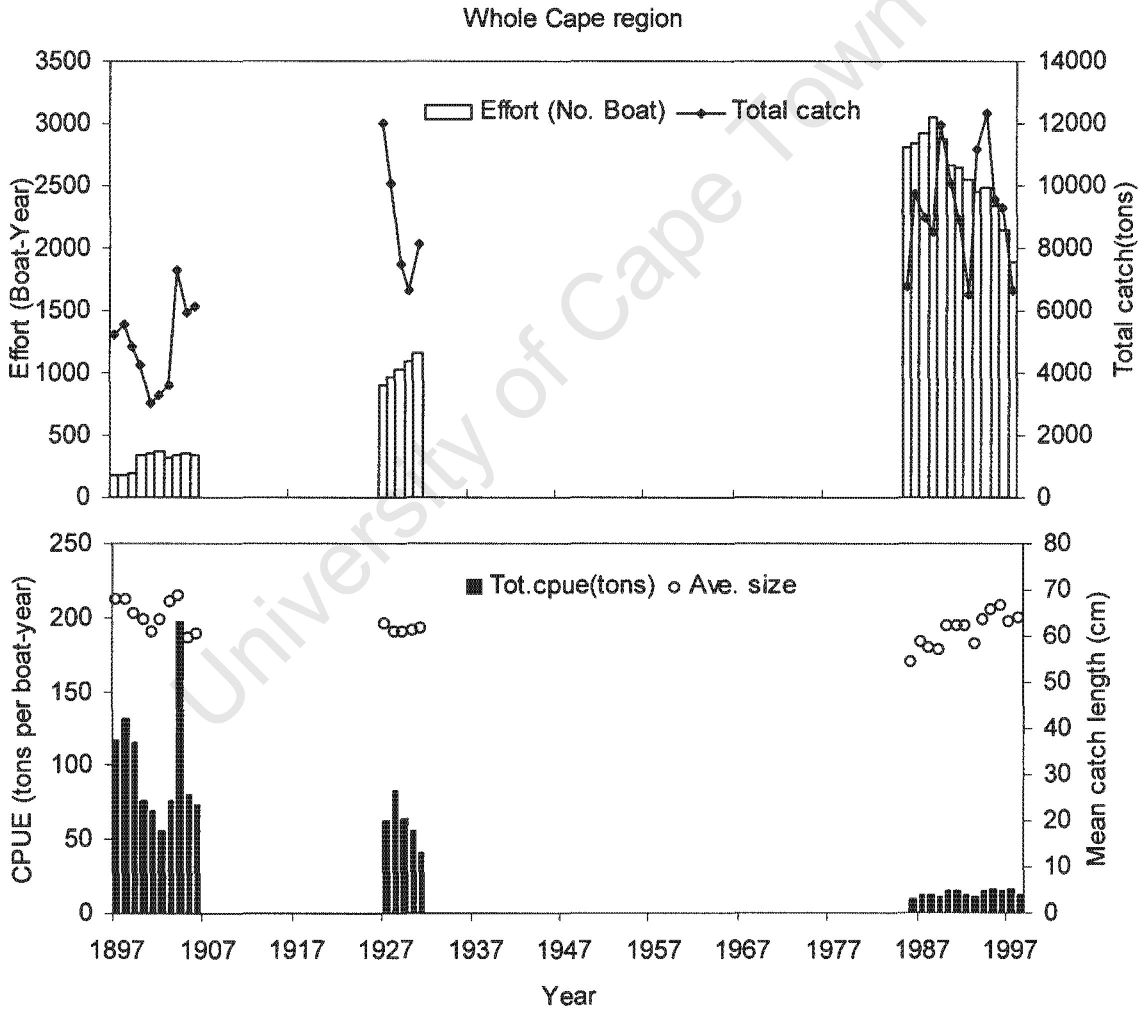


Figure 2.2. Long-term trend in the catch, effort, CPUE and weighted mean catch length of the whole Cape region.

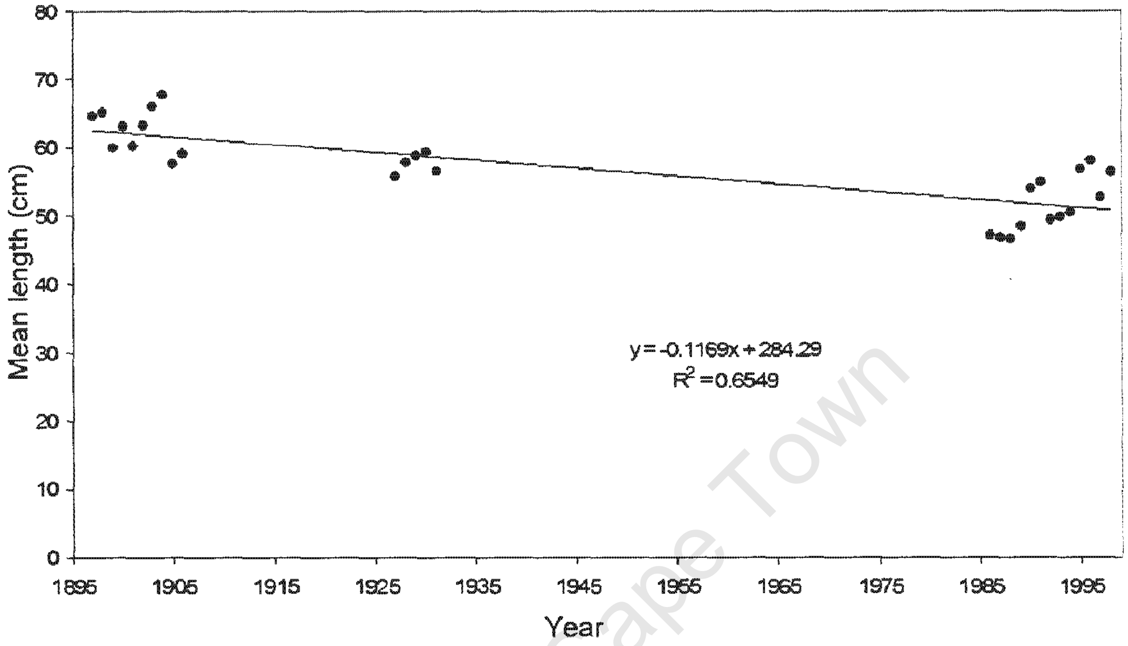


Figure 2.3. Long-term trend in the mean length of landings of the line fishery. Trends are calculated excluding the dominant species snoek from the Western cape.

2.3.2 Multivariate analysis of CPUE

The classification and ordination (using non-metric MDS) plot of years in the three periods are shown in Figure 2.5, based on the CPUE of each species included in the present study. The three periods cluster separately; ordination of the same data further confirms this. The two historical periods which are characterized by high CPUE for most of the linefish species and lower effort tend to be grouped close to each other and the years in the modern period characterized by high effort, when most species are over-exploited (Griffiths 2000), grouped together away from the other periods. This corroborates the observed trend in the aggregate CPUE and effort over the past 100 years.

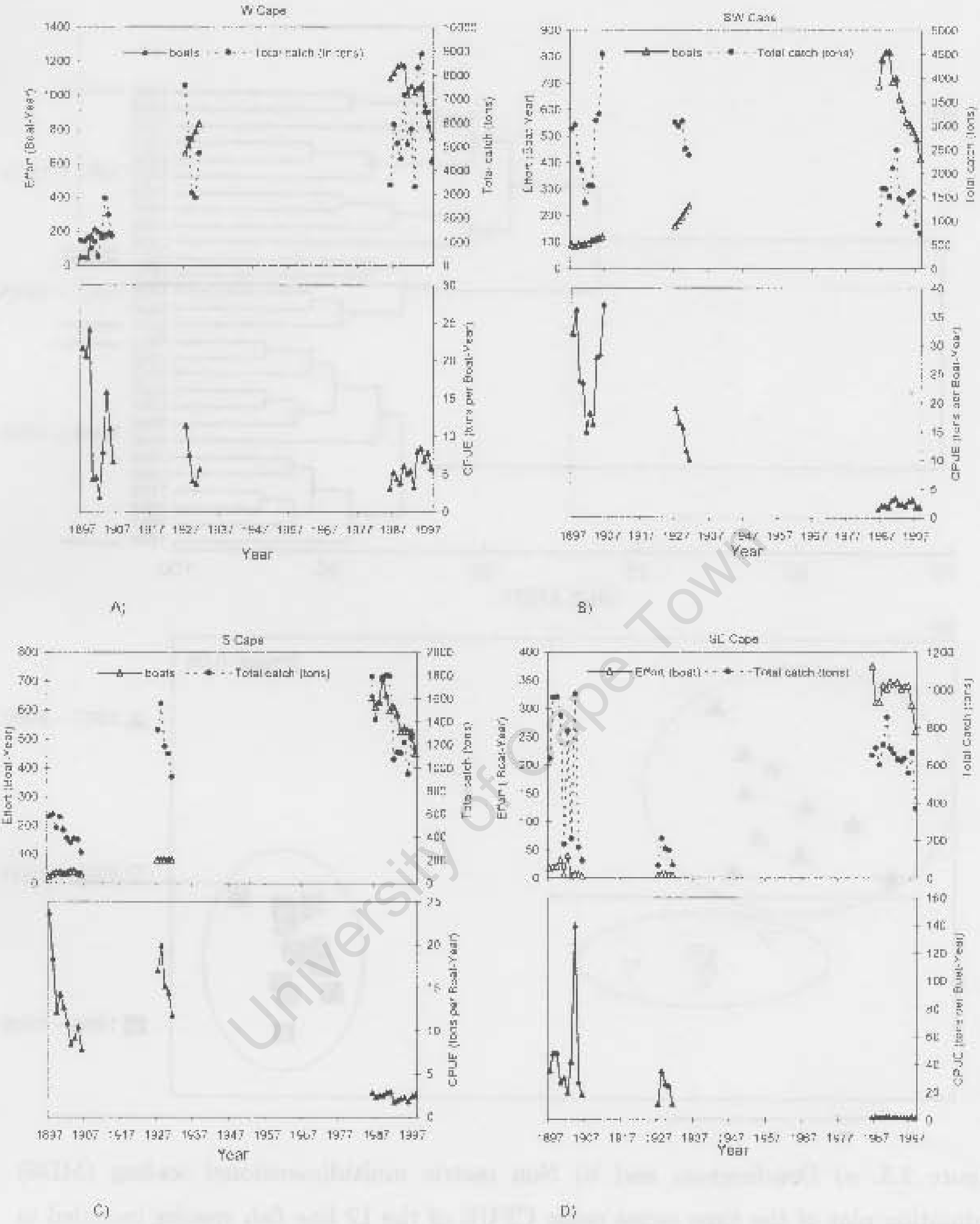


Figure 2.4. Long-term trend in the catch, effort and CPUE for the four sub-regions; (A) Western Cape, (B) Southwestern Cape, (C) Southern Cape, and (D) Southeastern Cape.

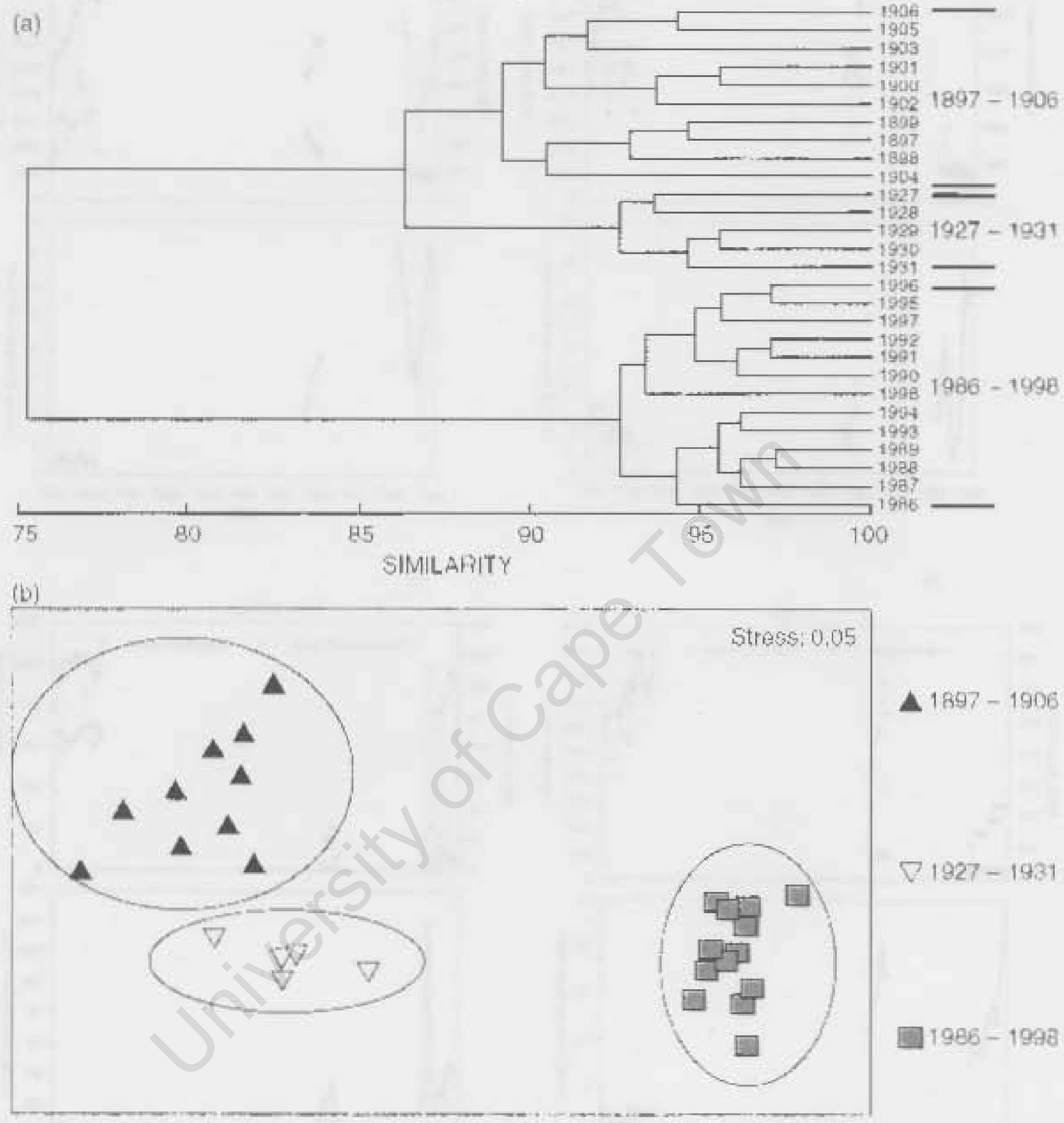


Figure 2.5. a) Dendrogram and b) Non metric multidimensional scaling (MDS) ordination plot of the time series using CPUE of the 12 line fish species included in this study. Both based on root-root transformed data and the Bray-Curtis measure of similarity.

2.3.3 Size composition

Mean length

The mean lengths of the species considered over the three periods are given in Table 2.1. Seven (58%) of the linefish species considered showed a decrease in the mean length between 1897 – 1906 and 1986 – 1998. The mean lengths of panga, chub mackerel, red stumpnose *Chrysoblephus laticeps* and white stumpnose have increased with time towards the present. The mean length of hottentot *Pachymetopon blochii* is unchanged. Decline in mean size are observed in the larger bodied species (snoek, roman, carpenter, yellowtail, geelbek, silver kob, and seventyfour). These are preferred species in the line fishery. The decrease in the mean length of seventy four appears extreme but it may to some extent be exaggerated by shortage of samples and the rarity of the species from catches. This shoaling species has, however, shown greatest decline in abundance (> 99%) (Griffiths 2000), thus a large decline in mean size is not surprising. Seventy-four had essentially become commercially extinct prior to the moratorium imposed in 1998.

The weighted mean catch length of the whole Cape region is shown alongside the catch, CPUE, and effort statistics in Figure 2.2. The trend in mean overall catch length over time was not significant when all the species were included in the analysis (slope = -0.031, t = -2.04, p = 0.052). This small trend may be the influence of the dominant species in the Cape region, snoek (*Thyrsites atun*), and possibly a switch towards a species that was not targeted in the historical period, yellowtail (*Seriola lalandi*) (Griffiths 2000). Exclusion of snoek from the calculation of mean length of the landings showed a significant decline in the mean length of the landings (slope = -0.1169, t = -7.02357, p = 0.000) (Fig. 2.3). In both cases inclusion and exclusion of snoek, the mean length of the landings within the modern period (1986 – 1998) increased (Fig. 2.2 and 2.3). Based on trends in CPUE and stock assessment, these fast growing pelagic nomads are the only two species targeted by the linefishery that do not appear to have been over-exploited (Griffiths 2000). Thus the increase in mean length of the landings in the modern period could be due to these two species.

Table 2.1. Mean lengths of main linefish species in the Cape region in the three different periods. The mean lengths in the 1917 – 1919 and 1986 – 1998 periods are weighted by the average CPUE of each species in each region.

Common name	1897 - 1906	1917 - 1919	1986 - 1998	% change 1890s-1990s
Panga	27.1	31.9	29.7	9.4
Chub mackerel	33.9	35.7	37.6	10.8
Red stumpnose	36.0	39.0	40.7	12.8
White stumpnose	27.7	25.3	32.6	17.8
Hottentot	29.9	26.6	29.7	-0.8
Snoek	83.5	83.3	75.9	-9.0
Roman	35.8	30.5	32.4	-9.5
Yellow tail	70.4	57.9	61.5	-12.6
Silver kob	61.3	58.9	52.4	-14.5
Carpenter	39.2	31.8	33.0	-15.7
Geelbek	84.6	78.6	68.5	-22.9
Seventy four	56.1	49.7	27.7	-50.7

Size spectrum

As examples the size spectra for selected years for each of the four coastal sub-regions of the Cape are depicted in Figure 2.6. The figure is intended to show a sample of the size spectra in each region and how an abundant species like snoek can affect the size spectra and in turn the spectrum statistics (slope and height). Size spectra of the Western Cape are strongly influenced by the abundant pelagic predator snoek. Snoek appears towards the tail of the size distribution, in the case of the historical data it contributes largely to size class 80 – 84 cm and in the modern data 75 – 85 cm. Similarly in the Southwestern Cape the size spectrum was affected by snoek, making the negative slope shallower. Figure 2.7 shows the long-term trend in the estimates of the size spectra of the whole Cape region plotted against time. Heights decreased significantly between the 1890s and 1990s (Table 2.2), though they fluctuate annually within each period. The slopes do not show a significant decline.

In the Western Cape the trends in the slopes of the size spectra do not show significant change over time when the large and abundant snoek is included, whereas the heights of the size spectra consistently decline with and without snoek over the past 100 years (Fig. 2.8a and 2.8b). This suggests a decline in the overall abundance of linefish. The insignificant change in the slopes of the size spectra can be explained by species composition of the sub-region between 1897 and 1998, where snoek was the dominant species, followed by hottentot, with other species contributing little to overall abundance (Griffiths 2000). When snoek is included in the size spectra the slopes tend to be shallower in both the historical and modern periods. When the size spectrum is constructed without snoek the slopes becomes steeper (more negative) in the modern period.

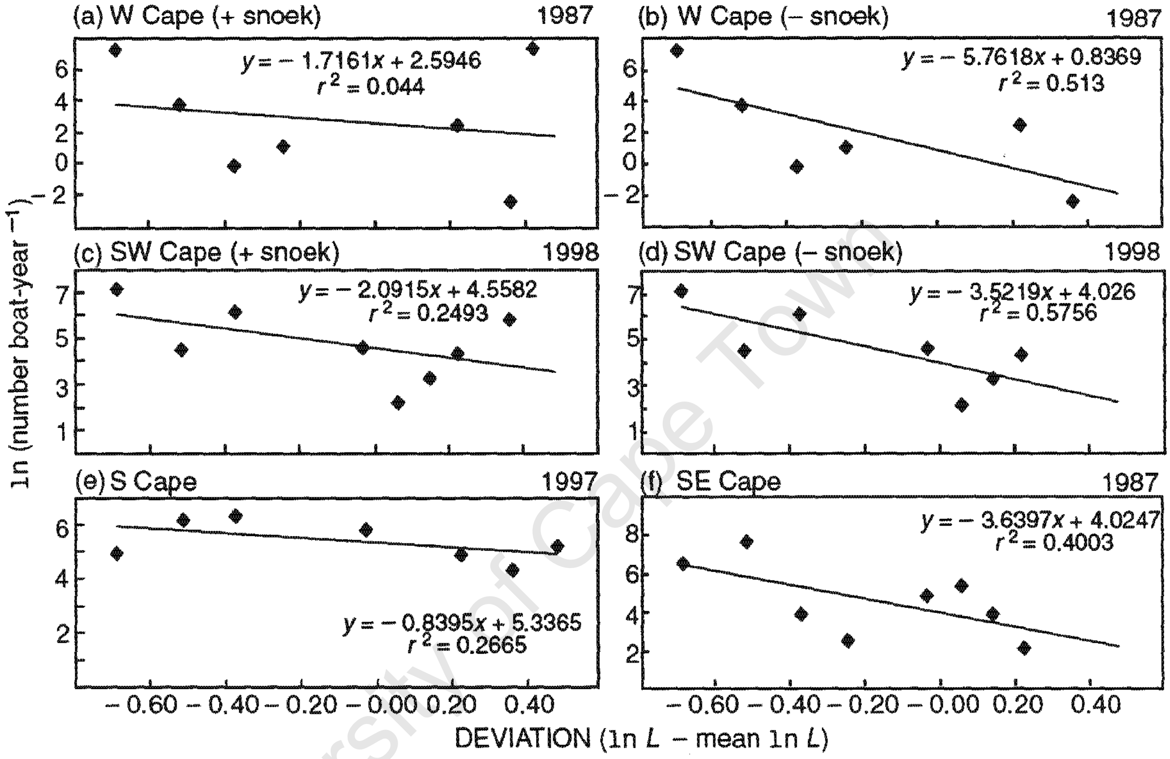


Figure 2.6. Sample size spectra of the four coastal regions in the Cape for selected years; Western Cape with snoek (n = 7), Western Cape without snoek (n =6), Southwestern Cape with snoek (n = 8), Southwestern Cape without snoek (n = 7), Southern Cape (n = 7), Southeastern Cape (n = 8).

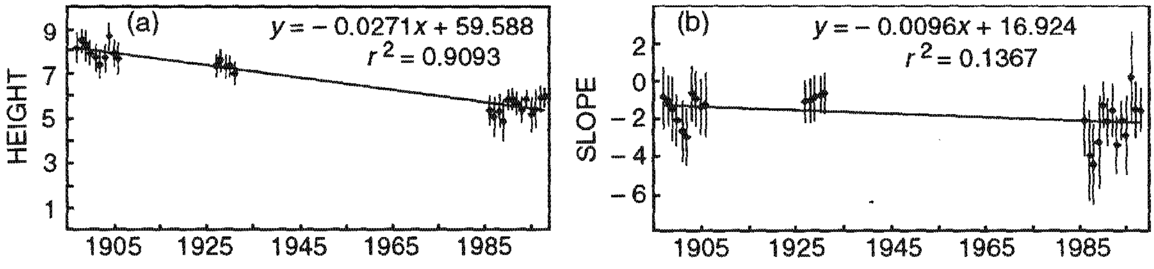


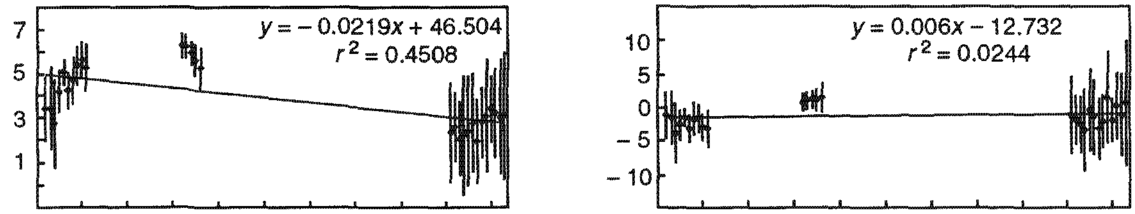
Figure 2.7. Long-term trends of the heights and slopes of the size spectra of the pooled data of the whole Cape region including snoek (Error bars ± 2 SE, n = 28).

Table 2.2. Significance tests of the long-term trends in the slopes and heights of the size spectrum over the three periods from 1897 - 1998 (see Figs. 2.6 and 2.7).

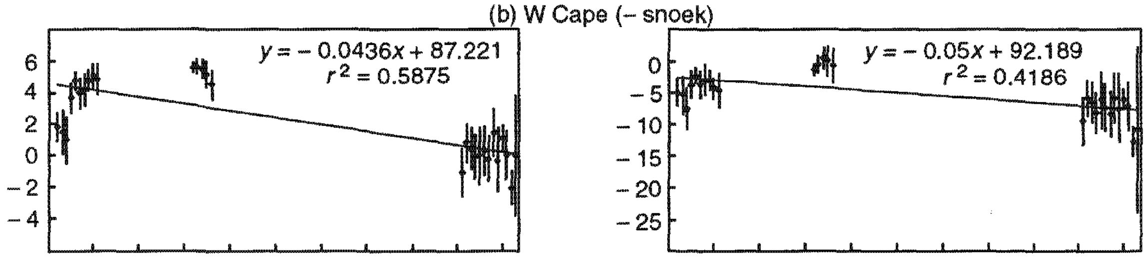
Region	Parameter	Estimate (*b*)	*SE*	*t*-value	*P*-value
Whole Cape	Slope Height	−0.010 −0.027	0.005 0.002	−2.029 −16.150	0.053 0.000
Western Cape with snoek	Slope Height	0.006 −0.022	0.007 0.005	0.807 −4.619	0.427 0.000
Western Cape without snoek	Slope Height	−0.050 −0.044	0.012 0.007	−4.326 −6.085	0.000 0.000
South-Western Cape	Slope Height	0.016 −0.048	0.004 0.003	3.644 −16.038	0.001 0.000
Southern Cape	Slope Height	0.016 −0.002	0.004 0.003	3.644 −0.617	0.001 0.542
South-Eastern	Slope Height	−0.035 −0.019	0.010 0.004	−3.477 −4.806	0.002 0.000

In the Southwestern Cape the slopes of the size spectra become significantly shallower with time and this is again attributed to the dominance of snoek (Fig. 2.8c) while the height declines over time. As with the Southwestern Cape the slopes in the Southern Cape flattened over time (Fig. 2.8d). This may be due to the catches of the large-sized yellowtail in the modern period that was not targeted previously. Surprisingly, the height did not show any trend over time. This is mainly because of yellowtail and silver kob that occupy the mean size classes (50 – 60 cm); in the 1890s seventy-four appeared in that size class. In the Southeastern Cape the slopes and heights of the size spectra decline significantly with time (Fig. 2.8e), suggesting both shifts in size composition, and reduction in overall linefish abundance.

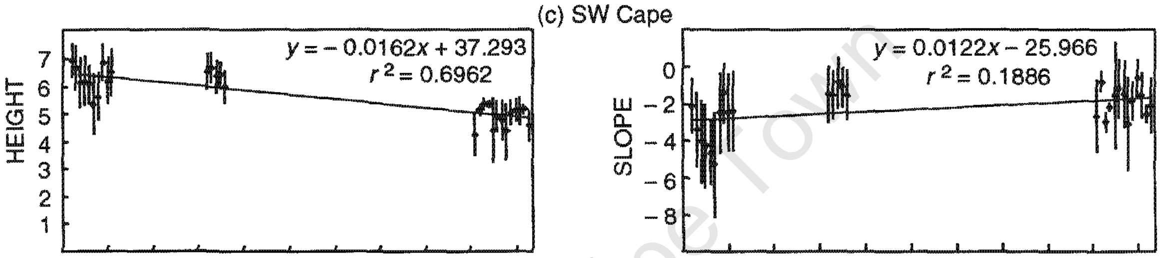
(a) W Cape (+ snoek)



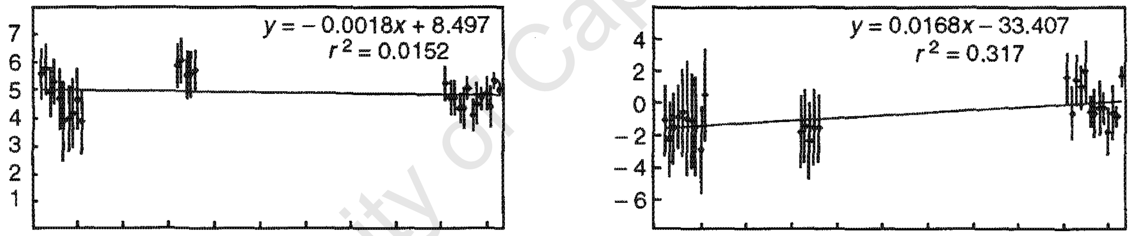
(b) W Cape (– snoek)



(c) SW Cape



(d) S Cape



(e) SE Cape

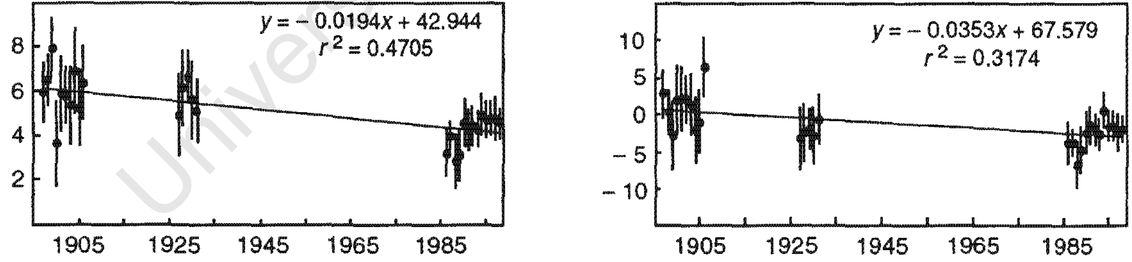


Figure 2.8. Long-term trends in the heights and slopes of size spectra in the four coastal sub-regions of the Cape (Error bars ± 2SE, n = 28). Western Cape with snoek (a), Western Cape without snoek (b), Southwestern Cape (c), Southern Cape (d), Southeastern Cape (e).

2.3.4 Regional comparison

The mean heights of the modern size spectra of the four coastal regions are plotted against the corresponding slopes (Fig. 2.9). It appears that there are distinct differences in the size spectra of the four regions and the position of the Western Cape on the plot appears to depend on the inclusion or exclusion of a dominant species. When snoek is included, all the four sub-regions group together. The exclusion of snoek from the size spectrum results in a dramatic shift of the position of the Western Cape towards the lower left hand side of the plot; the other regions remain in their original positions.

The pattern in the average slopes and heights of the sub-regions reflect the size composition and overall abundance of linefishes in the sub-regions. The shallow slope of the Southern Cape suggests relatively abundant larger individuals, this can be attributed to the dominant species (carpenter, silver kob, yellowtail, snoek, and geelbek); all of them except carpenter are large species (see Table 2.1). The Western Cape has the second shallowest slope, which is mainly because of snoek. The Southwestern Cape has a relatively steep slope indicating that smaller individuals dominate the catch here. The Southeastern Cape has the steepest slope, which implies a shift from large to small individuals. Catch in this region is dominated by the small carpenter and panga followed by silver kob.

Slopes and heights of the fish size spectra of different ecosystems from around the world have been compared (Bianchi *et. al.* 2000 Fig. 2, Bianchi *et. al.* 2001 Fig. 3). Both studies show distinct differences in size composition among the different ecosystems and between shelf and slope assemblages; they occur in an almost straight line on the plot of the slope versus intercept. This was partly a reflection of the correlation between the slope and intercept, where steeper slopes correspond to larger heights, as suggested by the authors. In the present study the four regions are not aligned linearly, mostly because of the removal of the correlation between the slopes and heights. This is clearly shown in Figure 2.10 where the four sub regions were arranged quasi-linearly. Regions with steeper slope are characterized by larger intercept and vise versa for regions with shallower slope.

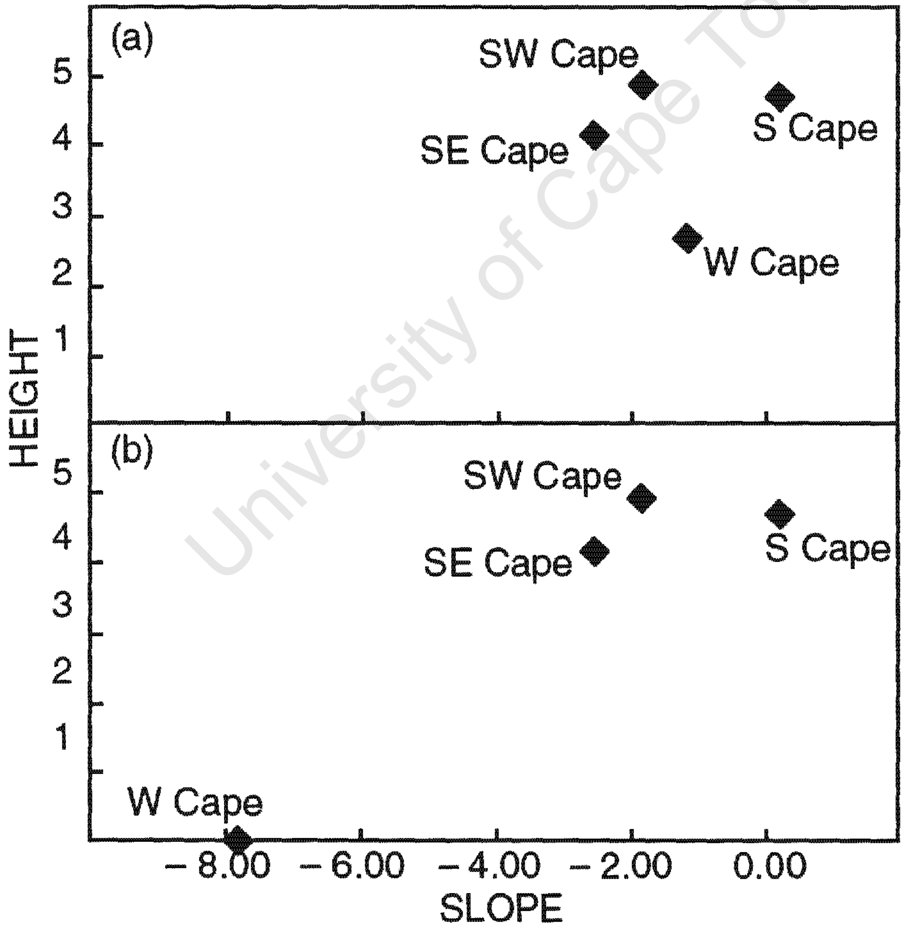


Figure 2.9. Regional comparison of size spectra using the slope and height in the modern period (1986 – 1998), with (a) and without (b) snoek.

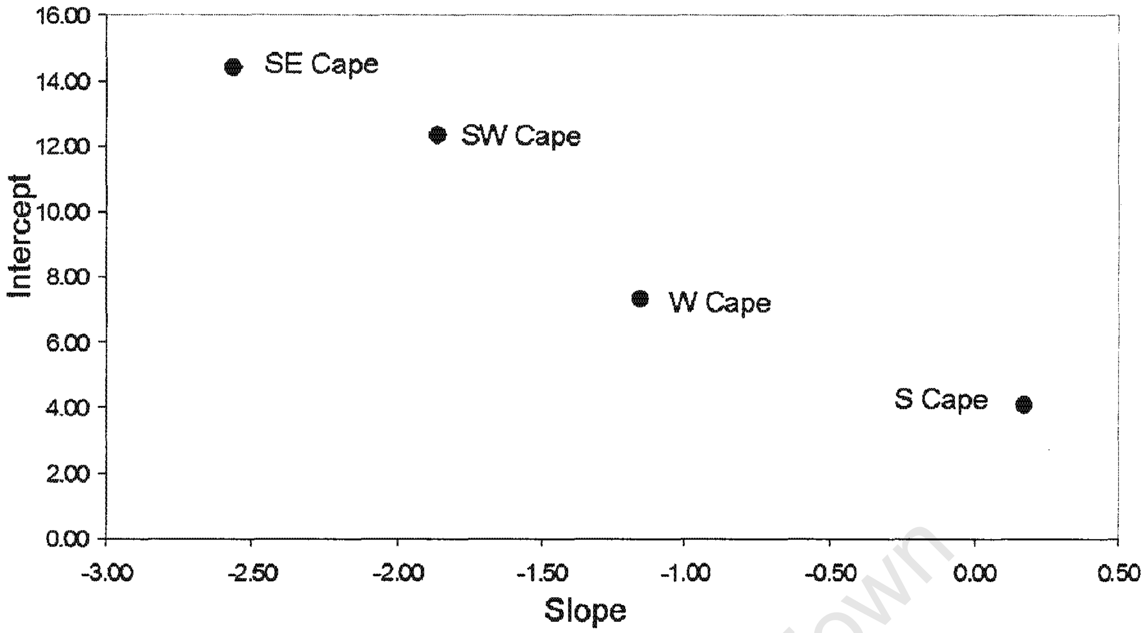


Figure 2.10. Regional comparison of size spectra using the slope and intercept in the period 1986 – 1998, with the inclusion of snoek in all regions.

2.3.5 Dominance

The *k*-dominance curves for the four sub-regions are depicted in Figure 2.11. There are considerable changes in dominance over the period between the 1890s and 1990s but the responses of the cool temperate and warm temperate regions are opposite. The cool temperate Western Cape tends to shift towards the catch being dominated by a few species with time; snoek contributes nearly 90% of the catch followed by hottentot. This sub-region has low species diversity historically as compared to the other sub-regions, so as the other species are depleted, there is a tendency for the system to be dominated by a single (fast-growing) species. In the Southwestern Cape there is not much change in the dominance plot between the historical and the modern periods, but there is a change in the dominant species from geelbek to snoek in the modern period (Griffiths 2000). The more species-diverse warm temperate regions (Southern and Southeastern Cape) show reversal of the trend from the catch being historically dominated by few species towards a more evenly spread modern catch (1986 – 1998).

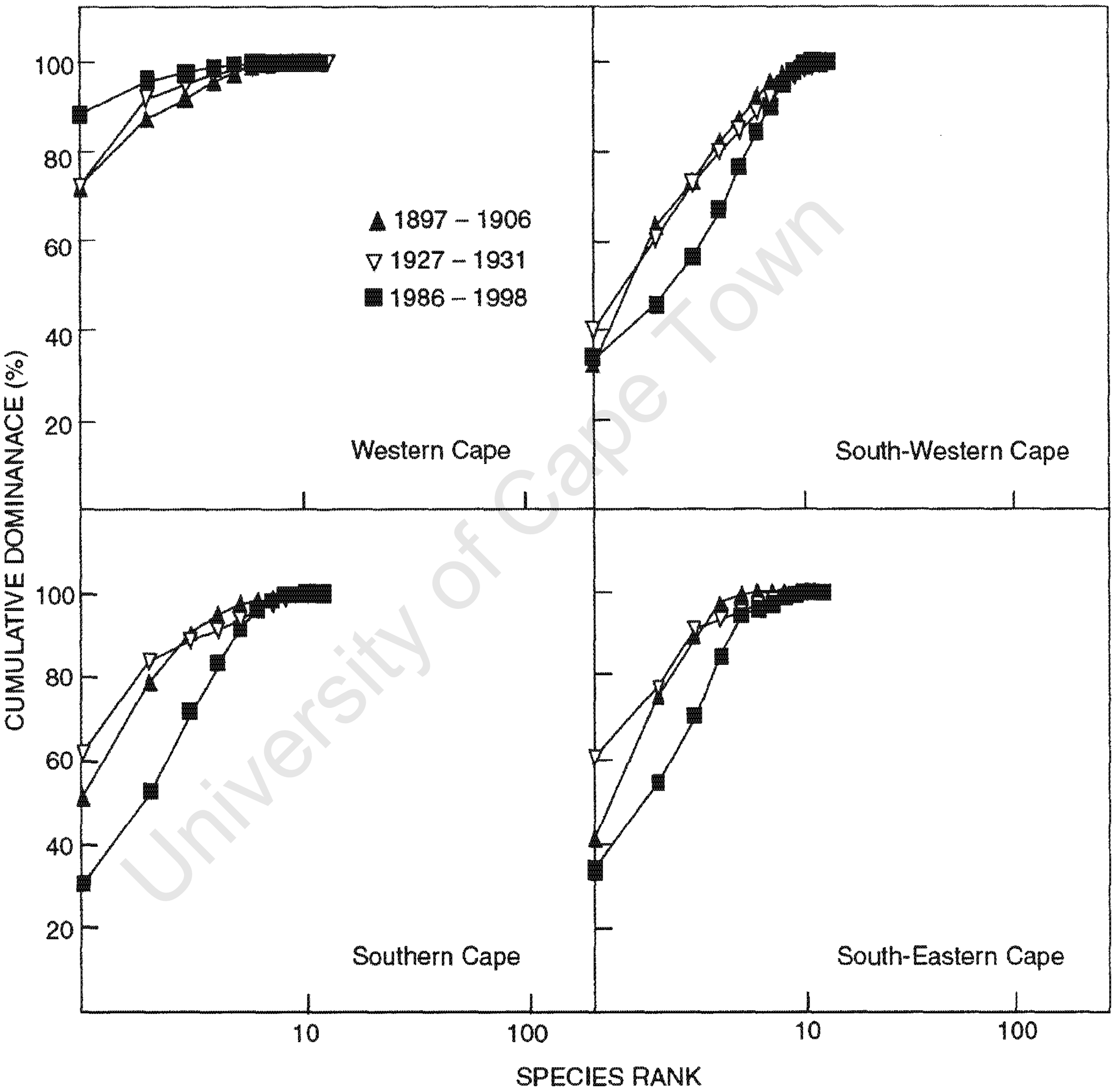


Figure 2.11. *k*-dominance plot of species biomasses of the four coastal regions for the three periods.

2.4 Discussions

This data set covers catch, effort, and fish size distribution records over a period of 100 years from the 1890s to the 1990s. The four sub-regions reflect different areas biogeographically as well as having different histories of development and exploitation.

2.4.1 Catch and effort: The dramatic declines in CPUE reflect the heavy commercial exploitation of the linefish. The reduction in CPUE is attributed to unregulated commercial effort and life history traits of the species in each region (Griffiths 2000). The depletion of most species is mainly attributed to over-fishing (Attwood and Farquhar 1999, Griffiths 2000). Although mis-reporting could theoretically have influenced the observed trends, the commercial handline trends were verified by similar trends in commercial trawl data sets (silver kob and carpenter), fishery independent linefish surveys (Southern Cape), and stock assessment (silver kob, geelbek, carpenter and yellowtail (*Seriola lalandi*) (Griffiths 2000).

The analysis of catch and effort shows that both catches and effort have increased several-fold over the past 100 years. The aggregate CPUE declined to less than 20% of its level in the 1890s. This is a very conservative estimate, as our estimates of the effort do not take account of major technological improvement in the fishery (e.g. motorization, echo-sounding, satellite positioning). This aggregate analysis also fails to take into account changes in catch composition and size.

2.4.2 Multivariate analysis of CPUE: This analysis shows the combined effect of the changes in CPUE for all 12 linefish species considered, confirming the conventional catch and effort analysis and showing that there was relatively little change in catch rate and catch composition from 1900 to 1930s, but a major change between the 1930s and 1980s, demonstrating a major change in abundances of the species, corresponding to the major change in fishing effort in this period; primarily as a result of developing technology and unregulated effort (Griffiths 2000). Previous studies on the effects of heavy fishing on fish assemblages have shown that changes in the catch composition often reflect changes in the assemblage considered (Gulland 1987, Pinnegar *et al.* 2002).

2.4.3 Analysis of mean size: The analysis of the trend in the mean size of individual species considered in this study shows that mean size of 58% of the species declined over the three periods whereas the rest showed an increase in mean size. The average size of species may decrease with changes in growth rate in response to environmental changes (e.g. change in the ambient temperature); However, there is no evidence that there has been a long term trend in coastal ocean temperatures in the Western or Southern Cape regions. If the data are from only a short period, size change may be the result of inter-annual dynamics in the recruitment of individual species (Haedrich and Barnes 1997). But, if the measured decreases in the mean length are assessed in conjunction with the trend in the CPUE of individual species reported in Griffiths (2000), it can be concluded that heavy exploitation is the most likely cause of the reduction in the mean length.

The average length in the modern period may also have been positively biased by the minimum size limit regulations introduced in 1940 and 1985, thus the reduction in size may have been greater than the data indicate.

On the other hand the mean length of the catch shows a minor (marginally non-significant) change in the overall mean length of the pooled catch in all four sub-regions and species. The gentle trend in declining overall mean length is attributed to the masking effects of the dominant, fast-growing snoek, and possibly to a switch in target towards migratory yellowtail in modern times. When snoek are excluded from the analysis the declines in overall mean length over the 100 year period are significant. Table 2.1 demonstrates the expected response to heavy fishing pressure: in seven out of 12 species considered the mean length of fish has declined substantially. Observed change in the mean length of individual species and hence fish communities could also be influenced, in addition to those mentioned above, by technical issues in the fishing practices: 1) change in discarding practices or high grading over time so that fishermen tend to target larger individuals or species, 2) increased landing of large proportion of the catch this may happen at the later stage of fishery and happens in response to increased demand for fish or in response to decline in the abundance of initial target species or combination of both, 3) non technical changes in genetic structure so that the continuous selection of the largest fast growing component of a population or community over longer time period in this case over 100 years. may result in juvenilizing the fish population or community. However as mentioned previously (page 5) there was no substantial change in the hook design or size used by the linefishery over the period considered.

2.4.4 Analysis of size spectra: Analysis of the combined distribution of fish sizes of the 12 species in logarithmic size classes is depicted in size spectra, summarized by the twin statistics of slope and height of the log-linear regression (Table 2.2). Slopes of the size spectra of some sub-regions become significantly more negative in the modern period, showing that the modern linefish catch has fewer large fish and relatively more small individuals than in the historical period, in spite of modern minimum-size regulations. The significant decline in the slopes of the Southeastern Cape size spectra indicates a long-term shift in the size composition towards smaller individuals (Table 2.2, Fig. 2.8e). This could be both the result of decreases in the abundances of larger individuals of all species and differential over-exploitation of larger, long-lived species. For the whole Cape linefishery both seem to be the case as the mean size (Table 2.1) and abundance of smaller species like carpenter and roman is substantially reduced in addition to the over-exploitation of the larger species seventyfour, kob, geelbek over the 100 year period (Griffiths 2000). On the other hand, the significant decline in the heights of the size spectra over time indicates an overall reduction in the abundance of all linefish in the landings. In the Western Cape (cool-temperate region) the size spectrum was strongly influenced by the abundant snoek and the slope does not change with time. Snoek is a large snake mackerel, which has socio-economic (valuable) and ecological (important pelagic predator) significance (Griffiths 2002, McQueen and Griffiths 2004) in the Cape region. Owing to its unpredictable longshore and offshore migrations, and r-selected life history traits such as fast growth, early maturity, and relatively short lifespan (Attwood and Farquhar 1999, Griffiths 2002), it is less vulnerable to overexploitation compared to the other linefish species. The Western Cape provides a good example of how the size spectrum can easily be influenced by a dominant species. If the dominant species is large like snoek, the slope of the size spectrum will tend to be shallower and may even become positive. This can mask changes in the size composition of the other species with changes in fishing effort. The height reflects overall abundance. The heights of the size spectra in the whole Cape region and all of the sub-regions, except the Southern Cape, have decreased significantly over the same period (100 years) suggesting an overall reduction in the abundance of all size classes. The substantial steepening in the slope of the Southeastern Cape and Western Cape without snoek was accompanied by a significant decrease in the height, thus not only the size structure but also the overall abundance of linefishes has been negatively impacted by heavy fishing as suggested by this study and the work of Griffiths (2000).

Furthermore, the linefish assemblage changes that are implied by changes in catch composition are different in the four sub-regions. The cool-temperate sub-regions differ from the warm-temperate ones, particularly with regard to the inclusion or exclusion of the fast-growing, nomadic, cool-water snoek. Inclusion of snoek gives the size spectrum of the cool-temperate sub-regions a shallower slope. The negative slope of the size spectrum was found to be directly proportional to the level of exploitation (Gislason and Rice 1998, Shin and Cury 2004). The work of Bianchi *et al.* (2000, 2001), which synthesizes size spectra and dominance structures of different marine ecosystems, added further support to the findings of Gislason and Rice (1998). The height of the size spectrum reflects overall fish abundance (Daan *et al.* 2005). This shows declines in overall abundance of the fish assemblages over the 100 year period considered in all four sub-regions, with statistically significant declines in all but one sub-region (Table 2.2).

2.4.5 Analysis of dominance curves: Dominance curves reflect the distribution of biomasses among species. Clearly these are also affected by the inclusion or exclusion of dominant species like snoek. The cool, upwelling-influenced Western Cape sub-region shows a trend towards increasing dominance in the modern period. Similar patterns of increasing dominance in temperate regions have been reported for the North-western North Sea (Greenstreet and Hall 1996), Southern North Sea (Rijnsdrop *et al.* 1996), Scotian shelf and Portugal (Bianchi *et al.* 2000). The warm temperate regions (Southern and Southeastern Cape) show decreased dominance with increasing fishing pressure. This is because, as the preferred species in the sub-regions, geelbek and silver kob were depleted, fishers tended to target other, less preferred, species (Griffiths 2000 Figs 17 and 18). Bianchi et al. (2000) found the same pattern of decreasing dominance in tropical regions (Ghana, Campeche Bank and Sofala Bank). This may be explained by taking into account life history traits, the relatively higher diversity, and the fact that most of the species are associated with rocky reefs. These species are usually long lived, *k*-selected species and have restricted ranges. When a fish community dominated by *k*-selected species is heavily fished their productivity is generally too low to cope with the fishing pressure, thus dominance decreases. If the Southeastern Cape is considered, the work of Griffiths (2000) shows that it was historically dominated by geelbek followed by silverkob and seventy four all of which are k-selected, slow growing species. These three species have subsequently been overexploited and the catch now tends to be dominated by the smaller carpenter and the overall dominance decreased. The use of *k*-dominance curves in assessing the effects of fishing may still need some refinement to analyze the direction of responses of the fish communities to disturbance.

This study shows that traditional analyses of overall catch rates are enhanced by multivariate analysis of the combined effects of fishing on all species, analysis of mean size, the slope and height of the size spectrum and dominance curves. These analyses are complementary and need to be assessed together with information on the life-history traits of the species, changes in target species, and other related aspects. Taking into account the fact that most of the linefishes considered in this study are predators at different trophic levels, over-exploitation and decreases in the abundance of larger individuals are likely to have tropho-dynamic implications for the functioning of the whole ecosystem.

Chapter 3 Comparison of fish community size spectra based on length frequencies and mean lengths

Abstract

Estimates of fish community size spectra are promising indicators of the impact of fishing on fish assemblages. Size spectra consist of logarithmic graphs of abundance plotted against fish body size. Size spectra may either be constructed from length-frequency data or estimated from the mean sizes and abundances of the species in an assemblage - very often mean sizes are the only historical data available. Changes in the slopes of size spectra are interpreted to indicate changes in the relative abundances of small versus large fish, whereas changes in intercept (height) suggest changes in the overall abundance of the fish assemblage. A comparison of the size spectra of linefish catches of the Cape region, South Africa, (1986-1998) revealed that statistics of the size spectra calculated from mean length data were significantly larger (heights) and shallower (slopes) than those calculated using length-frequencies (paired t-tests, $p<.001$). Thus use of mean lengths in size spectra overestimates the overall abundances of the community. Mean length was also found to overestimate the relative abundance of larger fish in the assemblage thereby underestimating the effects of fishing. In a time series of size spectra, it is therefore necessary to use one method consistently for comparative purposes.

Key words: size spectra, mean length, length frequency

3.1 Introduction

Fisheries affect marine ecosystems in a multitude of ways, causing or enhancing changes in the structure and function of the ecosystem (Gislason *et al.* 2000). Some of the effects of heavy fishing include over-exploitation of target species, changes in species composition, changes in the size structure, and differential effects on functional groups in the ecosystem. Many indicators have been proposed to capture the effects of fishing on fish communities: e.g. diversity indices, ordination plots of species abundance, proportion of piscivorous fish, proportion of non-commercial species, average size of fish in the community, size spectra, mass balance models, and dominance curves (Rice 2000, Rochet and Trenkel 2003). Size spectra are promising indicators still under development (Rice 2000, Rochet and Trenkel 2003).

Size spectra are generally constructed by plotting the abundance or biomass of components of a community against the log (bases: 2, 10, or e) of length or body mass respectively, with varying body size interval. For the purpose of this study size spectra are constructed by plotting the log of the number of individuals in a community per five-centimeter size class against the log of the class mark (Bianchi *et al.* 2000). Then linear regressions are fitted to calculate the slopes and heights of the size spectra. The slopes and intercepts (heights) of size spectra are reported to change proportionally to changes in the fishing level (Gislason and Rice 1998, Bianchi *et al.* 2000, Shin and Cury 2004). A steep (negative) slope of the size spectrum is attributed to selective removal of large individuals from the fish community. The height on the other hand, can be used as an index of community abundance if measured at the mean of the independent variable to avoid its correlation with slope (Daan *et al.* 2005). Temporal trends in the slopes and heights of the size spectra are used to infer changes in size structure and abundance.

Size spectra are ideally constructed from individual length measurements, but when these are not available (often the case with historical data), size spectra have been generated using information on the mean size and relative abundance of each species in a community/assemblage (Rice and Gislason 1996, Bianchi *et al.* 2000, Bianchi *et al.* 2001). Chapter two of this thesis constructs size spectra based on mean length of the species included. The consequences of different kind of data in the construction of size spectra have not been investigated and this note aims to show how estimates of the size spectrum parameters are affected by the kind of information used (mean length or length-frequencies) and possible misinterpretation that may result from the comparison of the slopes and heights calculated in different ways.

3.2 Methods

This study covers Western and Eastern Cape Provinces (here called the whole Cape), South Africa. It is sub-divided into four sub-regions: Western Cape, Southwestern Cape, Southern Cape, and Southeastern Cape. Each is characterized by a different history of fishing (Griffiths 2000) and experiences different oceanographic conditions (Schumann 1987, Shannon and Nelson 1996). The sub-regions fall into two different biogeographic zones (Branch and Branch 1981). See Chapter two for further details of the area and data used.

Construction of size spectra

3.2.1 Size spectra using length-frequencies

Length-frequency data of the 12 main linefish species (Table 2.1) were obtained from official observers at fishing harbours in the four sub-regions of the Cape. Length-frequency data of each species consisted of samples from 12 months in a year. Sampling frequency varies among the different sub-regions for all the species under study and ranges from a minimum of one month to whole year round sampling. It also varies among the years included in this study. Sample size varies among the species ($n = 20$ to $n = 1000$) for most species except for snoek and seventy-four. In extreme case smallest sample size $n = 1$ is observed for seventy-four and largest sample size $n > 20000$ is recorded for snoek in some years and sub-region.

The length-frequencies of individual species from samples, on a yearly basis, were raised to the total catch using raising factor (R_{ij}).

$$R_{ij} = \frac{T_{ij}}{S_{ij}}$$

Where R_{ij} = raising factor for species *i* in year *j*, T_{ij}= total catch of species *i* in year *j*, S_{ij} = sample weight of species *i* in year *j* from which length frequencies were obtained. An index of abundance was estimated by dividing the catch (numbers) per size class by the effort (boat-years) and expressed as numbers per boat-year. Size spectra for each year were constructed by allocating the numbers of individuals of each species into the appropriate five-centimeter size class, summing the numbers of all species in each size class, and plotting the logarithm of abundance against the logarithm of class mark. Linear regressions were fitted to estimate the slopes and heights of the size spectra. All heights were calculated at the mean of the independent variable to avoid their correlation with the slopes (Daan *et al.* 2005).

3.2.2 Size spectra using mean lengths

Size spectra using mean length was constructed in exactly the same way as in Chapter two. The only difference being in this case the size spectra is constructed for the modern period (1986 – 1998).

Paired t-tests were used to test the difference in the estimated slopes and heights of the size spectra between mean length and length frequency data. For this test estimates from all sub-regions were combined. In addition mean residual sums of squares (MRSS) were calculated for size spectra based on mean lengths and length-frequencies. The significance of the differences in MRSS using length-frequencies and mean lengths were tested using paired t-test.

3.3 Results

Figure 3.1 shows samples of the size spectra in each sub-region for selected years constructed using length-frequency data and the mean length of each species. Slopes and heights of size spectra calculated using length-frequency data were generally smaller than those estimated using mean lengths, with the exception of the Western Cape.

For the whole Cape region, the heights and slopes of the size spectra, obtained from the length-frequency data, tend to be smaller than those estimated using the mean lengths of each species (Fig. 3.2). Similar results were obtained for three of the four sub-regions: Southern Cape, Southeastern Cape, and Southwestern Cape (Fig. 3.3). In the Western Cape, however, the heights estimated from length-frequencies were larger than those from mean lengths whereas the slopes did not show any distinct pattern (Fig. 3.3). This is because of the influence of the dominant large species, snoek. In the Western Cape more than 90% of the catch is dominated by snoek followed by the smaller hottentot, (mean lengths 75.9 cm and 29.3 cm respectively for the period considered). The other linefish species contribute minor proportions to the catch in this sub-region.

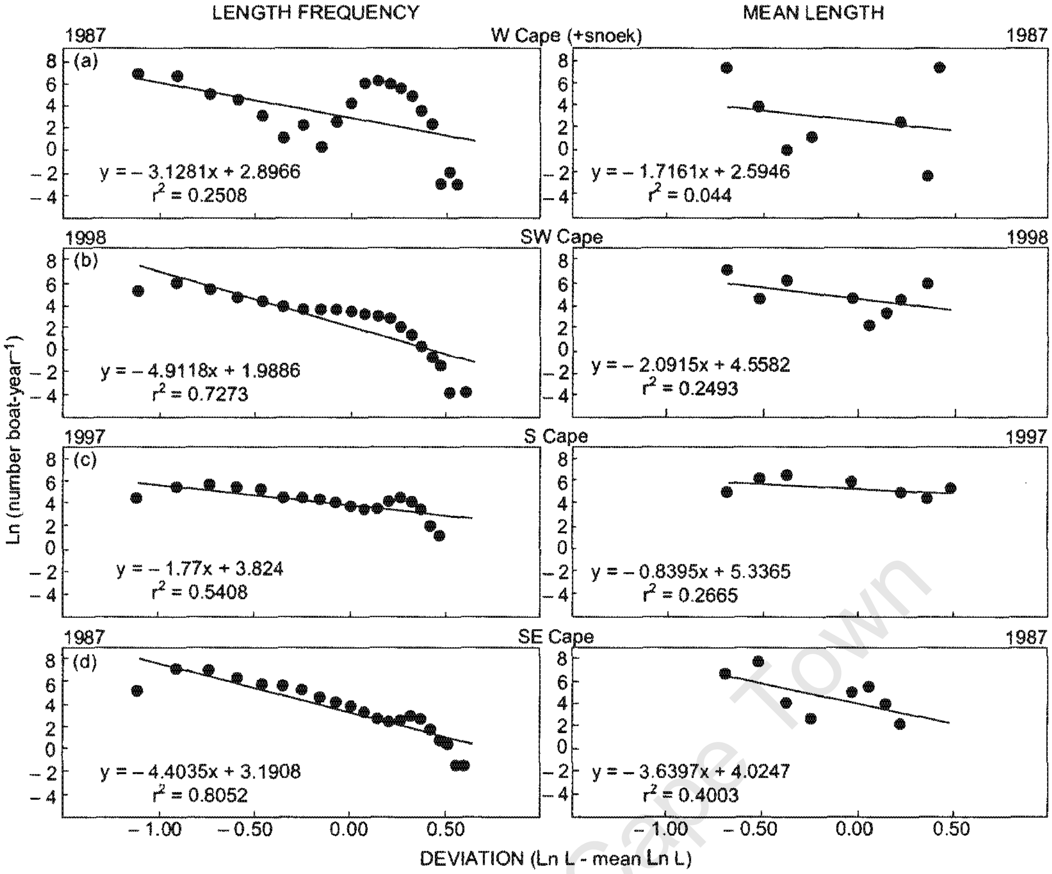


Figure 3.1. Examples of the size spectra of the four sub-regions for selected years constructed using length-frequency data and mean length. Western Cape (W Cape), Southwestern Cape (SW Cape), Southern Cape (S Cape), Southeastern Cape (SE Cape).

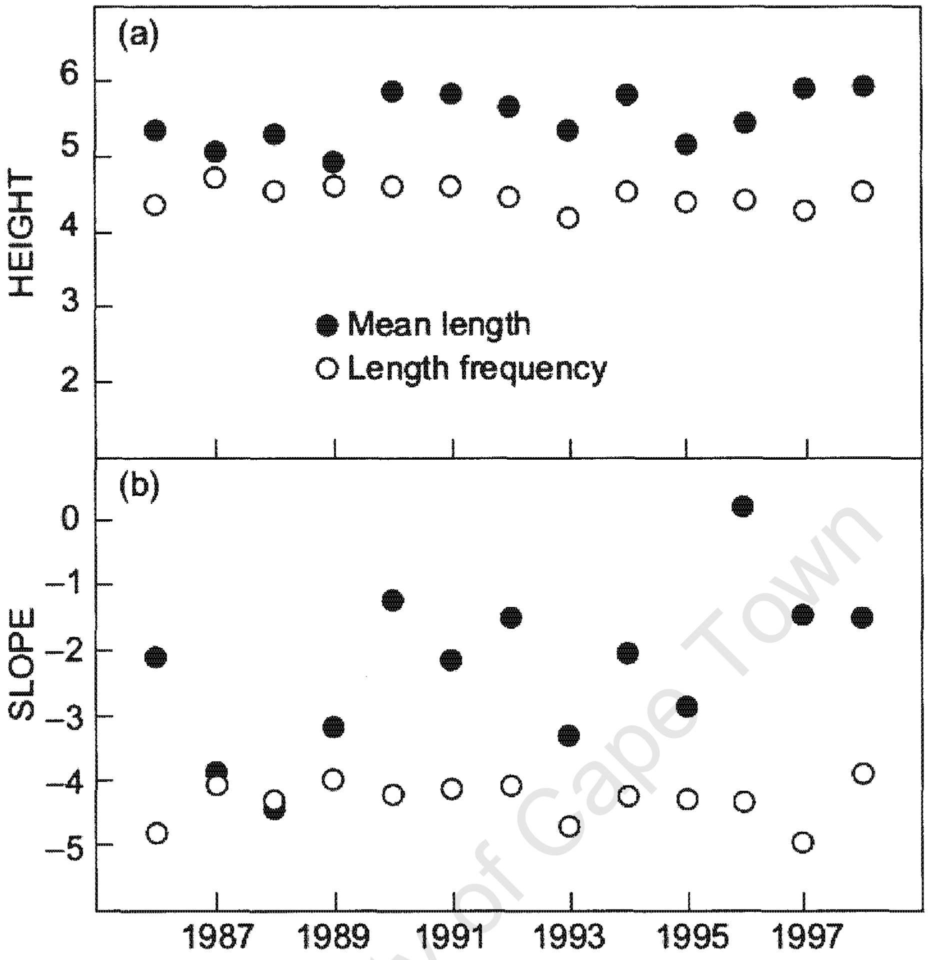


Figure 3.2. Temporal comparison of the heights and slopes of the size spectra of the whole Cape (see Fig. 2.1) based on mean lengths and length-frequencies for the period 1986 - 1998.

The paired t-test shows that slopes of the size spectra estimated from mean lengths are significantly shallower (less negative) than those calculated from length frequency data (t = 9.03, df = 12, p = 0.000). Similarly, heights of the size spectra estimated from mean lengths were significantly bigger than those calculated from length frequency data (t = 6.28, df = 12, p = 0.000).

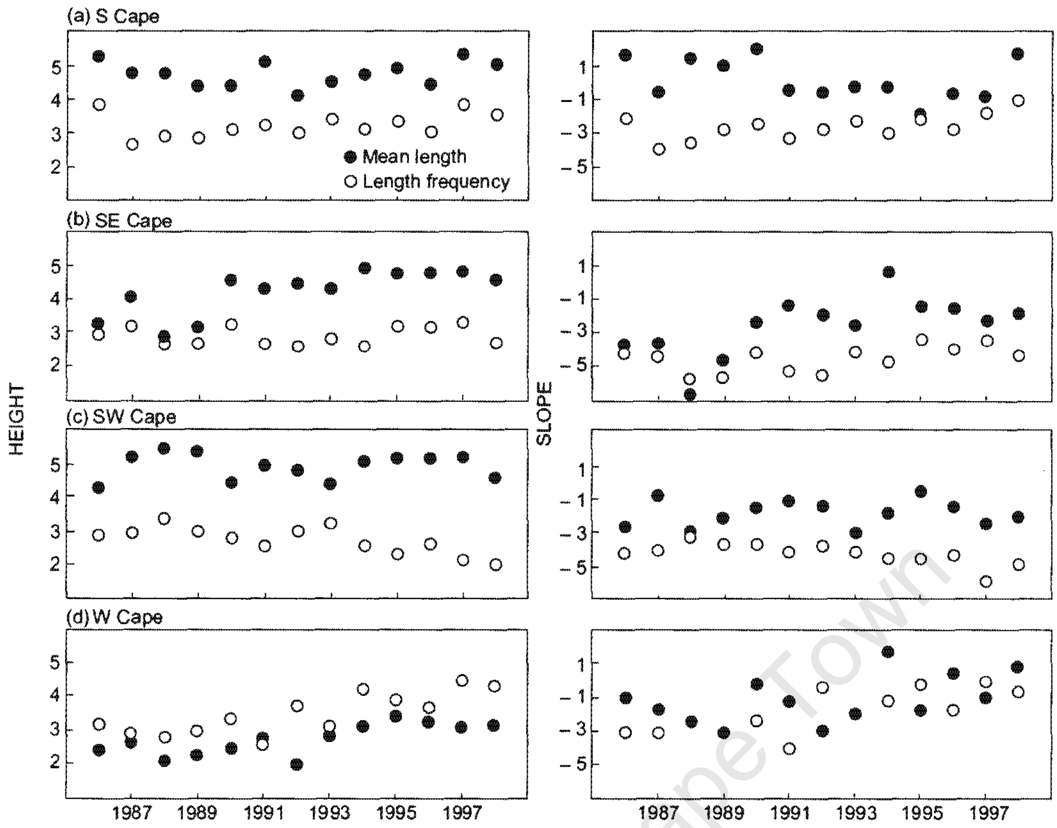


Figure 3.3. Comparison of the heights and slopes of the size spectra of the four sub-regions based on mean lengths and length-frequencies for the period 1986 – 1998. Southern cape (S Cape), Southeastern Cape (SE Cape), Southwestern Cape (SW Cape), Western Cape (W Cape).

Mean residual sums of squares of the size spectrum regressions ($\log_e$ abundance vs $\log_e$ body size) for length-frequency data (mean RSS = 3.22) were significantly smaller than, $p < 0.05$, for mean length data (mean RSS = 8.18); in both cases $N = 52$. Thus the length-frequency method gives statistically better linear fit to the data.

3.4 Discussion

The results show that the bias introduced by resorting to estimates based on the mean sizes of each species is usually towards an increase in the relative abundance of larger fish in the size spectrum. This will tend to underestimate the effects of fishing, which normally is targeted at larger fish. Several factors may bias size spectra based on the annual mean lengths of an assemblage of species. These include sample size, sampling frequency and the number of species in the analysis. In addition the shape and variance of the length distribution of individual species may bias the estimated size spectra.

Furthermore it also show the possible misinterpretation that could arise from the combined use of mean length data (for certain periods, especially historical periods when often the only information available is the mean size of species) and length-frequencies (usually for recent periods) in assessing the long-term trends in the slopes and heights of the size spectra. For example consider a time series for the Southern Cape (Fig. 3.3) constructed using the mean length methods (solid circles) for 1985-1991 and individual lengths for 1992-1998 (open circles). An artificially declining trend is created for both height and slope.

Based on the results of this study we recommend that size spectra should, wherever possible, be based on length-frequency data. However, in circumstances where only mean lengths are available for part of the study period, size spectra for all years should be based on the mean length method.

Chapter 4 The effects of fishing on the demersal fish communities of the south coast: assessing changes in size structure

Abstract

Heavy fishing is believed to change the size structure of fish communities through the differential removal of larger sized individuals and species. The size structure of the demersal fish communities off the south coast of South Africa is assessed using a variety of size-based indicators. The communities on this coast are subjected to different fisheries with wide ranging impacts. Changes in the size structure were assessed over the period from 1986 – 2003 for the whole south coast and two depth strata. There was a reduction in the mean length, mean maximum length (L_{max}), and proportion of large fish in the fish communities off the south coast of South Africa, and a corresponding increase in the proportion of small fish. Species with a large L_{max} declined in mean catch rate and mean length in contrast to species with small L_{max}. The trend in the size-based indicators suggests that there has been a change in the size structure of the communities. This change is characterized primarily by a reduction in the abundance of larger sized individuals and in species with a large maximum length.

Key words: size structure, size based indicators, demersal assemblages, South Africa

4.1 Introduction

The demersal fishery of South Africa started around the turn of the 20th century (Botha 1985), with intense harvesting after 1960s when the hake resource become widely sought (Payne 1995). The hake-directed bottom trawl fishery has been managed under a stock rebuilding strategy since South Africa declared the 200mile Exclusive Economic Zone (EEZ) in 1977 prior to that it was heavily exploited by foreign distant water fleets (Botha 1985, Rademeyer 2003). The demersal fishery on the south coast includes both inshore and offshore sectors, each of which is multi-gear and multi-species. Gears include line (both hand-line and long-line), pelagic mid-water trawl and bottom (otter) trawl (using 75, 85, and 110mm codends). The trawl sector targets Agulhas sole *Austroglossus pectoralis,* shallow-water Cape hake *Merluccius capensis*, deep-water Cape hake *Merluccius paradoxus*, Cape horse mackerel *Trachurus trachurus capensis* whereas the line sector targets shallow- and deep-water hake and a large number of shallow water (mainly reef dwelling) species. The longline fishery was initially introduced in the mid 1980s targeting kingklip *Genypterus capensis* was operational until 1990, after which it was banned because of its substantial impact on the resource (Punt and Japp 1994). The longline fishery was again reinstated in 1994 as experimental fishing targeting hake; this fishery is highly size selective, targeting fish above 60cm (Rademeyer 2003). As female hake grow faster, and attain a larger size than males (Punt and Leslie, 1991), the longline catch consists primarily of large, highly fecund females. Apart from the direct effect on the biomass of the target species and size distribution, the size-selective nature of this fishery may also have indirect effects: reduced reproductive output of the target species and effects on the trophic structure of the system, the magnitude of which depends on the functional role of the species as a predator. Furthermore, the longline fishery can target fish on rough ground where otter trawlers cannot operate.

All the different fishing sectors catch a variety of bycatch species that are either brought to landing or discarded offshore. In addition, all the above-mentioned gears catch various non-target demersal fish and cephalopod species.

One of the common features of these fishing gears is that they are all size-selective, although the degree of selectivity varies substantially within and among gears. Trawling tends to be less size selective than hand- and long-line fishing. Thus size selectivity represents one of the many ways in which fisheries interact with the structural and functional organization of marine ecosystems. The role of size as a structuring factor in marine ecosystems has been discussed in a number of studies (e.g. Platt and Denman 1978, Borgmann 1987, Moloney *et al.* 1991, Boudreau and Dickie 1992). In addition different studies ranging from terrestrial through to aquatic ecosystems have showed the allometric relationship between physiology of animals and body size (e.g. Calder 2001, Lominicki 2002), thus a change in the size structure of an assemblage has a major influence on the structure and functioning of the ecosystem.

A number of size-based indicators have been put forward to capture the effects of heavy fishing at different levels in marine ecosystems (Rochet and Trenkel 2003, Rice 2003); e.g. population level indicators (e.g. mean size, size at maturity), community level indicators (e.g. parameters of the size spectra, mean length of the community, proportion of size groups, proportion of L_{max} group), and ecosystem size spectra (biomass or abundance size spectra of the whole ecosystem from phytoplankton to fish).

The effects of fishing on the size composition of fish communities has been documented by empirical and theoretical studies from around the world: e.g. Haedrich and Barnes (1996) (looking at changes in mean size of fish species from Northeast Newfoundland and the Labrador shelf); Rice and Gislason (1996) (changes in the slope and intercept of abundance and diversity size spectra of North Sea fish assemblages); Gislason and Rice (1998) (modelling the response of size spectra to changes in fishing level using single-species and multispecies models); Bianchi *et al.* (2000) (using slopes and intercepts of size spectra for different ecosystems around the world); and Shin and Cury (2004) (applying an individual based model to assess the response of parameters of size spectra). The slope of size spectra has been shown to change proportionally to the change in fishing level (Gislason and Rice 1996, Rice and Gislason 1998, Shin and Cury 2004). The intercept of size spectra is believed to reflect the overall abundance or system productivity (Borgmann 1987, Boudreau and Dickie 1992, Bianchi *et al.* 2000). The mean size and mean Lmax of fish communities are also believed to change in response to fishing (Rochet and Trenkel 2003, Dulvy *et al.* 2004). In addition, the relative proportions of size groups in fish communities are reported to change with exploitation level (Daan *et al.* 2005).

This study aims to assess trends in the size composition of the South African south coast demersal fish communities using size-based indicators and the observed direction of response of the fish communities is discussed in the light of fishing impact and other possible driving factors.

4.2 Methods

4.2.1 Data source

The data used in all the subsequent analyses was obtained from the biannual demersal research trawl surveys of the south coast of South Africa conducted by the Branch: Marine and Coastal Management (MCM) of the Department of Environmental Affairs and Tourism (DEAT). The survey is conducted using a 180ft German otter trawl with 75mm mesh codend fitted with a 35mm mesh liner. Duration of trawls is limited to 30 minutes, in cases where it is exceeded or reduced for any reason; the catch is standardized to 30 minute tow duration. Towing speed and mouth width of the trawl are assumed to be constant (3.5knots and 26m respectively).

Therefore the area swept in a 30min tow is assumed to be constant (0.0246 square nautical miles).

At each station the whole catch (or sub-sample if the catch was too large) was sorted and identified to the lowest practical taxon (species whenever possible), then counted and weighed. Length frequency data was collected for commercial species and some common by catch species from the whole catch when possible or from a sub-sample when the catch for a species was large. The survey spans an 18-year period (1986 – 2003) and covers shelf and upper slope to the 500m isobath between 20^0 E and 27^0 E meridians (Southern and Southeastern Cape regions in Fig. 2.1).

This coast is characterized by distinct physical and hydrodynamic features (Schumann 1987). The Southwest flowing warm Agulhas current and physically a wider shelf down to 200m isobath with the edge of the shelf dropping steeply and the shelf getting narrower towards the East distinguishes this coast. The survey area is subdivided into four depth zones (0 – 50m, 51 – 100m, 101 – 200m, 201 – 500m), though for the purpose of this study the first two strata was pooled together. Each of the strata is subdivided into grids of size 5' x 5' (five X five nautical miles). Trawl stations during each cruise are distributed among the four strata, on a semi random basis, in proportion to the area of each stratum (Badenhorst and Smale 1991).

in response to fishing (Rochet and Trenkel 2003, Dulvy *et al.* 2004). In addition, the relative proportions of size groups in fish communities are reported to change with exploitation level (Daan *et al.* 2005).

This study aims to assess trends in the size composition of the South African south coast demersal fish communities using size-based indicators and the observed direction of response of the fish communities is discussed in the light of fishing impact and other possible driving factors.

4.2 Methods

4.2.1 Data source

The data used in all the subsequent analyses was obtained from the biannual demersal research trawl surveys of the south coast of South Africa conducted by the Branch: Marine and Coastal Management (MCM) of the Department of Environmental Affairs and Tourism (DEAT). The survey is conducted using a 180ft German otter trawl with 75mm mesh codend fitted with a 35mm mesh liner. Duration of trawls is limited to 30 minutes, in cases where it is exceeded or reduced for any reason; the catch is standardized to 30 minute tow duration. Towing speed and mouth width of the trawl are assumed to be constant (3.5knots and 26m respectively).

Therefore the area swept in a 30min tow is assumed to be constant (0.0246 square nautical miles).

At each station the whole catch (or sub-sample if the catch was too large) was sorted and identified to the lowest practical taxon (species whenever possible), then counted and weighed. Length frequency data was collected for commercial species and some common by catch species from the whole catch when possible or from a sub-sample when the catch for a species was large. The survey spans an 18-year period (1986 – 2003) and covers shelf and upper slope to the 500m isobath between 20^0 E and 27^0 E meridians (Southern and Southeastern Cape regions in Fig. 2.1).

This coast is characterized by distinct physical and hydrodynamic features (Schumann 1987). The Southwest flowing warm Agulhas current and physically a wider shelf down to 200m isobath with the edge of the shelf dropping steeply and the shelf getting narrower towards the East distinguishes this coast. The survey area is subdivided into four depth zones (0 – 50m, 51 – 100m, 101 – 200m, 201 – 500m), though for the purpose of this study the first two strata was pooled together. Each of the strata is subdivided into grids of size 5' x 5' (five X five nautical miles). Trawl stations during each cruise are distributed among the four strata, on a semi random basis, in proportion to the area of each stratum (Badenhorst and Smale 1991).

4.2.2 Data analysis: Size structure

The changes in the size structure are assessed systematically at a broad spatial level for the entire region and also for the first two of the three depth strata (0 - 100m, 101 – 200m, 201 – 500m). In addition all the analyses were conducted separately for autumn and spring surveys, to avoid the possible influence of seasonal dynamics in the migration of the demersal species. Previous studies reported an apparent inshore-offshore movement along the south coast (Badenhorst and Smale, 1991). Trends in the mean catch rate for the whole community on the south coast and communities associated with each depth stratum were used together with the trend in the nominal fishing effort of the commercial trawl and longline fisheries on the South coast.

Size spectra

Length frequency data for all species were adjusted to estimated numbers per size class per 30min tow duration. For each species the mean number of individuals per five-centimeter size class per stratum was calculated for each cruise and weighted by the area of the stratum for pooling across strata:

$$N_{ij} = \left(\frac{\sum_{k=1}^{S_j} n_{ijk}}{s_j} \right) * A_j$$

Where N_{ij} = number per size class i in stratum j, n_{ijk} = number per size class in stratum j at station k, S_j = total number of station in stratum j, A_j = area of stratum j.

These were then summed across depth strata to get the area-weighted numbers per five-centimeter size class for the whole south coast. The construction of the size spectra and estimation of its parameters are similar as in Chapter three. Size spectra were constructed for the 0 – 100m and 101 – 200m depth strata for each year. For reasons of limited trawls and incomplete sampling over the survey year (Table 4.1) separate size spectra were not constructed for the 201 – 500m depth stratum, however when data were pooled to construct size spectra for the entire region data for this stratum was included. A size range of 26cm – 120cm was used in the construction of the size spectra, to avoid the smallest size classes where escapement might distort the size-spectrum.

Proportion of length classes

Temporal trends in the proportion of the three length classes (1 - 40cm, 41 – 80cm, 81 – 120cm) were assessed by calculating the proportion of the different length classes in each year. In this case all size classes were included. The proportion of each size category in each survey was calculated as follows:

$$P_{ij} = \frac{N_{ij}}{\sum_{i=1}^{3} N_{ij}}$$

Where:

P_{ij} = proportion of length category i in year j

N_{ij} = the pooled number of individuals in the length category i and year j

Abundance per size class was also estimated and assessed over the period of 1986 – 2003 for the following size ranges (1 – 40cm, 41 – 80cm, 81 – 120cm). Log transformed abundance per size class was plotted against time and the trend was assessed using linear regression.

Mean length and L_{max}

The mean length and L_{max} of the community were calculated for the entire south coast and for the 0 – 100m and 101 – 200m depth strata. L_{max} was calculated from the pooled length frequency data as the length below which 95% of the individuals occur. Generally L_{max} can be calculated in three different ways: 1) as a weighted (by the catch or abundance of each species) measure of the L_{max} of species comprising the community concerned; 2) as a weighted measure of the L_{inf} of the species comprising the community concerned, or; 3) as a larger percentile (in this case 95%) from the length frequency distribution of the species in the community. The first two usually reflect the relative abundance of species of different L_{max} or L_{inf} in the community whereas the third could reflect an additional aspect not only the relative abundance of the different species but also of relative abundance of various size groups. Further various percentiles 95% to 99% could also be explored. The significance of the trend over time in the proportions of the length groups, mean length and mean L_{max} was tested using student t-tests (Zar 1999).

Mean length by species

Mean length of each species for the whole south coast was calculated from the length frequency data. The correlation in mean length of species with year was conducted using Spearman's rank correlation (Zar, 1999).

Mean catch rate

The mean catch rate per standard tow (30 min) for the whole south coast was calculated by summing the total catch in each stratum and dividing by the total number of stations sampled.

Table 4.1: Distribution of stations by depth range and range of value of environmental variables measured and the stations from which it was measured are shown in parentheses. Surveys conducted in autumn are shown shaded in grey.

Date	Depth range (meter)	Number of station at each depth range			Temperature (°C)	Oxygen (ml/L)	Salinity (ppt)
		0 - 100	101 - 200	201 - 500			
Sep-86	26 - 465	27	41	12	5.45 - 17.09 (75)	3.26 - 5.83 (72)	34.04 - 35.46 (73)
Sep-87	17 - 395	41	40	7	7.43 - 17.03 (78)	3.38 - 5.63 (75)	34.75 - 35.54 (78)
May-88	30 - 450	44	41	8	8.28 - 14.9 (84)	1.97 - 5.44 (87)	34.78 - 35.45 (84)
May-89	32 - 185	31	31		8.80 - 16.05 (57)	1.85 - 5.19 (57)	34.77 - 35.19 (57)
May-90	30 - 480	33	24	1	9.54 - 17.17 (52)	1.54 - 5.42 (56)	34.76 - 35.49 (52)
Sep-90	24 - 224	43	29	1	8.11 - 16.87 (72)	3.25 - 5.27 (72)	34.71 - 35.65 (72)
Jun-91	33 - 397	52	31	13	8.13 - 16.25 (79)	2.47 - 5.56 (79)	34.56 - 35.33 (77)
Sep-91	31 - 289	55	20	1	9.97 - 17.44 (68)	3.76 - 5.99 (68)	34.68 - 35.51 (67)
Mar-92	30 - 400	42	35	5	9.29 - 13.16 (44)	2.02 - 4.90 (43)	34.77 - 35.13 (44)
Sep-92	25 - 124	60	27		9.33 - 16.42 (70)	3.16 - 5.87 (69)	34.80 - 35.50 (70)
Apr-93	29 - 440	45	54	10	6.33 - 19.43 (96)	2.72 - 5.21 (95)	34.63 - 35.35 (96)
Sep-93	29 - 186	71	34		8.40 - 16.30 (56)	3.55 - 5.08 (54)	34.64 - 35.36 (56)
Jun-94	35 - 500	33	42	10	6.59 - 16.75 (68)	1.35 - 5.65 (65)	34.57 - 35.61 (65)
Sep-94	30 - 200	54	28		9.50 - 15.15 (50)	3.12 - 4.95 (49)	34.78 - 35.33 (47)
Apr-95	29 - 463	40	44	14	5.29 - 16.2 (71)	1.81 - 6.02 (69)	34.57 - 35.21 (71)
Sep-95	28 - 193	68	30		8.73 - 16.62 (59)	3.03 - 5.59 (59)	34.68 - 35.47 (50)
Apr-96	27 - 440	39	35	5	5.59 - 11.56 (55)	2.31 - 4.71 (53)	
Apr-97	33 - 426	37	49	12	6.96 - 17.35 (65)	2.77 - 4.90 (68)	34.00 - 35.25 (66)
Apr-99	30 - 469	34	38	10	5.98 - 13.5 (58)	2.41 - 5.55 (67)	34.58 - 35.14 (58)
Aug-01	35 - 384	32	41	7	8.79 - 15.81 (50)	4.22 - 5.77 (50)	34.72 - 35.48 (50)
Apr-03	35 - 441	32	43	12	5.73 - 14.37 (84)	2.17 - 4.59 (83)	34.56 - 35.18 (84)

4.3 Results

Figure 4.1 shows the size spectra per survey, pooled for the whole south coast and the temporal trend in the heights and slopes of the size spectra are depicted in Figure 4.2a. The height of the size spectra for autumn surveys increased slightly from the mid 1980s to the 1990s then declined until 1994. In 1994 the autumn spectrum height increased sharply, thereafter it declined until the end of the study period. The slopes follow a similar pattern. The trend in the slopes and height for the spring season are less clear. These trends were also apparent at the spatial scale of individual stratum when the size spectra were analyzed for the 0 - 100m and 101 – 200m depth ranges (Fig. 4.2b). The trends in the slopes and heights of the size spectra for the autumn and spring seasons follow the same pattern. The trends in the heights for both depth ranges suggest an initial increase in the overall abundance towards the early 1990s then a consistent decline beginning in the late 1990s. The slopes of the size spectra also declined after 1995, suggesting changes in the size composition of the demersal communities in both depth ranges.

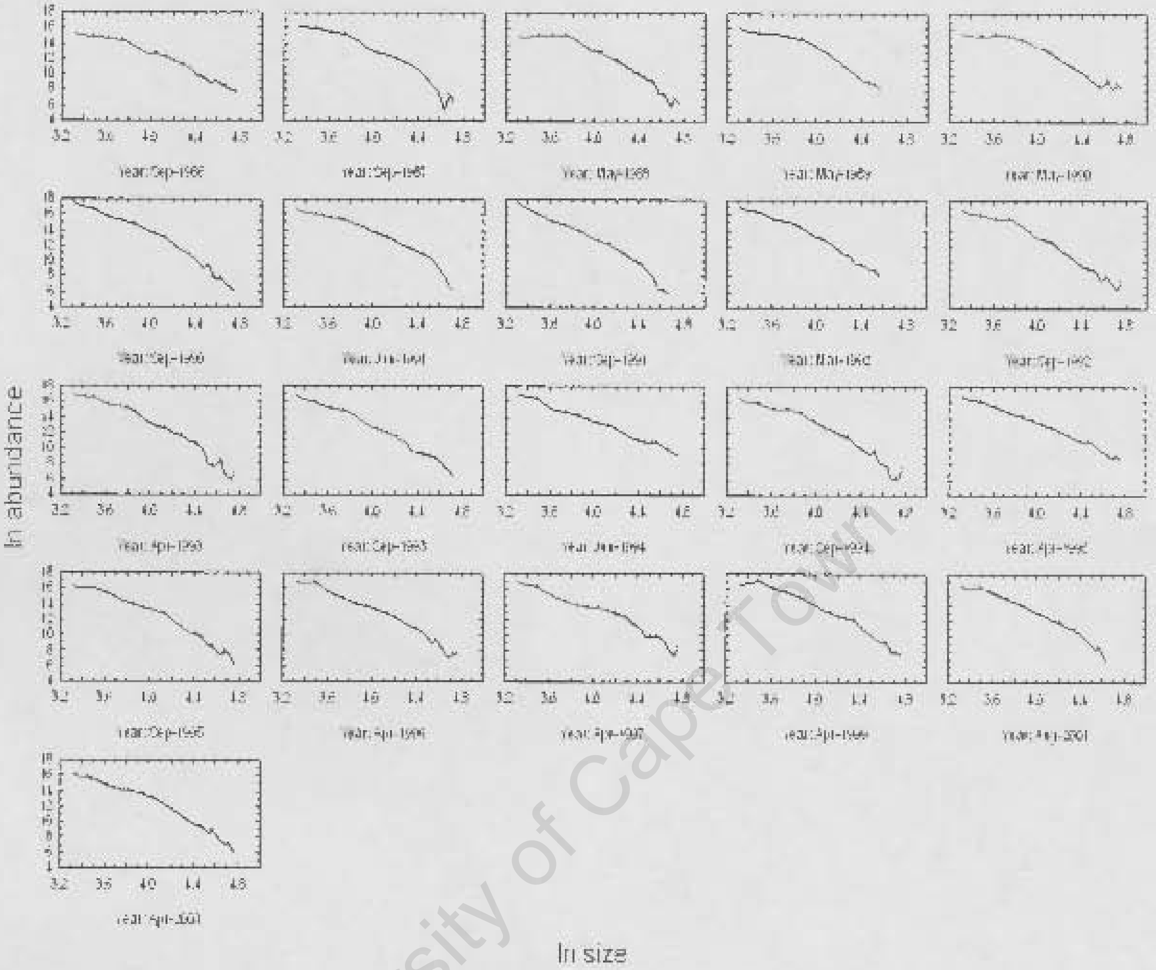


Figure 4.1. Size spectra for the pooled data of the south coast demersal fish communities. The size spectra cover size range of 26cm – 120cm. Each graph plots log abundance against log length (cm). The slope and height are calculated by linear regression, with the height calculated at the mean length standardized to zero.

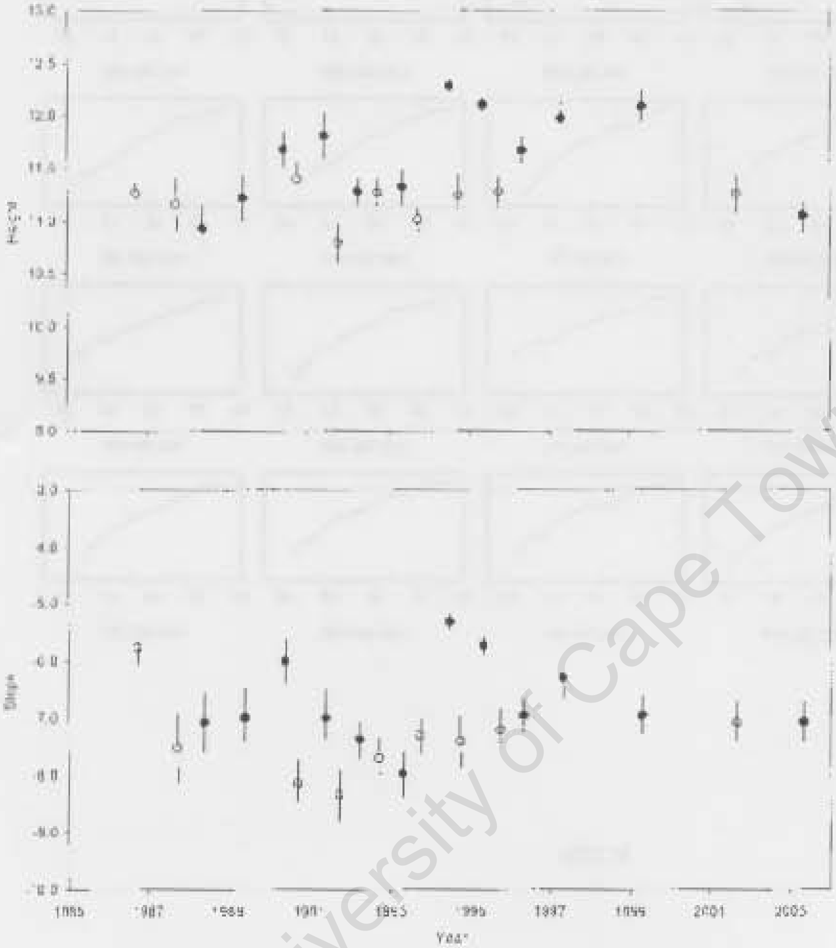

13.0
12.5
12.0
11.5
11.0
10.5
10.0
9.5
9.0
Height
-3.0
-4.0
-5.0
-6.0
-7.0
-8.0
-9.0
-10.0
Slope
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

Figure 4.2a

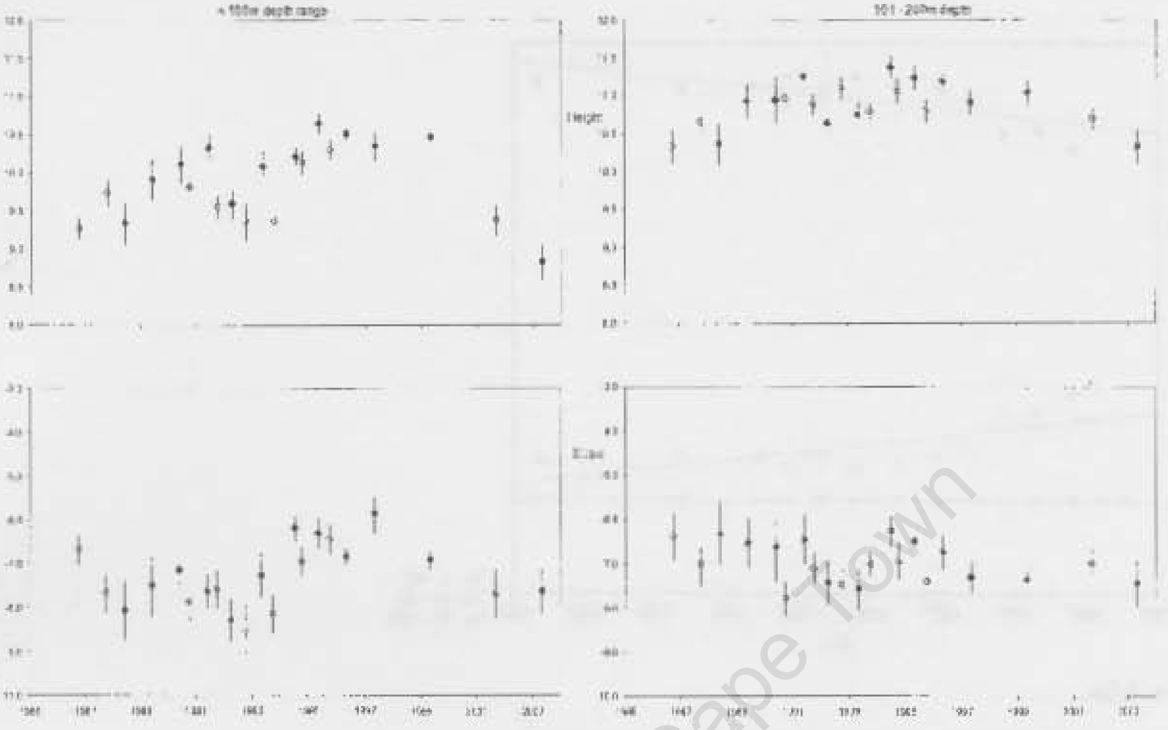


Figure 4.2b

Figure 4.2. Temporal trend in the heights and slopes of the size spectra: (a) pooled depths, and (b) 0 - 100m and 101 200m depth ranges (± two standard error). Open and solid circles represent spring and autumn, respectively.

The decline (increasing steepness) in the slopes of the size spectra suggests changes in the relative abundance of small vs large individuals in the community, with a progressive decline in the abundance of larger individuals. This temporal change in the relative abundance of the different size groups in the communities for the autumn surveys is further shown in the trend in the proportions of three size categories, 1 40cm, 41 – 80cm, 81 – 120cm (Figs. 4.3a, 4.3b, 4.3c).

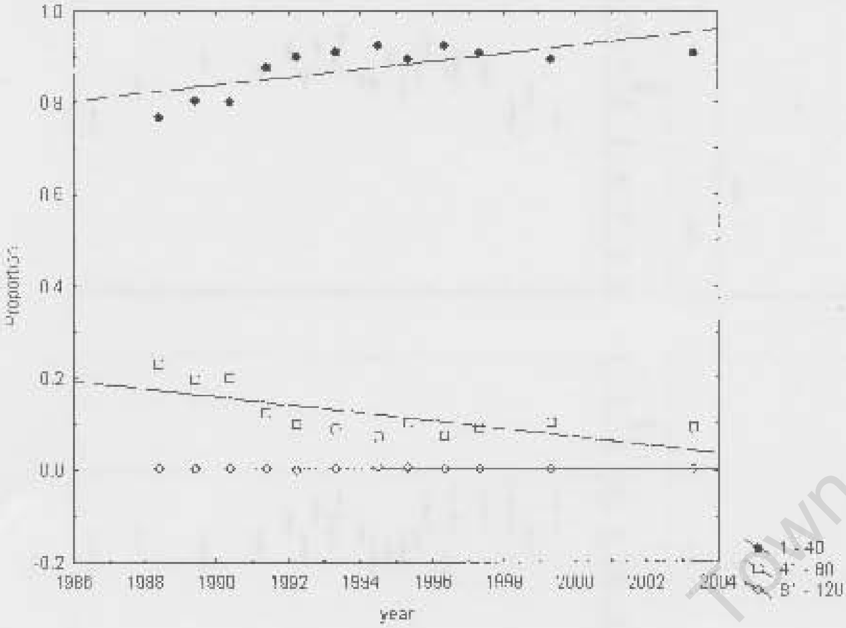


Figure 4.3a

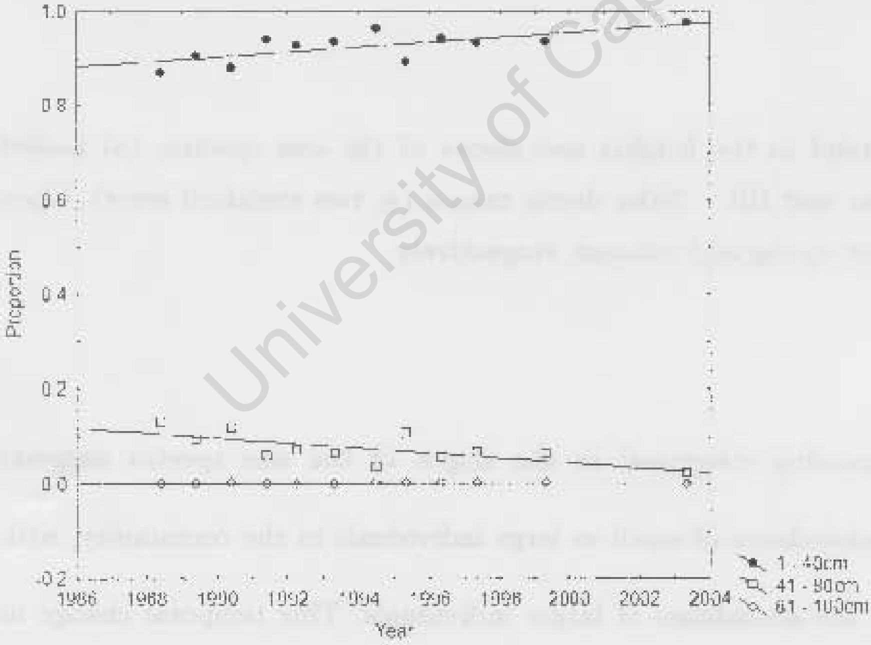


Figure 4.3b

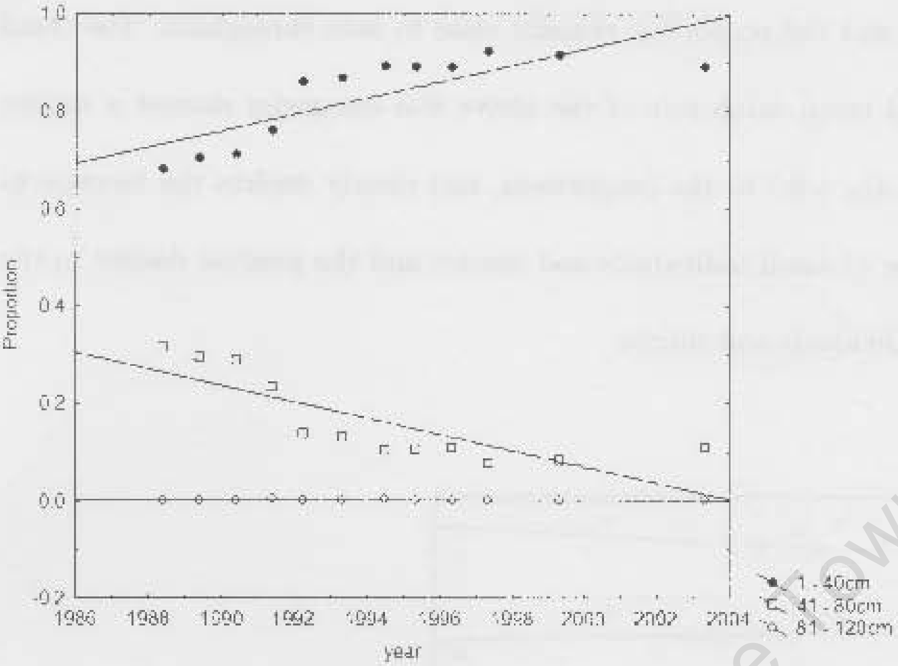


Figure 4.3c

Figure 4.3. Temporal trends in the proportions of three size classes for the autumn surveys: (a) Pooled depths, (b) 0 - 100m depth range, (c) 101-200m depth range

The trends in the proportions of the three size categories show the same pattern at different spatial scales, those of the whole south coast and each depth stratum. The proportion of individuals in the 1 40cm increased significantly over time at both spatial scale of the entire south coast ($t = 3.1224$, $n=12$, $p<0.05$) and for individual depth strata (0 100m: $t = 4.3764$, $n= 12$, $p< 0.05$; 101 200m: $t = 3.08507$, $n= 12$, $p< 0.05$). In contrast the proportion of individuals in the 41 – 80cm size category decreased significantly over time for the entire south coast ($t = -3.1139$, $n= 12$, $p< 0.05$) and for individual depth strata (0 – 100m: $t = -4.34476$, $n= 12$, $p< 0.05$; 101 - 200m: $t = -3.13765$, $n= 12$, $p< 0.05$). For the 81 120cm size category there was no clear trend over time and the proportion remains close to zero throughout. The trend in the log-transformed mean catch rate of the above size categories showed a similar pattern (Figs. 4.4a, 4.4b, 4.4c) to the proportions, and clearly depicts the increase in the relative abundance of small individuals and species and the gradual decline in the abundance of large individuals and species.

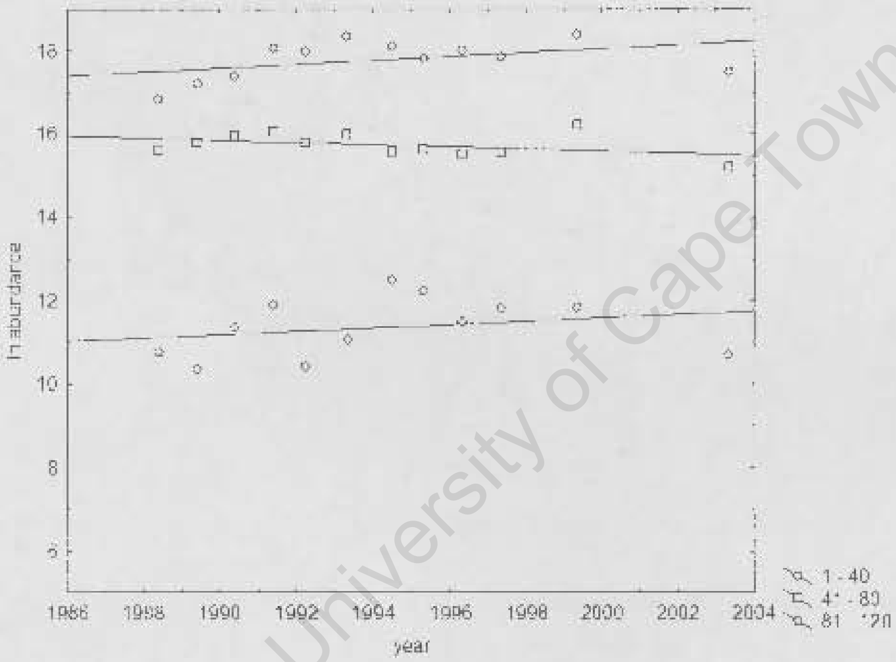


Figure 4.4a

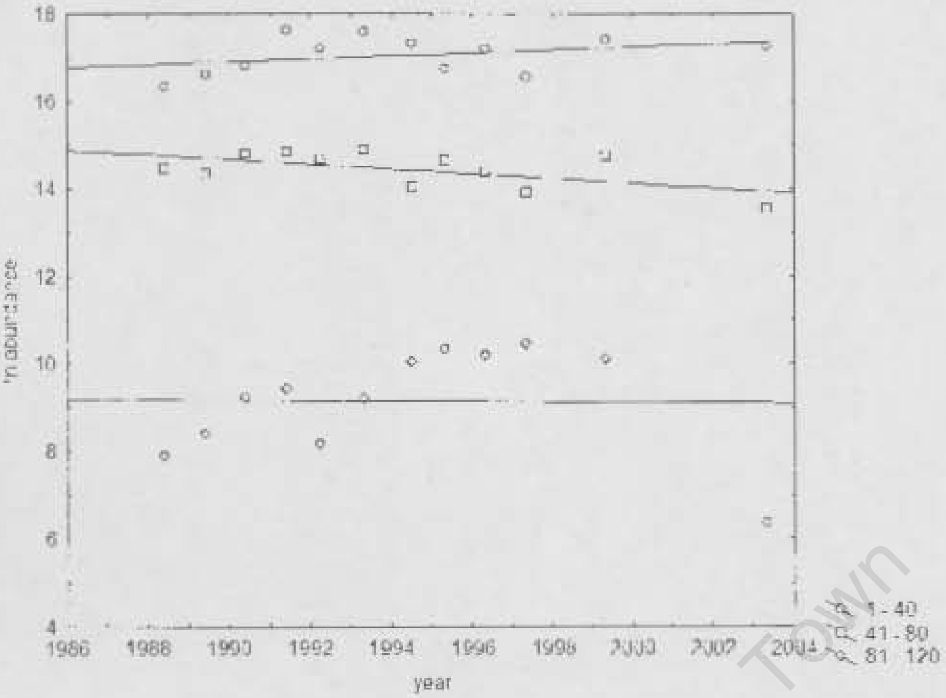


Figure 4.4b

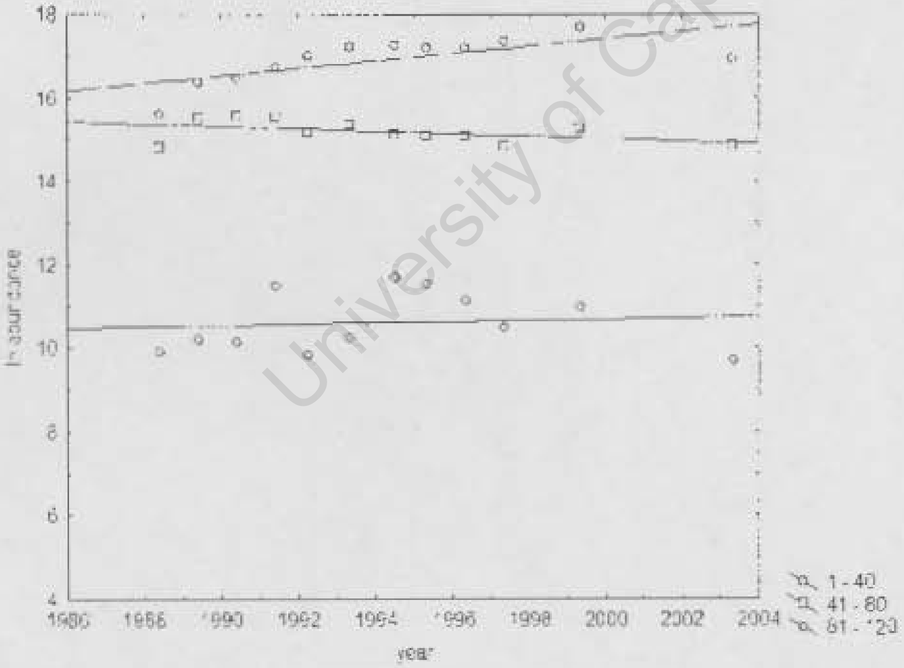


Figure 4.4c

Figure 4.4. Trend in the abundances (numbers per 30min tow) of the different size classes over the period 1986 – 2003, for the autumn surveys. (a). Pooled depths, (b). 0 – 100m depth, (c). 101 – 200m depth.

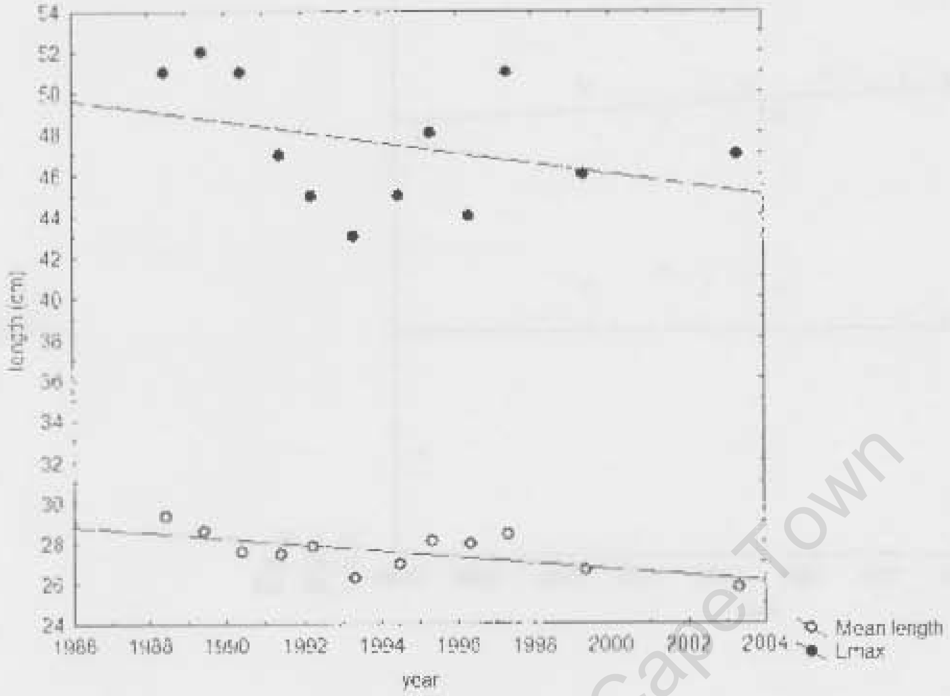


Figure 4.5a

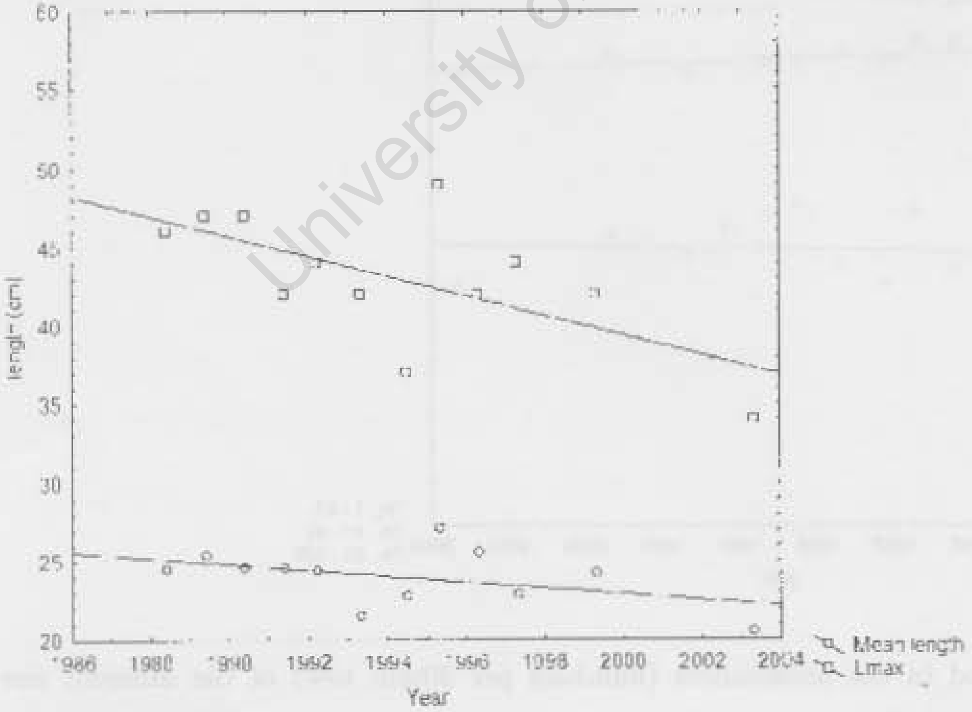


Figure 4.5b

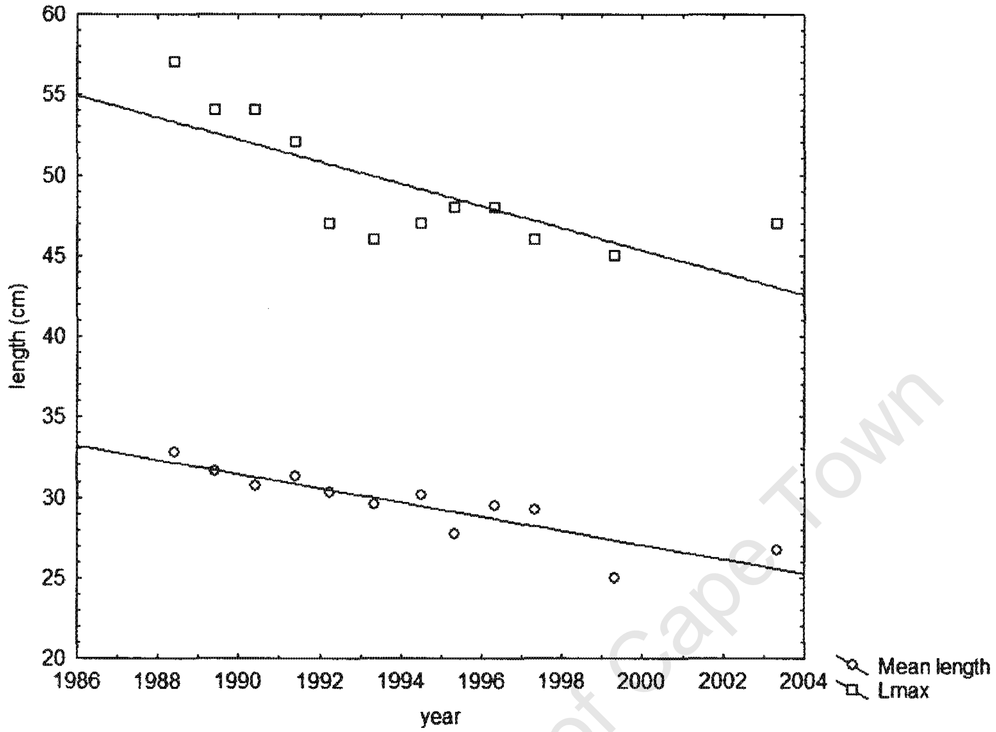


Figure 4.5c

Figure 4.5. Trends in the mean length and L_{max} of the demersal fish and cephalopod assemblages for the autumn surveys. (a). Pooled depths, (b). 0 – 100m (c). 101 – 200m.

In addition the mean length of the demersal community as a whole for the entire south coast declined substantially (t = -2.65205, n= 12, $p < 0.05$), however the decline in L_{max} was slight and was not significant (Fig. 4.5a). In the 0 – 100m depth stratum, only the L_{max} showed (Fig 4.5b) a significant decline with time (t = -2.65452, n= 12, $p < 0.05$) whereas both mean length and L_{max} (Fig. 4.5c) declined significantly in the 101 – 200m depth stratum over time (t = -5.77497, t = -3.70566, respectively, n=12 and $p<0.05$ for both cases).

An exploratory analysis of the response of species, either by a change in mean size or in mean catch rate, over time shows that more and more species with a large L_{max} tend to decrease in abundance and in mean size as compared to those with a smaller L_{max} (Figs. 4.6a, 4.6b). This suggests that not only does the proportion of larger individuals in the population of all species decline, but that species with a large L_{max} also decline in abundance.

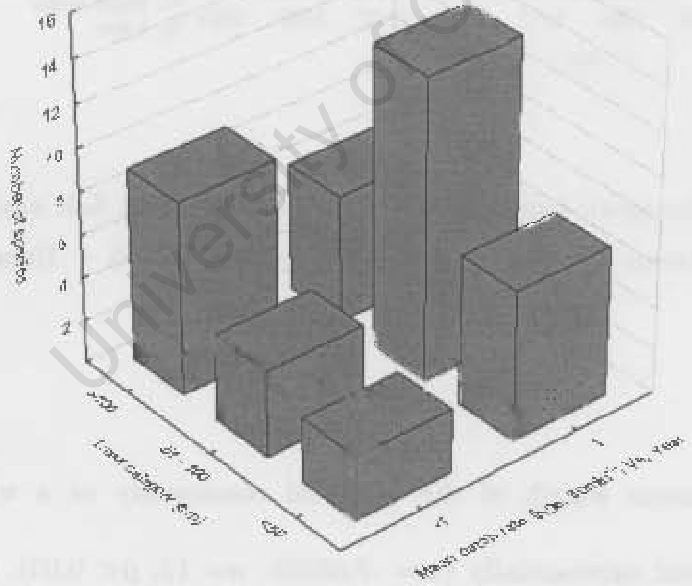


Figure 4.6a

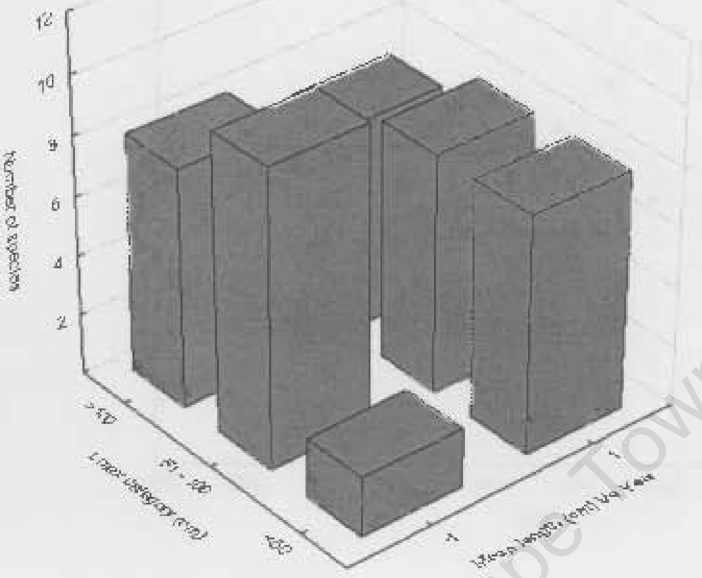


Figure 4.6b

Figure 4.6. Bivariate plots of the number of species that either declined (-1) or increased (+1) in the different L_{max} groups. (a). in abundance (catch rate) (b). in mean length

The temporal trends in the mean catch rate for the whole south coast (Fig. 4.7a) and for three depth strata (Fig. 4.7b) show a similar pattern to those of the heights of the size spectra (Figs. 4.2a, 4.2b) and there is a significant correlation between them (Spearman R = 0.6713, t = 2.864, $p < 0.05$, n =12), indicating that the heights of the size spectra capture the trends in the index of abundance of the community.

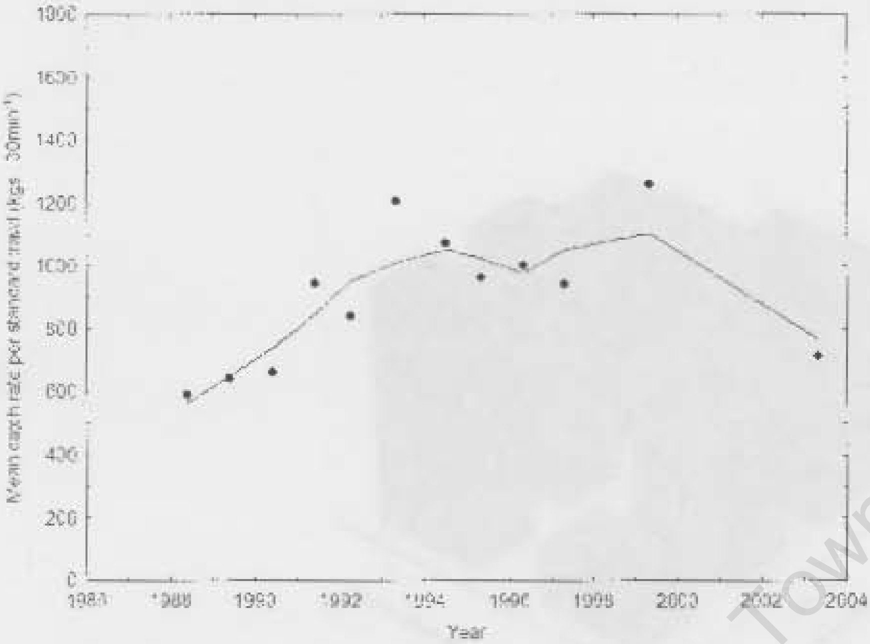


Figure 4.7a

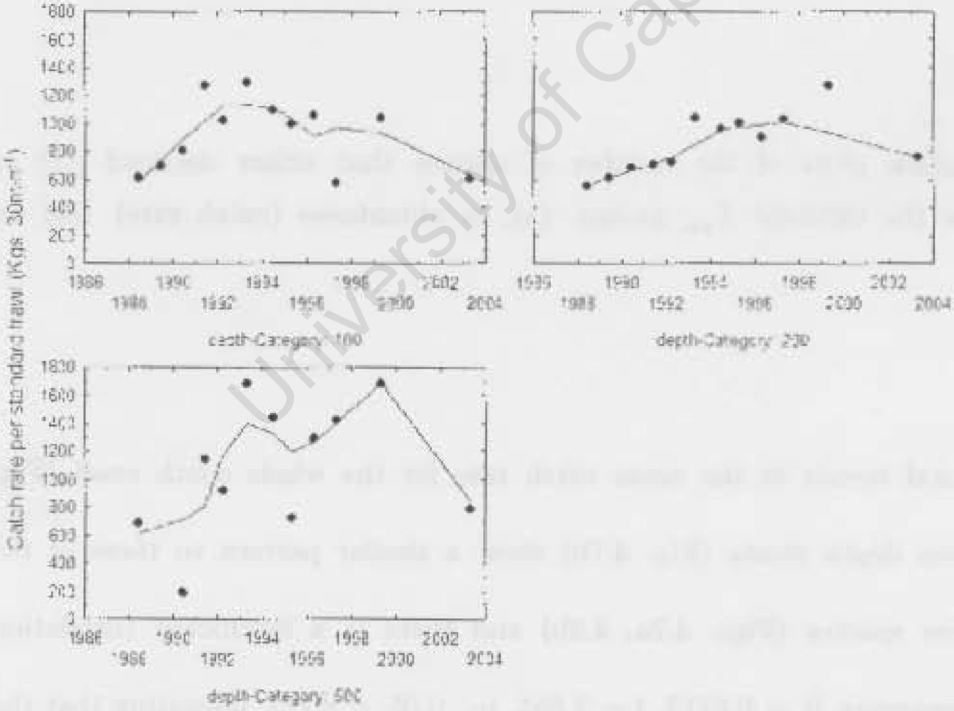


Figure 4.7b

Figure 4.7. Trend in the mean catch rate per standard trawl, Loess smoothed, for the autumn surveys. (a). pooled depths, (b) 0 - 100m depth, 101- 200m, 201 - 500m depth.

The temporal trends in the nominal fishing effort of the hake-directed trawl and longline fisheries, categorized by depth strata, on the south coast are shown in Figures 4.8 and 4.9. Most of the trawling effort is concentrated in the 0 – 100m depth stratum with some temporal variation, though it has been declining since the mid 1990s to its recent historical low points. For the 101 – 200m depth stratum the effort has been declining since the mid 1980s (Fig. 4.8). In the hake-directed longline fishery, effort has been increasing since its inception in 1994, with the majority of the effort concentrated in the 101 – 200m depth range (Fig. 4.9).

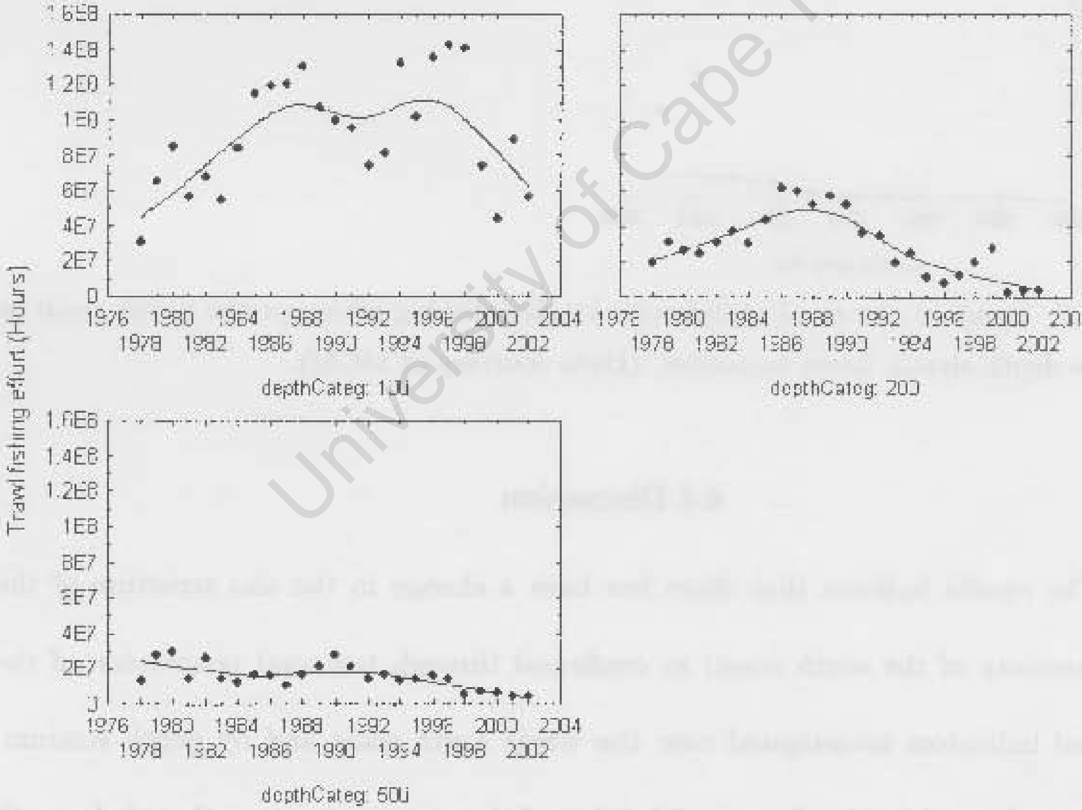


Figure 4.8. Trend in the total nominal effort of the commercial hake directed trawl fishery categorized by three depth strata, Loess smoothed. (Data courtesy of MCM).

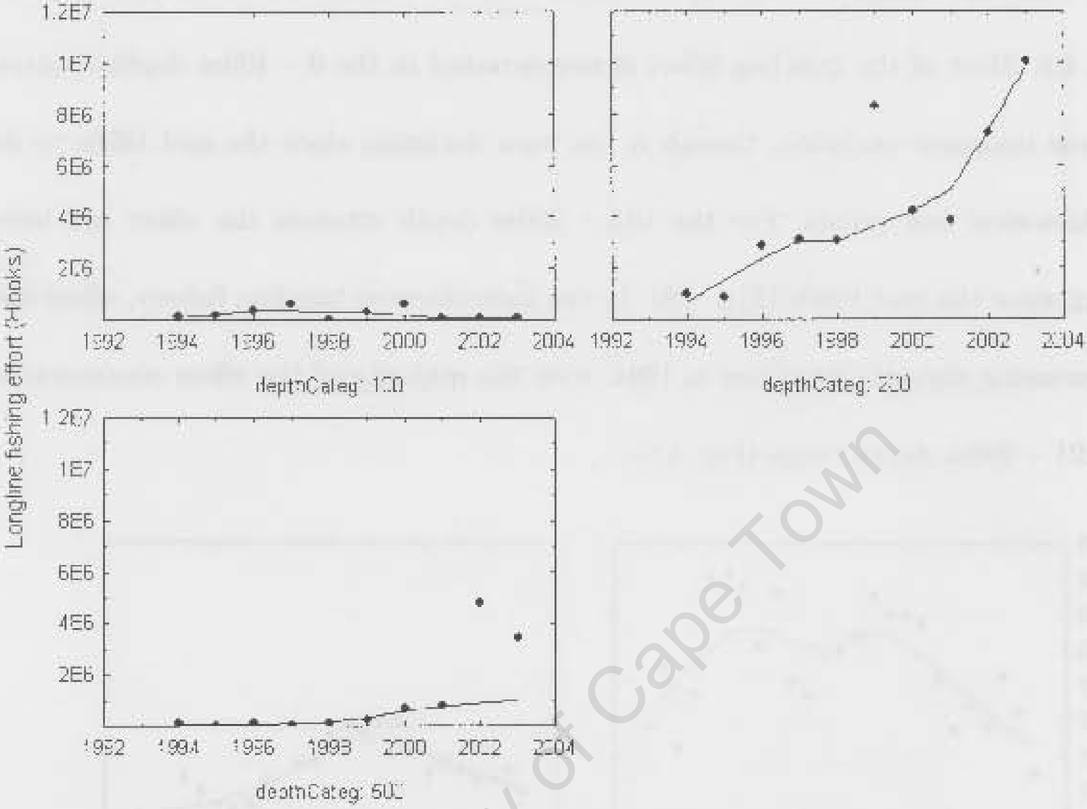


Figure 4.9. Trend in the total commercial longline fishing effort on the South coast in the three depth strata, Loess smoothed. (Data courtesy of MCM).

4.4 Discussion

The results indicate that there has been a change in the size structure of the fish community of the south coast: as confirmed through temporal progression of the size based indicators investigated over the whole south coast and by depth stratum. The temporal trend in the slopes and heights of the size spectra over the whole south coast and in each stratum suggests a changes in the size structure towards a community with lower abundance of larger individuals (larger sized species). A similar temporal progression (steepness) of the slopes of the size spectra is reported from other heavily fished fisheries (Rice and Gislason 1996, Bianchi *et al.* 2000) and was attributed to the size selective nature of fishery. Such response of the parameters of the size spectra to fishing was also confirmed through modeling study using various modeling approaches (Gislason and Rice 1998, Shin and Cury 2004). The observed response of the size spectra was further confirmed by the temporal trend in the proportion of individual in three size category where proportions of individuals in the smaller size categories increased while those in the larger size classes declined. The temporal trend in the mean catch rate of the different size categories also confirmed an increase in the smaller sized individuals, a likely indirect consequence of overexploitation, and a decline in abundance of larger sized individuals. In addition the decline with time of the mean length of the community and mean L_{max} of the community further supports the assertion that the size structure of the fish community has changed over the period considered in this study. The observed response of the size-based indicators over the study period can be linked to the inherent nature of fishing practices, their highly size selective nature resulting in increased mortality on larger sized individuals and limited or no mortality on smaller sized individuals (Beverton and Holt 1993). Indirect effects of fishing can also be expected theoretically as a result of size related trophodynamic interactions which suggests that reduction of larger individuals or species, usually the main predators of a fish community, lowers predation pressure on smaller sized individuals or species, resulting in turn in an increase in the abundance of individuals in the smaller size classes (Fogarty and Murawsky 1998, Dulvy *et al.* 2004, Daan *et al.* 2005). Despite the apparent relationship, as reported from previous theoretical and empirical works, between the impact of fishing and response of the size-based indicators used in this study, observed trends can also be influenced by factors other than those related to fishing, for example; chronic environmental changes through effects on growth, density dependent processes, and variability in recruitment of component species (Ottersen and Loeng 2000, Lekve *et al.* 2002, Wilderbuer *et al.* 2002). An increase with time in the recruitment of some species in the community can result in the steepening of slope of the size spectra and decline in mean length, thus confounding the response attributable to heavy fishing. Similarly effects on growth rate or other biotic processes can influence the trends in the size-based indicators. During the progress of this study there were no reports of such a consistent pattern of rise or decline in temperature (other than those shown in Chapter 5, where a decline in bottom temperature and salinity was observed only for surveys conducted in autumn). Thus effects on growth rate and recruitment of component species suggest that observed trends are unlikely to be caused by environmental factors, although this can not be ruled out.

On the other hand there has been substantial increase in the biomass of small pelagic species (sardine and anchovy) after the mid 1990s, although no clear trend in the environmental factors has been observed (Carl van der Lingen, pers.comm, MCM). None of the pelagic species are included in this study. They make up main prey item of some of the dominant demersal species (e.g. the shallow and deep water hake) but this increase in small pelagic biomass did not have positive effect on their predators.

When observed responses are viewed in relation to the history of fishing activity on this coast, attributing the effects to any of the fishing sectors operating is difficult. However if the trawl fishery is considered, it was established in the early 1900s and peaked in the 1970s, therefore the major changes caused by trawling had likely happened prior to 1986 where the demersal surveys began. Fishing strategy and technology continually changes which would change the fish community continuously. The introduction of longlining in South Africa increased access to the Spanish fresh fish market, which places a premium on large fish, this led to a change in the fishing strategy of the trawl fleet to selectively target larger fishes. In addition, longlining selectively targets larger fish. Therefore there was a marked change in fishing strategy in the early 1990s, which could be the underlying cause of marked community changes reported in this study.

Generally changes in the size structure of fish communities is believed to reflect changes in trophic structure, as larger individuals of a species or larger species tend to feed higher in the marine food web (Jennings *et al.* 2002, Pauly and Watson 2005). Thus observed changes in the size structure may have tropho-dynamic consequences.

Chapter 5 Spatio-temporal dynamics in the community structure of the south coast demersal fish communities

Abstract

The community structure of the south coast demersal communities has been studied based on survey data collected biannually from 1986 – 2003. A snapshot of the community structure for a selected year confirms that the communities on this coast are strongly structured by depth with environmental variables varying among the depth strata. Temporal and spatial trends of the measured environmental variables tend to vary between the spring and autumn seasons. A significant increase in the non-target species has been observed whereas the other components remained stable with a slight decline in the 2000s. Analysis (using non-metric multidimensional scaling, MDS) based on catch rate averaged by survey year showed a consistent change in community structure in both autumn and spring. However, when the whole station by species matrix was analyzed a significant change in species composition was observed only in autumn. Similar responses in the community structure in both seasons in contrast to the different temporal pattern in temperature and salinity between seasons suggest that these environmental factors are less important as drivers of the observed temporal changes in community structure than increased size-selective fishing pressure.

Keywords: community structure, multivariate analysis, depth, longitude, south coast, South Africa

5.1 Introduction

The continental shelves of many marine ecosystems around the world are highly productive and support diverse groups of fishes, cephalopods, and of macro- and meio-benthos. The continental shelves are also the most heavily fished areas of the ocean, yielding the majority of the global landings from capture fisheries (Pauly and Christensen 1995). For most of the nekton, these regions represent spawning grounds and nursery areas. Thus there have been a number of studies with varying degrees of depth and scope addressing issues ranging from population dynamics and recruitment success of single species, to multi-species structure and biogeochemical cycles. The community structure of nekton and macro-benthos has also been studied in the context of disturbance and understanding the structuring of the community in relation to physico-chemical factors in several regions around the world.

Fish community structure is governed by a multitude of biotic and environmental factors acting either in isolation or in concerted. Structuring of the community along environmental gradients is related to the differential preference of component species to the prevailing environmental conditions. On the other hand, biotic interactions among component species; trophic interaction and competition for space or resource, also contribute to the structuring of the community along a gradient that ensures or maximizes the coexistence of all the species in the environment. Several studies in the marine environment have reported the structuring of communities along depth, temperature, oxygen concentration, substrate type, latitude, longitude, and other physico-chemical characteristics. Jaureguizar *et al.* (2004) studied the main environmental parameters structuring fishing communities in Rio de la Plata estuary in Southwest Atlantic between Uruguay and Argentina. They found distinct assemblages corresponding to the inner, central and outer part of the estuary and bottom salinity was the most important factor responsible for the observed spatial structuring of the community. Temperature has the strongest influence on the seasonal structuring of the community, furthermore, seasonal migration of component species of the communities is manifested in the community structure. Smale *et al.* (1993) found that the fish and cephalopod component of the fauna on the south coast of South Africa are structured along depth strata into three assemblages and the prevailing temperature and oxygen concentrations also varied among the different strata. Various demersal fauna are also reported to have preferences for different bottom substrate types. The community of the demersal fishes around Kodiak island, Alaska, was mainly structured along depth and temperature gradients with sediment composition and geographic area of sampling site playing a substantial role in structuring the community (Mueter and Norcross 1999). Such structuring of the communities along the biotic and abiotic dimensions suggests these communities are vulnerable to any substantial change, other than the inherent variability in the system, in either or both of the dimensions (biotic and abiotic) along which they are structured. There is a considerable literature, from works around the world, documenting substantial anthropogenic impact on marine ecosystems: changes in the biogeochemical cycle, biotic changes: accelerate loss of species, and increased invasion, increasing eutrophication of coastal waters in many regions around the world (Vitousek *et al.* 1997), and heavy fishing with direct and indirect effects that cascade through the structure of the community (Gislason *et al.* 2000).

Heavy fishing affects community structure both directly and indirectly. Directly through differential biomass removal from certain components of the community usually larger individuals of a given species and species that attain a larger size (Haedrich and Barnes 1997, Baum and Myers 2004), and habitat destruction mainly due to interaction of the gear with the seabed (Jennings and Kaiser 1998, Jennings *et al.* 1999). Indirect impacts includes reduction in the reproductive output of some populations as a result of age or size truncation (Berkeley *et al.* 2004, Palumbi 2004), increase in the abundance of species that were competitively suppressed by overexploited species (Fogarty and Murawsky 1998), changes to the trophic structure of the community depending on the biomass and trophic role of the overexploited species (Pauly *et al.* 1998, Pauly *et al.* 2000, Pauly *et al.* 2001, Link and Garrison 2002, Pinnegar *et al.* 2002), impact on bottom feeding species as a result of effect on their benthic prey due to direct mortality and habitat destruction by bottom trawling. Jennings and Kaiser (1998) reported a decline in diversity of the fish communities related to the impact of fishing. Rogers *et al.* (1999) suggested that heavy fishing might be a key cause of change in the diversity of fish community in the Northeast Atlantic. Other indirect impacts of heavy fishing are suggested to result from a heavy selective heavy fishing are; loss of genetic diversity, and impact on ecosystem stability (Jennings *et al.* 2001b). It is mainly due to these serious and harmful effects of the global capture fishery on the structural and functional organization of marine ecosystems, that fisheries managers and scientists have been promoting an Ecosystem Approach to Fisheries (EAF). This requires the development of indicators or metrics to gauge the impact of heavy fishing on the ecosystem. To this end a number of indicators or approaches have been put forward, including multivariate clustering and ordination techniques (Rice 2000, 2003). Multivariate measures of change in community composition are more sensitive to changes in the community structure, than are univariate indices of species composition (Austen and Warwick 1989). Assessments of the effects of fishing on the fish communities on the south coast of South Africa are restricted to few studies and they are limited either in the geographic coverage or the number of taxa included in the study; for example Booth and Hecht (1998) looked into the changes in the Eastern Cape demersal fishery over time.

The south coast of South Africa supports a number of demersal fish and cephalopod species, some of which are directly targeted by different fishing sectors while others are caught as bycatch species. These species are captured using single gear or caught by multiple gears, each with its own characteristic selectivity for certain species or size classes, and with varying degree of interaction with the bottom habitat, and targeting various species. There are a number of studies addressing different aspects (trophic interaction, spatial distribution, biology and population dynamics) of the fish communities (Chapter 4). Few studies address the community structure, based on demersal survey data, and relate it to the prevailing physical and environmental factors Smale *et al.* (1993). On the other hand Walmsley *et al.* (2006) looked at issues of bycatch problem in the whole South African demersal trawl fishery, noting that it is a serious problem, and suggested various measures to reduce and manage bycatches. Furthermore Booth and Hecht (1998) assessed changes in the Eastern Cape demersal inshore trawl fishery between 1967 and 1995. They found a change in the composition of the catch, reduction in age at 50% recruitment to the fishery for shallow water Cape hake, horse mackerel, and panga. A comprehensive study of the community structure of the demersal fish communities over space and time has not been undertaken.

The main objective of this chapter is to assess the community structure of the south coast demersal fish communities over the spatial and temporal bounds of the data available using multivariate measures of change in community structure. In addition the relationships between measures of community structure and the physical variables (depth and longitude) measured will be investigated and the temporal trends in the mean catch rate of the community will be investigated to help assess the changes in community structure.

5.2 Methods

The sources of data, spatial and temporal bounds, and data standardization, are discussed in detail in Chapter 4. The distribution of trawling stations by cruise and depth is shown in Table 5.1.

5.2.1 Multivariate analysis

Community structure was investigated using two multivariate techniques, cluster analysis and ordination using non-metric multidimensional scaling (MDS). The multivariate analysis was conducted for selected surveys separately and for the pooled data from all the surveys together. Teleosts, elasmobranchs, and cephalopod identified to species level were considered for the multivariate analysis. The catch rate (by mass) of each species was then root-root transformed, to reduce the influence of abundant species on the resemblance matrix. Then a resemblance matrix was created using the Bray-Curtis measure of (dis)similarity. This measure of resemblance is most favored, among the other measure of resemblance [see Clarke and Gorley (2006), for some of the available measure of distance or (dis)similarity], due to its possession of important properties of significance for ecological data: a) joint absence of species from samples has no effect on the coefficient, b) a scale change in the measurement does not affect the value of the coefficient, c) it takes the highest value (100% for similarity) when samples are identical in the biotic composition and lowest value (0% for similarity) when two samples do not have species in common (Field *et al.* 1982, Clarke and

Warwick 2001, Clarke *et al.* 2006). Cluster analysis was performed on the resemblance matrix using group average linkage. Based on the resulting dendrogram groups of stations were identified. Ordination of the multivariate data was also performed on the resemblance matrix, using non-metric multidimensional scaling (MDS). Before further use of the result of the ordination plot the measure of fit, stress value, inter-stations similarity in the high dimensional space and the inter-station distance in the two and three dimensions were checked. Though a stress value of < 0.05 is generally considered a good fit for the two-dimensional ordination plot (Clarke and Gorley 2006), cross comparison of groups from the cluster analysis and that of the multidimensional scaling is suggested as good practice for checking the satisfactory and consistent representation of the multivariate data (Clarke and Gorley 2006).

Differences in community structure by depth strata were assessed using one-way ANOSIM Analysis of similarity, (Clarke and Warwick 2001). The station by species data matrix was averaged into years by species matrix, for each season, for assessment of temporal changes in community structure. The resemblance matrix was then constructed based on the root-root transformed catch rate data. The Bray-Curtis measure of similarity was used as a measure of resemblance. Ordination by MDS was done on the resemblance matrix.

All the multivariate analyses are done in PRIMER-E, version 6 (Clarke and Gorley 2006). The Analysis of Variance on the MDS axis scores was done in STATISTICA version 7.

Processing of axis scores

As the data matrix for the whole survey period comprised 1800 stations by 110 species, visual assessment of the dendrogram and ordination plot is difficult; thus for the case where individual stations are included, the axis scores for the three dimensional configuration were analyzed using main effects two-way Analysis of Variance. The analysis was conducted for each season separately. The main effect ANOVA comprised 12 years for the autumn season and nine years for spring and three depth strata (100m, 200m, and 500m). Interaction effects were not included as the design was not fully crossed. Sampling of the 201 – 500m depth stratum (Table 4.1) was insufficient for full analysis.

The following two-way main effect ANOVA model was used

$$y_{ijk} = \mu + \alpha_i + \beta_j + \varepsilon_{ijk}$$

Where y_{ijk} is the axis score for year i depth stratum j and station k

μ is the intercept

α_i is year effect pooling over all depth strata

β_j is depth stratum effect pooling over all years

ε_{ijk} is the residual error term

5.2.2 Analysis of environmental data

A set of environmental data was collected during each survey and analyzed for trends over time and relationships among the environmental variables (temperature, salinity, and oxygen concentration), depth and longitude, investigated using Pearson's correlation coefficient. As can be seen in the correlation matrix in Table 5.1 most of the environmental variables were highly correlated, except for depth and longitude of the survey stations, thus raising the issue of co-linearity for the subsequent use of the variables in relating to the community structure. Quinn and Keough (2002) highlighted the important effects of co-linearity in regression type analysis where severe co-linearity affects: the estimated regression parameter, inflation in the standard error and hence in the confidence interval of the regression slopes. The simplest way to remove the impact of co-linearity is to exclude the redundant variables. A second method is to do a principal component regression analysis, where regression is done on the principal component extracted from the variables by sample matrix. The third, which the authors acknowledge as biased, is to do ridge regression analysis (Quinn and Keough 2002). Thus in this study, because of co-linearity and the large number of missing values in the environmental variables, and because the depth contours in the study area generally run east/west (Fig. 2.1) only depth and longitude of individual stations are used in relating the community structure to the environment.

5.2.3 Analysis of catch rate

The mean catch rate was analyzed for its spatial and temporal change over the study period. The catch rate was related to depth and longitude of the stations. The temporal trend was assessed using Analysis of Covariance (ANCOVA), with depth and longitude as covariates. The analysis was conducted for the whole demersal community and for target and non-target species separately. The following ANCOVA model was fitted to the data:

$$C_{ij} = \mu + \alpha_i + \beta(x_{ij} - \bar{x}) + \gamma(l_{ij} - \bar{l}) + \varepsilon_{ij}$$

Where: C_{ij} is the catch in station j in year i

μ is the intercept term

α_i is the year effect

β and γ are coefficients of the covariates depth and longitude of a station in a particular year, respectively

x_{ij} is the depth of station j in year i, and $\bar{x}$ is the mean depth

l_{ij} is the longitude of station j in year i, and $\bar{l}$ is the mean longitude

ε_{ij} is the residual error term

5.2.4 Spatial and temporal trend in the fishing effort

The temporal progression in the spatial distribution of the commercial demersal trawl fishing effort is summarized for four periods (1980 – 1984, 1985 – 1989, 1990 –

1994, 1995 – 1999, and 2000 – 2002) and for the long line fishery two periods (1994 – 1998, 1999 – 2003).

5.3 Results

5.3.1 Analysis of environmental data

The pair-wise correlation among temperature (^{0}C), salinity (ppt), oxygen (ml/L), depth (m), and longitude is shown in Table 5.1. Longitude was positively correlated to temperature, salinity, and oxygen in autumn but negatively correlated in spring. The correlation between depth and oxygen concentration also changed from positive in spring to negative in autumn. All other correlations were the same direction in spring and autumn, although the strength varies. The weak but significant correlation between depth and longitude is probably the reflection of the configuration of the coast where as one moves toward the east, the shelf tend to be narrower and steep gradient develops from shallower to deep water. The spatial pattern of distribution of temperature, salinity, and oxygen was explored graphically by fitting a second order polynomial regression to the pooled data from the whole survey (Fig. 5.1). In autumn temperature and salinity decline with depth to about 300m and increased with longitude towards the east whereas oxygen concentration increased towards deeper water and towards the east. In spring both temperature and salinity declined with increasing depth but the trend with longitude is reversed and shows a decline towards the east. The spatial pattern of oxygen concentration in spring also reversed and showed a slight decline with increasing depth and towards the east.

The temporal trend in the environmental variables is shown in Figure 5.2. The trends differ between the two seasons, in autumn only salinity declined significantly with time ($t = -2.82$, $n = 11$, $p < 0.05$), temperature also declined slightly (but not significant) over the study period whereas oxygen concentration varied inter-annually with no clear trend. In contrast none of the environmental variables showed a consistent rise or decline in spring during the study period.

Table 5.1. Correlation matrix of environmental variables in the two seasons based on Pearson's product moment correlation, r. Correlations are calculated for the pooled data from all the surveys. The shaded/upper triangular matrix is for spring and the lower triangular matrix is for autumn. All correlations are significant at 0.05 level of significance.

Autumn / Spring	Longitude	Depth	Temperature	Salinity	Oxygen
Longitude		0.09	-0.13	-0.20	-0.15
Depth	0.08		-0.61	-0.56	-0.15
Temperature	0.29	-0.55		0.95	0.49
Salinity	0.32	-0.47	0.83		0.51
Oxygen	0.43	0.17	0.29	0.21	

Figure 5.1. The relationship of the three environmental variables to depth and longitude for autumn and spring. Quadratic fit to the data to show the form of the relationship.

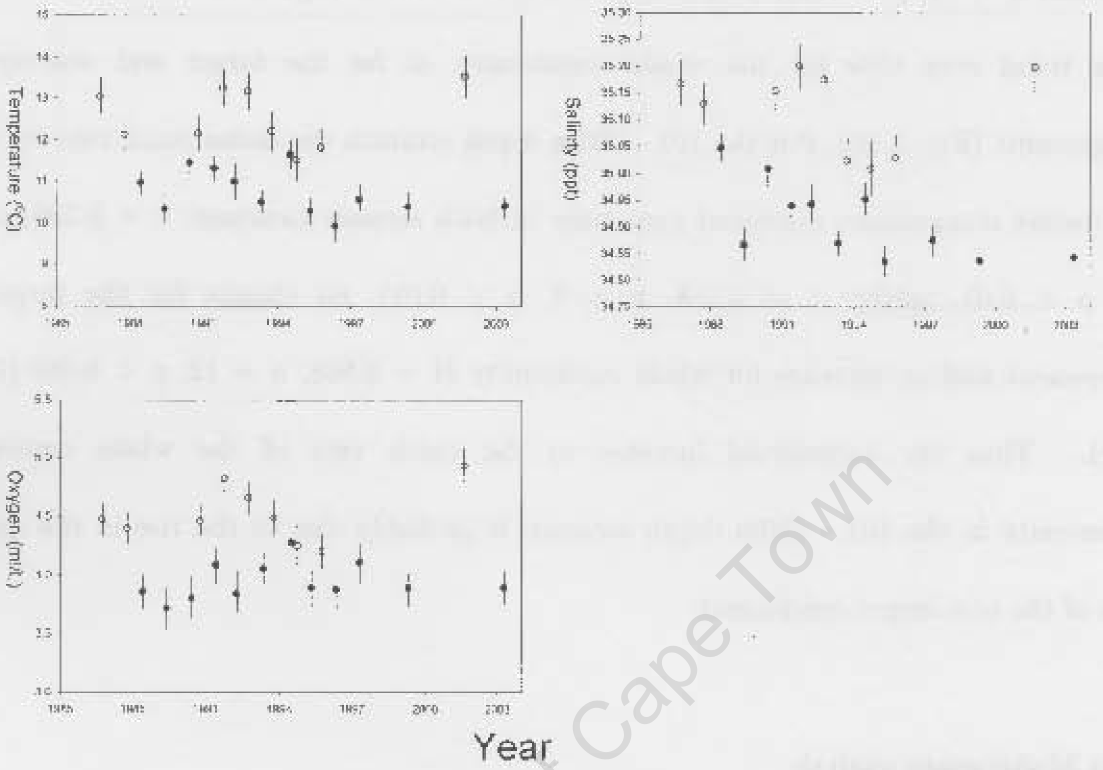


Figure 5.2. Temporal trend in the least square means of temperature, salinity and oxygen for autumn (closed circle) and spring (open circle).

5.3.2 Catch rates

The changes in catch rates of the demersal species were assessed for the whole community and for the target and non-target components separately. The least square means of the standardized catch rates of the whole community, target and non-target components for the entire south coast and two depth strata, 0 – 100m and 101 – 200m, are shown in Figure 5.3. The catch rates of the whole demersal community and the targeted component show an initial increase towards the mid 1990s after which they stabilize, whereas the non-target component showed a significant increase (autumn: t

$= 2.868$, $n = 12$, $p < 0.05$) (Fig. 5.3a). For the 0 - 100m depth stratum there was no clear trend over time for the whole community, or for the target and non-target components (Fig. 5.3b). For the 101 - 200m depth stratum the mean catch rate for the non-target components increased over time in both seasons (autumn: $t = 3.396$, $n = 12$, $p < 0.01$, spring: $t = 3.568$, $n = 9$, $p < 0.01$), no change for the targeted component and an increase for whole community ($t = 2.868$, $n = 12$, $p < 0.05$) (Fig. 5.3c). Thus the substantial increase in the catch rate of the whole demersal community in the 101 - 200m depth stratum is probably due to the rise in the catch rate of the non-target component.

5.3.3 Multivariate analysis

As the multivariate structure of the demersal communities on this coast has already been investigated (Smale *et al.* 1993), here a snapshot of the community structure will be presented with more emphasis being given to the temporal aspect of the community structure. The community structure of the south coast from the 1993 survey is analyzed.

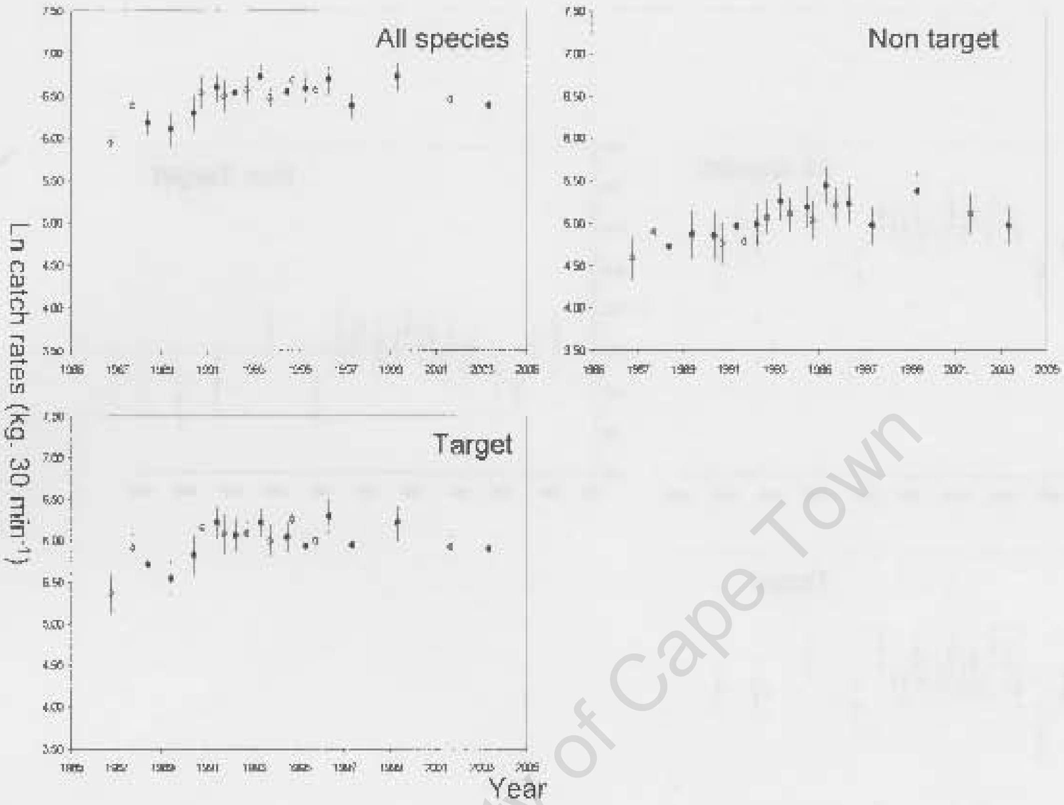

All species
Non target
Target
Ln catch rates (kg. 30 min-1)
Year
7.50
7.00
6.50
6.00
5.50
5.00
4.50
4.00
3.50
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
2005

Figure 5.3a

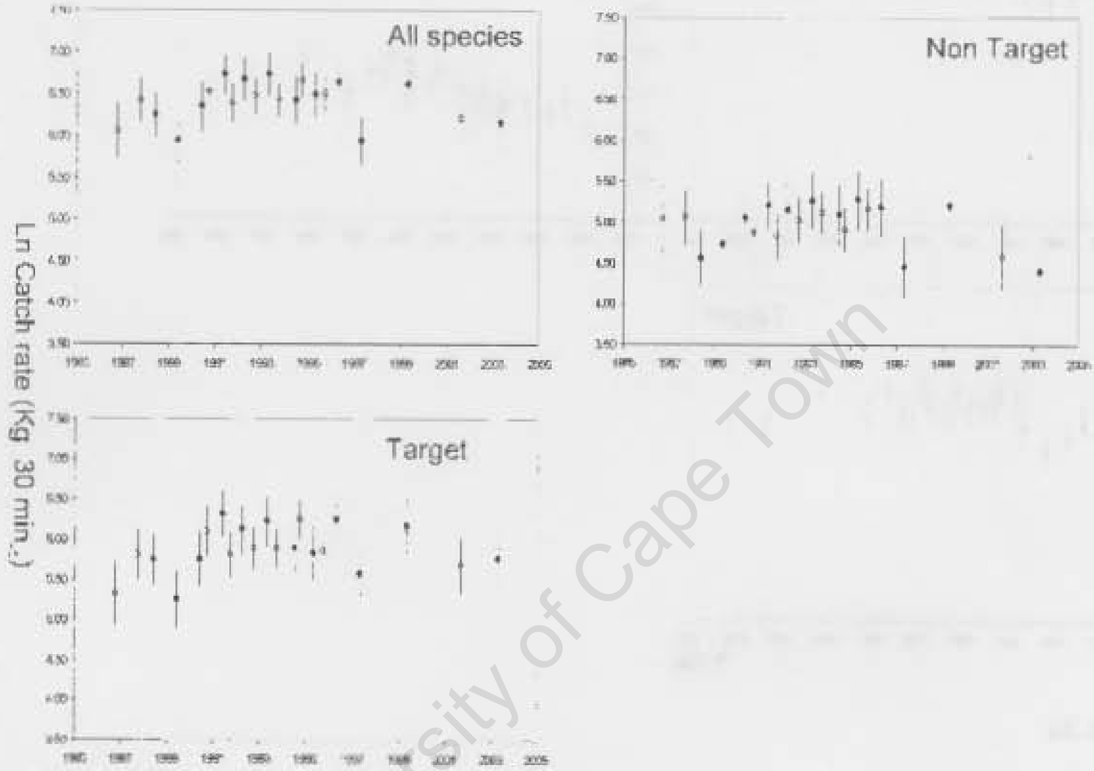

All species
Non Target
Target
Ln Catch rate (Kg 30 min.)
7.50
7.00
6.50
6.00
5.50
5.00
4.50
4.00
3.50
1985
2005

Figure 5.3b

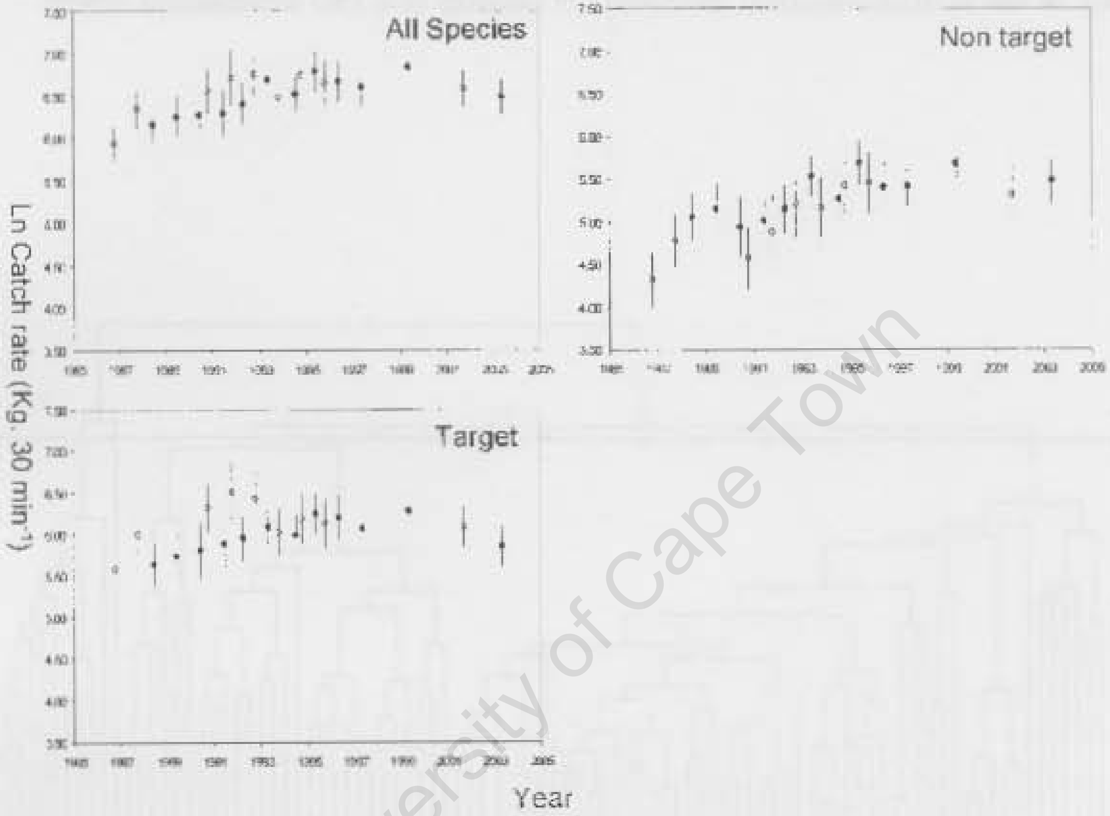


Figure 5.3c

Figure 5.3. Trend in the mean catch rate of the whole demersal community, targeted component, and non-target component, for the whole south coast (a), for the 0 – 100m depth stratum (b), and for the 101 – 200m depth stratum (c). open circle (spring) and closed circle (autumn).

Figure 5.4 shows the dendrogram from the cluster analysis; three distinct clusters appear at the cut-off similarity level of 43%. These groups approximately correspond to the three depth strata (A = 0 – 100m, B = 101 – 200m, and C = 201 –

500m). The corresponding ordination plot for the same data is shown in Figure 5.5: the stress value of 0.14 for the ordination in two dimensions suggests a reasonable summary of the multidimensional ordination of samples into two dimensional spaces.

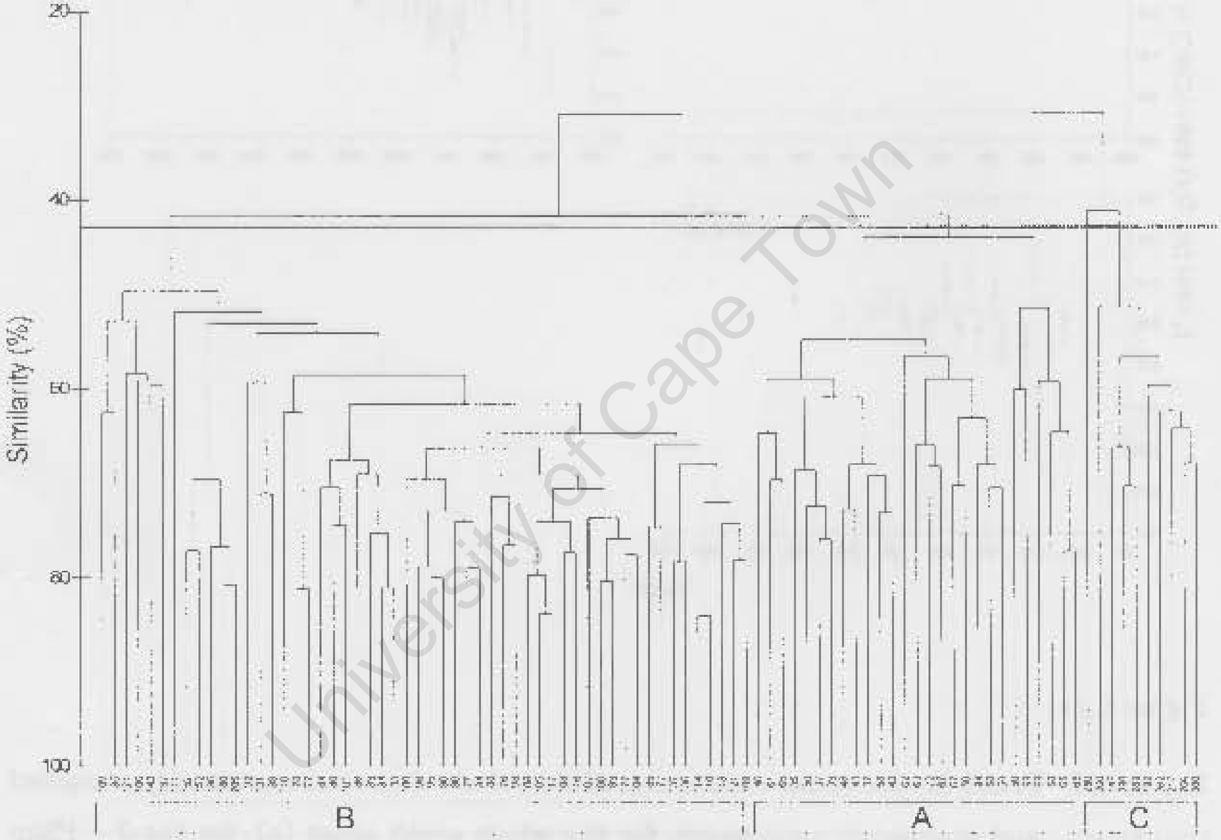


Figure 5.4. Dendrogram of the sample by species matrix for the 1993 demersal survey (0 – 100m (A), 101 – 200m (B), 201 – 500m (C)). The label denote depth of the trawling station.

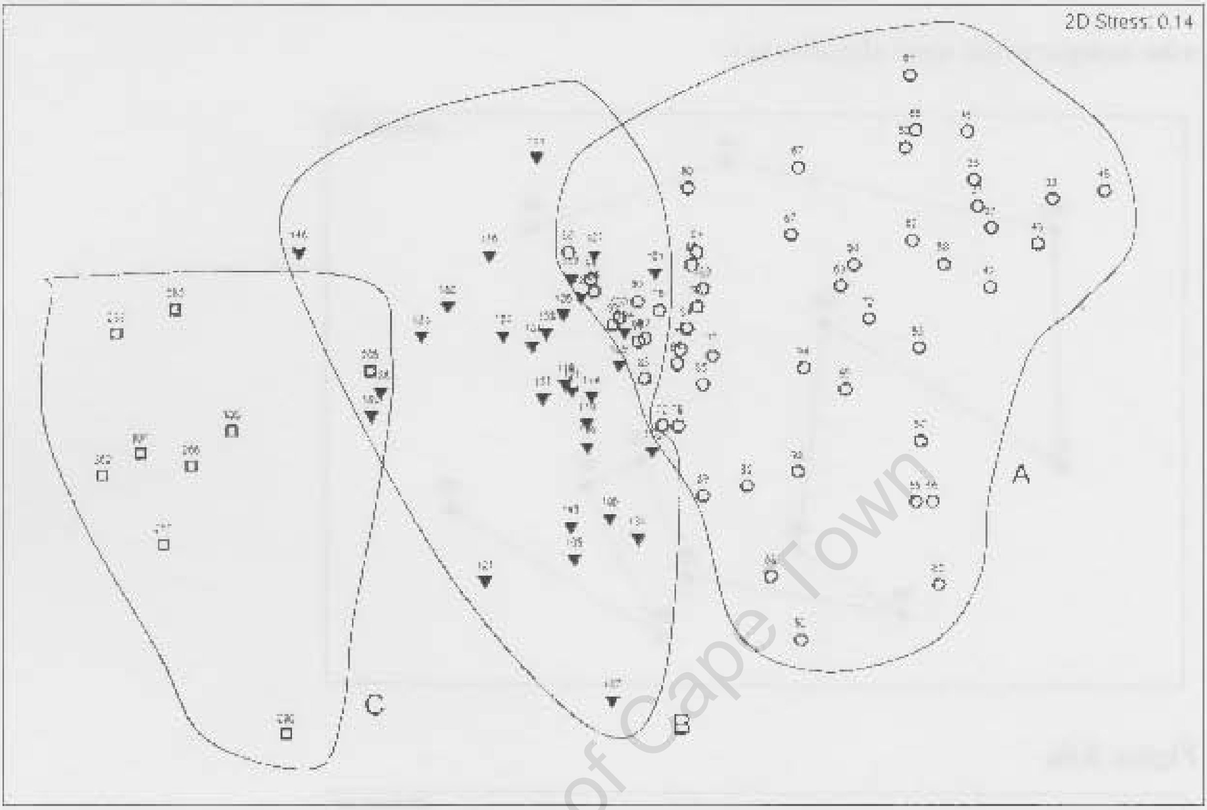


Figure 5.5. Ordination plot of the sample by species matrix for the 1993 survey. Open circle (0 – 100m depth stratum), closed triangles (101 – 200m depth stratum), open square (201 – 500m depth stratum).

The significance of structuring of the community by depth strata was assessed using one way ANOSIM. The global test shows a significant grouping of the communities by depth stratum (global R = 0.469, p = 0.1%), similarly the pair-wise comparison of the three depth strata confirmed significant difference among the depth strata (0 – 100m vs 101 – 200m, R = 0.288, p = 0.1%; 0 – 100m vs 201 – 500m, R =

0.945, p = 0.1%; 101 – 200m vs 201 – 500m, R = 0.797, p = 0.1%, all the three pair-wise comparisons were significant).

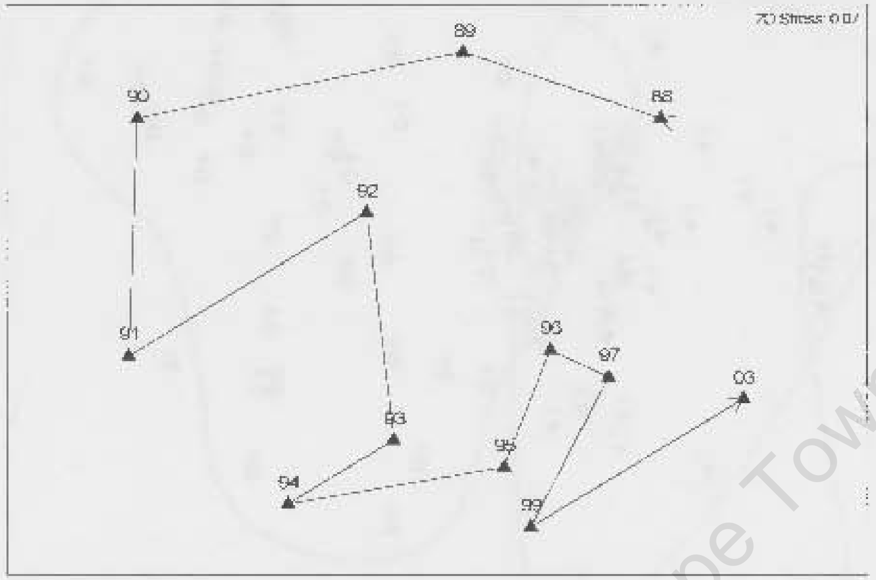


Figure 5.6a

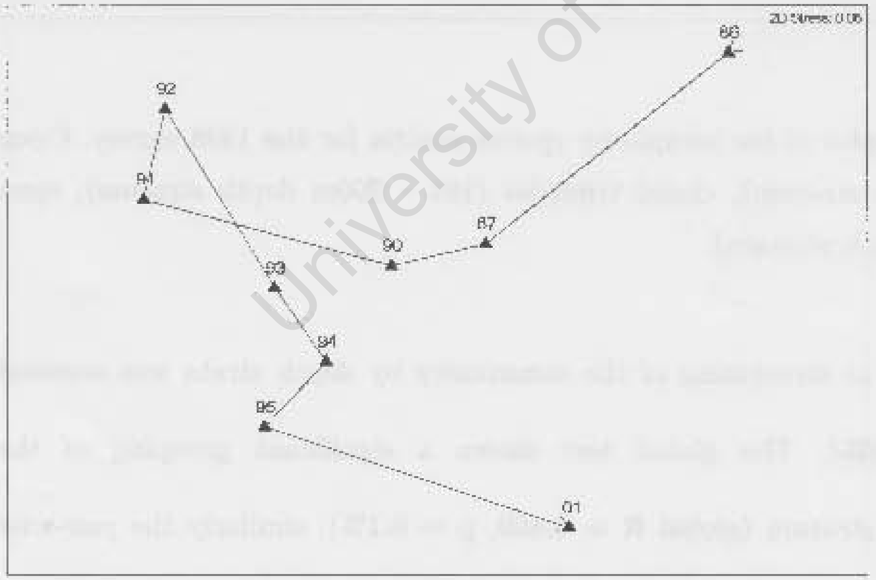


Figure 5.6b

Figure 5.6. MDS ordination plots of mean catch rate of species by year matrix for the autumn (a) and spring (b) seasons. Numbers at each point denote survey year.

The temporal aspect of the community structure was investigated in two ways; first, ordination of samples by species matrix, in this case the sample represent survey years so that the catch rate of each species is averaged by year. This was done for both the autumn and spring seasons. The second approach was analyzing the axis scores for each survey station from the multidimensional scaling using main effect two-way Analysis of Variance (ANOVA).

Figure 5.6 shows the ordination plots for the south coast demersal community based on mean catch rate by year of all the species for the surveys in both autumn and spring. It is clearly shown that the community structure has changed with time, for the autumn survey, from the beginning of the 1990s to the year 2003 (Fig. 5.6a). A similar pattern of change in the community structure has also been observed for spring (Fig. 5.6b), thus suggesting consistent trends over time despite seasonal differences. The trend in the species groups related to the axis scores of the MDS for autumn surveys is depicted in Figure 5.7.

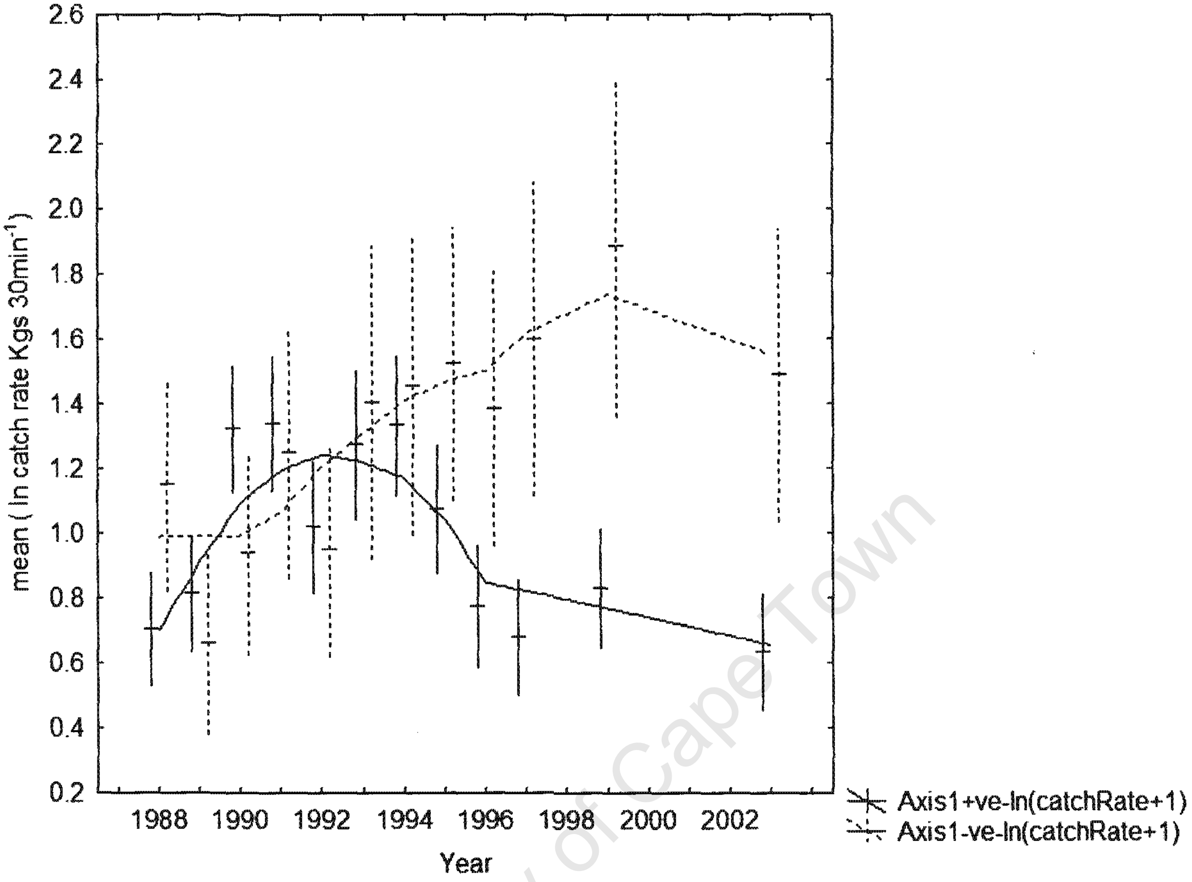


Figure 5.7. Trend in the mean catch rate of species groups that were positively (axis1+ve-ln(catchRate+)) and negatively correlated with axis 1 score (axis1-ve-ln(catchRate+)).

The changes in the community structure were mainly driven by two contrasting changes. Groups of species that were positively correlated with scores of axis 1 declined with time whereas those that were negatively correlated with axis 1 scores increased in relative abundance over time. Spearman's rank correlation coefficient (ρ) was used to assess the correlation between the mean catch rate of each species and the MDS axis 1 score. Species were assigned to either of the two groups (positively correlated to axis 1 and negatively correlated to axis 1), and a cutoff value of correlation (ρ >=|0.4|) was used, arbitrarily selected, for grouping.

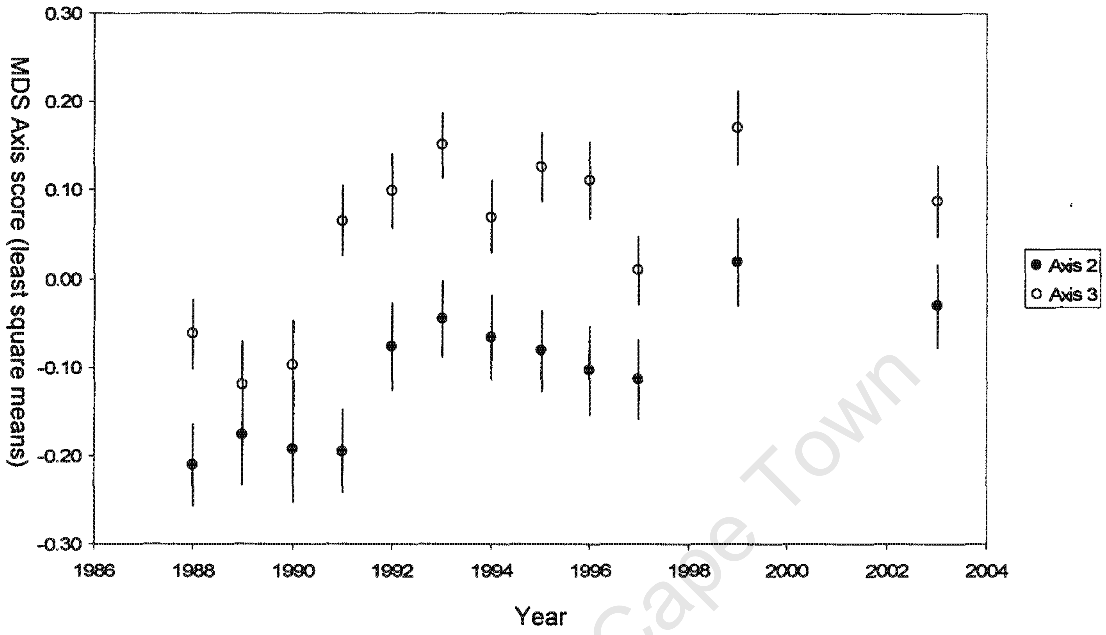


Figure 5.8. Trend in the least square means of the axis scores of the second and third axis for surveys conducted in autumn. Vertical bars are ± 2 standard errors.

The result of the main effect ANOVA is shown in Table 5.2. Except for axis 1, survey year has a significant effect on the axis 2 and axis 3 scores for all the autumn surveys. The corresponding least square means of these axes is shown in Figure 5.8. Both axes scores have increased over time, as the different axes are supposed to represent different aspects of species composition it is apparent that the species composition on this coast has changed with time. However, analysis of the scores for the three MDS axes still suggests that the major mode of variation in the community structure is along the depth gradient, while the second and third MDS axes summarize the temporal component of variation in species composition.

Table 5.2. Result of the main effect two way ANOVA test on the axis scores of each sampling stations over the whole survey period, for the autumn and spring survey separately.

Season	Axis	Effect	Sum of Square	Degr. of Freedom	Mean sum of Square	F	p
Autumn	Axis 1	Intercept	113.612	1	113.612	580.72	0.0000
		Year	2.670	11	0.243	1.24	0.2549
		Depth_category	433.004	2	216.502	1106.64	0.0000
		Error	197.400	1009	0.196		
	Axis 2	Intercept	6.563	1	6.563	35.15	0.0000
		Year	4.870	11	0.443	2.37	0.0068
		Depth_category	33.959	2	16.979	90.93	0.0000
		Error	188.410	1009	0.187		
	Axis 3	Intercept	1.496	1	1.496	10.96	0.0010
		Year	7.744	11	0.704	5.16	0.0000
		Depth_category	5.155	2	2.577	18.88	0.0000
		Error	137.758	1009	0.137		
Spring	Axis 1	Intercept	71.079	1	71.079	273.61	0.0000
		Year	4.375	8	0.547	2.10	0.0331
		Depth_category	196.853	2	98.426	378.87	0.0000
		Error	198.737	765	0.260		
	Axis 2	Intercept	4.541	1	4.541	18.52	0.0000
		Year	3.792	8	0.474	1.93	0.0524
		Depth_category	15.507	2	7.753	31.61	0.0000
		Error	187.613	765	0.245		
	Axis 3	Intercept	3.335	1	3.335	20.93	0.0000
		Year	0.954	8	0.119	0.75	0.6486
		Depth_category	6.642	2	3.321	20.85	0.0000
		Error	121.866	765	0.159		

5.3.4 Analysis of fishing effort

Figure 5.9 shows the spatial distribution of the commercial demersal trawl fishing effort and longline fishing effort. On the south coast, the majority of the demersal fishing effort is concentrated between 20^0 and 23^0 E and on the east coast. For the longline fishery comparison of the distribution of the effort in the two periods shows that both the magnitude and the spatial coverage of the fishing effort have increased over the recent period.

5.4 Discussion

Assessment of the spatial and temporal trends of measured environmental variables suggests that they differ between autumn and spring seasons, though bottom (within 10m of the sea floor) temperature and salinity declined with time in the autumn season with no clear trend in spring. These contrasting trends between the two seasons suggest different responses of the demersal community over time in each season if observed changes in community structure are solely to be attributed to a strong environmental driver. A snapshot of the community structure of the demersal fishes (Fig. 5.6) confirms the conclusion of previous studies (Smale *et al.* 1993), that depth is the main structuring physical factor separating three distinct demersal communities. But the strong correlation between depth and the environmental variables suggests observed depth related structuring could also be confounded by the environmental variables (temperature, oxygen concentration, and salinity).

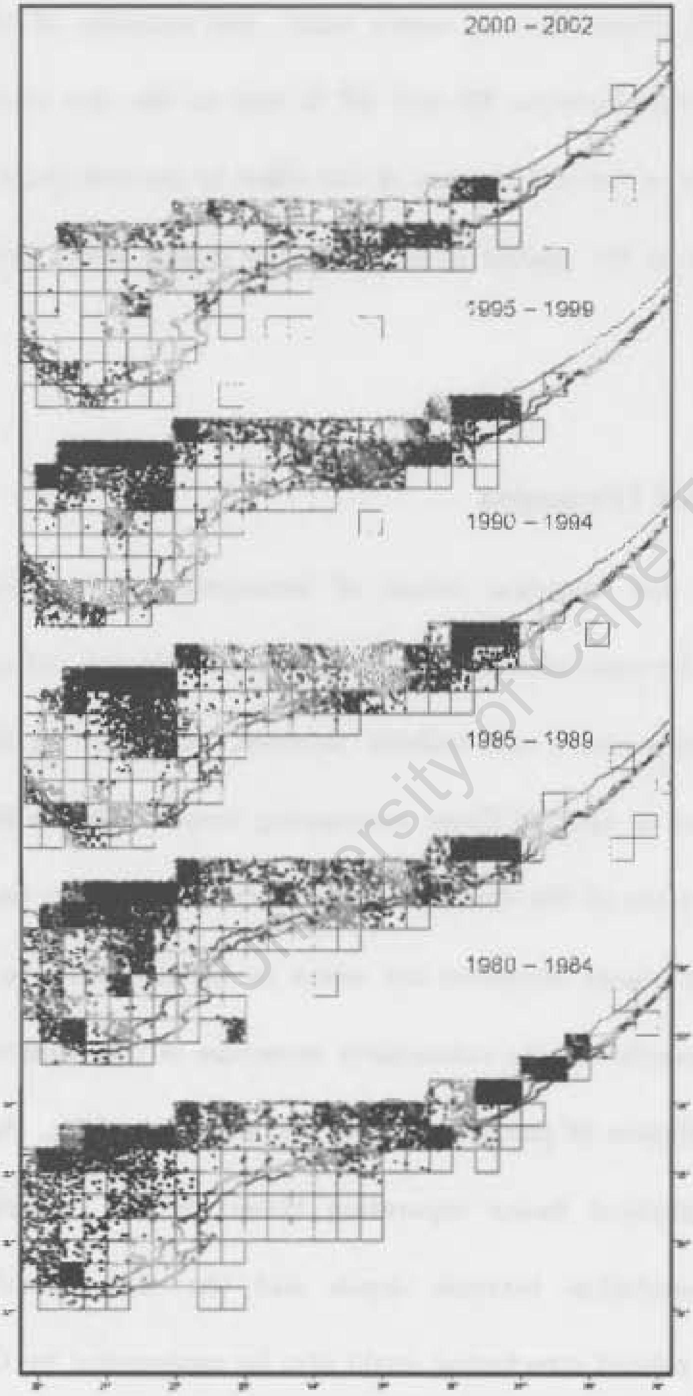


Figure 5.9a.

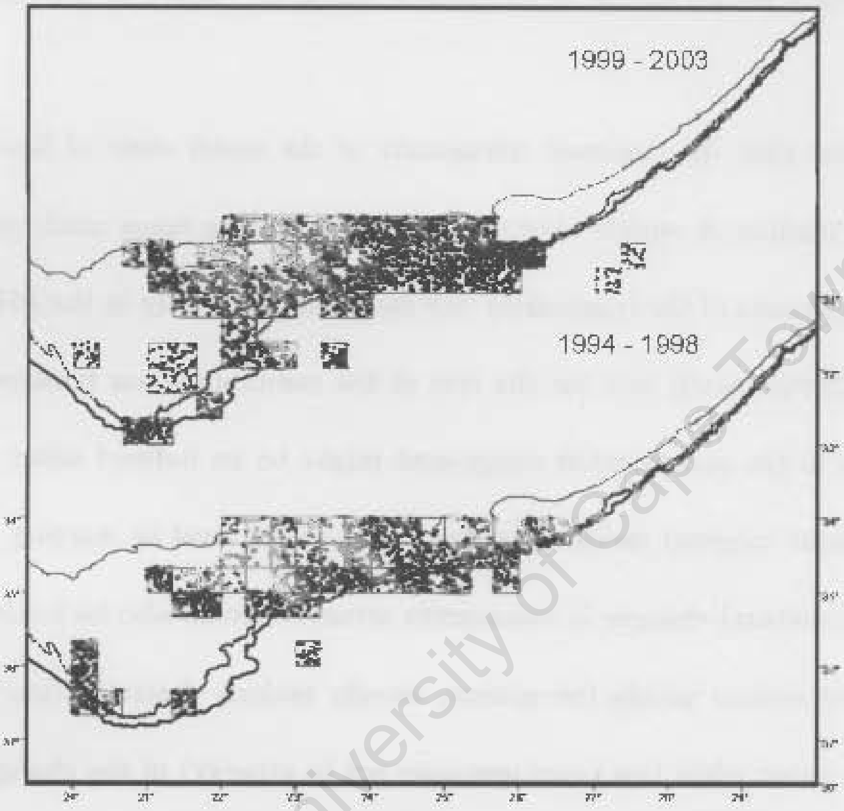


Figure 5.9b

Figure 5.9. Spatial distribution of the demersal trawl fishing effort (a), and the long line fishing effort (b) for different periods. Each dot in the map for the demersal trawl fishing effort represent 200 hours of fishing, for the long line fishery each dot represent 200 hooks.

Similar depth-related changes in community structure of demersal fish communities have been reported from studies elsewhere for example off Alaska, Mueter and Norcross (1999) and off Angola, Bianchi (1992). Strongly depth related change in the diversity of this community is also shown in Chapter 6, based on variety of diversity indices.

The results suggest that the demersal community of the south coast of South Africa has changed in a number of aspects over the past 18 years. The mean catch rate of the non-targeted components of the community has increased, especially in the 101 - 200m depth stratum, whereas catch rate for the rest of the community has remained stable. Such an increase in the non-targeted component might be an indirect effect of fishing where the dominant targeted species has kept at a certain level or starting to decline due to fishing. Structural changes in community structure could also be further enhanced by trophic interactions within the system, usually making determination of the cause (or important cause when two more processes act in synergy) of the changes difficult, if not impossible. A related temporal response of fish communities has been reported for the Georges Bank, where over harvesting of the dominant species was followed by an increase in the abundance of species that were suppressed competitively or by their predators (Fogarty and Murawsky 1998). A similar but rather substantial shift has been observed in the demersal community of the Gulf of Alaska, which has shifted from a system dominated by shrimp and small forage fishes to a system dominated by large piscivorous gadid and flatfish species (Mueter and Norcross 2000).

The overall mean catch rate and mean catch rate of the target component appears to stabilize with a slight decline in the 2000s after an initial increase in early 1990s.

Both the results of the MDS ordination on the detailed station by species matrix, and year by species matrix highlight that there has been temporal change in the community structure. This change in community structure, in both seasons, is due to changes in the relative abundance of groups of species which may be attributed to the direct and indirect effects of fishing. Furthermore this impact of fishing might also be acting in synergy with the decline in bottom temperature and salinity on this coast, though only observed in autumn, which may also be an important source of change through their effect on the growth rate. A case of similar biotic response but opposite trend in the environmental variables has been reported for the Canadian Scotian shelf; where a decline in the mean weight of the species and steepness of the slope of the size spectra over time was observed on the east and west Scotia while a decline and an increase in the bottom temperature was observed for the Scotia shelf (Zwanenburg 2000). The trend in the mean catch rate of the two groups of species that were positively and negatively correlated with the MDS axis 1 score suggests that the temporal changes in community structure on this coast are reflected in the contrasting trends of relative abundance of the two groups of species. Those species that were positively correlated with axis 1 declined over time whereas those that were negatively correlated increased over time. The overall output strongly indicates that the structure of the demersal fish community has changed with time over the temporal bounds of the study. These changes in the community structure may be attributed to the impact of increased fishing from the longstanding demersal trawl fishery and mainly the newly introduced long line fishery combined with the other fishing operations on this coast.

Chapter 6 Patterns in the diversity of demersal fish communities off the south coast of South Africa

Abstract

The diversity of ecological communities has been the focus of many studies. Some of the context for this is to track the impact of disturbances, on communities and to study the role of community structure in the functioning of ecosystems. The spatial and temporal patterns in the diversity of the south coast demersal fish communities have been investigated using selected sets of diversity indices. Species diversity declined with increasing depth. Diversity is related in an inverted bell shape to longitude, with regions around the middle of the south coast being characterized by lower diversity. On the other hand, the taxonomic distinctness index (Δ^*) showed an increase in the taxonomic heterogeneity of the demersal community below the 200m isobath. Assessment of the temporal trend in diversity indicates that survey year has a significant effect on all diversity indices except the taxonomic distinctness index. An increase in diversity and decline in dominance was observed with time. This may be result of a decline in the abundance of dominant species or an increase in the abundance less dominant species, or a combination of both. Multivariate analysis of the set of diversity indices produced three groups of indices; those reflecting species richness (S, Margalef's d), those measuring mainly taxonomic relatedness (Δ^*), and those balancing the richness and evenness components of diversity (J', H', λ, Δ, *Hill's N1*, and *Hill's N2*). The relationship between evenness, catch rate, and size was also investigated. Size classes with highest evenness were found to have lowest catch rate and vice versa. This highlights the need to consider the size and/or trophic level of species when linking diversity to the functioning of ecosystems.

Keywords: diversity, maximum length, catch, depth, longitude, South Africa

6.1 Introduction

The diversity of ecological communities has been studied in different ecosystems around the world in various contexts ranging from purely descriptive studies of the structural and functional heterogeneity of the community, as comparative measures between ecological communities, as metrics for tracking changes in a community resulting from natural phenomena and those resulting from anthropogenic causes, to complex situations where it is related to the functioning of ecosystems. There are a number of studies in terrestrial ecosystems, relating diversity at the base of the food web or across food webs to the functioning of ecosystems, through its influence on ecological processes (Grime 1997, Hooper and Vitousek 1997, Tilman *et al.* 1997). For example Hooper and Vitousek (1997) found that, based on experimental manipulation, the functional richness and composition of plants influence some of the processes of production and nutrient cycling. In their study plant composition was a more important factor in explaining the variability in the nitrogen dynamics and production as compared to functional richness. Similarly the work of Tilman *et al.* (1997) on terrestrial primary producers demonstrated the influence of functional diversity and functional composition on various ecological attributes: productivity, percent of nitrogen, and total nitrogen of plants and light penetration. The marine counterparts of the terrestrial diversity and ecosystem process studies, with experimental manipulation, includes those of Bolam *et al.* (2002) and Hall *et al.* (2000). The study of Bolam *et al.* (2002) addresses the issue by experimental manipulation of richness and biomass of marine benthos in Blackness, Scotland, and found that except for oxygen consumption, none of the ecosystem processes or functions were related to the level of richness or biomass of macro-invertebrate fauna. On the other hand, Hall *et al.* (2000) looked at nutrient enrichment and the response of the fauna and flora of a mud flat community: the diversity of flora increased in enriched experimental plots but the diversity of the fauna did not follow that of the flora linearly, instead it had a bell-shaped relationship with the diversity of the flora. Unfortunately biodiversity of various ecosystems is affected by the direct and indirect impacts of mans action: through habitat destruction, harvesting of components of the ecological community, the result of the direct impact manifested in the trophic or competitive interaction of the biotic community, nutrient overload of coastal systems that seriously alter the composition and diversity, and changes in the planets biogeochemical cycles (Vitousek *et al.* 1997).

One of the direct and indirect impacts of man on many marine ecosystems is over harvesting, and in the process, habitat damage by capture fisheries. There are a number of studies around the world documenting the substantial impact of heavy fishing on the structure of fish communities (Pauly 1998, Bianchi *et al.* 2000, Jennings *et al.* 2001a, Jennings *et al.* 2002). One of the reported responses of fish communities, in terms of diversity, is increasing steepness of the diversity size spectra (Rice and Gislason 1996, Gislason and Rice 1998), which suggests a progressive decline in the diversity within the larger size classes and an increase in the diversity within the smaller size classes. Greenstreet *et al.* (1999) found a decline in the diversity of non-target species in heavily fished regions. They also found spatial differences in the diversity of the Northeast Atlantic shelf sea areas where inshore and Southern areas were characterized by a higher diversity of demersal fishes whereas the offshore and Northern regions had a lower diversity.

A number of studies relate diversity of nearshore, shelf, and slope communities of different marine ecosystems to the prevailing environmental parameters (temperatue, oxygen concentration, and salinity), depth, latitude and longitude. Analysis of survey data from the Gulf of Alaska showed that diversity of the demersal fish communities was related to depth in a bell shaped form where lower diversity was observed in shallow water, with an increase in diversity down to 200 – 300m below which it declined (Mueter and Norcross 2002). They also found a lower diversity and higher Catch Per Unit Effort (CPUE) of demersal fishes on the Western part of the gulf whereas the Eastern part is characterized by higher diversity and lower CPUE. McClatchie *et al.* (1997) found that species richness of demersal fishes off New Zealand decreased with latitude, moving South, but increased with depth. Areas of increased species richness were also found associated with regions of high productivity. In addition they reported that richness was positively related to catch rates whereas evenness was inversely related to catch rate. Macpherson and Duarte (1994) investigated the pattern of change in the richness, size, and distributional range of East Atlantic fishes and found that richness of both teleost and elasmobranches increased towards higher latitudes. Richness, maximum size and latitudinal range of the fish communities were also found to increase with depth. The trend in the diversity or richness of other taxa (benthos) also appears to increase with depth (Grassle and Maciolek 1992). They found higher diversity and richness of benthos off the East coast of the United

States around depth of 1500 – 2500m than shallower. There are few studies that relate evenness or any measure of diversity to catch rate and trophic level or size composition (as a proxy for trophic level).

A number of diversity indices have been proposed by ecologists, mainly those based on balancing the richness and evenness components of diversity. Selecting among these indices is difficult, highlighting a need for a way to explore the influence of a variety of diversity indices on the assessments that an investigator wishes to make. To this end Clarke and Gorley (2006) showed a neat way to achieve the above objective through multivariate analysis of sets diversity indices. This study makes use of this opportunity to investigate the relationship among the various diversity indices and discusses the findings in light of the possible conclusions that could be drawn about the fish community under study.

This study is based on the demersal fish communities of the south coast of South Africa which supports a number of demersal fish communities. There are a number of studies addressing different aspects these communities: feeding ecology and trophic interactions (Sauer and Lipinski 1991, Smale 1992, Pillar and Wilkinson 1995), spatial distribution (Botha 1985, Badenhorst and Smale 1991, Smale 1991), biology and population dynamic (Bennett 1993), fisheries (Japp *et al.* 1994). The demersal fish communities of the south coast of South Africa are exploited by a number of fishing sectors using a variety of fishing gear and varying in their selectivity, degree of interaction with the bottom habitat, and targeting various species. The only study on this coast that looked into aspects of the community structure was that of Smale *et al.* (1993), and using multivariate techniques which showed the existence of three assemblages related to depth. Temperature and oxygen concentration were found to be different among the three depth ranges.

This study aims to assess the temporal changes in the diversity of the south coast demersal fish communities (teleosts, elasmobranches, and cephalopods) and to investigate the relationship of diversity to physical and environmental conditions. Temporal patterns in the diversity of fish communities on the south coast of South Africa have not been investigated previously. Further this study also attempts to show empirical relationships between catch rate, diversity and maximum observed length (L_{max}) of a species (generally believed to reflect the trophic level of the species) in an ecosystem and discuss this issue in the light of possible consequences of impact on the diversity of any groups to the functioning of the whole ecosystem.

6.2 Methods

Details of the sources of the data used, the spatial and temporal bounds, standardization of the data, and distribution of trawling stations by depth stratum (Table 5.1) are given Chapter 4. The spatial boundary of the study represents the South and Southeastern Cape in Figure 2.1, between 20^0 E and 27^0 E.

6.2.1 Measures of diversity

There are numerous diversity indices available and in use. As the choice of diversity index could affect the conclusion drawn, a variety of diversity indices was calculated for each trawling station and a correlation matrix (based on Pearson's product moment correlation) was created describing pair-wise correlations of each of the diversity indices. This correlation matrix was then converted to similarity percentages by taking the absolute value of the correlation values and multiplying by 100 (Clarke and Gorley 2006).

The following diversity indices were calculated to explore the issue of choice of diversity indices, formulas are as outlined in Clarke and Gorley (2006) and Magurran (2004): catch rates of each species were used in calculating the indices.

$$\textit{Species richness} = S$$

$$\textit{Margalef's (d)} = \frac{(S-1)}{\log_e(N)}$$

$$\textit{Shannon-weiner index } (H') = -\sum P_i * \log_e(P_i)$$

$$\textit{Pielou's evenness index } (J') = \frac{H'}{\log_e(s)} \text{ or } \frac{H'}{H'\max}$$

Simpson's index $(\lambda) = \sum P_i^2$

Hill's first index (N1) $= \exp(H')$

Hill's second index (N2) $= \dfrac{1}{\sum P_i^2}$ or $\dfrac{1}{\lambda}$

Where H'max is where the Shannon-Weiner index reaches a maximum

S is the total number of species

N is abundance of all the species

P_i is proportion of species i in the sample

Diversity indices based on taxonomic relatedness

The following diversity indices were calculated base on catch rate data of each species and information on the taxonomic relatedness of each species (which is provided on additional data matrix reflecting the taxonomic hierarchy of each species).

Average taxonomic diversity (Δ)*, and Average taxonomic distinctness* (Δ^*) (Warwick and Clarke 1995)

$$\Delta = \frac{\left(\sum\sum_{i<j} W_{ij}\, X_i\, X_j\right)}{\left(N(N-1)/2\right)}$$

$$\Delta * = \frac{\left(\sum\sum_{i<j} W_{ij} X_i X_j\right)}{\left(\sum\sum_{i<j} X_i X_j\right)}$$

Where W_{ij} is the weighting given to each taxonomic hierarchy

X_i and X_j are abundance of species i and j respectively

N is the total abundance of all species in the sample

The double summation in the numerator of both indices and denominator of taxonomic distinctness index (Δ*) is over all pairs of species i and j such that (i, j = 1, 2, 3, ……., S; $i < j$)

Pielou's evenness index (J'), Shannon-weiner diversity index (H'), Simpson's index (λ), average taxonomic diversity (Δ) and average taxonomic distinctness (Δ*) were used to investigate the temporal trend. The same indices (except that λ was replaced by species richness S) were used to investigate spatial patterns (relationship to depth and longitude) in the diversity.

The temporal trend in the diversity of the demersal assemblages, based on few selected indices, was investigated using a GLM model of the following type:

$$D_{iy} = \mu + (\text{Year})_y + \beta_1 * Z_{iy} + \beta_2 * L_{iy} + \beta_3 * C_{iy} + \varepsilon_{iy}$$

Where D_{iy} is the diversity index for station i in year y

μ is the intercept; Z_{iy} is depth of station i in year y

L_{iy} is longitude of station i in year y; C_{iy} is ln(total catch) of station i in year y; ε_{iy} residual error term higher diversity at 20^0 E, declining towards the middle of the south coast and increasing again from about 24^0 E eastwards (Fig. 6.1d – 6.1f). The two indices based on taxonomic relatedness (taxonomic diversity Δ and taxonomic distinctness Δ^*) show different patterns with depth. Initially both indices decline steeply with increasing depth, but Δ remain relatively stable below the 200m isobath (Fig. 6.2a) whereas Δ^* increases (Fig. 6.2b). They also show slightly differing longitudinal trends, with Δ similar to both J' and H' whereas that of Δ^* is more similar to S (Figs. 6.2c and 6.2d). All the diversity indices suggest that part of the south coast (between Platenberg Bay and Cape St. Francis, around 24^0E) has the lowest diversity.

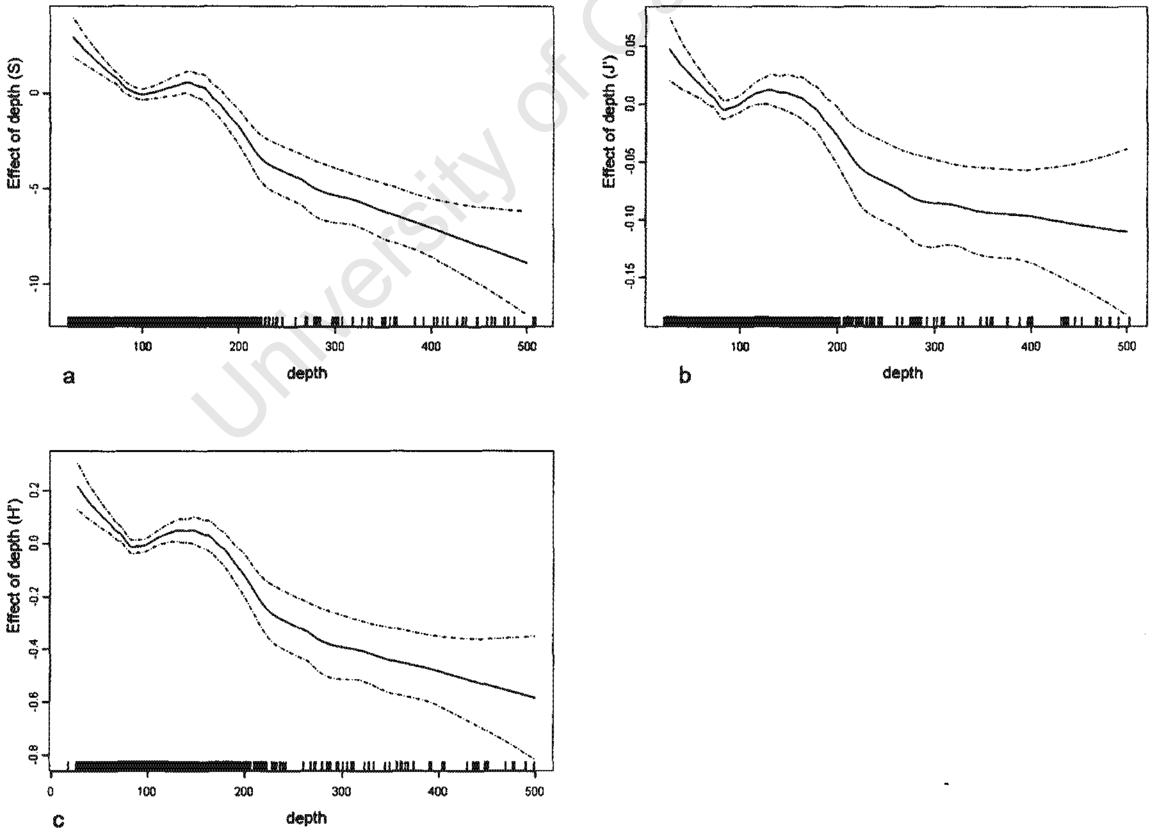


Figure 6.1a, b, and c.

The temporal trend in both species- and taxonomic-based diversity indices was assessed using a General Linear Model (GLM). The results of the GLM analyses show that for almost all of the diversity indices depth is the most important factor followed by longitude and survey year (Table 6.1). Survey year is a significant effect for all of the diversity indices, except for Δ^*. Figure 6.3 shows a positive trend over time in the least square means of J', H', Δ, Δ^*, whereas the trend is negative for Simpson's index (λ). There is a significant increase in evenness J' and diversity H' over time, conversely a decline in dominance λ (Table 6.1).

Table 6.1. Result of the GLM test of the diversity indices.

Response	Effect	Sum of Square (SS)	Df	Mean sum of square (M.S.S.)	F	p
Species richness (S)	Intercept	3495.803595	1	3495.803595	140.7724	0.000000
	Longitude	25.43787578	1	25.43787577	1.050530	0.297046
	Depth	3190.000377	1	3190.000377	135.5520	0.000000
	Catch rate	1378.954635	1	1378.954635	58.92067	0.000000
	Year	1039.72533	11	94.47954619	4.04108	0.000008
	Residual	23564.46956	1008	23.3875134		
Margalef d	Intercept	108.7484055	1	108.7484055	250.9950	0.000000
	Longitude	0.019742359	1	0.019742359	0.045565	0.831000
	Depth	70.33111928	1	70.33111928	162.3272	0.000000
	Catch rate	12.43981406	1	12.43981406	28.65579	0.000000
	Year	23.79511710	11	2.163273381	4.982949	0.000000
	Residual	435.7997773	1008	0.43326763		
Pielou's evenness (J')	Intercept	2.346200965	1	2.346200965	173.3923	0.000000
	Longitude	0.09064702	1	0.09064702	6.716281	0.009602
	Depth	0.584096663	1	0.584096663	44.01522	0.000000
	Catch rate	4.463641588	1	4.463641588	330.9455	0.000000
	Year	0.334347270	11	0.030396834	2.250815	0.006320
	Residual	13.60450192	1008	0.01349655		
Shannon-wiener (H')	Intercept	22.63932044	1	22.63932044	139.8727	0.000000
	Longitude	0.906592230	1	0.906592282	5.616874	0.017976
	Depth	14.13495274	1	14.13495274	87.34934	0.000000
	Catch rate	28.57761434	1	28.57761434	176.3677	0.000000
	Year	4.841287034	11	0.440116722	2.719334	0.001822
	Residual	163.1273599	1008	0.16183524		
Hill's N1	Intercept	247.2897122	1	247.2897122	42.89441	0.000000
	Longitude	40.56865064	1	40.56865064	7.036456	0.008017
	Depth	479.0103298	1	479.0103298	83.28105	0.000000
	Catch rate	574.0017052	1	574.0017052	99.70739	0.000000
	Year	182.0906711	11	16.55431420	2.870770	0.000983
	Residual	5797.644581	1008	5.751671558		
Hill's N2	Intercept	118.980481	1	118.980481	36.67783	0.000000
	Longitude	15.09211153	1	15.09211153	4.655875	0.031547
	Depth	178.0882168	1	178.0882168	55.73077	0.000000
	Catch rate	321.4387788	1	321.4387788	99.13143	0.000000
	Year	69.9574516	11	6.359758327	1.938134	0.029359
	Residual	3208.562759	1008	3.24258278		
Taxonomic diversity (Δ)	Intercept	34930.57364	1	34930.57364	211.2825	0.000000
	Longitude	294.6831007	1	294.6831007	1.782418	0.182154
	Depth	16916.40169	1	16916.40169	102.3208	0.000000
	Catch rate	43330.20553	1	43330.20553	261.3352	0.000000
	Year	3299.058009	11	299.9144972	1.814059	0.047474
	Residual	166650.4205	1008	165.327030		
Taxonomic distinctness (Δ*)	Intercept	67880.7373	1	67880.7373	1718.019	0.000000
	Longitude	52.43176854	1	52.43176854	1.3228	0.250365
	Depth	6025.324188	1	6025.324188	152.1587	0.000000
	Catch rate	3349.154574	1	3349.154574	84.61213	0.000000
	Year	650.7475909	11	52.70430005	1.342089	0.198452
	Residual	39851.33964	1008	39.53596255		

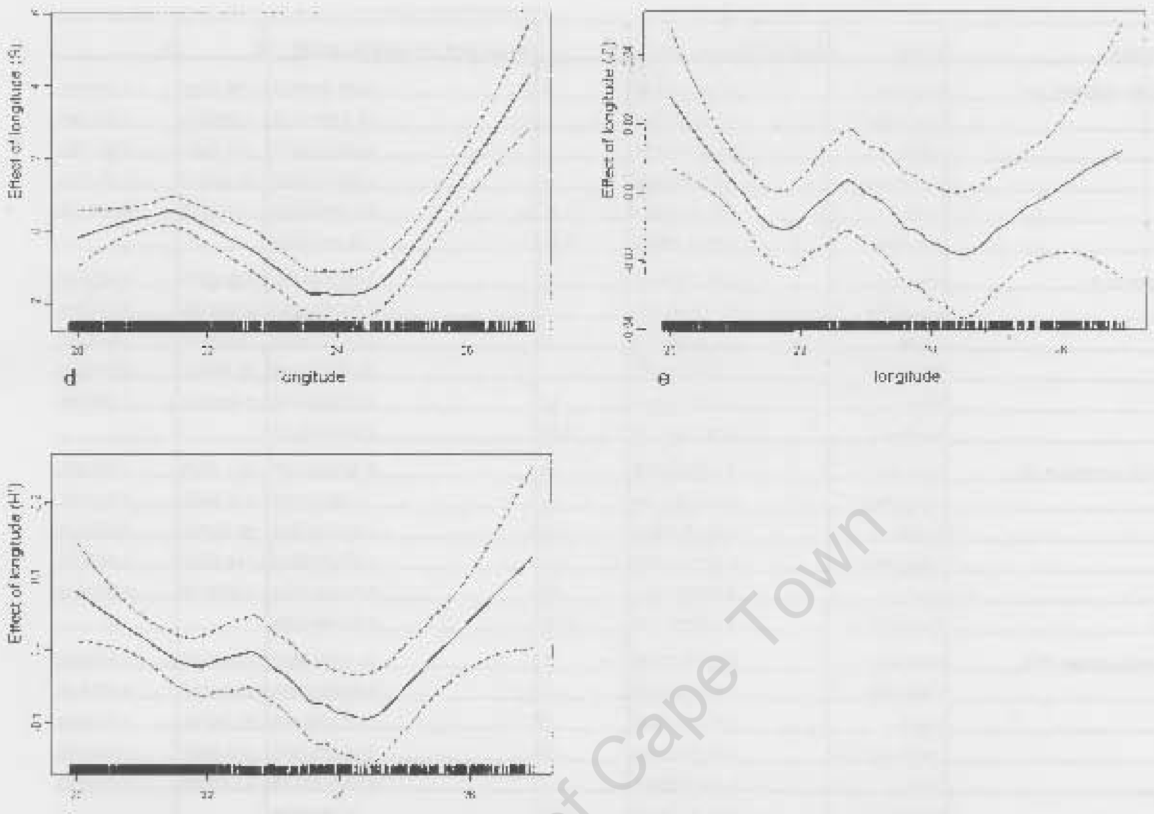


Figure 6.1d, e, and f.

Figure 6.1. Trend in the diversity of the fish assemblages in relation to depth (a, b, c) and longitude (d, e, f). Loess smoothed with ± 2 standard error dashed lines.

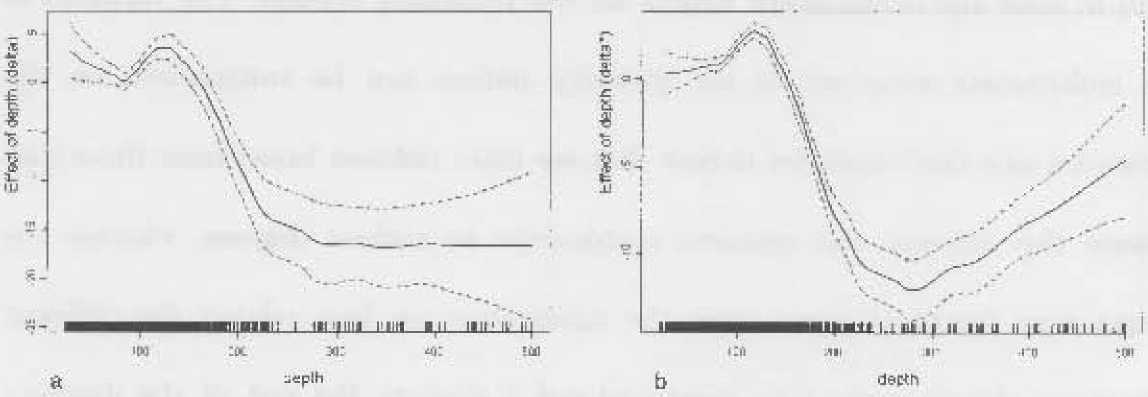


Figure 6.2a and b.

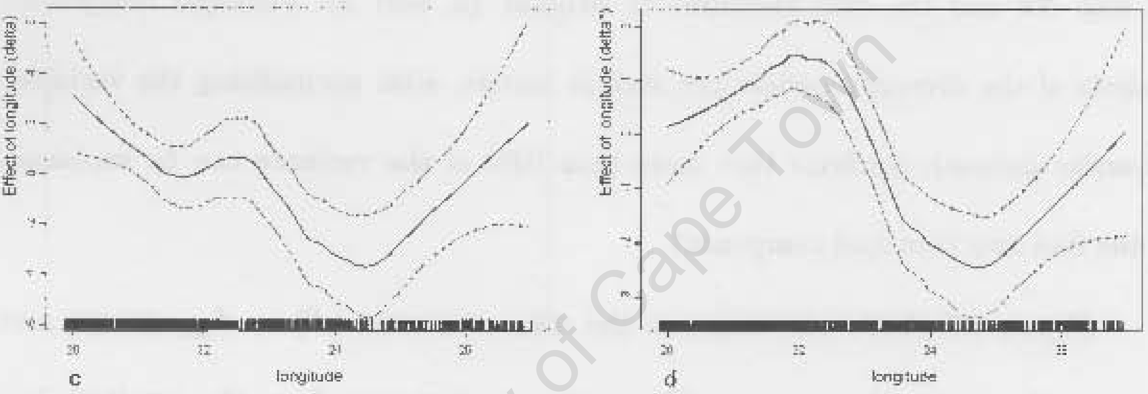


Figure 6.2c and d.

Figure 6.2. Trend in the taxonomic relatedness indices (taxonomic diversity and taxonomic distinctness) in relation to depth (a and b) and longitude (c and d). Loess smoothed with ± 2 standard error dashed lines.

Multivariate analysis of the diversity indices illustrated in Figure 6.4a shows that the nine diversity indices cluster into three groups, one containing measures of species richness (*S*, and Margalef's *d*), another containing diversity indices that consider evenness and richness (*H'*, *J'*, Hill's *N1* and *N2*, Δ, λ), and Warwick and Clarke's taxonomic distinctness Δ* (Warwick and Clarke 1995) far from both groups. A further MDS was carried out on the diversity indices excluding Δ* (Fig.

6.4b) to show the relationships within the two remaining clusters. The variation in the multivariate structure of the diversity indices can be summarized on the horizontal axis that separates indices that are more richness based from those that balance the richness and evenness components to various degrees, whereas the second axes (vertical) summarizes the information on how related the different indices are, for example Δ is closely related λ than to the rest of the diversity indices. Similarly H' and J' are more close to each other; the same applies to Hill's *N1* and *N2* and the two measures of richness (S, and d). Principal component analysis of the diversity indices per station matrix, after normalizing the variables (diversity indices), confirms that more than 93% of the variance can be explained by the first two principal component.

Figure 6.5 shows the trend in the mean evenness (J') vs L_{max} groups and mean catch rate vs L_{max} groups. The catch rate increases from the smallest L_{max} classes 36.2cm to the medium L_{max} class 125.2cm and declined for the two largest L_{max} classes whereas the evenness showed the opposite trend. A different form of the relationship between catch rates, evenness, and L_{max} is shown in Figure 6.6. This figure shows that the above three factors are related in complex ways and size groups with high catch rates tend to have lowest evenness. High catch rate were associated with the second and third L_{max} classes and that have low to medium evenness. Largest L_{max} classes and higher evenness values were associated with lower catch rates.

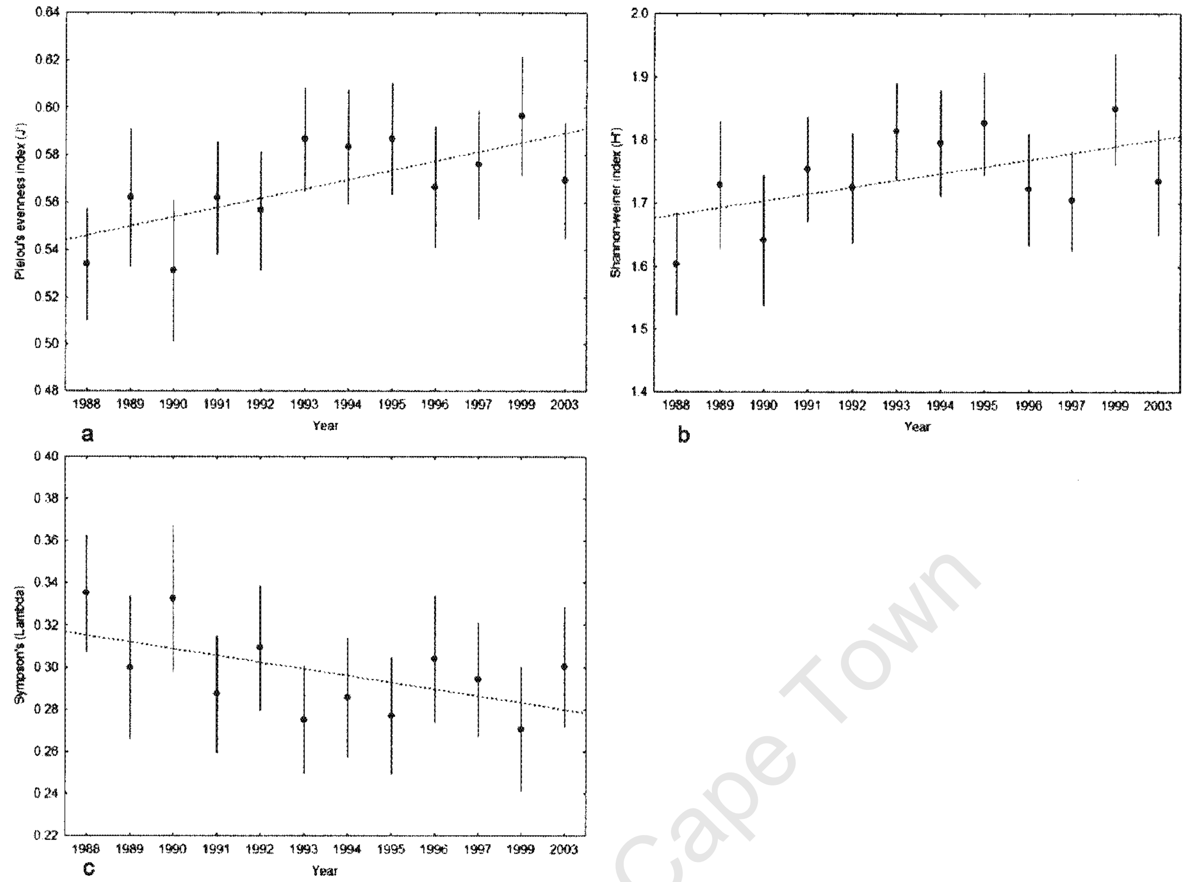


Figure 6.3a, b, and c.

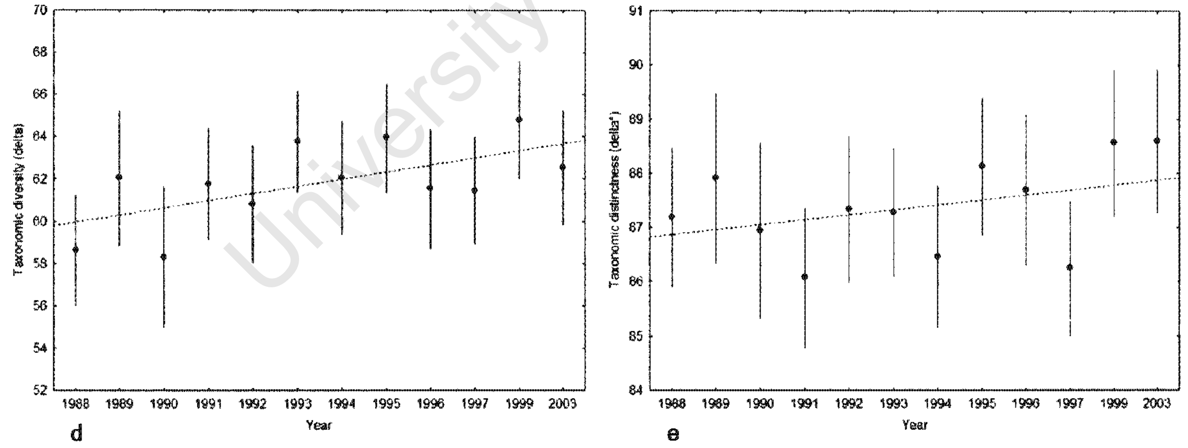


Figure 6.3d and e.

Figure 6.3. Temporal trend in the least square means of species diversity; pielou's evenness index (J'), Shannon-weiner index (H'), Simpson's index (λ) (a, b, and c), diversity indices based on taxonomic relatedness; taxonomic diversity (Δ), taxonomic distinctness (Δ*) (d and e). Vertical bars give 95% confidence intervals.

6.4 Discussion

The relationship of the various diversity indices to depth and to longitude shows that, the diversity of the demersal assemblage on the south coast declines quasi-linearly with depth. This decline in the diversity indices is likely to be the combined effects of both the richness and evenness components of diversity, as clearly shown in Figure 6.1. In contrast to our observation, Mueter and Norcross (2002) found that diversity of demersal fish community in the Gulf of Alaska was uni-modally related to depth with highest diversity around 200 – 300m; their study was also based on surveys conducted within the same depth range as this study (15 – 500m). On the other hand McClatchie *et al.* (1997) reported that richness of the demersal fish community off New Zealand increased with depth, however their study covers a wider depth range (80 – 898m). Similarly, an increase in species richness with depth was reported for East Atlantic fishes by Macpherson and Duarte (1994). Thus the increase in richness as reported in the two studies (Macpherson and Duarte 1994, McClatchie *et al.* 1997) occurred out side the depth range covered by this study. The increase in richness in waters deeper than 500m seems also to be the case for fishes and crustaceans off the West and south coast of South Africa (Dr. Rob Leslie, MCM, Pers.comm).

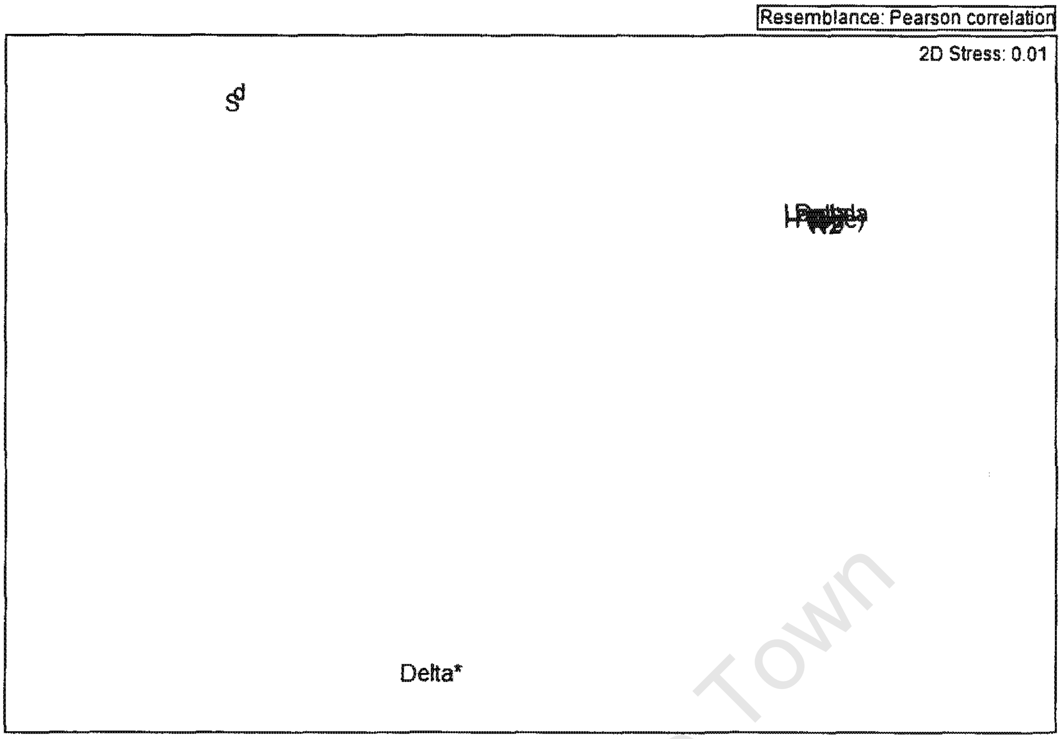


Figure 6.4a.

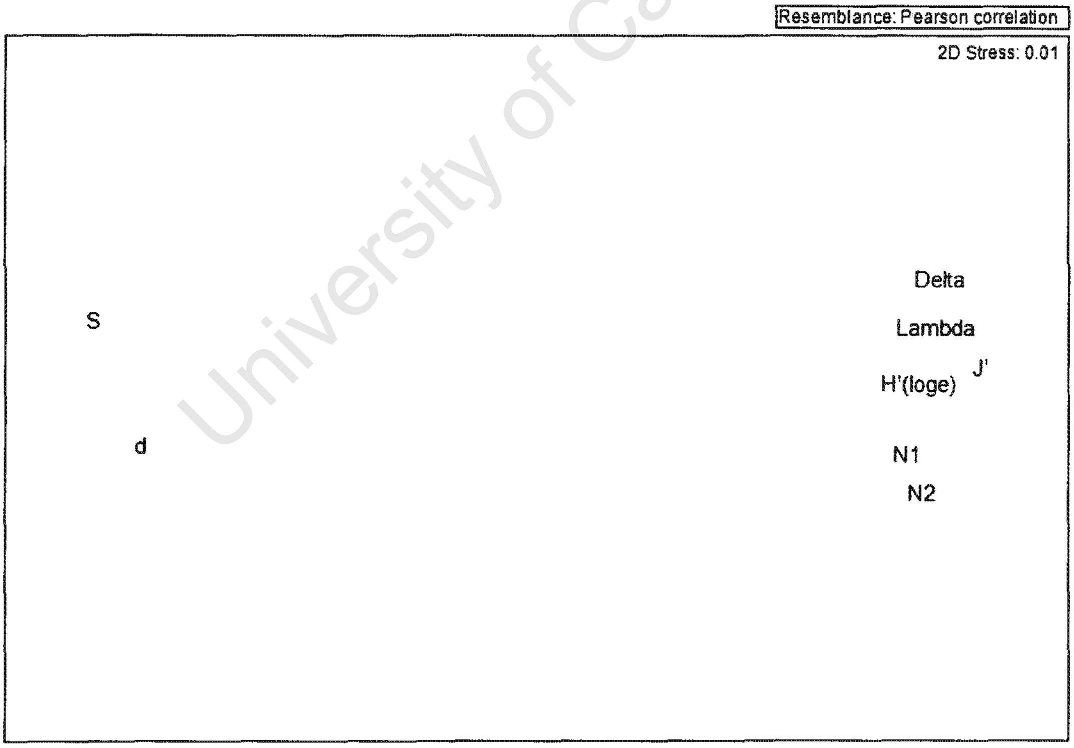


Figure 6.4b.

Figure 6.4. Multivariate analysis of the nine diversity indices using the nonmetric multidimensional scaling (a), and similar ordination for the subset of the diversity indices excluding the taxonomic distinctness index (b).

Though the direction, the form, and the rate of change in species diversity differs between this study and those mentioned above, they all agree that depth is the main physical factor along which the diversity of marine demersal fishes changes. The differences in the form of response of diversity to depth may be result of the sampling strategy and gear, for example Mueter and Norcross (1999, 2000) they only sampled juveniles and small adults. Some of the reasons for higher diversity in waters shallower than 200m, reported here, could be due to the greater structural heterogeneity of the bottom and possibly higher productivity in contrast to deeper waters. McClatchie *et al.* (1997) associated of diversity hot-spots with areas of higher productivity. The relationship of taxonomic diversity (Δ) to depth was slightly different from that of the rest of species diversity indices where it declined sharply to the 200m depth below which it stabilized. This might be a reflection of constancy in the taxonomic heterogeneity of the community or in the evenness component. On the other hand the rise in the taxonomic distinctness below 200m highlights an increase in the taxonomic heterogeneity of the demersal community as the taxonomic distinctness is a pure measure of taxonomic relatedness (Clarke and Warwick 1998). Thus, the pattern of change in the taxonomic diversity (Δ) and taxonomic distinctness (Δ^*) with depth indicates that the demersal community in the deeper regions is characterized by greater richness above the species level, and constant evenness.

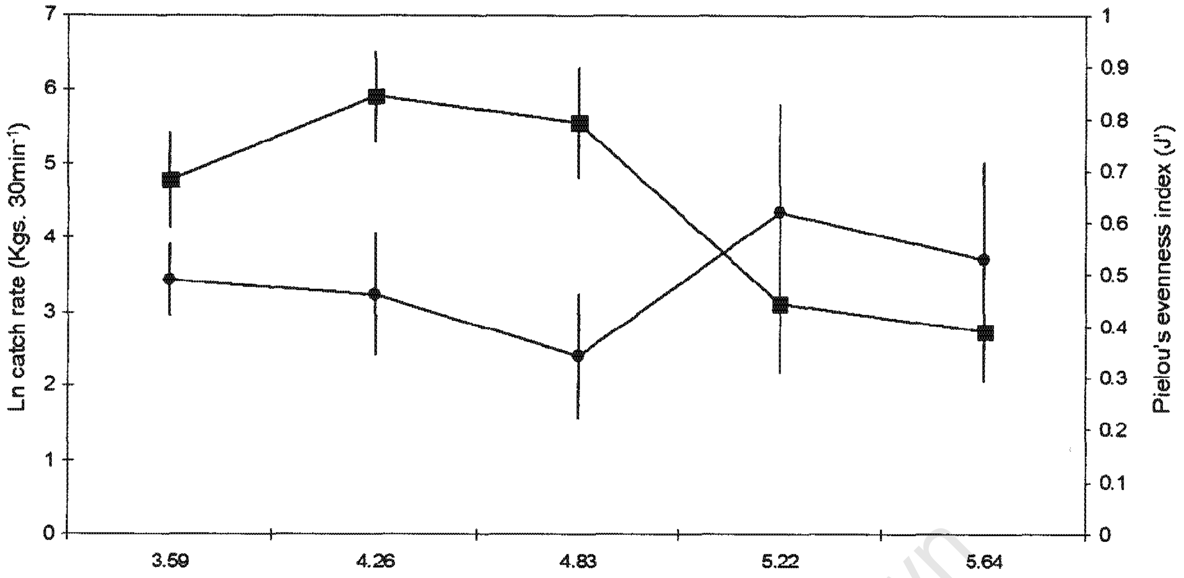


Figure 6.5. Plot of the mean catch rate (closed boxes) and pielou's evenness index (J') (closed circles) vs mean L_{max}. Error bars are standard deviations.

The temporal change in the species diversity indices and taxonomic diversity, in the direction of increasing diversity and decline in dominance over time, (except for that of taxonomic distinctness) could be the result of an increase in abundance of species or groups of species that were previously less abundant. They could also be result of a decline in the abundance of previously dominant species (mainly the shallow water Cape hake and deep water hake, horse mackerel *Merluccius capensis*, *Merluccius paradoxus*, *Trachurus trachurus capensis* respectively). This kind of response with time is the same as the one reported for tropical ecosystems (Bianchi *et al.* 2000), for the Northern North Sea (Greenstreet and Hall 1996, Greenstreet *et al.* 1999) and for the linefish community on this coast (Chapter 2) and is also believed to be a consequence of the differential impact of exploitation. The trend in the dominance of the south coast demersal community over the study period, is in accord with the study that assessed long-term changes in the linefish community structure (reported in Chapter 2) where a decline in the dominance structure was observed from the comparison of the dominance structure among three periods (1897 – 1906, 1927 – 1932, and 1986 – 1998). Though the time scale of this study and that on the linefish community is different, the trend in the dominance structure over the three periods suggests over harvesting of the previously dominant species, on this species rich coast, is likely to result in increasing evenness. Studies from other tropical regions, though the south coast is a warm temperate region, also documented similar response over time (Bianchi et al. 2000), whereas studies in the Northern temperate regions (Rijnsdorp *et al.* 1996, Bianchi *et al.* 2000) and on the linefish community of the West coast of South Africa (Chapter 2) showed a reversal of the trend in dominance over time. As part of the impetus behind an EAF is the protection or maintenance of biodiversity of a system, this necessitates the need to use an appropriate set of diversity indices, but there are large number of diversity indices to choose from. The result (Fig. 6.4) of this study shows that diversity indices could be grouped into a few families so that the use of any index from within such a family will not change the final conclusions drawn.

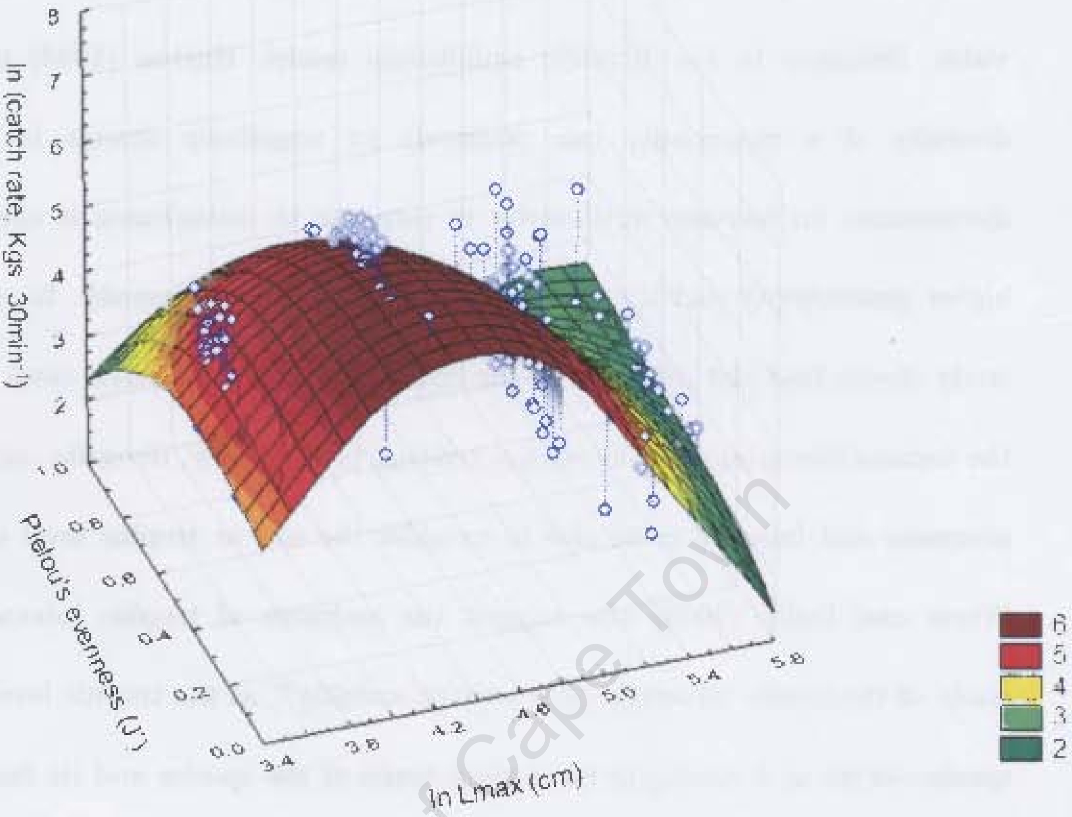


Figure 6.6. 3-d surface plot, smoothed using a spline, of the relationship between mean catch rate, evenness index (J') and mean L_{max}. Cubic spline fitted to show the form of the relationship.

The relationship between catch rate, evenness, and L_{max} category (which could be used as a proxy for trophic level of a species, since as a fish gets larger it tends to move up in the foodweb (Jennings *et al.* 2002, Pauly and Watson 2005)), adds an additional dimension to the usual discussion in the ecological literature relating diversity to the productivity of ecosystems. The study of the demersal fish community off the continental slope of Western Australia by Williams *et al.* (2001) showed a relationship between diversity and density. Areas of higher diversity were associated with lower fish density and areas of low productivity; on the other hand areas of lower diversity were associated with high productivity of the overlying water. Similarly in his dynamic equilibrium model, Huston (1994) predicts that diversity of a community can positively or negatively change in response to disturbance; an increase in diversity in response to disturbance is associated with higher productivity and the converse is true with lower diversity. In addition, this study shows that the diversity of the fish community and catch rates vary among the various size groups. Thus studies relating productivity, diversity, and ecosystem processes and function need also to consider the size or trophic level of the fauna. Worm and Duffy (2003) also suggest the inclusion of trophic interaction in the study of the triads "diversity-productivity-stability", as the trophic level or size of a species serves as a surrogate for various traits of the species and its function in the ecosystem.

This study clearly shows that the diversity of the south coast demersal fish community is strongly related to physical factors: depth and longitude, though observed changes could also be confounded by environmental variables (such as temperature, oxygen concentration, salinity), and potentially substrate type of the sea floor. Multivariate analysis of sets of diversity indices suggests that the same conclusions could be reached by the use of alternate diversity indices from among the three groups identified. Exploratory analysis shows a non-linear relationship among catch rate, diversity (Pielou's evenness index) and L_{max}. Analysis of the temporal trend in the diversity indices suggests an increase in species diversity and a decline in dominance over time and with increased fishing pressure.

Chapter 7 Assessing changes in the demersal fish community of the south coast using Abundance Biomass Comparison ABC curves

Abstract

The possible effect of fishing on dominance patterns in the South African south coast demersal fish community over the period 1986 – 2003 is assessed using Abundance Biomass Comparison (ABC) curves. The ABC method compares the ranked distribution of abundance among species against that of biomass. The temporal pattern in the ABC curves and the *W-statistic* for two depth groups (0 – 100m and 101 – 200m) and for the whole area combined shows a gradient of change in the demersal assemblages from neutral ($W >= 0$) towards negative ($W < 0$) suggesting a disturbed or stressed condition. This corresponds to the increase in long-line fishing effort from 1994 – 2003, superimposed upon temporally variable hake-directed trawl fishing effort in the region. The ABC method shows promise as a guide for assessing the effects of fishing on fish communities, and is based on established *r*- and *k*-selection theory. More modelling and comparative work is needed to establish acceptable ranges for the *W-statistic* and their application in an Ecosystem Approaches to Fisheries.

Key words: ABC curves, effects of fishing, fish assemblages, *r*- and *k*- selection

7.1 Introduction

Heavy fishing is a major threat to the structural and functional organization of marine ecosystems. Such effects manifest themselves directly (as a spatial or temporal gradient in abundance of target species, habitat destruction or decrease in mean size: Jennings *et al.* 2001b, Haedrich and Barnes 1997), or indirectly (causing or enhancing changes in community structure or differential effect on functional groups of the ecosystem; Greenstreet and Hall 1996, Garison and Link 2000) and at different times. Despite the effects of fishing on fish communities and the environment, previous attempts to regulate the effects of fishing have focused mainly on the target species. Currently, because some important indirect effects have been documented (Fogarty and Murawski 1998, Pauly *et al.* 1998) and the collapses of some fisheries (e.g Canadian Atlantic cod fishery), tremendous effort is being exerted towards understanding the wider effects of fishing and measuring them. Many indicators have been proposed to capture such effects, which all have their own merits and drawbacks, based on different scoring criteria (Rice 2000, Rochet and Trenkel 2003, Rice 2003, Shin *et al.* 2005, this thesis).

Multivariate clustering methods such as classification and ordination (Field *et al.* 1982) are very sensitive at detecting changes in community structure but they do not show whether the changes are in the direction of a climax community (presumably positive) or due to natural or human-induced disturbance (presumably undesirable or negative). The Abundance Biomass Comparison (ABC) method was initially proposed by Warwick (1986) as a technique for monitoring disturbance (mainly pollution effects) on benthic invertebrate communities by comparing dominance in terms of abundance with dominance in terms of biomass. Subsequently it has been applied in different regions and in most cases showed the expected changes in response to disturbance (Warwick *et al.* 1987, Agard *et al.* 1993). ABC curves have a basis in classical evolutionary theory of *r*- and *k*-selection. In undisturbed states, the community is expected to be dominated by *k*-selected species. As they are slow-growing and larger-sized they are dominant in biomass but not numerically, therefore the biomass curve lies above the abundance curve. With increasing disturbance the slow-growing species cannot cope and the system starts to be dominated by *r*-selected species (fast-growing, smaller in size and opportunistic) and the biomass curve will be below the abundance curve (Fig. 7.1). The difference between the two curves is given by the *W-statistic*, which represents the area between the two curves and takes a different sign depending on whether the biomass curve is above or below the abundance curve. A negative sign indicates that the biomass curve lies below the abundance curve and suggests a disturbed community. The ABC method takes into account the number of species included in the analysis (Warwick and Clarke 1994). An advantage of the method is that each curve for any area or time will indicate the status of the community without the need for a spatial or temporal control against which to compare the index, because the biomass is compared with the abundance for the same time and place (Clarke and Warwick 1994).

ABC curves have only recently been used in a few studies on fisheries (Bianchi *et al.* 2001, Blanchard *et al.* 2004). For example Bianchi *et al.* (2001) investigated whether there is evidence of disturbance in the Namibian demersal fishery. They found differences between the shelf and slope assemblages but without a clear temporal trend for the shelf community, but with an increase in the gap between the biomass and abundance curve for the slope community, though they have not shown the trend in *W-statistic*. Validity of the method therefore remains to be confirmed for fisheries.

This study attempts to assess the status of the South African south coast demersal fish community using ABC curves. A description of the fishery on this coast is given in Chapter 4.

7.2 Methods

Details of data source, spatial and temporal bound, and data standardization are the same as Chapters 4 to 6. The distribution of the number of trawl stations among the three depth strata, and environmental variable recorded are given in Table 4.1. All the survey catch data were extracted for each species where there are abundance data, corrected for sample weight and catch weight difference, standardized to 30-minute trawl duration and summarized into depth categories. Smale *et al.* (1993) found three demersal communities of fish and cephalopods on the south coast: an inshore community less than 100m depth; a shelf community 90m ÷ 190m depth, and; a shelf edge or upper slope community greater than 200m depth. Therefore catch data was summarized into the following depth categories: 0 – 100m, 101 – 200m, and 201 – 500m.

ABC curves were constructed and *W-statistics* calculated using PRIMER software (Clarke and Warwick, 1994) for depth groups and the aggregate of all depth ranges. Only species for which there is information on the numbers and weight caught are included. The number of species included in the analysis ranged from 17 (May 1988) to 72 (in April 1999 when for large number of species both abundance and biomass information were recorded). But this variable number of species included in the analysis is supposed not to affect the *W-statistic* as the calculation standardises the value of *W* by the number of species included in the analysis. Time series of *W-statistics* were assessed for significant trends over the period considered using non-parametric Spearman rank correlation R (Zar, 1999). The ABC curves and the *W-statistics* for the depth ranges 0 – 100m and 101 – 200m were calculated but not for the 201 – 500m depth range as there were only few species for which information on numbers and weight were available and this depth range was not sampled in all surveys (Table 4.1), but this depth range was included in the overall analysis for the south coast. For each of the two depth ranges (0 – 100m and 101 – 200m) separate ABC curves were plotted for each season but presented on the same graph. The autumn and spring data were not pooled to capture the influence of seasonal dynamics.

Longline fishing effort data for the period 1984 – 1988 were obtained from Japp (1989) while the rest were obtained from the Marine and Coastal Management (MCM) division of the South African Department of Environmental Affairs and Tourism (DEAT).

Calculation of *W-statistic* (Warwick and Clarke 1994, Magurran 2004)

$$W = \sum_{i=1}^{S}(B_i - A_i) \Big/ [50*(S-1)]$$

Where: S = the total number of species

B_i = percentage in biomass of species rank i

A_i = percentage in abundance of species rank i

Note: B_i and A_i do not necessarily refer to the same species as dominance in biomass and abundance may not be occupied by the same species in the community

Theoretically *W* takes values between +1 (when biomass is dominated by a single species and abundance evenly distributed among the species in the community), and -1 (when abundance is dominated by a single species and biomass evenly distributed among the species in the communities) (Clarke and Warwick 2001).

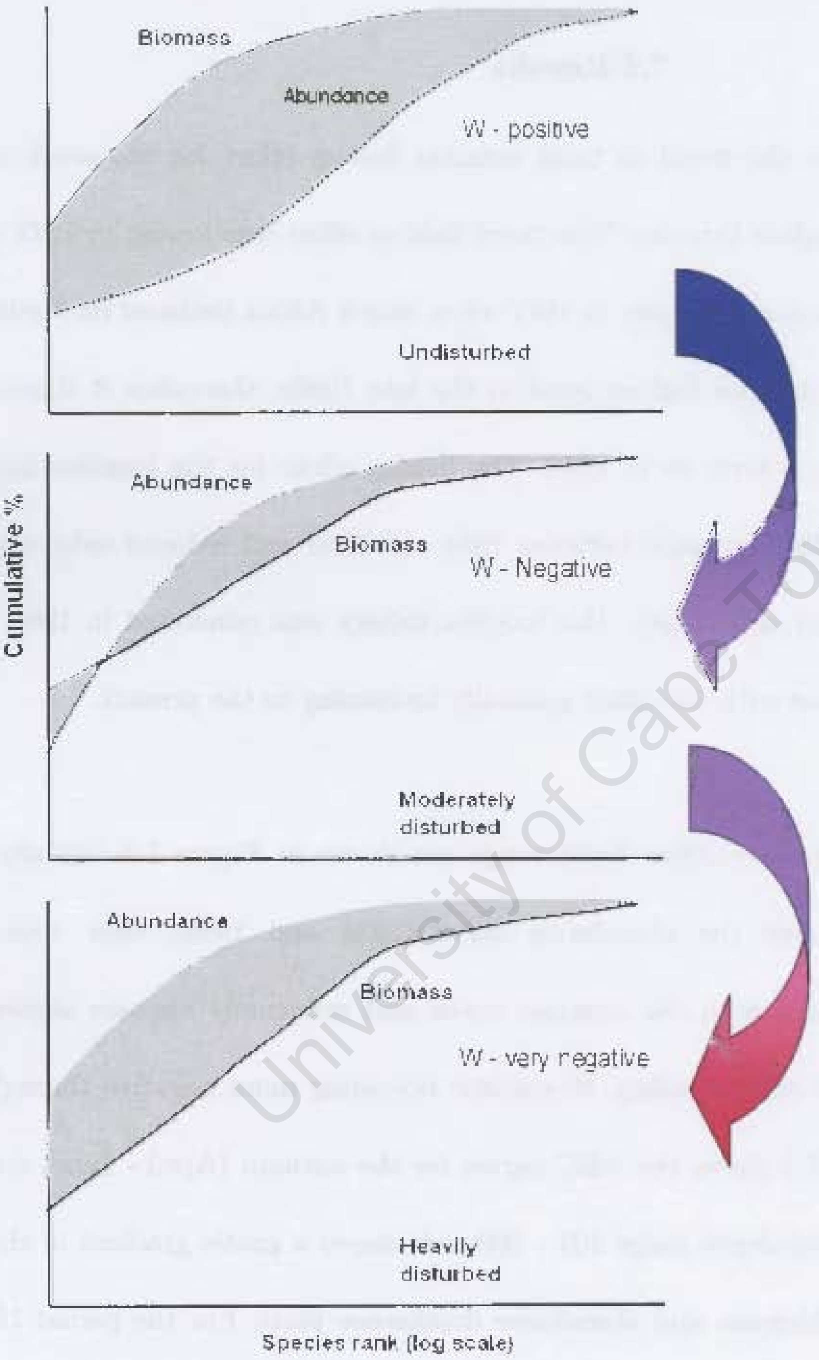


Figure 7.1. Theoretical ABC curves showing the pattern in the abundance and biomass of undisturbed, moderately disturbed and heavily disturbed assemblages (modified from Clarke and Warwick, 1994). *W* measures the area between the biomass and abundance curves.

7.3 Results

Figure 7.2 shows the trend in total nominal fishing effort for the south coast demersal trawl and longline fisheries. The trawl fishing effort was lowest in 1978 after the ban of foreign distant-water fleets in 1977 when South Africa declared its Exclusive Economic Zone. It reached its highest level in the late 1980s; thereafter it fluctuated and declined to the same level as in 1978. The fishing effort for the longline fishery, when it targeted kingklip, increased between 1984 and 1986 and reduced substantially in 1988 when the fishery was closed. The longline fishery was reinstated in 1994, this time targeting Cape hake with the effort generally increasing to the present.

ABC plots for the 0 – 100m depth range are shown in Figure 7.3. Initially the biomass curve was above the abundance curve (1988 and 1989); over time the abundance curve overlaps with the biomass curve and eventually appears above the biomass curve with the corresponding *W-statistic* becoming more negative throughout the time series. Figure 7.4 shows the ABC curves for the autumn (April - June) cruises from 1988 to 2003 for the depth range 101 - 200m. It shows a gentle gradient of change in the patterns of the biomass and abundance dominance plots. For the period 1988 - 1993 the biomass curve lies above the abundance curve and has a positive *W-statistic* (suggesting a relatively undisturbed state, according to the theory of *r*- and *k*-selection, Warwick and Clarke, 1994). Thereafter the abundance and biomass curves cross each other once or twice over the length of the curves and *W-statistic* is negative except for 2003 (Fig. 7.5). The *W-statistic* is significantly negatively correlated with year (Spearman R = -0.54, $p < 0.05$, n = 21) considering the value of *W-statistic* for both seasons. The ABC curves for the depth range of 0 – 100m follow a similar pattern (Fig. 7.3) and the corresponding *W-statistic* becomes more negative over the period 1986 – 2003 (Spearman R = -0.68, $p < 0.05$, n = 21).

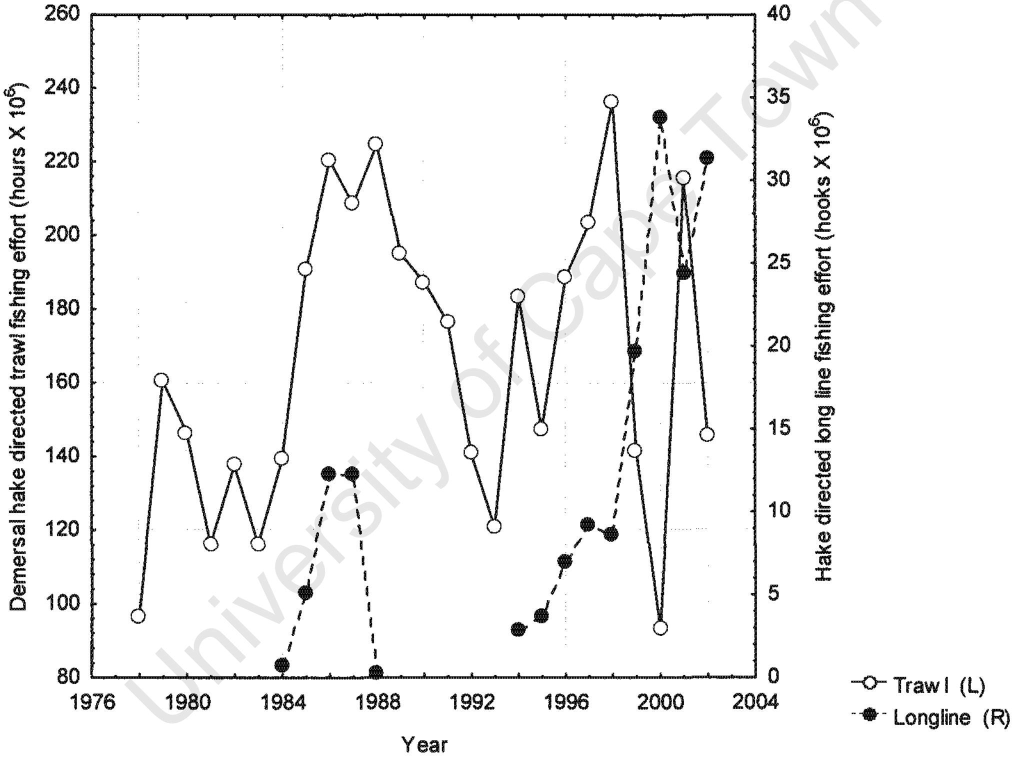


Figure 7.2. Long-term trend in the total fishing effort of the south coast demersal trawl fishery and longline fishery (From MCM data and Japp (1989)).

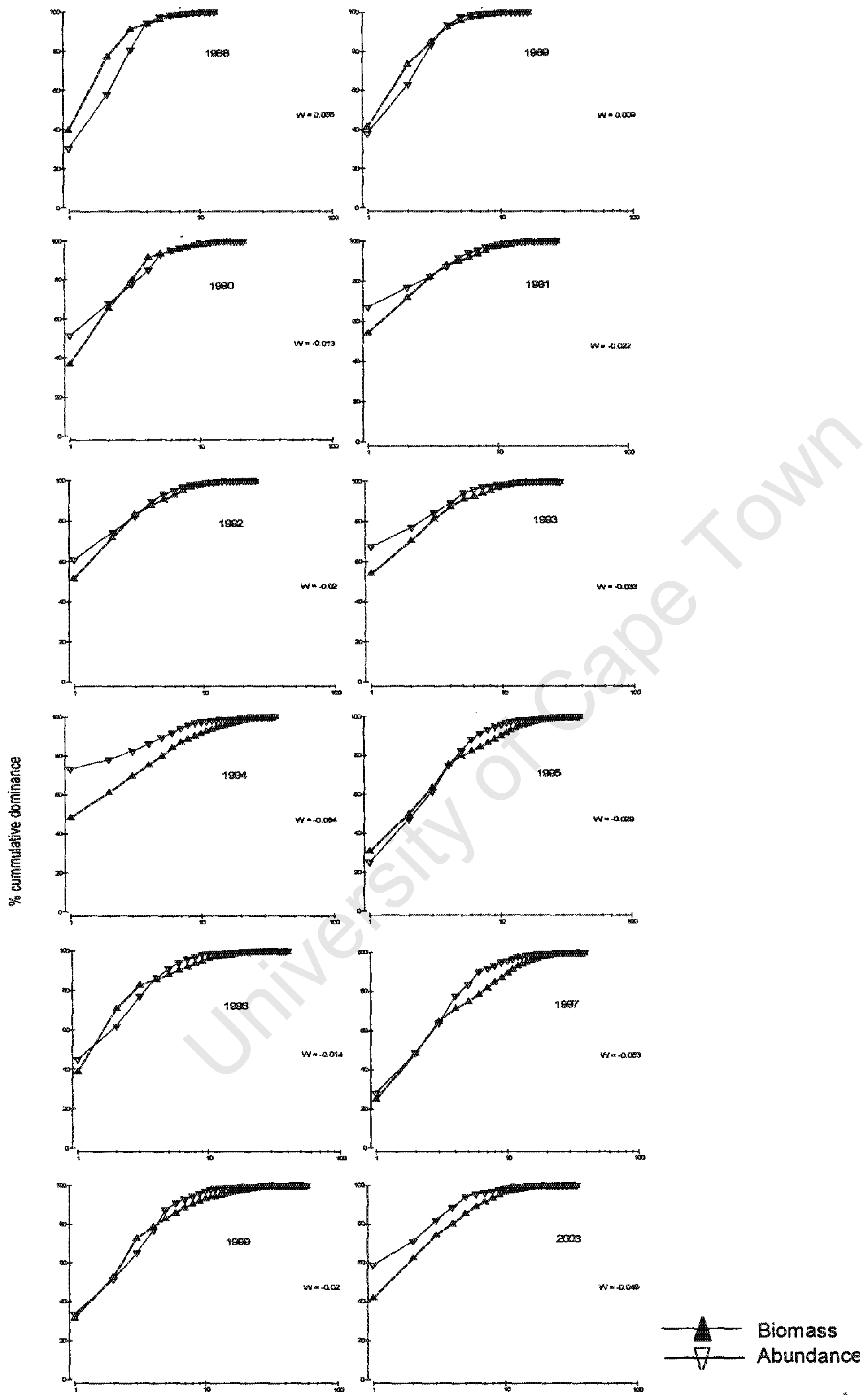


Figure 7.3. ABC plots of 0 – 100m depth range for the demersal fish community of the south coast. Plots are for surveys conducted in autumn.

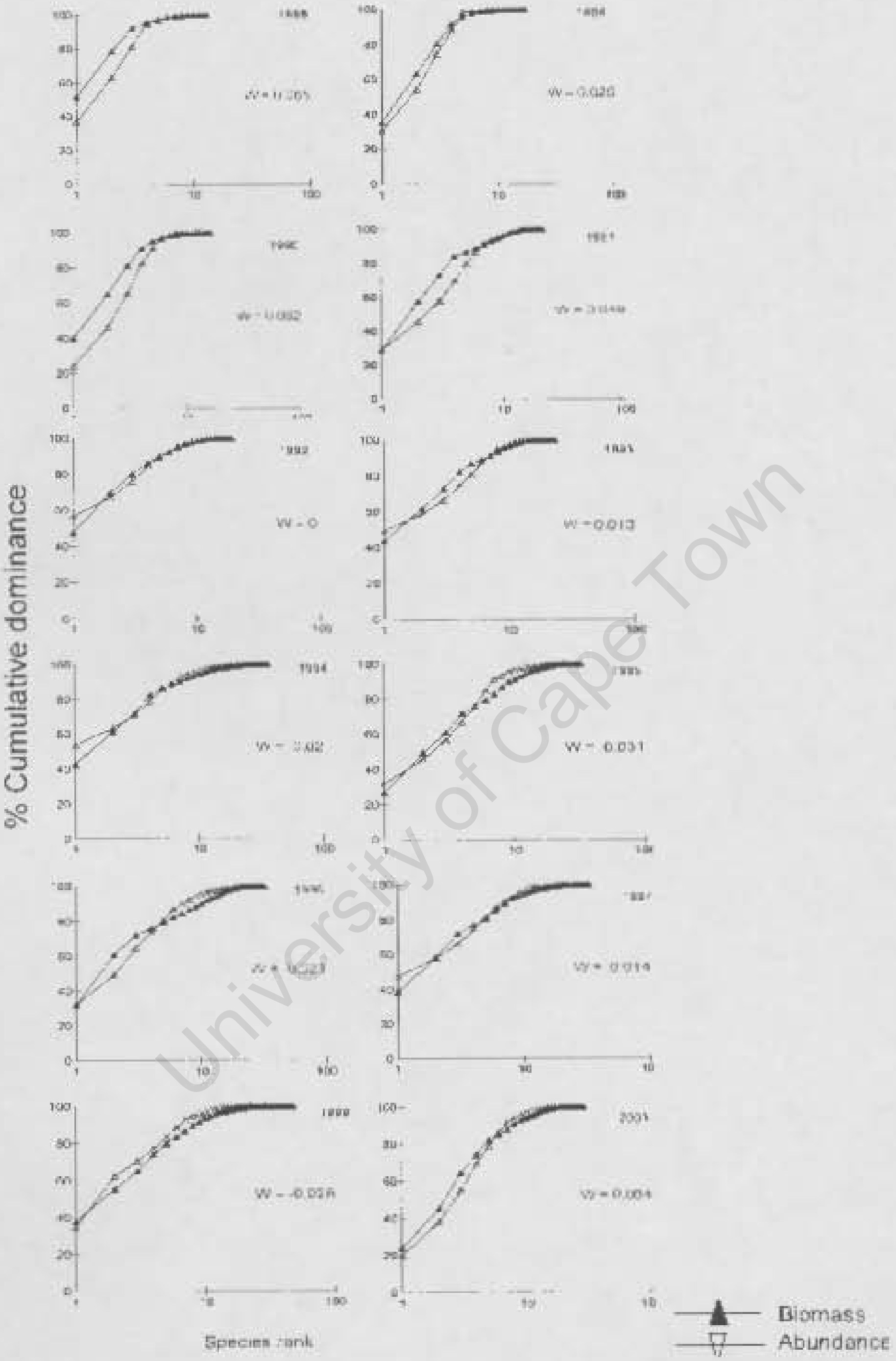


Figure 7.4. ABC curves for the 101-200 m depth range of the demersal fish community on the south coast of South Africa, 1988-2003.

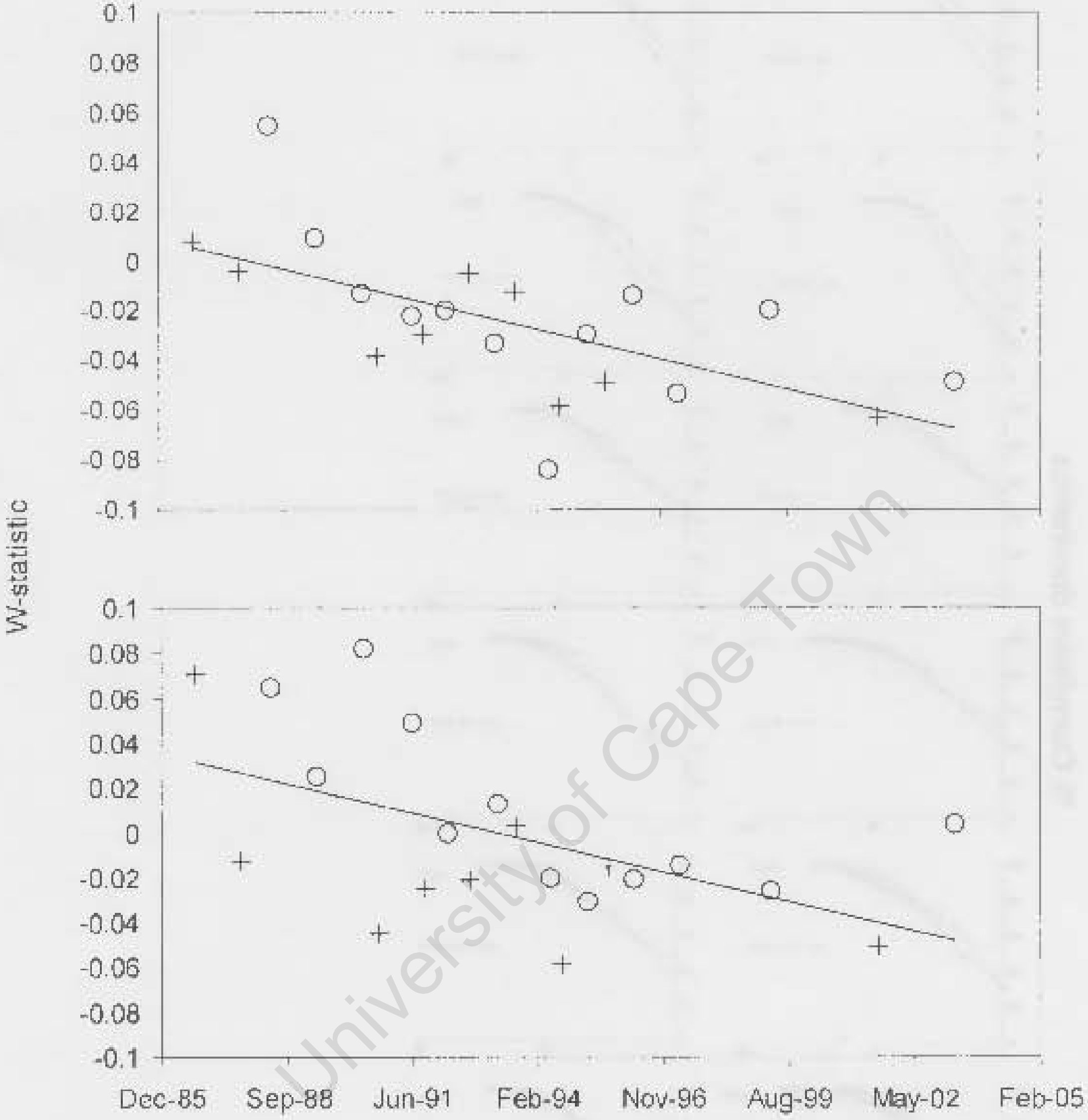


Figure 7.5. Trend in the *W-statistic* for the 0 – 100m (top panel) and 101 – 200m (bottom panel) depth ranges of the south coast demersal fishery autumn (open circles) and spring (crosses) over the period 1986 - 2003. Spearman R for the 0 – 100m, R = -0.54; for the 101 – 200m R = -0.68. Values of R are for both seasons combined. Regression line to show direction of trend.

Figure 7.6 shows the temporal trend in the *W-statistic* for the whole south coast and for both seasons (autumn and spring). The results are generally similar to those for each depth range and the two seasons follow the same pattern. There is a significant negative correlation between *W-statistic* and year (Spearman $R = -0.66$, $p < 0.05$, $n = 21$).

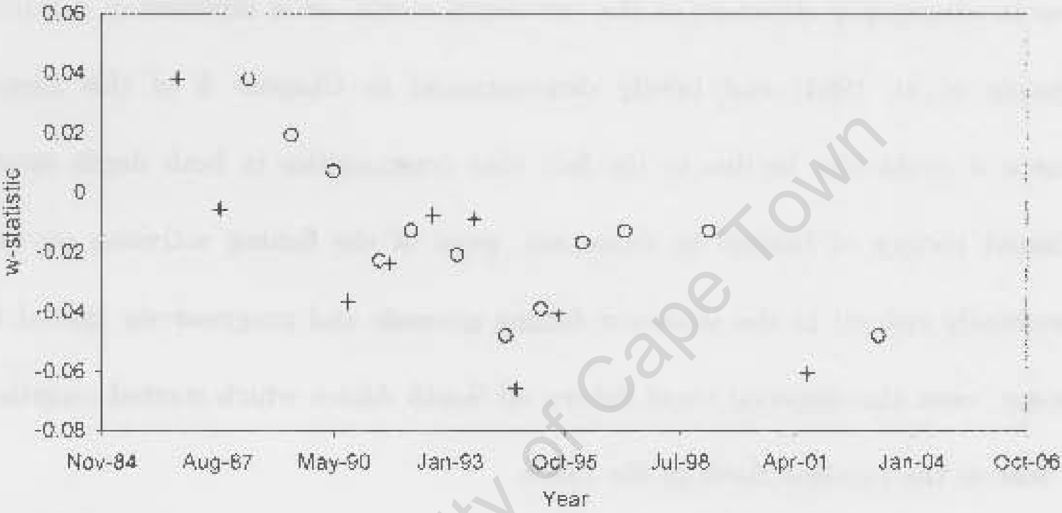


Figure 7.6. Trend in the *W-statistic* for the whole south coast demersal fishery for autumn (open circles) and spring (crosses) over the period 1986 - 2003. Spearman $R = -0.66$, R is computed for both seasons combined.

7.4 Discussion

The trends in the *W-statistic* for the whole south coast and the two depth strata show some important points. First the effect of season such that though the trend in autumn and spring is relatively the same, towards more negative values of *W-statistic*, the values do vary. Second large differences in *W-statistic* are observed between the first few years in the time series and the rest of the years where only gradual declines are observed, except for 1994. The other difference is the response between the two depth strata; a gradual change happened in the 0 – 100m depth stratum whereas rapid change in *W-statistic* was observed in the 101 – 200m depth stratum. This difference between the two depth strata could be a reflection of the differences in community structure of the two depth strata, as is reported in previous study (Smale *et al.* 1993) and briefly demonstrated in Chapter 5 of this thesis. Furthermore it could also be due to the fact that communities in both depth strata have different history of fishing. In retrospect, most of the fishing activities on this coast historically started in the shallower fishing grounds and progressively moved to deeper water, even the demersal trawl fishery off South Africa which started targeting Agulhas Sole on the Agulhas Bank in the 1890s.

The results of the ABC curves and their corresponding *W-statistics* at different scales (each depth group separately and aggregating depth groups) suggest that the south coast demersal fish communities are becoming increasingly stressed, following the classification of the ABC plots by Warwick (1986). This gradient of community change towards a more stressed state, as illustrated by the temporal trend in *W-statistic*, may be attributed to the change in fishing strategy and pressure from the long established demersal trawl fishery and the newly introduced demersal longline fishery. This fishery is extremely size selective (Japp 1989). Overall, the possible impact of chronic environmental damage affecting demersal assemblages over a much longer period cannot be ruled out. Observed changes based on the ABC curves could also be related to the finding of the previous chapters: Chapter 4, changes in the size structure of the fish community both at the level of the whole south coast and in two depth stratum 0 – 100m and 101 – 200m; Chapter 5, changes in community structure in both the autumn and spring seasons; Chapter 6, changes in diversity of the demersal fish community where an increase in diversity and decrease in dominance was observed for the whole south coast.

A large flux of recruit of dominant species could bias ABC analyses and lead to a reduction in the value of *W-statistic*; however, this is unlikely to be the case here because the trend continues for over 6 years. Nevertheless, complementary results from other indicators, which could be purely taxonomic or ataxonomic, would help confirm the observed changes, as it seems from results of previous chapters. According to Warwick and Clarke (1994) the response of ABC curves is mainly due to shifts in phyletic proportions in the benthic community and changes in the relative proportion of abundance and biomass of species of polychaetes. In fisheries ABC may respond to changes in the relative abundance of large and small species in communities and/or changes in size composition.

The application of the ABC method to the management of multi-species fisheries would be better justified if it were applied to simulated theoretical fish communities, with different life history traits, subjected to different fishing and environmental perturbations. Application of the method to different fisheries with different histories of fishing around the world would also help in understanding the response of the ABC method and in establishing a safe range of *W-statistic* within its theoretical range of -1 to +1. Some of the applications of the method in fisheries context include that of Bianchi *et al.* (2001) for the demersal fish community off Namibia; Blanchard *et al.* (2004) for fish and benthic invertebrates of the Bay of Biscay, France; and Jouffre and Inejih (2005) for the demersal fish community off Mauritania. The application of the method off Mauritania clearly shows that the method is robust to different levels of taxonomic aggregation; species, genus, and family (Jouffre and Inejih 2005), further the study also highlights the fact that with various levels of aggregation the value of *W-statistic* varies but the temporal trend still remains. Thus, due to the limited application of the ABC method in fisheries, inference based on the direction of the trend in the *W-statistic* is a much better approach than relying on the actual value. Furthermore, the result of this study and that of the study off Mauritania suggests that at present relying on the direction of the response is better as it is difficult to associate the actual values of the *W-statistic* with the limit reference state or target reference state of the community in question. Therefore discussion regarding observed trends in *W-statistics* for the demersal fish communities of the south coast is based on reference direction. In conclusion results of this study suggest that the ABC method may provide a useful guide for an Ecosystem Approach to Fisheries, having a sound theoretical basis in *r-* and *k-* selection and needing only abundance and biomass data to derive ABC curves.

Chapter 8 Exploring the effects of non-uniform distribution of fishing mortality on fish communities: an individual based modelling approach

Abstract

The current increase in interest towards an ecosystem approach for the management of fisheries results in the wider use and development of ecosystem models. These models are used for understanding the response of ecosystems or some of their components to different sources of disturbance, such as heavy fishing. In this study the individual-based model (IBM) Object-oriented Simulator of Marine Eco-system Exploitation (OSMOSE, the acronym is derived from the French name of the model) is used to investigate alternative spatial implementations of fishing mortality (uniform and spatialized fishing mortality). In both implementations, the overall variability and trends in biomass of the system with increasing fishing mortality are similar but the absolute biomass of the species and of the system differs between the two scenarios. The response of the modelled species and the whole system to the establishment of Marine Protected Areas (MPAs) was investigated by simulating the introduction of three particular MPAs separately or simultaneously. Although some differences in the response of the species to the different MPAs were observed, overall the introduction of MPAs results in the increase of the relative biomass of large predatory species and a decline in the biomass of potential prey and/or competitor species. This simulation study shows that consideration of trophic interactions is necessary when introducing MPAs, with indirect effects that may be detrimental to some species.

Key words: Individual Based Models, spatial fishing, Marine Protected Areas, southern Benguela.

8.1 Introduction

8.1.1 The use of ecosystem models for an Ecosystem Approach to Fisheries

The recent shift in focus from single-species towards a multi-species or ecosystem approach in the management of fisheries is associated with various initiatives to facilitate its timely and appropriate implementation. These mainly include developing indicators, understanding processes, structures, and functions of marine ecosystems that are directly or indirectly affected by the overexploitation of certain resource components and by habitat damage. Although most of the current evidence on the effects of heavy fishing comes from retrospective data analyses of fisheries data and some experimental fishing activities, various modelling approaches have helped in understanding possible future consequences of current fisheries management policies.

Ecosystem models have been developed for different aquatic systems, with different scopes and degrees of complexity. These include from the simplest to the more complex versions of, among others, biogeochemical models (e.g. Murray 2001, Fulton et al. 2004a), mass balance models (Pauly et al. 2000), multispecies stock assessment models (Hollowed *et al.* 2000) and individual-based models (e.g. Shin and Cury 2001). The main focuses of these models are: (a) parts of the life-history of target species (recruitment), (b) trophic interactions, (c) biogeochemical cycles, and various combinations of the above three. Ecosystem models are used for better understanding of past dynamics and forecasting of future consequence of various types of disturbance on the components of the system (different levels of nutrient load, and overexploitation of components of the ecosystem). As all models are approximations of reality, they are mainly designed to reflect some specific aspect of the modelled system (Gurney and Nisbet 1998), thus there are many ecosystem models designed to understand different aspects of ecosystems. A review of the various ecosystem models, in the context of fisheries, is given by Hollowed et al. (2000). They classified various ecosystem models according to three regulatory processes and their interaction: predation, competition, and environmental impact. In the recent move towards integrating ecosystem process into fisheries models, different modelling methods emerge, with an increasing use of Individual Based Models (IBMs). Some of the areas where IBMs are successfully applied in marine ecosystems include the understanding of recruitment dynamics of various fish species (Hinckley et al. 1996, 2001, Parada et al. 2003, Miller 2006), the migration patterns of schooling fish species (Huse et al. 2002). These IBMs of early life stages of marine fishes are used coupled with biogeochemical and hydrodynamic models in order to identify the factors controlling fish recruitment (retention, nursery ground, food availability, and predation). Integrating the whole life cycle of fish, OSMOSE is another IBM developed recently, with emphasis on trophic interactions (Shin and Cury 2001, 2004). It is a multispecies model devoted to assess the indirect effect of fishing through trophic interactions and allows one to calculate various types of ecosystem indicators.

The impetus behind the steadily increasing use of IBMs, other than the increase in computing power and storage capacity, is that they allow one to address various ecosystem processes at different scales, especially at the level of individual fish (Huston et al. 1988). These include the consideration of variability among individuals, local interactions, complete life cycle of an individual, an individual's history, and individual behaviour adapting to its changing internal and external conditions (Grimm 1999, Grimm and Railsback 2005). IBMs also allow researchers to study how system level properties emerge from adaptive behaviour of individuals and how the system affects the individuals (Grimm and Railsback 2005).

8.1.2 Spatially variable fishing mortality

As mentioned above, with the increasing interest towards whole ecosystem considerations in the management of living aquatic resources, there has been a variety of ecosystem models developed to aid in the understanding of the dynamics of marine ecosystems and the indirect ecosystem effects of fishing. To the variety of these ecosystem models, there corresponds a variety of ways to represent species interactions and life history processes (e.g. growth, mortality, predation), which has consequences for the simulation of the modelled system (Murray and Parslow 1999). In addition, the representation of the above-mentioned processes in a spatially explicit manner in ecosystem models has been demonstrated to be of crucial importance in capturing the dynamics of ecosystems (Fulton et al. 2004b, Gribble 2004).

Spatial issues in ecosystems are a major focus in a number of ecological studies, mainly because space in all its aspects (structural heterogeneity, resolution, and extent) affects the structural and functional organizations of the biota in an ecosystem. Also ecological or physical processes operate at specific spatial scales so that choosing appropriate spatial scales of analysis is crucial to detect interactions and to avoid amplified or exaggerated signals. The spatial heterogeneity of a habitat affects a number of ecological processes at different levels of organization (population dynamics affected by the patchiness in food availability; at the community level trophic interactions are conditioned by the spatial co-occurrence of predators and prey) so that mortality or survival of marine biota varies spatially over the range of the population, community or ecosystem considered. There is patchiness in the resource in an environment and also patchiness in the amount, frequency, and type of stress applied to an ecosystem. This stress includes those disturbances from natural phenomena, abiotic (waves, storms, currents, climate change) or biotic in nature (trophic interactions, competition, invasive species), and stress of anthropogenic origin (pollution, overfishing).

This study focuses on the direct and indirect consequences of overfishing, with consideration of spatial patchiness in the fishing mortality on the various components of the ecosystem upon which the pressure is exerted. In addition to overall effort reduction, introduction of spatial management strategies, through the implementation of “no-take” zones of various size, is one of the measures to avoid or reduce serious consequences of overexploitation, (Gell and Roberts 2003, Roberts et al. 2005). Stefansson and Rosenberg (2005) investigated the role of different control measures in fisheries management (quotas, effort limitation, and protected areas). They used a variety of performance measures to assess the consequence of introducing each of the control measures individually and in combination. They observed that the use of the control measures in combination (especially catch quota control in combination with closed areas) gives the best result, in terms of reducing the risk of stock collapse and maintaining both the short term and long term economic performance, as compared to their application in isolation. The choice of the size and location of no-take zones is crucial to achieve the management objectives and benefits. Furthermore, various simulation studies have demonstrated the significance of considering trophic interactions. Various ecological aspects have to be considered; mobility of the species, biodiversity within an area, spawning ground, and nursery area. The consequences of the implementation of "no-take" zones individually and as a network can be investigated through a modelling approach. The prediction of ecological responses is not trivial when considering complex multispecies assemblages, and requires systematic exploration of indirect and non-linear effects on all species considered, resulting from species interactions, migration patterns and life histories. Among the existing multispecies models in fisheries science, the OSMOSE model allows one to account for the spatial dynamics of the fish community (Shin and Cury 2001). It is an individual-based model with the effective unit being a super-individual (referred to as a fish school) characterized by key life history traits (size, reproductive output, etc.) and interacting with its local environment. From such interactions at the individual level with some prescribed rules for basic biological processes, emergent properties appear at different hierarchical levels of biological organization (population, community, and ecosystem). OSMOSE is spatially explicit with size-based opportunistic predation as a main structuring process (Fig 8.1), provided that there is spatio-temporal co-occurrence of the predators and their prey (Shin and Cury 2001). Thus each individual can be a prey or predator depending on its size and the size of the fish with which it is interacting. OSMOSE has been used previously in the Southern Benguela ecosystem in two different contexts. The first aimed at conducting a cross comparison with the Ecopath-Ecosim model for the system (Shin et al. 2004) and reported reasonable agreement when simulating the effects of fishing on the structure and function of the Southern Benguela system. The second application aimed at investigating the sensitivity of different indicators to fishing intensity (Travers et al. 2006). In the existing model, mortality due to fishing is assumed to be uniform throughout the simulation grid of the model.

This study mainly intends to investigate the response of the modelled system to a heterogeneous spatial distribution of fishing mortality, as measured by the spatial distribution of different indicators of the structure and function of the fish community. Furthermore the implication of the introduction of newly proposed no-take zones will be explored through the sequential and simultaneous introduction of the no-take zones. It is expected that localized effects (spatially variable fishing mortality) of fishing will be manifest in the structure of the community through changes in the size structure of the fish community or individual species. In addition such heterogeneous distribution of fishing mortality is expected to affect community organization.

8.2 Methods

8.2.1 The model: OSMOSE

A short description of the OSMOSE model is given in the following paragraphs. Written in Java programming language, the OSMOSE model includes a hierarchical structure of model classes corresponding to those in an ecosystem. The model includes three biological classes; school, cohort, species, and two classes representing the spatial domain of the ecosystem: cell, and grid. This hierarchical structure allows features of the system to be assessed at different levels in the hierarchy (for example size, abundance, or biomass can be tracked at the population and community level, and locally in sub regions). The model time step is 6 months. Reproduction and fishing occur once a year in the model. The following biological processes are invoked in the order as outlined in Figure 8.2. The structure and details of the model have been described in previous works (Shin and Cury 2001, 2004, Travers et al. 2006), this chapter will provide a brief note of the processes. The nature of trophic interaction that OSMOSE is based on: size structured predation process is given Figure 8.1.

8.2.2 Modelled Biological processes

Carrying capacity constraint

The maximum biomass of non-piscivorous fish in the model corresponds to the carrying capacity constraint. Non-piscivourous fish include egg, larval and juvenile stages of piscivorous fish and all stages of forage fish. At the beginning of each time step and in each cell of the grid the biomass of non-piscivorous fish is compared to the carrying capacity and if the biomass exceeds that of the carrying capacity then it will be reduced proportionally. Additional mortality is applied to the eggs and the larval stages of fish to account for the higher natural mortality these stages suffer, in fact this parameter is used for calibrating the model (Shin et al. 2004a).

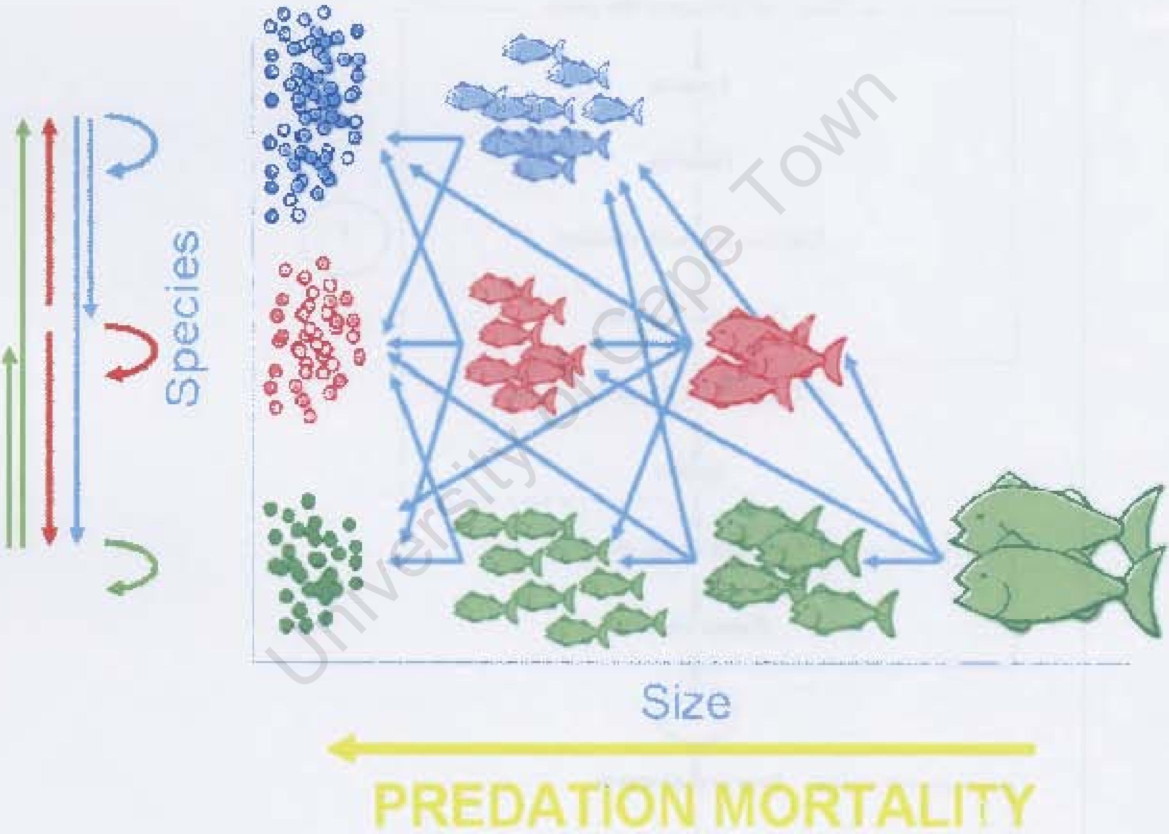


Figure 8.1. Schematic diagram of trophic interaction in a size structured ecosystem: body size and the interwoven marine food web. (Courtesy of Dr. Yunne J. Shin).

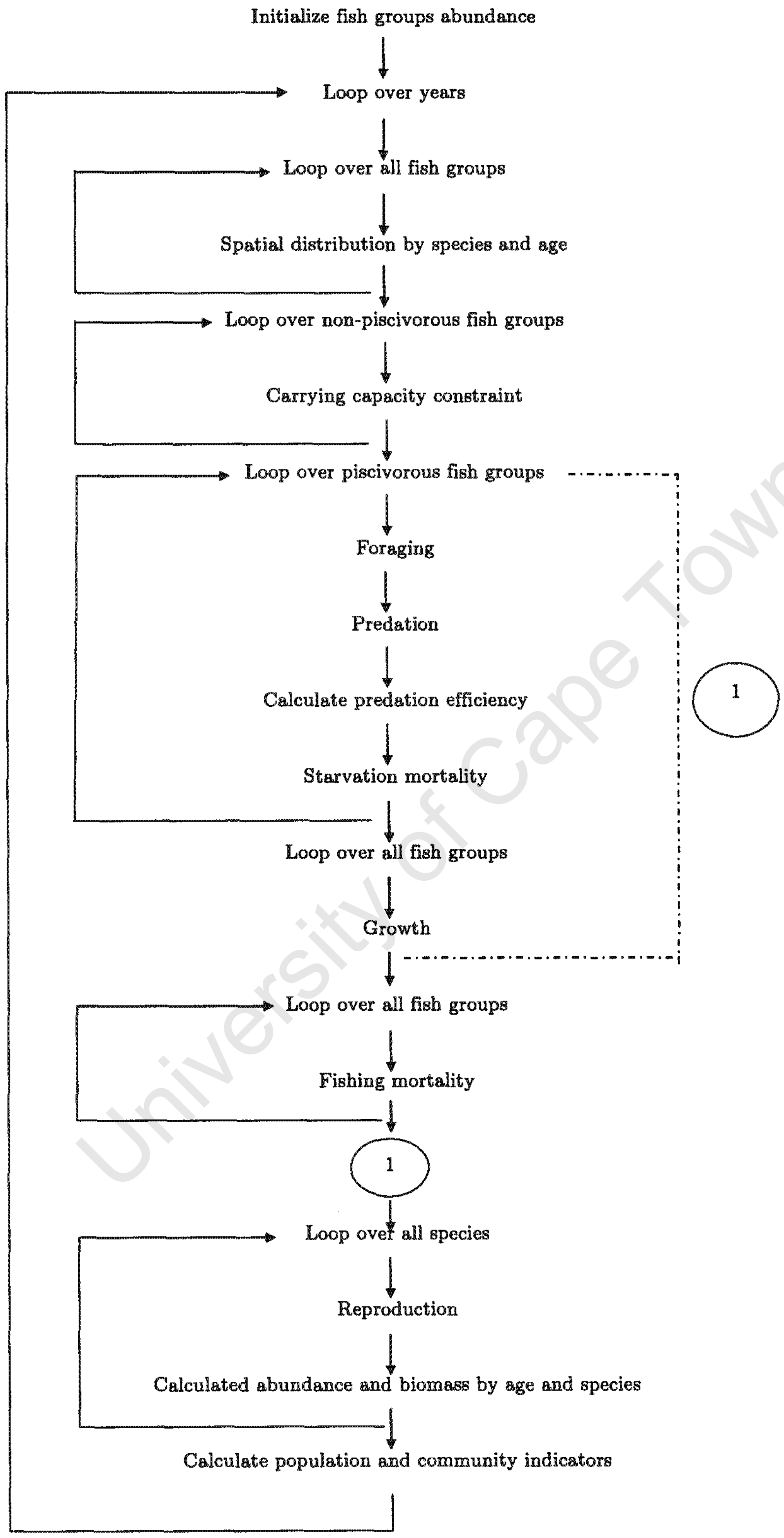


Figure 8.2. Process flow chart for OSMOSE according to the order of execution in the model. Modified from Shin and Cury (2004).

Foraging and predation

Both foraging and predation processes are applied to the piscivorous groups of the community. Foraging represents the movement of fish toward neighbouring cells with high potential prey biomass. Potential preys are defined according to their size relative to that of a predator. Then predation in OSMOSE occurs once the following two criteria are satisfied; first there must be a spatio-temporal co-occurrence of a predator and its prey as such a predator only affects those in its vicinity, second the predator-prey size ratio must exceed the critical ratio 3.5 estimated from FishBase. Once predators exerted predation mortality on their prey, a predation efficiency is calculated, as the ratio of the amount of ingested food by a predator to the amount required to fulfil its vital functions (Shin and Cury 2001).

Growth

The mean annual growth rate of fish of at each age is calculated using the von Bertalanffy growth model. This mean growth rate is thereafter adjusted to take into account the amount of food ingested in relation to the critical ration for maintenance, so that the growth rate in length increases linearly with predation efficiency when the predation efficiency is greater than the maintenance threshold. This threshold is calculated as the ratio of the annual maintenance ration over the annual mean ration, which is around 0.57. If the amount ingested is less than the critical value then the growth rate will be set to zero (Shin and Cury. 2001).

Starvation mortality

As the food ration drops below the threshold, or as predation efficiency decreases, the mortality due to starvation increases. When the amount of ingested food is too low to fulfil maintenance requirements, then the starvation mortality rate is calculated as a linear negative function of predation efficiency.

Fishing mortality

Mortality due to fishing is applied at the end of the first 6 month period. In the previous version of the OSMOSE model, the theoretical number of fish removed from each school is computed using the exponential decay model of the type:

$$N_{F,a,s} = N_{a,s} * (1 - \exp(-F_s)) \quad \text{with } a \in [a_{r,s}, a_{\max,s}]$$

Where: $N_{F,a,s}$ = Total number of fish removed from the cohort of age a, of species s due to fishing

$N_{a,s}$ = numbers of individuals in the cohort of age a of species s

F_s = fishing mortality rate for species s

$a_{r,s}$ = age of recruitment of species s

$a_{max,s}$ = longevity of species s

Once $N_{F,a,s}$ is calculated it will be equally distributed among all schools in each cohort above age of recruitment to the fishery, regardless of the spatial location of each school. Thus each school has equal chance of mortality regardless of its spatial location across the spatial domain of that cohort.

Adding to the existing model structure, I computed the possibility of taking into account a spatial distribution of fishing mortality. This is achieved by imposing the observed relative distribution of fishing effort from two fisheries using different gears: the small pelagic purseseine fishery and the hake-directed demersal trawl fishery (Figs. 8.3 and 8.4). The relative spatial distribution of the fishing effort is assumed to approximate reasonably the relative distribution of mortality due to fishing. The relative value of fishing effort in each grid cell is calculated as the ratio of the total number of hours and average hours; this was done for the 1990s period. This value is then used as a weighting in the calculation of the total number of removed individuals in each cell. Thus regions with higher relative fishing effort tend to account for most of the mortality due to fishing as compared to less intensively fished regions. The weighting from the pelagic fishery effort (Fig. 8.3) is applied to the following species: anchovy, sardine, round herring, lanternfish, and lightfish; whereas the weighting from the demersal fishery (Fig. 8.4) is applied to: shallow water hake, deep water hake, silverkob, kingklip, and horse mackerel.

Reproduction

Each species in the model reproduces once at the end of each time step. The number of eggs spawned by each species is calculated using the relative fecundity parameter of each species, the spawning biomass and a 1:1 sex ratio. The recruitment level is an output of the model once the eggs and larval stages have undergone explicit predation and starvation mortalities. Details of model formulation and existing structure of OSMOSE are provided in Shin and Cury (2001, 2004).

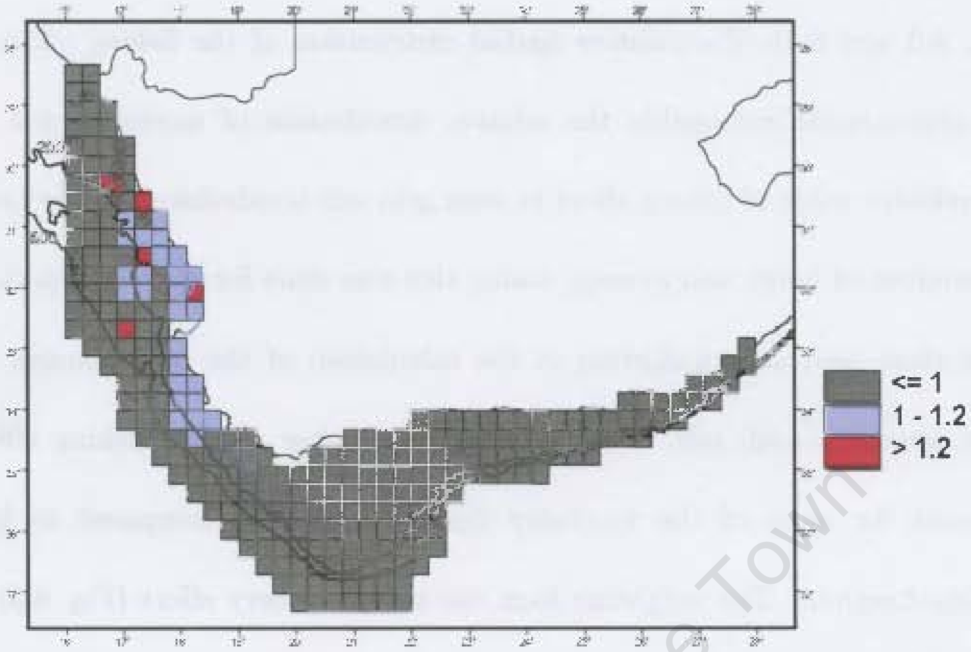


Figure 8.3. Distribution of relative fishing effort (hours) for the pelagic purseseine fishery for the 1990s (Data courtesy of MCM). The value in each grid cell is expressed as a ratio of the average of all cells. The size of each grid is of 18 nautical miles.

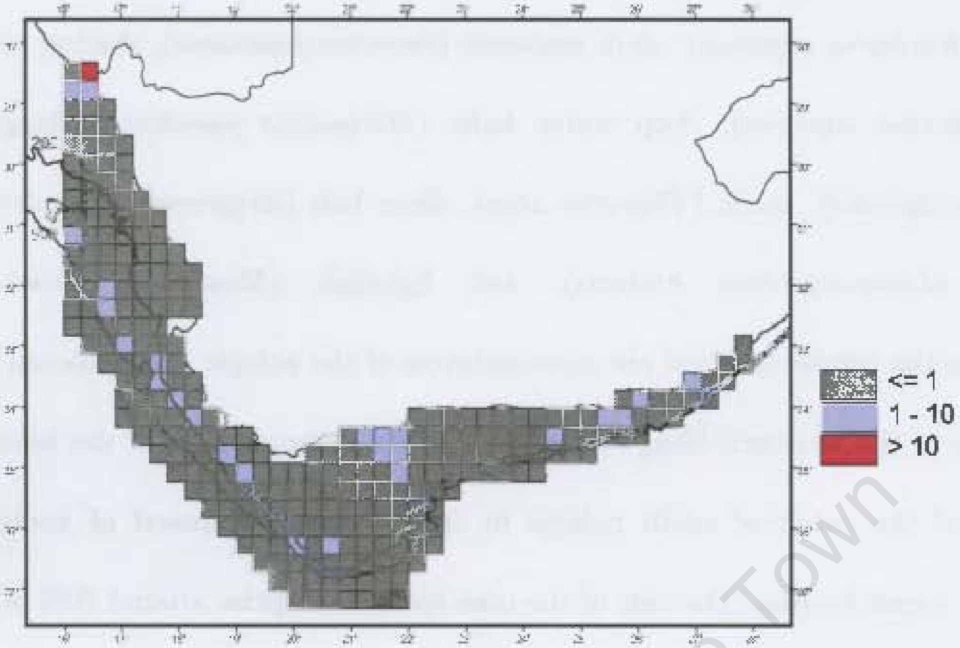


Figure 8.4. Distribution of relative fishing effort (hours) for the demersal hake directed trawl fishery for the 1990s (Data courtesy of MCM). The value in each grid cell is expressed as a ratio of the average of all cells. The size of each grid cell is 18 nautical miles.

8.2.3 Model parameterization

The selection of the species to be included in the model was based on the following justification; the selected species represent around 76% of the biomass in the system and around 94% of the total catch, as reported from previous studies using the Ecopath with Ecosim approach (Shannon *et al.* 2003). In addition Shannon *et al.* (2003) reported that these species account for 84% of the total consumption by the different groups in the model and for 72% of consumption of the production of small pelagic fishes. The modelled fish community includes the following 12 species in the southern Benguela: anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), round herring (*Etrumeus whiteheadi*), horse mackerel (*Trachurus trachurus capensis*), chub mackerel (*Scomber japonicus*), shallow water hake (*Merluccius capensis*), deep water hake (*Merluccius paradoxus*), kingklip (*Genypterus capensis*), snoek (*Thyrsites atun*), silver kob (*Argyrosomus inodorus*), lanternfish (*Lampanyctodes hectoris*), and lightfish (*Maurolicus muelleri*). Furthermore, the species selected are representative of the pelagic and demersal fish communities in the southern Benguela ecosystem: for example 97% of the biomass and 99.9% of the catch of small pelagic in the 1990s is composed of anchovy, sardine, and round herring. The rest of the nine species comprise around 70% of the biomass of commercially important demersal species in the system, as reported from the west and south coast biomass survey in 2001 and 90% of the demersal commercial catch during the period 1992 – 1999 (Travers *et al.* 2004, 2006). All the biological parameters of the twelve species that are used in input to the model as well as the species spatial distributions that account for life history migration patterns on a 6-monthly basis are obtained from Travers et al. (2006). The various input parameters of each species in the model are given in Table 8.1.

Table 8.1. Input parameters of the model for each of the species modelled

	Reproduction		Survival				Growth				Initialization Biomass
	φ eggs.g⁻¹	a_mat years	a_max years	A_sr years	M_adult years⁻¹	F year⁻¹	L∞ cm	k year⁻¹	t₀ years	c g.cm⁻³	1990s tons
Anchovy	4000	1	5	1	0.403	0.23	14.6	1.37	0.05	0.007	796143
Chub mackerel	300	3	6	2	0.143	0.07	68	0.237	0.99	0.005	100000
Shallow water hake	900	4	15	3	0.228	0.23	270.6	0.039	-0.73	0.005	398300
Deep water hake	900	4	15	3	0.174	0.33	219.4	0.049	0.914	0.005	647900
Horse mackerel	250	3	6	2	0.314	0.56	94.5	0.163	0.65	0.009	532900
Kingklip	600	5	24	3	0.182	0.11	180	0.105	0.06	0.001	11583
Lanternfish	646	0.5	2	1	0.226	0.0003	7	1.86	0.01	0.008	1128820
Lightfish	334	0.5	2	1	0.226	0.0003	6	1.15	0.01	0.008	1126520
Round herring	750	1	5	1	0.208	0.04	30.1	0.71	0.28	0.009	1358720
Sardine	2400	2	10	1	0.355	0.16	26	0.26	-1.5	0.009	480000
Silver kob	150	2	25	3	0.226	0.191	116	0.12	-1.47	0.007	10400
Snoek	130	3	10	2	0.132	0.25	115.3	0.294	-0.1	0.018	74140

8.2.4 Spatial domain of model

The spatial bounds of the modelled system cover the whole southern Benguela ecosystem from around the Orange River (25° 33' S, 16E) in the north to east of East London (37° 33' S, 28E) (Figs., 8.3, 8.4, and 8.5). In addition, locations of proposed MPAs are highlighted in the Fig. 8.5 (Dr. Colin Attwood MCM, pers. comm). The overall spatial domain covers almost the same area as Figure 2.1. This spatial grid comprises 542 square cells of 18 x 18 nautical miles in size.

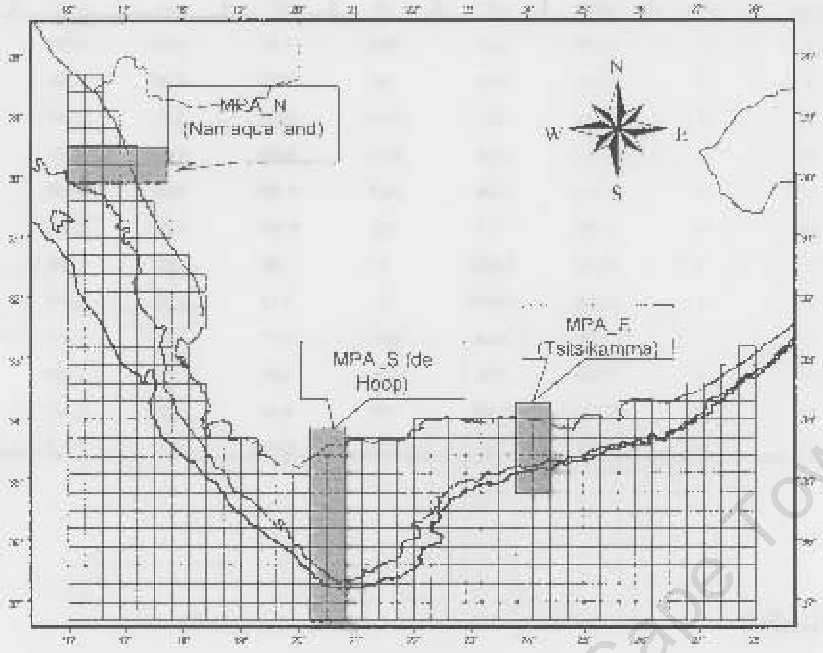


Figure 8.5. Map of South Africa showing the spatial domain and cells of the OSMOSE model between (25° 33' S, 16 E) and (37° 33' S, 28 E). The location of proposed no-take MPA zones are shown in grey shading.

8.2.5 Model runs: Calibration and reference state

Before running any of the simulation experiments, the model was calibrated to a reference state, in this case the 1990s (1990 – 1999). The calibration of the model is done by estimating the additional larval mortality parameters, and using the biomass of each species as a performance measure. This is done using a genetic algorithm which was developed specifically (Versmisse et al. 2007 submitted to ecological modelling). The target biomasses are the same as those used by Travers et al. (2006), biomasses of modelled species for the 1990s are shown in Table 8.1.

8.2.6 Analysis of model output

Model outputs were analysed qualitatively through comparison of the spatial distribution of output variables and quantitatively through the use of the multivariate technique second stage Multidimensional Scaling (2 stage MDS).

8.2.7 Simulation experiments

Each simulation experiment is based on the average of 30 simulations run for 200 years; the outputs from the last 100 years only were used for calculating the average. Two simulation experiments are conducted to investigate the consequence of spatially variable mortality due to fishing. This was addressed: (1) by imposing the spatial distribution of fishing effort to derive regions (grid cells) with higher fishing mortality and then compare the differential effects of heterogeneous and uniform fishing mortality on the fish community; (2) by the introduction of no-take zones as a management strategy.

The effect of accounting for a spatially variable mortality due to fishing (versus uniform mortality) is assessed by comparing the distribution of output variables (biomasses and mean lengths of the community and species). Outputs are compared globally for the whole model spatial domain and locally by grid cell.

1) Comparison of spatially variable versus uniform fishing mortality.

In this study the alternative implementations of the fishing mortality either uniformly over the spatial domain or in a spatially explicit manner are compared.

The comparison is made at the reference state (with the fishing mortalities of the 1990s) and with an increase in the fishing mortalities of all species as a function of a multiplier. The value of the multiplier ranges from 1 to 3 with 0.1 increments. The comparison is undertaken on two features of the modelled ecosystem using classical ecological indicators: the size structure (mean size for the whole community), and the species composition (Non-metric Multidimensional Scaling, MDS). The biomass of each species, and of the whole community, and mean length of the community are used to compare the two alternative implementations of fishing mortality. Multivariate ordination, using the MDS, is carried out to compare the two implementations in terms of the component species biomass (282 cells X 12 species). Of the 543 cells only 282 are occupied by the species modelled in OSMOSE.

The relative changes in biomass and mean length over the different fishing scenarios are expressed as the ratios of the biomass and mean length over that in the reference state (B_{sc} / B_{ref}, ML_{sc} / ML_{ref}) respectively.

Second stage multidimensional scaling (2 stage MDS)

Model outputs from the two implementations of fishing mortality (uniform, heterogeneous) were compared for different fishing intensities. For the purpose of this study, two stage MDS (also referred to as MDS of MDSs) (Clarke and Gorley 2006), is used to compare two aspects of the modelled community: first the effects of increasing the global fishing mortality on the community structure, and second to compare the effects of accounting for the spatial heterogeneity of fishing mortality on the community structure. 2 Stage MDS is a recently proposed approach for investigating changes in community structure and has been mainly used in marine benthic ecology. There are two general cases in which it has been used. The first one is the investigation of temporal changes in community structure for sampling where repeated sampling of sites has been conducted over time. The second case is for comparing multiple resemblance matrices to assess changes in community structure. Here the resemblance matrix is created based on the biomasses of the species in each cell after root-root transformation to reduce the impact of dominant species over-influencing the measure of resemblance. The Bray-Curtis measure of similarity is used as a measure of resemblance. 42 Resemblance matrices corresponding to the 21 fishing mortality scenarios in the two implementations of fishing mortality (uniform and spatialized) are used in the second stage MDS. Spearman rank correlation (ρ) is used as a measure of match between each pair of resemblance matrices and then an MDS is constructed based on the resulting correlation matrix.

2) Spatial fishing strategy: exploring the response of the modelled fish community to the implementation of the MPAs

The ecological effects of the implementation of various no-take zones at different locations of the coast is also investigated (Fig. 8.4). Three proposed no-take zones are modelled, with the size and location specified after consultation with experts (Dr. Colin Attwood, Marine and Coastal Management, pers.com). The effects of such spatial management strategy, on the basis of the 1990s status of the ecosystem (fishing and natural mortality, initial abundance based on the 1990s biomass estimate), are simulated by introducing each of the proposed no-take zones separately and simultaneously. The approach followed in this modelling investigation consists in redistributing the fishing mortality from the no-take zones to the part of the exploitable component of the species outside the no-take zones. The uniform fishing option was applied. Changes in the biomass and mean length of each of the modelled species in the three no-take zones are quantified relative to the situation where no restrictions were implemented. The multivariate technique 2 stage MDS is also used to compare the community structure under the four no-take options, and when no spatial restriction is introduced. The resemblance matrices were constructed based on the biomass by species matrix from the whole model domain (282 cells X 12 species). A total of five resemblance matrices is used for the 2 stage MDS.

As the main aim of this study is to explore the consequence of the spatially variable mortality due to fishing, more emphasis is placed on the comparison of the model dynamics with and without the implementation of any of the spatial fishing mortality schemes (spatial distribution of fishing mortality, and implementation of no take zones). Thus no emphasis is given to testing the sensitivity of various ecosystem indicators to an increase in fishing mortality, as this aspect has already been dealt with in a previous application of the OSMOSE model to this region (Travers et al. 2006).

8.3 Results

8.3.1 Comparison of uniform and heterogeneous implementations of fishing mortality

The consequences of the two alternative implementations of fishing mortality are investigated by comparing maps of the distribution of the relative change in biomass and mean length of the community. Figure 8.6 shows the distribution of community biomass with increasing fishing mortality relative to that at the reference level (the fishing mortality of the 1990s, mF 1). The distribution of the relative change in biomass does vary between the two implementations of fishing mortality where overall higher biomasses are observed when spatialized mortality is applied, and a lower biomass is observed when fishing mortality is assumed to be uniform. These apparent differences in the biomass between the two implementations are also captured in the trend in the mean, median and 95% of the biomass (Fig. 8.7). Figure 8.7 also shows that although the relative values vary the overall pattern of change in response to increase in fishing mortality remains the same.

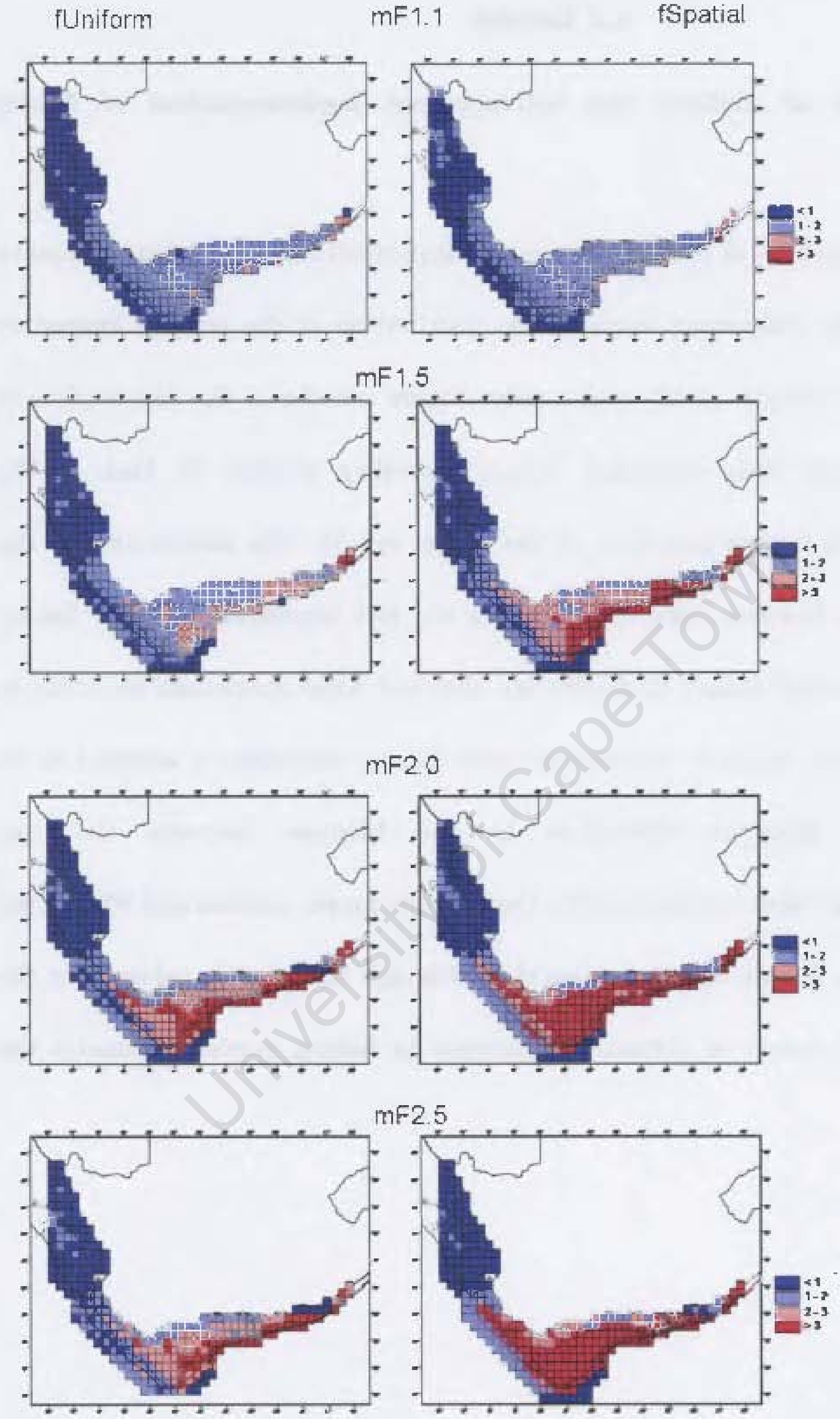


Figure 8.6. Distribution of the community biomass relative to the reference state (which is unity) with increasing fishing mortality. Multiplier *m* of the initial vector of mortality rate F per species. Left panel: Uniform fishing, Right panel: heterogeneous fishing.

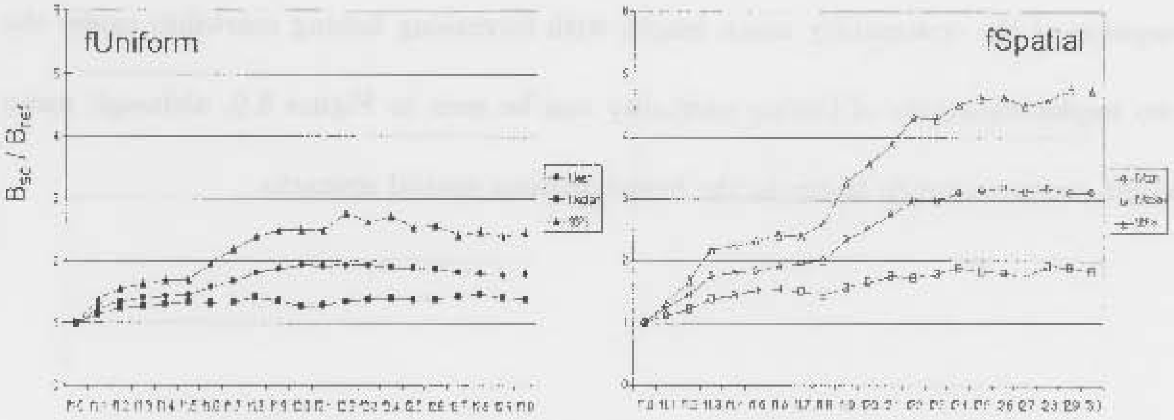


Figure 8.7. Trend in the mean, median, and 95 percentile of the community biomass with increasing fishing mortality scenario under the two implementations of fishing mortality (left panel; simulation with uniform fishing, right panel: simulation with heterogeneous fishing). The plots show the relative change in biomass.

The pattern of change and response in the modelled species are similar in the two implementations (Fig. 8.8a and 8.8b). The species that responded most positively to the global increase in fishing mortality is round herring, followed by horse mackerel. Similar to the global trend in the community biomass, the biomasses of species under the spatial fishing option are generally higher than those under a fishing uniform strategy. Furthermore, the influences of these two spatial implementations of fishing on the size structure of the community are investigated using the mean length of the community. Similar to the community biomass, the relative change in the community mean length also varies between the two implementations with a rapid decline in the community mean length observed on the west coast in the uniform fishing option whereas a rather gradual change was observed in the spatial fishing option (Fig. 8.9). But the overall similarity in the response of the community mean length with increasing fishing mortality under the two implementations of fishing mortality can be seen in Figure 8.9, although mean length increases much faster in the heterogeneous spatial scenario.

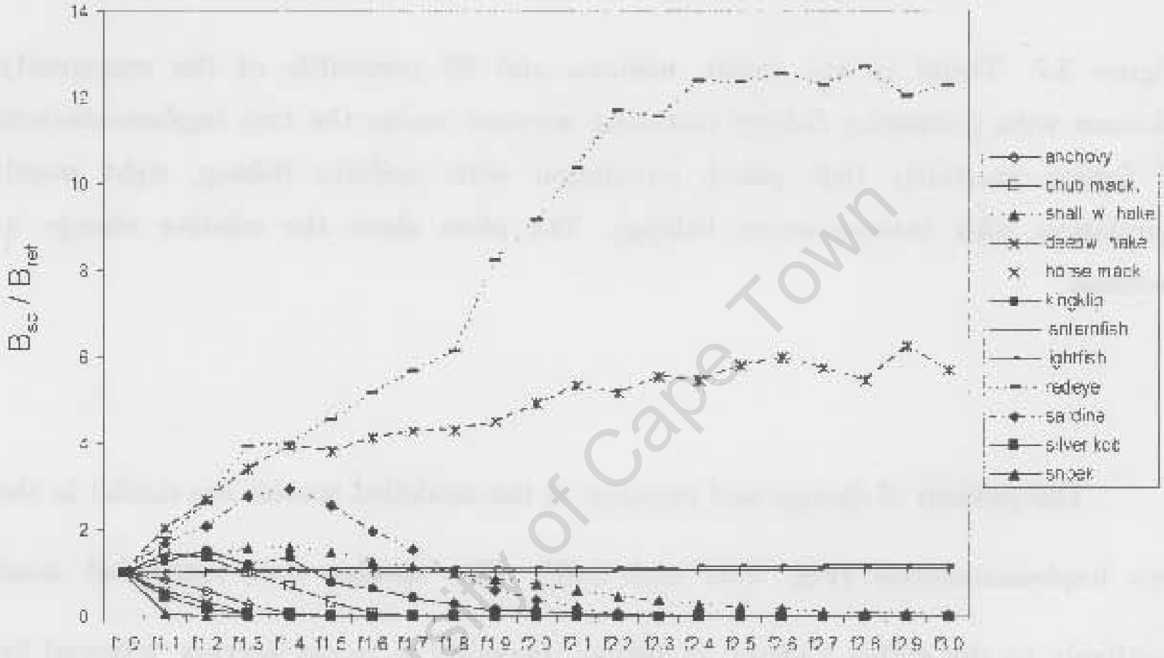


Figure 8.8a

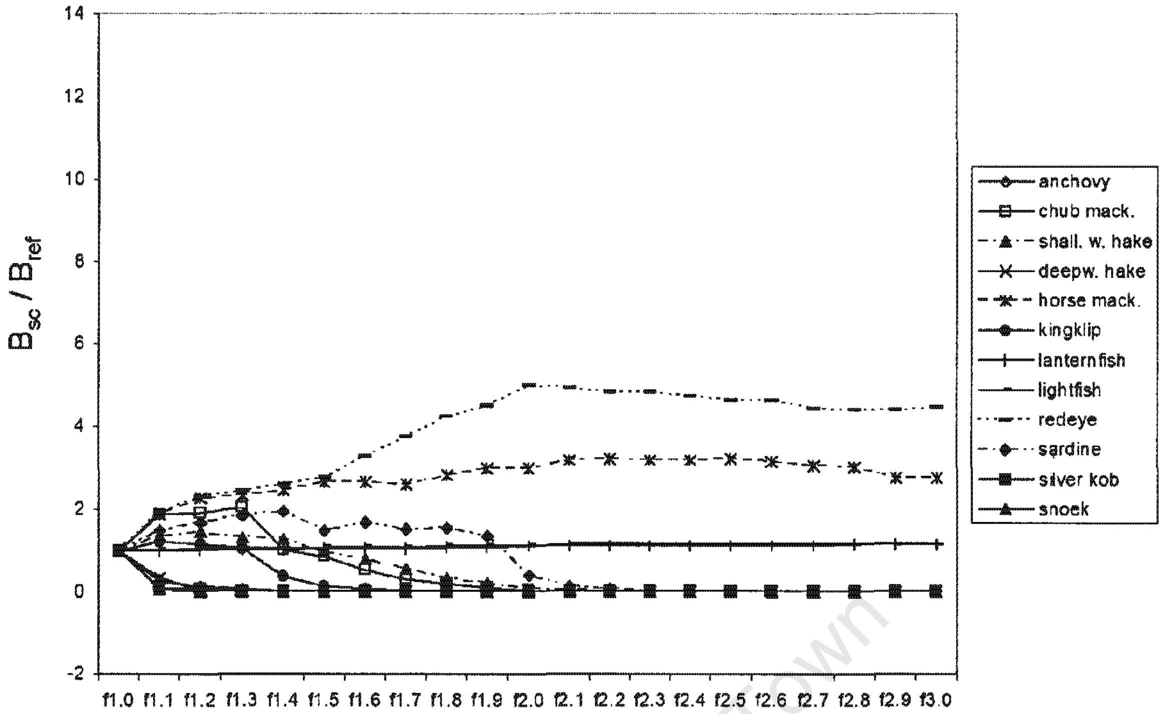


Figure 8.8b

Figure 8.8. Relative change in biomasses of the modelled species when heterogeneous (a) and uniform fishing mortality (b) are applied. Trends show relative changes over the simulated increase in fishing mortality from mF1.0 to mF3.0 (x-axis f1.0 to f3.0).

These patterns of change in the community mean length are also observed for individual species, when relative changes in the mean length of each species are tracked with the increase of fishing mortality (Fig. 8.10a and 8.10b). The mean length of the species shows a gradual change under the spatial fishing option as opposed to the rapid change observed under the uniform fishing option. This response of individual species is about the same in the two fishing scenarios, although the amplitude of variation is higher in the uniform scenario.

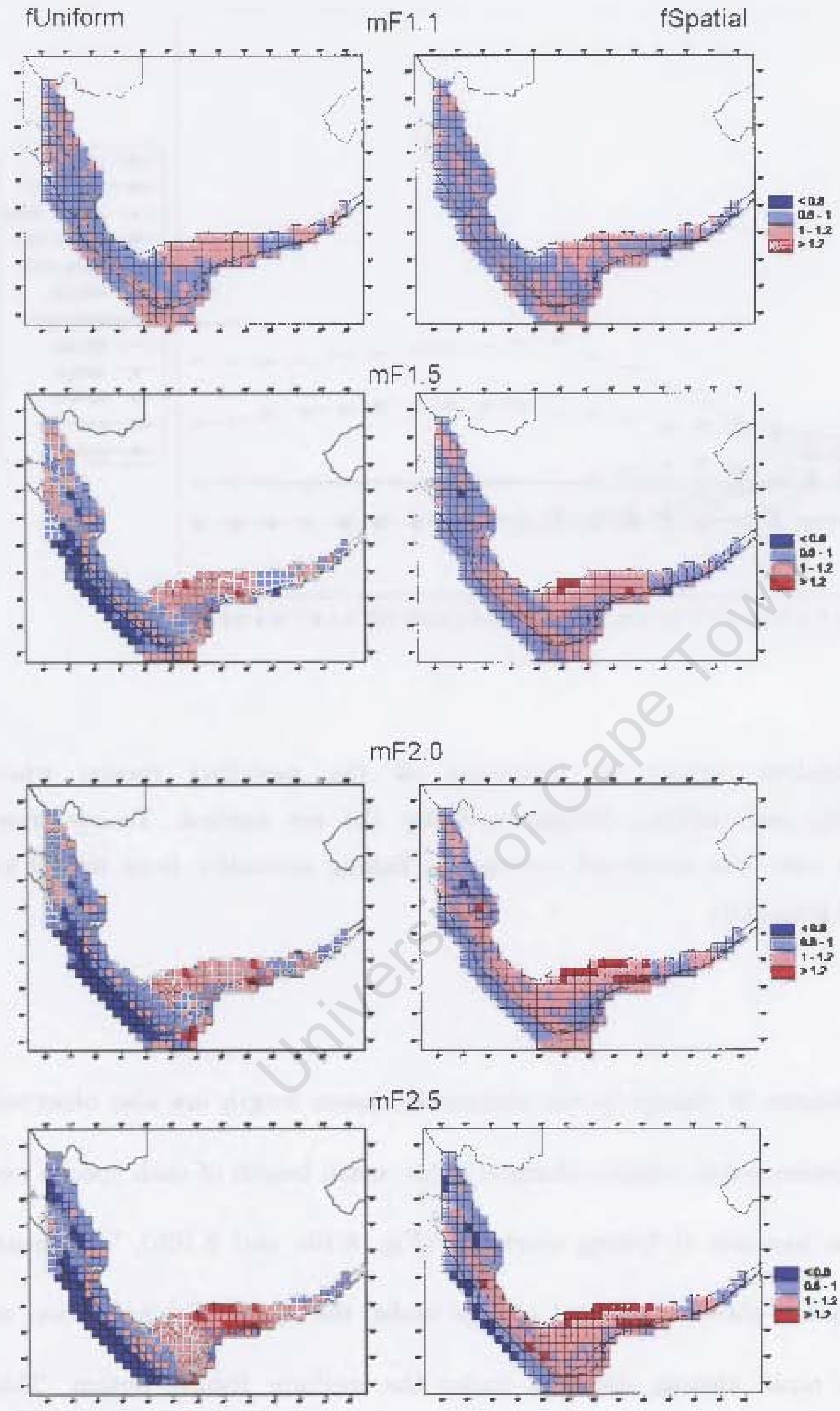


Figure 8.9. Distribution of the relative community mean length relative to the reference state (unity) with increasing fishing mortality F. Left panel: scenario with uniform F, Right panel: scenario with heterogeneous F.

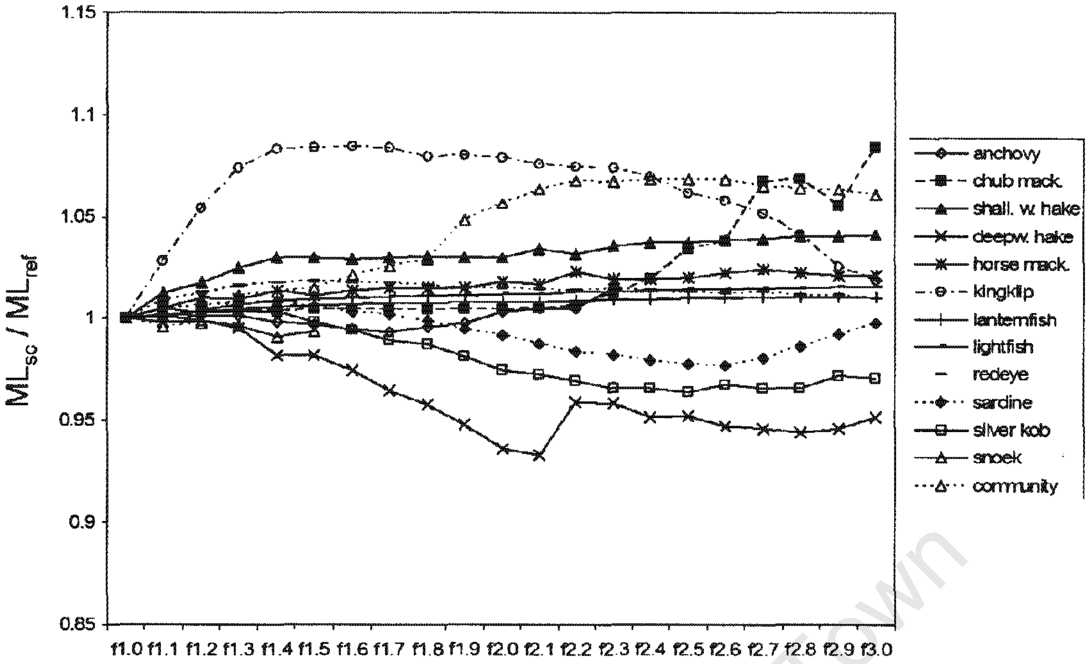


Figure 8.10a.

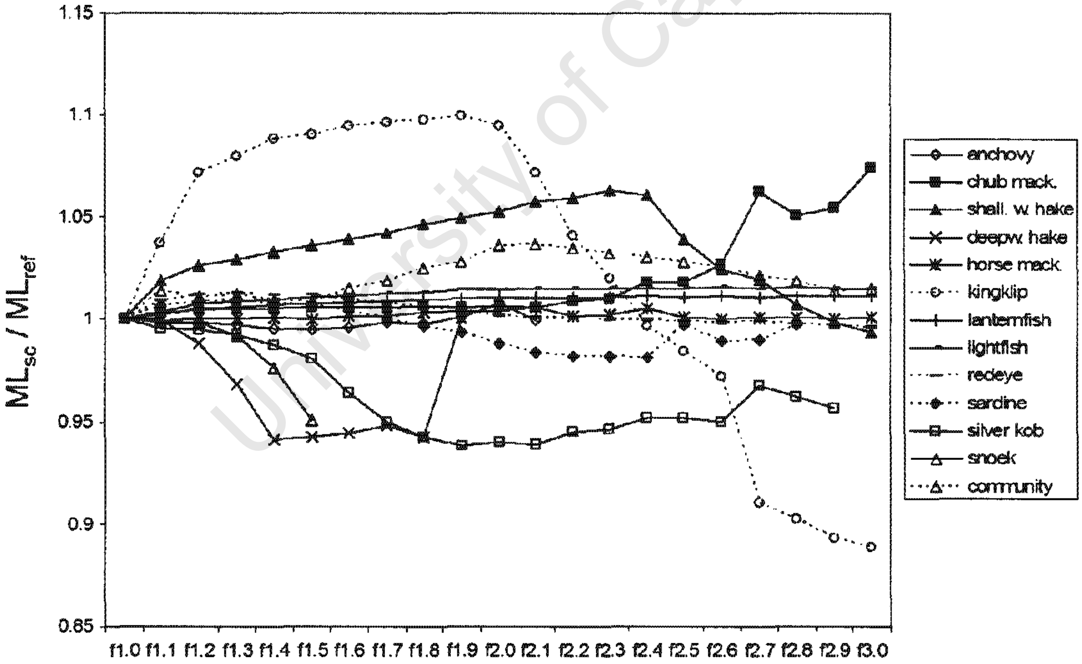


Figure 8.10b.

Figure 8.10. Relative change in mean length of the modelled species when heterogeneous (a) and uniform (b) fishing mortality is applied. Trends show relative changes over the simulated increase in fishing mortality from mF1.0 to mF3.0 (x-axis f1.0 to f3.0).

In addition the outputs from the two implementations are compared in terms of the community structure. A 2 stage MDS is used to assess if both implementations of fishing mortality could track the same changes in community structure (Fig. 8.11). The figure shows that the uniform and spatialized implementations of fishing mortality tend to produce relatively similar trajectories of community structure with increasing fishing mortality, although there is a slight divergence between the two implementations towards higher values of F. In both cases with the global increase in fishing mortality, as specified by the multiplier used, the community structure gradually moves away from the baseline resulting in structurally and possibly functionally too, different communities. These changes might be the result of differential responses of the modelled species to the increase in fishing mortality.

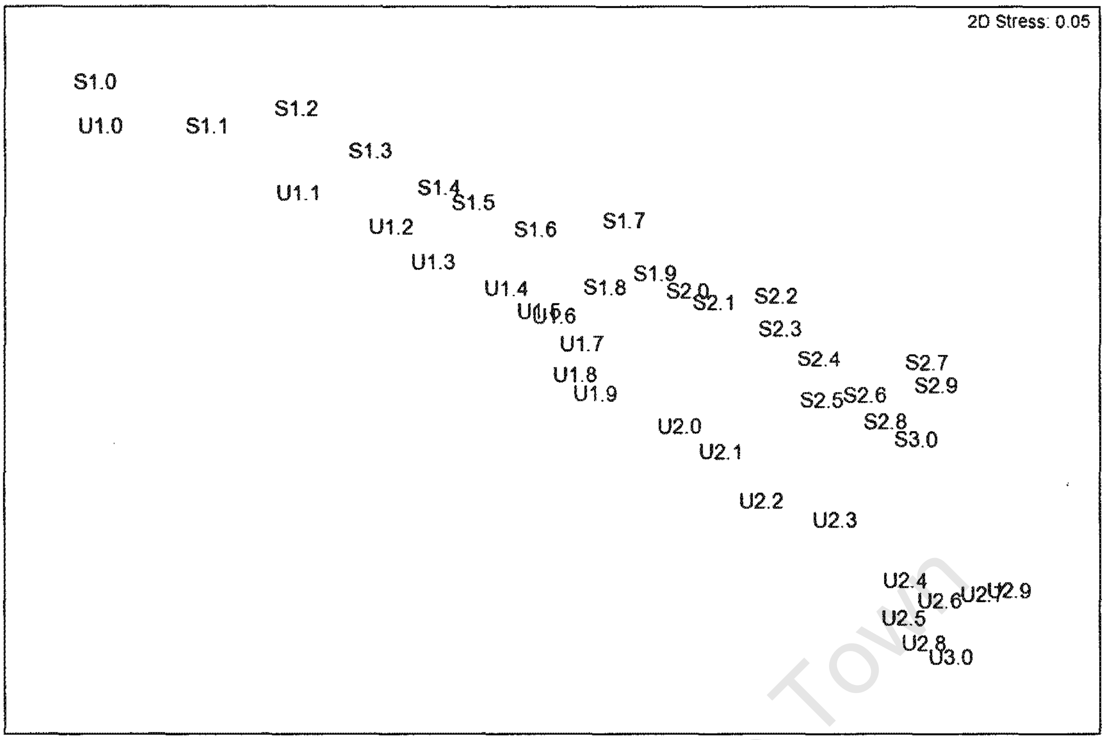


Figure 8.11. 2-stage MDS plot of the community structure from output under the uniform and spatialized fishing mortality (where U stands for uniform fishing mortality and S stands for spatialized fishing mortality, the numbers 1.0 to 3.0 represent the multiplier for the increasing fishing mortality scenario).

8.3.2 Response to the introduction of MPAs

Percentages of the distribution area of the exploitable component of each species (above age of recruitment to the fishery) and of the whole community that fall within the three MPAs are shown in Figure 8.12. When the MPAs are introduced individually the largest percentage of the distribution area of most species is protected by the MPA_S. The simultaneous introduction of the MPAs as a network results in the protection of 5% to 17% of the distribution area of the exploitable component of the species and around 12% of the distribution of the community.

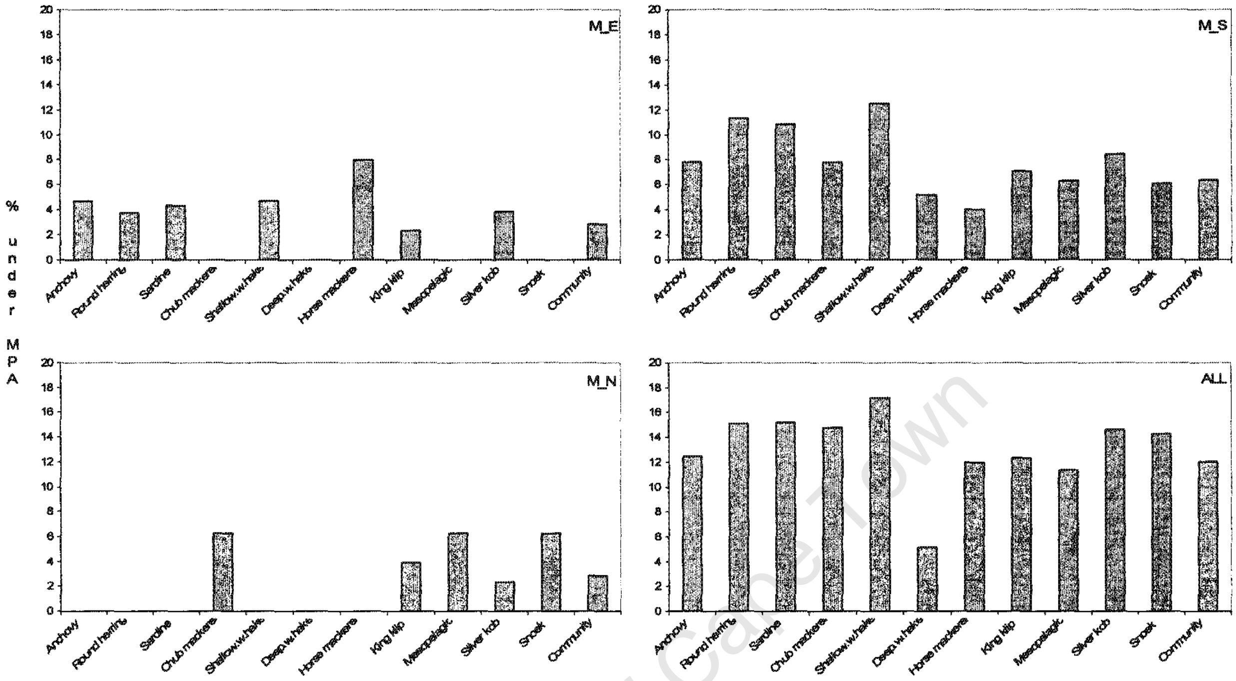


Figure 8.12. Percentage of each species and the whole community distribution areas under the three MPAs when implemented individually and simultaneously. The coverage by the MPAs is calculated relative to the distribution area of age classes above age of recruitment to the fishery. When no value is reported either the species do not occur in that particular MPA or only their early life stages occur there.

The consequences of the introduction of no-take zones when implemented individually and simultaneously are shown in Figure 8.13. The relative changes in biomass of the modelled species tends to differ when the no-take zones are implemented alone and in combination. Changes are expressed relative to the reference state (model calibrated for the 1990s biomasses). The introduction of the no-take zone off Tsitsikamma (MPA_E) results in a slight increase in the biomass of sardine and kingklip within the MPA whereas the other species that occurred in the protected zone remained close to the value before the introduction of the MPA (reference state). On the other hand when the reserve is established off de Hoop (MPA_S), a huge increase in the biomass of deep water hake followed by silver kob, is observed with all the small pelagic species, chub mackerel, and horse mackerel reduced to a lower abundance as compared to the reference state. Similar to the case where MPA_E is introduced, when simulating the instauration of MPA_N corresponding to an area off Namaqualand most of the species that occur in the region did not vary in biomass and an increase in the biomass of the large predatory species: kingklip, silver kob, and shallow water hake is clearly shown. The simultaneous introduction of the three no-take zones as a network results in an increase in the biomass of some large predatory fishes (deep water hake and silver kob) with the forage fishes (small pelagics) kept at relatively lower biomass. Remarkably, deep water hake responded disproportionately to the creation of the MPAs whereas it has the smallest proportion of its distribution area protected. On the other hand the introduction MPAs or of their combination does not affect the biomass of the mesopelagic species (lanternfish and lightfish). Relieving the large predators from mortality due to fishing does not result in enhanced mortality due to predation on the mesopelagic species. Another conclusion of this study is that the response of the species within a particular MPA tends to vary (either amplified or dampened) with the individual and simultaneous applications of the MPAs. For example, the responses of silverkob and deep water hake are amplified within

MPA_N when all the three MPAs are introduced together as compared to the situation when MPA_N is applied alone; on the other hand, the response of kingklip within MPA_N is dampened when all the three MPAs are introduced together. The effect of the establishment of the no-take zones was also investigated for the whole model domain (Fig. 8.14). The establishment of these reserves has cascading effects beyond the community in the reserve. The option which seems to have less impact on the biomass of the modelled species relative to the reference state is the introduction of a reserve off the Tsitsikamma (MAP_E). Under this option the biomass of most species remained around the reference state with higher biomass only for sardine and silverkob. With other options, the instauration of MPAs resulted in differential responses of the modelled species. There are a few common responses to those scenarios, i.e. an increase in the biomass of few large predatory fishes (silver kob, deepwater hake) and substantial reduction in the biomass of some forage fishes (chub mackerel, redeye, horse mackerel) and reduction in the biomass of snoek.

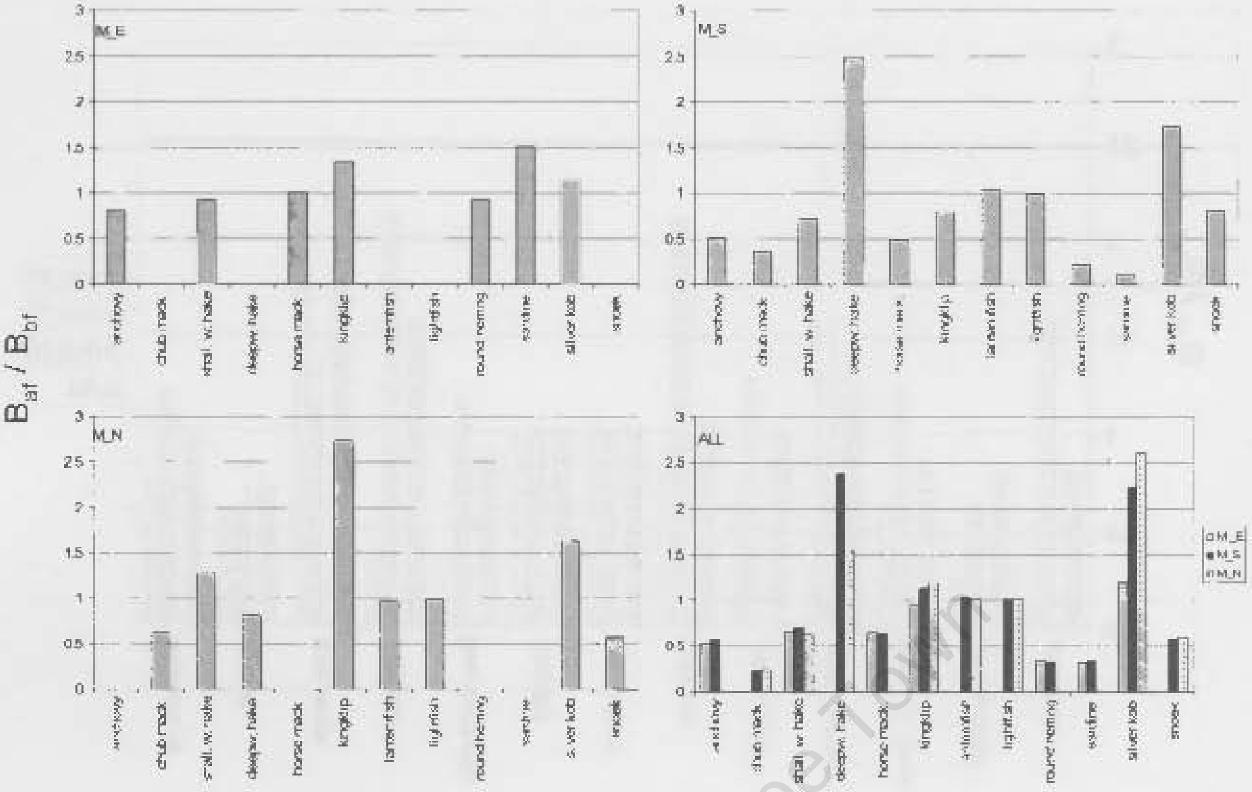


Figure 8.13. Relative change in the biomass of each species in the MPAs when the MPAs are applied one at a time (E, S, N) and simultaneously (ALL). Observed biomass in each zone is expressed (B_{af}) relative to the biomass before the no-take zone restriction was introduced (B_{bf}) in the model. Species that do not have values in the figures are those that do not occur in that particular MPA or only their early life stages occur there.

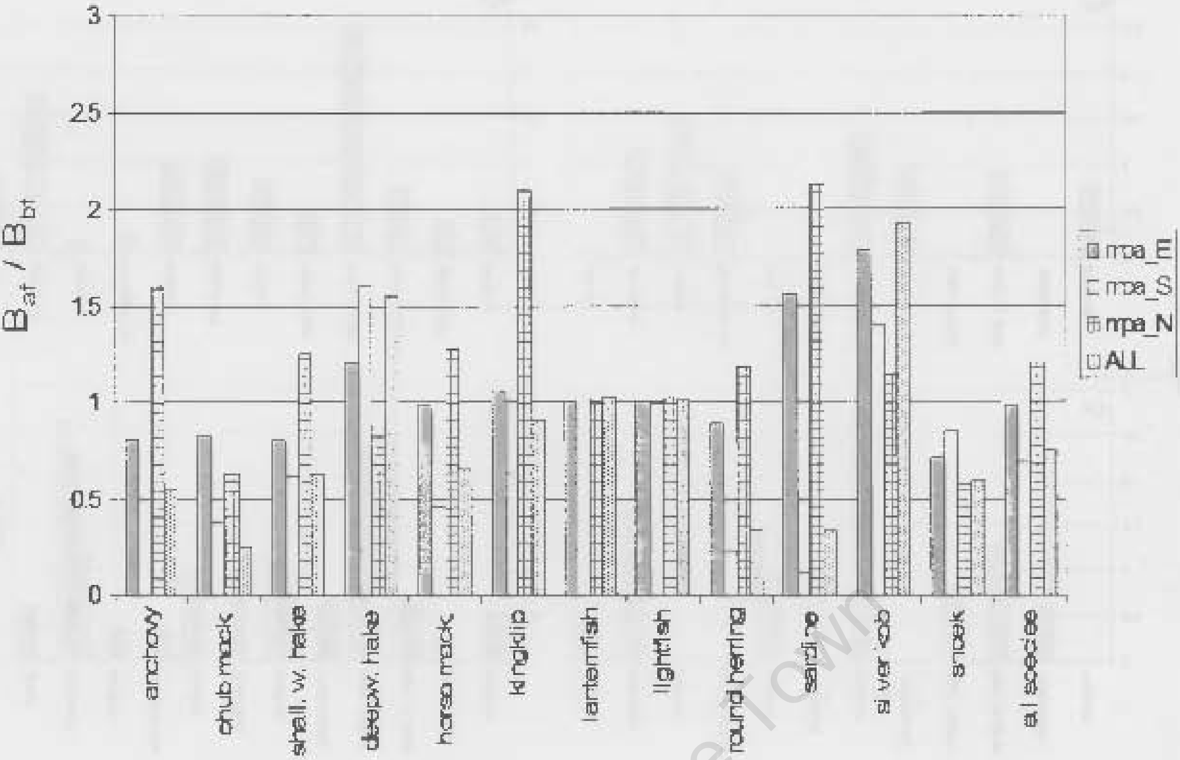


Figure 8.14. Relative change in the biomass of all the species pooled data (global output over the whole spatial domain), when the reserves are implemented sequentially and simultaneously. B_{bf} and B_{af} stand for the biomass of each species before and after the implementation of MPAs, respectively.

The variable responses are also reflected in the subsequent multivariate analysis of the output using 2 stage MDS (Fig. 8.15), which compared the resemblance matrices from the three individual applications of the reserves, one simultaneous application, and a resemblance matrix when no reserve was introduced. Three separate groups of community structure emerged, with the no-reserve option clearly separating out from the rest in one corner (no_MPA), the community structure from the option when reserve off de Hoop is established on the other corner (MPA_S), and the community structure obtained when grouping together (MPA_E, MPA_N, and all3_MPA). This exploratory study allows one to show some of the expected responses of fish communities, either within reserves or its cascading effects towards the rest of the community.

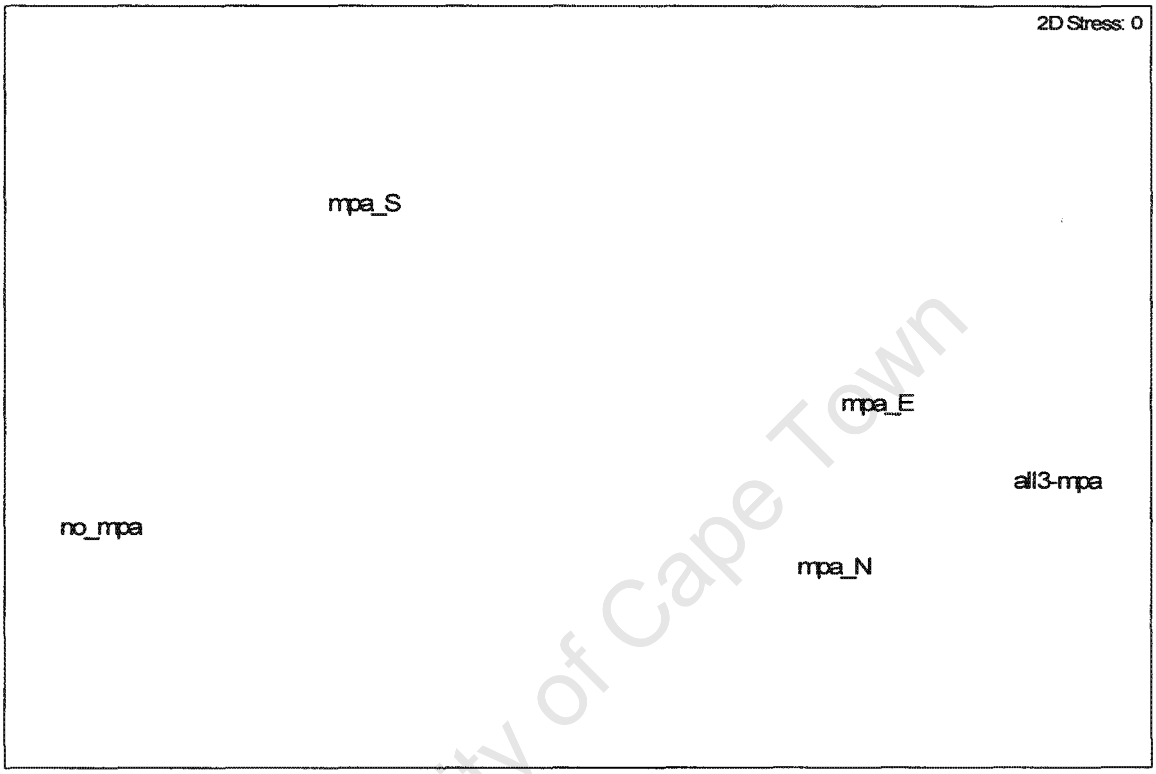


Figure 8.15. 2-stage MDS plot of the community structure under the four MPA options (MPA_E, MPA_S, MPA_N, all3-MPAs), and the reference state without MPA (no_MPA).

8.4 Discussion

8.4.1 Comparison of the two fishing mortality implementations

Spatial or uniform implementation of fishing mortality resulted in relatively similar patterns of change in biomass and in mean length over the simulated increase in fishing mortality. Observed differences in the rate of change in biomass between the two implementations might be the result of the distribution of the relative fishing effort along the coast (Figs. 8.3 and 8.4). Most of the cells on the East side of the coast have values of fishing effort less than 1, explaining the rather rapid rise in biomass observed on the south coast when the spatial fishing option is applied. Although the overall response is the same under both options, what this study highlights is that the strength of the response may vary. Both the qualitative comparison of output variables (spatial distribution, and graphs of relative changes) and quantitative comparisons (multivariate analysis using 2-stage MDS) confirmed that under either option for fishing mortality (uniform and heterogeneous), the overall behaviour of the model does not differ much. This agreement between the two implementations could be due to the fact that in the uniform fishing scenario, the fishing mortality is provided as input for each species by age class. This may inherently take into consideration the spatial variation in fishing mortality, as it is natural for fishermen to concentrate their effort in an area or region where they can find abundant fish above certain size classes. However, this finding does not discount the fact that the distribution of fishing effort and hence fishing mortality varies among localities in the entire ecosystem under study. Instead it suggests that fishermen are rather efficient in finding the resource, and that the fish prospecting area covers the spatial extent of the recruited fish distribution.

The observation that with an increase in fishing mortality the overall system biomass tends to increase more on the south coast than on the west coast (Fig. 8.6) has something to do with the general stage-dependent migration towards, and availability of older age classes on the south coast and younger age classes on the west coast. This apparent and complex migration/movement patterns for small pelagics, cape hakes, and horse mackerel is reported in Barange *et al.* (1998). First of all this rise in the biomass of the system is due to round herring and horse mackerel populations and in fact the system biomass without these two species declines with an increase in global fishing mortality. Older age classes (above age 2) of round herring are mainly restricted on the south coast whereas the younger age class (age 1) is found on both coasts; age 0 are not included in the calculation but they are mainly found on the west coast. Similarly, older age classes (above age 1) of horse mackerel are found East of 18^0 E whereas the younger age classes (age 0) are found on both coasts. Currently there is a general shift in the distribution of small pelagics, and in the centre of gravity of catches towards the southeast along the shelf (Fairweather *et al.* 2006). The rapid explosion of round herring and horse mackerel may be related to the combination of various factors: the lowest initial fishing mortality (F = 0.06 for horse mackerel, and F = 0.04 for round herring Table 8.1), and the trophic interactions with the rest of the modelled community. Round herring shares prey items with the rest of the small pelagics (anchovy and sardine); it is also prey of the shallow and deep water Cape hake (Payne *et al.* 1987). Similarly horse mackerel is prey of shallow and deep water hake at some stage during their life cycle. Previous empirical works on the feeding ecology of horse mackerel reports the following: juvenile horse mackerel share same diet as juveniles of anchovy and sardine, further the diet of adult horse mackerel is the same as adult hakes of the same size (Crawford 1989). Thus horse mackerel interacts with different species at different life stages, making complex the expected response to any kind of perturbation of the system as it interacts with different species embedded in a complex foodweb. With the increase in fishing mortality, proportional to the F multiplier, the biomass of the competitors and predators of horse mackerel and round herring declines, thus relieving both species from competitive and predation pressure while they continue to be exploited at very low levels, as opposed to the other species in the modelled system which become rapidly overexploited.

8.4.2 Consequences of the introduction of MPAs

Simulating the implementation of no-take zones resulted in substantial changes in the relative biomass of the species within the no-take zones or in the whole model domain. According to the simulations, the introduction of any of the three no-take zones tends to favour the large predator component of the modelled community, mainly deep water hake, kingklip, and silverkob, under the fishing strategy in the 1990s. On the contrary, the creation of MPAs can be detrimental to some forage species such as redeye, horse mackerel and chub mackerel. Deep water hake experiences the highest fishing mortality of all the modelled species, thus the results suggest that relieving part of the species in the MPA_S from fishing mortality has a positive impact on its biomass, but with a negative impact on the rest of the species in the MPA and throughout the model domain. In the scenario with all the three MPAs, deep water hake has the smallest proportion of its area protected, but the subsequent increase in the biomass is the second most important within the community. The fact that deep water hake feeds heavily on mesopelagic fish (Shannon *et al.* 2003) while other forage populations decrease substantially in abundance, may amplify the response of deep water hake to the creation of MPA_S. Shallow water hake remained below the reference level most of the time. This could partly be explained by competition with other large predators on small pelagic fish, and increased predation on their juveniles by large deep water hake. Thus observed responses, an increase in large predators and decline in small forage species, could be the result of both direct predation on adults of prey species so that it indirectly reduces their competitive and predatory impact on the early life stages of the large predators. This process is known as the "Cultivation effect" (Walters and Kitchell 2001) which has been shown to have an impact on the dynamics and resilience of demersal species (e.g. Bundy and Fanning 2005). The results of this study show that the effects of introducing the MPAs individually or together, cascades to the rest of the modelled community. Further this study shows that the responses of some species within a particular MPA vary, depending on the way the MPAs are introduced: individually (e.g. either one of the three MPAs studied in this simulation experiment), or simultaneously. The responses of some species get amplified within an MPA when this MPA is introduced simultaneously with others, and the converse holds true for some other species.

The indirect effects of introducing MPAs are not trivial, and one way to grasp them is to model local species interactions explicitly. This exploratory analysis further echoes the results suggested by various empirical studies on the role of marine reserves; although MPAs provide benefit for a few species within an assemblage, maximum benefit of their implementation may be achieved when used in conjunction with other fisheries management tools (Roberts et al. 2005) such as an overall reduction in fishing effort, and introduction of size limits. From a management perspective, setting aside part of the coast (extending from inshore to offshore) as a no-take zone needs to consider the location, size, and biological interactions of the species within the reserves. Although most of the species are highly mobile over the modelled spatial domain, cases where reserves are believed to be least effective, this study shows that protecting a minor proportion of the coastal area results in changes in the individual species abundance within the reserves and can cascade to the whole system.

The effectiveness of MPAs as management tools, especially in temperate zones, has been doubted for various reasons. Here the simulation results show that MPAs indeed do affect the protected community but not all species, and benefits from doing so could be maximized by careful selection of the localities and the number of MPAs in combination with other management measures.

Some of the benefits of this type of ecosystem modelling in conjunction to empirical data analyses can be considered in terms of the insights that can be gained with respect to the response of the modelled components of the ecosystem these are usually not obvious. Such information includes unexpected species or community response to an increase in any form of disturbance, resulting from complex species interactions (released or enhanced competition and predation, indirect effects on distant trophic levels, local interactions) and inherent population dynamics (compensation and depensation effects). With the current increasing concern about ecosystem approaches to fisheries management, marine reserves are viewed as one of the key management measures for rebuilding overfished stocks, for protecting critical habitats, and for reducing the risk of stock collapse (Gell and Roberts 2003). As this type of management measure is often implemented as bet-hedging in the face of risking management failures, exploring the population and community consequences of doing so through simulation experiments, before practical implementation, it is of tremendous importance to get a range of the possible responses of the fish community to the planned reserve. To do so a good understanding of community interactions is crucial for the selection of the location and size of reserves (Walters 2000, MacAll 2002, Knowlton 2004, Micheli et al. 2004). Using a model comprising two species of rockfish Sebastes, one of them being a large target predatory fish (*Sebastes ruberrimus*) whereas the other is smaller in size with no targeted fishing (*Sebastes wilsoni*) but is preyed upon by the larger species, Baskett et al. (2006) investigated the role of trophic interactions in the recovery of the overexploited large predatory species within a marine reserve. They found that when trophic interactions are considered, the recovery of the overexploited large predatory species depended on the initial densities of the predator (adults and juveniles) and those of its prey, and on the size of the reserve. Both initial community composition and the distribution of life stages are crucial to the recovery of overexploited species. Therefore, careful selection of reserve location where biomass of the overexploited species is higher and that of its potential competitors is lower may be more efficient than areas with an overall high biomass and diversity.

protecting critical habitats, and for reducing the risk of stock collapse (Gell and Roberts 2003). As this type of management measure is often implemented as bet-hedging in the face of risking management failures, exploring the population and community consequences of doing so through simulation experiments, before practical implementation, it is of tremendous importance to get a range of the possible responses of the fish community to the planned reserve. To do so a good understanding of community interactions is crucial for the selection of the location and size of reserves (Walters 2000, MacAll 2002, Knowlton 2004, Micheli et al. 2004). Using a model comprising two species of rockfish Sebastes, one of them being a large target predatory fish (*Sebastes ruberrimus*) whereas the other is smaller in size with no targeted fishing (*Sebastes wilsoni*) but is preyed upon by the larger species, Baskett et al. (2006) investigated the role of trophic interactions in the recovery of the overexploited large predatory species within a marine reserve. They found that when trophic interactions are considered, the recovery of the overexploited large predatory species depended on the initial densities of the predator (adults and juveniles) and those of its prey, and on the size of the reserve. Both initial community composition and the distribution of life stages are crucial to the recovery of overexploited species. Therefore, careful selection of reserve location where biomass of the overexploited species is higher and that of its potential competitors is lower may be more efficient than areas with an overall high biomass and diversity.

Chapter 9 Synthesis: putting it all together

Results reported in the previous chapters (Chapter 2 to Chapter 8) show changes in the community with respect to the size or community structure and make up pieces of the story with respect to the effects of fishing in the two empirical case studies and on a theoretical basis using simulation modelling. Furthermore, there are different issues relevant for the overall objective of the thesis that needed to be considered. Thus this section of the thesis tries to address various aspects related to the approaches adopted, data sources, and various indices used and then attempts to answer the questions outlined in Chapter 1.

Relevant issues

The issue of reference direction

Although reference direction is advocated and adhered to in this thesis there are technical implications for practical application in a management context. By virtue of their complexity and uncertainty in measuring their attributes, ecosystems and their properties respond differently and non-linearly in different time frames. Thus *a-priori* delimitation of a time frame must be set within which the direction of change in the ecosystem indicators can be used in setting management actions to mitigate or enhance observed changes (depending on the reference direction). A related conclusion, in terms of power analysis, has also been reached for size-based indicators by Jennings and Dulvy (2005). They found that size-based indicators could be used for medium-term management (5 – 10 years), but the power of the size-based methods to detect trends is weaker at shorter time scales.

Issues of the use of catches

As mentioned in Chapter 2 results based on the analysis of landings are often biased when assessed over time because changes in discarding practices, high grading, and market forces affect which components of the catch are landed. Therefore changes in species composition or in size structure of the landings do not necessarily reflect changes in the populations. Equally marked changes in the catches may not be reflected in the landings. Thus initial landings from historical records may be biased towards catches mainly composed of larger individuals of target species or larger species. This could bias estimates of fishing mortality in historical data and estimates of size structure (such as mean size). However the influence of this bias on the results reported in Chapter 2 is assumed to be limited for the following reasons: there is no indication of changes in hook sizes used by the traditional linefishery off the coast of South Africa, this fishery generally used the same kind of hook (simple J-hooks) over time, as the line fishery is selective compared to trawling, fishermen would target most valuable species first, usually larger ones, so discarding is probably limited. Furthermore as also outlined in Chapter 2, changes in hook size or type are usually responses to declining catches of the initial target size class or species, thus indicating problems with the fishery.

Issues related to the use of survey data to study community level changes

The reported changes in community structure may be influenced by variability in the catchability of species. The catchability of the various species varies in response to different factors; survey vessel type, survey gear type, spatial distribution, and length composition of the species. But the data for the south coast demersal community was collected consistently using the same vessel and gear except for the starting year (which was experimental), in addition the spatial coverage has remained constant. The assumption of using the survey catch rate estimates of the species as reflecting its abundance should be valid because most of the factors that could potentially influence catchability are kept constant. In addition recent work by Trenkel et al. (2004) shows that consistent changes in the community structure of demersal species could be obtained from different surveys, except for size spectra, although they caution against the use of different surveys to assess abundance trends of a population.

Questions posed in Chapter 1 and findings

1) Are there spatio-temporal changes in the size structure, species composition, and community structure of the fish communities?

Changes in the size structure were observed for the main linefish species landed by the line fishery off the four sub-regions of the Cape region. These changes were evidenced both in terms of a reduction in the mean length over three periods, and in changes in the slope of the size spectra. Changes in species composition for the linefish species were shown using *k*-dominance curves, where the temporal trend in the *k*-dominance curves clearly shows the change in dominance structure of the community with the Western and Southwestern Cape responding by an increase in dominance over the three periods (1890s, 1930s, 1990s) whereas the Southern and Southeastern Cape responded by decline in dominance. Multivariate analysis using multidimensional scaling and dendrograms shows the distinct changes in structure of the community over the three periods (Chapter 2).

One of the observations of this study and others is the response of dominance curves and diversity indices to the effects of fishing. It seems that the contrasting response of diversity and dominance to disturbance is a general pattern rather than an exception. This contrasting response has been related to the productivity of the system concerned. It might also have to do with the species composition of the system being studied (Chapter 2 and 6).

For the south coast demersal fish communities, changes in size structure were investigated using various size-based indicators (mean length, mean Lmax, slope of the size spectra, proportion of different size categories, and abundance of different size categories). The temporal trend in all the indicators suggests a change in the size structure of the south coast fish community towards a community with reduced abundance of larger individuals (Chapter 4).

Changes in the community structure of the south coast demersal fish community were investigated using: multivariate clustering and ordination, a variety of univariate diversity indices (Chapter 5 and 6), and Abundance Biomass Comparison (ABC) curves (Chapter 7). The multivariate analysis for selected survey year shows that the fish communities on this coast are strongly structured by depth, confirming findings of a previous study on this coast (Smale *et al.* 1993). As the main emphasis of the multivariate analysis was to investigate temporal trends, study of the community structure in relation to depth and longitude was restricted to a few sample survey cruises. Based on the axis scores of the ordination by multidimensional scaling, the community structure of the fish communities on this coast has changed over time (Chapter 5). The result of analysis of the univariate diversity indices showed that diversity of the fish communities changes substantially with depth, and with longitude. Furthermore, similar to the results of the multivariate analyses, the diversity on this coast has changed over time. This change is characterized by an increase in diversity and decline in dominance (Chapter 6). The ABC method, though with limited previous application in fisheries, also suggests changes in the demersal fish community of the south coast. Temporal trends in the *W-statistic* (the summary statistic of the ABC curve) shows a more negative value of *W-statistic* over time towards the 2000s, again indicating a reduction in abundance of larger fish and / or relative increase in small fish (Chapter 7).

2) How does fishing modify the structure of fish communities and ecosystems?

This question is important in terms of its implication for management. With the current thrust towards an Ecosystem Approach to Fisheries management, understanding of the impacts of overexploitation on the structure of the communities and of the ecosystem they are part of, is crucial. There are various world wide investigations towards achieving that goal. Some of the outcomes of those investigations include: changes in size structure towards a community with fewer large individuals, and populations or communities characterized by smaller average size, and in some cases indirect responses were observed in the form of an increase in the abundance of smaller individuals and species with smaller Lmax. Changes in the community structure as a result of differential impact of fishing are observed as changes in relative abundance of species in the community and assessed using multivariate techniques, univariate diversity indices, dominance curves, and others. The results of this study from Chapter 2 to Chapter 7 also corroborate the above mentioned response of communities to fishing. What remains is to translate these changes into decision criteria when formulating management procedures.

The theoretical study of fish communities using an IBM (Chapter 8) shows how important consideration of trophic interaction is in the assessment of the effects of heavy fishing. An unexpected response to increase in total fishing mortality for all modelled fish species was the increase in biomass of some species that were able to take advantage of the vacant niche in the ecosystem created by selectively overfishing a species, this in turn resulting in an increase in the system biomass. The second lesson from the modelling study was the response of fish communities when part of population is protected from fishing using MPAs. In general the responses of fish communities when afforded protection from fishing, was the relative increase in biomass of large predatory fishes and relative decline in biomass of prey and competitor species. A slightly different response of the fish communities was observed when MPAs were introduced individually and as a network. Furthermore, it was observed that consequence of introducing MPAs cascades to the rest of the modelled community (Chapter 8). Thus the theoretical modelling study is consistent with the empirical case studies and can be taken further to ask "what-if?" questions related to how MPA may help in sustainable fisheries management.

3) Has fishing effort increased?

Temporal trends in fishing effort for both case studies are based on nominal fishing effort. They are thus crude and probably underestimate the real increase in fishing effort. For the line fishery the trend in the nominal fishing effort has increased over a period of 100 years based on three brief periods (1897 – 1906, 1927 – 1931, and 1986 – 1998) (Chapter 2).

Analysis of fishing effort for the fish communities of the south coast is based on the demersal hake directed trawl fishery and the demersal hake-directed longline fishery. Though there are also other types fishing activity on this coast, analysis is based on these as the most important fishing activities: the trawl fishery and longline fishery. The nominal hake-directed trawl fishing effort showed strong interannual variability over the period 1978 – 2002, whereas the hake-directed longline fishery effort has been increasing rapidly since its introduction in 1994 (Chapter 4 and 7).

4) Are there signs of overfishing at either of the ecological hierarchy levels (population, community) assessed?

An earlier study by Griffiths (2000) has shown that most of the linefish species are severely overexploited, one species even to the level of commercial extinction. Thus in Chapter 2 of this thesis no attempt has been made to repeat the same work as that of Griffiths (2000), instead the changes in catch rate of the whole linefish community are assessed over the three periods and substantial reduction in the landings and CPUE of the whole linefish community was observed.

For the demersal fish community of the south coast inference regarding the abundance of the species was based on the trend in the catch rate of collective groups (target vs non-target, and abundance by size classes). Thus, as the main interest of the thesis concerns effects above the species level, no attempt has been made here to assess the abundance of individual species caught during the demersal trawl survey (Chapter 4 and 5).

After an initial increase from the mid-1980s, a gradual decline in the catch rate of the south coast fish community for all depth strata and for each depth stratum individually when the catch rate was assessed for the whole community was observed after the mid 1990s. For the target and non-target components, a slightly different image emerges. The trend also depends on the depth stratum; when all depth strata were pooled together the catch rate of both the target and non-target components of the community declines after the mid-1990s. A similar result was obtained when the catch rates were assessed for the 0 – 100m depth stratum alone. For the 101 – 200m depth stratum the trends was different with an increase in the catch rate of the non-target species, which was also evident in the whole communities catch rate for this depth range, whereas the catch rate of the targeted component declined after the mid-1990s (Chapter 5).

Additional contributions of this thesis are in connection with the kind of data used for construction of size spectra, and multivariate analysis of diversity indices. Issues regarding the use of data of different resolution such as length frequency data versus mean length (especially application for the case where two separate data sets, of different resolution, are used to construct size spectra). This study cautions against the assessment of changes in the size structure of a community based on the slopes of size spectra derived from two different data sources with different resolution (size spectra based on length frequencies and size spectra based on mean lengths) (Chapter 3). The second relates to the choice of diversity indices for tracking changes in demersal fish communities. Multivariate analysis of a selection of diversity indices, all calculated from the same data source, shows that sub-sets of the diversity indices that summarise similar information tend to group together on ordination plots (Chapter 6). For example: those that summarise mainly the richness component of diversity, those indices that balance the richness and evenness component, and those that measure taxonomic distinctness cluster separately. This suggests that the alternative use of indices from within the sub-sets would not change the final conclusion reached about the diversity of the community under study. In the same chapter exploratory analysis shows the non-linear relationship between diversity of communities, catch rate and

Lmax. Smaller Lmax classes tend to have a higher catch rate and lower evenness, whereas larger Lmax classes have relatively smaller catch rate but higher evenness.

In conclusion the diversity of approaches followed in this thesis allowed assessing and confirming the response of the various indicators of fishing impacts. As the main concern of this thesis is to assess the effects of fishing at the community level, results from the two case studies clearly highlight and emphasize those effects. Consistent response of the various indicators was observed in the two case studies and in the modelling approach. For the two case studies despite the difference in spatial and temporal coverage, species composition, and data sources, changes in community and size structure were observed in agreement with the expected effects of fishing. The results further highlight that although there still remains a challenge to incorporate observed changes in the management context, an Ecosystem Approach to Fisheries is indeed a necessity for responsibly managing fisheries as the effects of targeted fishing extend well beyond the targeted stocks.

REFERENCES

Agard, J. B. R., J. Gobin, and R. M. Warwick. 1993. Analysis of marine macrobenthic community structure in relation to pollution, natural oil seepage and seasonal disturbance in a tropical environment (Trinidad, West Indies). Mar Ecol Prog Ser **92**: 233 – 243.

Austen, M. C., and R. M. Warwick. 1989. Comparison of univariate and multivariate aspects of estuarine meiobenthic community structure. Est Coast Shelf Sci **29**: 23 – 42.

Attwood, C. D and B. A. Bennett. 1995. A procedure for setting daily bag limits on the recreational shore-fishery of the South-Western Cape, South Africa. S Afr J Mar Sci **15**: 241 – 251.

Attwood, C. D. and M. Farquhar. 1999. Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. S Afr J Mar Sci **21**: 415 – 432.

Badenhorst, A. 1988. Aspects of the South African longline fishery for kingklip *Genypterus capensis* and the Cape hake *Merluccius capensis* and *M. paradoxus.* S Afr J Mar Sci **6**:33 - 42.

Badenhorst, A., and M. J. Smale. 1991. The distribution and abundance of seven commercial trawlfish from the cape south coast of South Africa, 1986 - 1990. S Afr J Mar Sci **11**: 377 – 393.

Barange, M. S. C. Pillar and I. Hampton. 1998. Distribution patterns, stock sizes and life history strategies of Cape horse mackerel *Trachurus trachurus capensis,* based on bottom trawl and acoustic survey. In Benguela Dynamics: Impacts of variability on Shelf-Sea Environments and their Living Resources. S. C. Pillar, C. L. Moloney, A. I. L. Payne, and F. A. Shillington (Eds). S Afr J Mar Sci **19**: 433 – 447.

Baskett, M. L., M. Yoklavich, and M. S. Love. 2006. Predation, competition, and the recovery of overexploited fish stocks in marine reserves. Can J Fish Aquat Sci **63**: 1214 – 1229.

Baum, J. K., and R. A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecol Lett **7**: 135 – 145.

Bennett, B. A. 1993. Aspect of the biology and life history of white steenbras *Lithognathus lithognathus* in Southern Africa. S Afr J Mar Sci **13**: 83 – 96.

Beverton, R. J. H., and J. S. Holt. 1993. On the dynamics of exploited fish populations. Chapman and Hall, London.

Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology **85**: 1258 – 1264.

Bianchi, G. 1992. Demersal assemblages of the continental shelf and upper slope of Angola. Mar Ecol Prog Ser **81**: 101 – 120.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F., and K. Zwanenburg. 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES J Mar Sci. **57**: 558 – 571.

Bianchi, G., Hamukuaya, H., and O. Alvheim. 2001. On the dynamics of demersal fish assemblages off Namibia in the 1990s. S Afr J Mar Sci **23**: 419 – 428.

Blanchard, F., Leloc'h, F., Hily, C., and J. Boucher. 2004. Fishing effects on the diversity, size, and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. Mar Ecol Prog Ser **280** :249 – 260.

Bolam, S. G., T. F. Fernandes, and M. Huxham. 2002. Diversity, Biomass, and Ecosystem processes in the marine benthos. Ecol Monogr **72**: 599 – 615.

Borgmann, U. 1987. Models on the slope of, and biomass flow up, the biomass size spectrum. Can J Fish Aqua Sci **44**: 136 – 140.

Booth, A. J., and T. Hecht. 1998. Changes in the Eastern Cape demersal inshore trawl fishery between 1967 and 1995. S Afr J Mar Sci **19**: 341 – 353.

Botha L. 1985. Occurrence and distribution of Cape hakes *Merluccius capensis* Cast. and *Merluccius paradoxus* Franca in the Cape of Good Hope area. S Afr J Mar Sci **9**: 327 – 357.

Boudreau, P. R. and L. E. Dickie. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. Can J Fish Aqua Sci **49**: 1528 – 1538.

Brouwer, S. L., B. Q. Mann, S. J. Lamberth, W. H. H. Sauer, and C. Erasmus. 1997. A survey of South African shore-angling fishery. S Afr J Mar Sci **18**: 165 – 177.

Branch, G. M. and M. L. Branch. 1981. The living shores of South Africa. Cape own; Struik: 272pp. +60pp. Plates.

Bundy, A. and L. P. Fanning. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanation for the non-recovery of the cod stock on the eastern Scotian shelf, Canada. Can J Fish Aquat Sci **62**: 1474 – 1489.

Calder, W. A. 2001. Ecological consequence of body size. Encyclopedia of Life Science

Chapman, J. L., and M. J. Reiss. 1992. Ecology: Principles and Applications. Cambridge University Press, Cambridge. 294pp.

Clarke, K. R. 1990. Comparisons of dominance curves. J Exp Mar Biol Ecol **138**: 143 – 157.

Clarke, K. R., and R. M. Wawick. 1994. Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth: Plymouth Marine Laboratory: 144pp.

Clarke, K. R., and R. M. Warwick. 1998. A taxonomic distinctness index and its statistical properties. J Appl Ecol **35**: 523 – 531.

Clarke, K. R. and R. N. Gorley. 2001. PRIMER v5: User Manual/Tutorial. PRIMER-E Ltd.

Clarke, K. R., and R. M. Warwick. 2001. Changes in marine communities: an approach to statistical analysis and interpretations, 2nd edition. PRIMER-E: Plymouth.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: User manual/tutorial. PRIMER-E Ltd.

Clarke, R. K., P. J. Somerfield, and M. G. Chapman. 2006. On resemblance measure of ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. J Exp Mar Biol Ecol **330**: 55 – 80.

Crawford, R. J. M. 1989. Horse mackerels and saury. Pages 122 – 129. *in* A. I. L. Payne, R. J. M. Crawford, and A. P. van Dalsen, editors. Oceans of life off Southern Africa. Valberg, Cape Town.

Daan, N., H. Gislason, J. G. Pope, and J. Rice. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES J Mar Sci **62**: 177 – 188.

Dulvy, N. K., N. V. C. Polunin, A. C. Mill, and N. A. J. Graham. 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Can J Fish Aquat Sci **61**: 466 – 475.

Fahey, F. J., G. S. H. Russouw, A. J. Stals, and D. H. Steyn. 1934. The fishing industry, board of trade and industries **180**: Pretoria; Government Printer: 90 pp + 1 chart

Fairweather, T. P., C. D. van der Lingen, A. J. Booth, L. Drapeau, and J. J. van der Westhuizen. 2006. Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus.* Afr J Mar Sci **28**: 661 – 680.

Fauth, J. E., J. Bernardo, M. Camara, W. J. J. Resetarits, J. V. Buskirk, and S. A. McCollum. 1996. Simplifying the jargon of community ecology: A conceptual approach. Am Nat **147**: 282 – 286.

Field, J. G., K. R. Clarke and R. M. Warwick. 1982. A practical strategy for analysing multivariate distribution patterns. Mar Ecol Prog Ser **8**: 37 – 52.

Fogarty, M. J., and S. A. Murawski. 1998. Large scale disturbance and structure of marine systems: fishery impacts on Georges bank. Ecol Appl **8**: s6 – s22.

Jouffre, D. and C. A. Inejih. 2005. Assessing the impacts of fisheries on demersal fish assemblages of the Mauritanian continental shelf, 1987 – 1999, using dominance curves. ICES J Mar Sci **62**: 380 – 383.

Froese, R. and D. Pauly, Editors. 2000. FishBase 2000: Concepts, design and data sources. ICLARM, Los Banos, Laguna, Philippines. 344p

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2004a. Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems. Ecol Model **174**: 267 – 307.

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2004b. Effects of spatial resolution on the performance and interpretation of marine ecosystem models. Ecol Model **176**: 27 – 42.

Garcia, S. M., and K. L. Cochrane. 2005. Ecosystem approach to fisheries: a review of implementation guidelines. ICES J Mar Sci **62**: 311 - 318.

Garison, L. P., and J. S. Link. 2000. Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. ICES J Mar Sci **57**: 723 - 730.

Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol **18**: 448 - 455.

Gilchrist, J. D. F. 1898. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1897. Cape Town; Government Printer: 148 pp. + 1 Chart.

Gilchrist, J. D. F. 1899. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1898. Cape Town; Government Printer: 362 pp. + 21 Charts.

Gilchrist, J. D. F. 1900. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1899. Cape Town; Government Printer: 124 pp.

Gilchrist, J. D. F. 1901. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1900. Cape Town; Government Printer: 180 pp. + 3 Charts.

Gilchrist, J. D. F. 1902. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1901. Cape Town; Government Printer: 104 pp. + 2 Charts.

Gilchrist, J. D. F. 1903. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1902. Cape Town; Government Printer: 283 pp. + 3 Charts.

Gilchrist, J. D. F. 1904. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1903. Cape Town; Government Printer: 194 pp.

Gilchrist, J. D. F. 1906. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1904. Cape Town; Government Printer: 40 pp.

Gilchrist, J. D. F. 1907. Report of the Marine biologist, Department of Agriculture, Cape of Good Hope, for the year 1906. Cape Town; Government Printer: 44 pp.

Gislason, H., and J. C. Rice. 1998. Modeling the response of size and diversity spectra of fish assemblage to changes in exploitation. ICES J Mar Sci **55**: 362 – 370.

Gislason, H., M. Sinclair, K. Sainsbury, and R. O'Boyle. 2000. Symposium overview: incorporating ecosystem objectives within fisheries management. ICES J Mar Sci **57**: 468.

Grassle, J. F., and N. J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. Am Nat **139**: 313 - 341.

Greenstreet, S. P. R., and S. J. Hall. 1996. Fishing and the ground fish assemblage structure in the North-westen North Sea: An analysis of long-term and spatial trend. J Anim Ecol **65**: 577 - 598.

Greenstreet, S. P. R., F. E. Spence, and J. A. McMillan. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish species assemblage between 1925 and 1996. Fish Res **40**: 153 - 183.

Gribble, N. A. 2004. A spatially explicit multi-competitor coexistence model of penaeid (shrimp) distribution on the Australian Great Barrier Reef. Ecol Model **177**: 61 - 74.

Grime, J. P. 1997. Biodiversity and ecosystem function: The debate deepens. Science **277**:1260 - 1261.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecol Model **115**: 129 - 148.

Grimm, V., and S. F. Railsback. 2005. Individual based modelling and ecology. Princeton University Press, Princeton.

Griffiths, M. H., and T. Hecht 1995 – On the life history of *Atractoscion equidens,* a migratory sciaenid off the east coast of southern Africa. J Fish Biol **47**: 962 – 985.

Griffiths, M. H. 1997a. Management of South African Dusky Kob *Argyrosomus japonicus* (Sciaenidae), based on per recruit models. S Afr J Mar Sci **18**: 213 – 228.

Griffiths, M. H. 1997b. The application of per recruit models to *Argyrosomus inodorus*, an important South African sciaenid fish. Fish Res **30**: 103 – 115.

Griffiths, M. H. 2000. Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: Snapshots of the 20th century. S Afr J Mar Sci **22**: 81 – 110.

Griffiths, M. H. 2002. Life history of South African snoek, *Thyrsites atun* (Pices: Gempylidae): a pelagic predator of the Benguela ecosystem. Fish Bull **100**: 690 – 710.

Gulland, J. A. 1987. The effect of fishing on community structure. S Afr J Mar Sci **5**: 839 – 849.

Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological dynamics. Oxford University Press, Oxford.

Hall, S. J., S. A. Gray, and Z. L. Hammett. 2000. Biodiversity-productivity relations: an experimental evaluation of mechanisms. Oecologia **122**: 545 - 555.

Haedrich, R. L. and S. M. Barnes. 1997. Changes over time of the size structure in an exploited shelf fish community. Fish Res **31**: 229 – 239.

Hilborn, R., J.-J. Maguire, A. M. Parma, and A. A. Rosenberg. 2001. The Precautionary Approach and risk management: can they increase the probability of successes in fishery management? Can J Fish Aquat Sci **58**: 99 - 107.

Hinckley, S., A. J. Hermann, and B. A. Megrey. 1996. Development of spatially explicit, individual based model of marine fish early life history. Mar Ecol Prog Ser **139**: 47 - 68.

Hinckley, S., A. J. Hermann, and B. A. Megrey. 2001. Importance of spawning location and timing to successful transport to nursery areas: simultation study of Gulf of Alaska walleye pollock. ICES J Mar Sci **58**: 1042 - 1052.

Hollowed, A. B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope, and J. C. Rice. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES J Mar Sci **57**: 707.

Hooper, D. U., and P. M. Vitousek. 1997. The effect of plant composition and diversity on ecosystems processes. Science **277**: 1302 - 1305.

Huse, G., S. Railsback, and A. Ferno. 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. J Fish Biol **60**:571 - 582.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer model unify ecological theory. BioScience **38**: 682 - 691.

Huston, M. A. 1994. Biological diversity: The coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (Gadus morhua). Can J Fish Aquat Sci **62**: 824 - 832.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**: 629 - 638.

Japp, D. W. 1989. An assessment of South African long line fishery with emphasis on stock integrity of kingklip, *Genypterus capensis* (Pisces: Ophidiidae). MSc. Thesis, Rhodes University.

Japp, D. W., P. Sims, and M. J. Smale. 1994. A review of the fish resources of the Agulhas bank. S Afr J Sci **90**: 123 - 134.

Jaureguizar, A. J., R. Mennic, R. Guerrero, and C. Lasta. 2004. Environmental factors structuring fish communities of the R´ýo de la Plata estuary. Ecol Model **66**: 195 - 211.

Jennings, S. and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. Adv Mar Biol **34**: 201 – 251.

Jennings, S., S. P. R. Greenstreet, and J. D. Reynolds. 1999. Structural changes in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. J Anim Ecol **68**: 617 - 627.

Jennings, S., T. A. Dinmore, D. E. Duplisea, K. J. Warr, and J. E. Lancaster. 2001a. Trawling disturbance can modify benthic production processes. J Anim Ecol **70**: 459 - 475.

Jennings, S., M. J. Kaiser, and J. D. Reynolds. 2001b. Marine Fisheries Ecology. Blackwell Science Ltd.

Jennings, S., S. P. R. Greenstreet, L. Hill, G. J. Piet, J. K. Pinnegar, and K. J. Warr. 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable isotope analysis, size-spectra and community metrics. Mar Biol **141**.

Jennings, S., and N. K. Dulvy. 2005. Reference points and reference directions for size-based indicators of community structure. ICES J Mar Sci **62**: 397 - 404.

Jouffre, D., and C. A. Inejih. 2005. Assessing the impact of fisheries on demersal fish assemblages of the Mauritanian continental shelf, 1987 - 1999, using dominance curves. ICES J Mar Sci **62**: 380 - 383.

Jukic-Peladic, S., Vrgoc, N., Krstulovic-Sifner, S., Piccinetti, C., Piccinetti-Manfarin, G., Marano, G., and N. Ungaro. 2001. Long-term changes in demersal resources of the Adriatic Sea: comparison between trawl surveys carries out in 1948 and 1998. Fish Res **53**: 95 – 104.

Kaiser, M. J., K. Ramsay, C. A. Richardson, F. E. Spence, and A. R. Brand. 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. J Anim Ecol **69**: 494 - 503.

Knowlton, N. 2004. Multiple "stable" states and the conservation of marine ecosystems. Prog Oceanogr **60**: 387 - 396.

Lekve, K., G. Ottersen, N. C. Stenseth, and J. Gjosaeter. 2002. Length dynamics in juvenile coastal Skagerrak cod: effects of biotic and abiotic processes. Ecology **86**: 1676 - 1688.

Link, J. S., and L. P. Garrison. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. Fish Res **55**: 71 - 86.

Link, J. S. 2005. Translating ecosystem indicators into decision criteria. ICES J Mar Sci **62**: 569 - 576.

Lomnicki, A. 2002. Physiologically structured populations. Encyclopedia of Life Science

Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Ecol Appl **3**: 547 - 549.

MacAll, A. D. 2002. Fishery-management and stock rebuilding prospects under conditions of low-frequency environmental variability and species interactions. Bull Mar Sci **70**: 613 - 628.

Macpherson, E., and C. M. Duarte. 1994. Patterns in species richness, size, and latitudnal range of East Atlantic fishes. Ecography **17**: 242 - 248.

Magurran, A. E. 2004. Measuring Biological diversity. 2nd Edition. Blackwell Science Ltd., Oxford.

McClatchie, S., R. B. Millar, F. Webster, P. J. Lester, R. Hurst, and N. Bagley. 1997. Demersal fish community off newzealand: Is is related to depth, latitude, regional surface phytoplankton? Deep-Sea Res Part I **44**: 647 - 667.

McQueen, N., and M. H. Griffiths. 2004. Influence of sample size and sampling frequency on the quantitative dietary descriptions of a predatory fish in the Benguela ecosystem. Afr J Mar Sci **26**: 205 - 217.

Mann B. Q. (Ed.) 2000 – Southern African marine linefish status reports. Oceanographic Research Institute, Special Pub. **(7)**: 1 – 257.

Mansergh L., Nicholson, G. T., and R. A. Leigh. 1926. Fishing Harbours Report (Part 1 – 3), Department of Mines and Industries. Cape Town; Government Printer: 70pp. + 36 plates and 10 charts.

Mansergh L., Nicholson, G. T., and R. A. Leigh. 1927. Fishing Harbours Report (Part 4 and 5), Department of Mines and Industries. Cape Town; Government Printer: 85pp. + 19 plates and 8 charts.

Mansergh L., Nicholson, G. T., Leigh R. A., and C. Von Bonde. 1928. Fishing Harbours Report (Part 6 and 7), Department of Mines and Industries. Pretoria; Government Printer: 85pp. + 19 plates and 8 charts.

Micheli, F., P. Amarasekare, J. Bascompte, and L. R. Gerber. 2004. Including species interactions in the design and evaluation of marine reserves: some insights from a predator-prey model. Bull Mar Sci **74**: 653 - 669.

Miller, D. C. M. 2006. An individual based modelling approach to examine life history strategies of Sardine *Sardinops sagax* in the southern Benguela ecosystem. PhD Thesis. University of Cape Town, Cape Town.

Moloney, C. L., Field, J. G. and M. L. Lucas. 1991. The size-based dynamics of plankton foodwebs. II. Simulations of three contrasting southern Benguela food webs. J Plankton Res **13**: 1039 – 1092.

Murray, A. G. 2001. The use of simple models in the design and calibration of a dynamic 2D model of a semi-enclosed Australian bay. Ecol Model **136**: 15 - 30.

Murray, A. G., and J. S. Parslow. 1999. The analysis of altenative formulations in a simple model of a coastal ecosystem. Ecol Model **119**: 149 - 166.

Mueter, F. J., and B. L. Norcross. 1999. Linking community structure of small demersal fishes around kodiak island, Alaska, to environmental variables. Mar Ecol Prog Ser **190**: 37 - 51.

Mueter, F. J., and B. L. Norcross. 2000. Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alska. Can J Fish Aquat Sci **57**: 1169 - 1180.

Mueter, F. J., and B. L. Norcross. 2002. Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alska. Fishery Bulletin **100**:559 - 581.

Ottersen, G., and H. Loeng. 2000. Covariability in early growth and year class strength of Barents Sea cod, haddock, and herring: the environmental link. ICES J Mar Sci **57**: 339 - 348.

Palumbi, S. R. 2004. Why mothers matter. Nature **430**: 621 - 622.

Parada, C., C. D. van der Lingen, C. Mullon, and P. Penven. 2003. Modelling the effects of buoynacy on the transport of anchovy eggs from spawning to the nursery grounds in the souhtern Beguela: An IBM approach. Fish Oceanogr **12**: 170 - 184.

Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature **374**: 255 - 257.

Pauly, D. 1998. Large marine ecosystems: analysis and management. S Afr J Mar Sci **19**: 487 - 499.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and F. Torres. 1998. Fishing down marine food webs. Science. **279**: 860 – 863.

Pauly, D., V. Christensen, and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci **57**: 697 - 706.

Pauly, D., V. Christensen, R. Froese, and M. L. Palomares. 2000. Fishing Down Aquatic Food Webs. Am Sci **88**:1 - 5.

Pauly, D., M. L. Palomares, R. Froese, Pascualita Sa-a, M. Vakily, D. Preikshot, and S. Wallace. 2001. Fishing down Canadian aquatic food webs. Can J Fish Aquat Sci **58**: 51 - 62.

Pauly, D., J. Alder, E. Bennett, V. Christensen, P. Tyedmers, and R. Watson. 2003. The Future for Fisheries. Science **302:** 1359 - 1361.

Pauly, D., and R. Watson. 2005. Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. Phil. Trans R Soc B **360**: 415 - 423.

Payne, A. I. L, Rose, B., and R. W. Leslie. 1987. Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. S Afr J Mar Sci **5**: 471 - 501.

Payne, A. I. L. 1995. Cape Hakes. Pages 380 *in* A. I. L. Payne and R. J. M. Crawford, editors. Oceans of life off southern Africa. Vlaeberg, Cape Town.

Pikitch, E. K., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mengel, M., McAllister, M. K., Pope, J., Sainsbury, K. J. 2004. Ecosystem-Based fisheries management. Science **305**: 346 - 347.

Pillar, S. C., and I. S. Wilkinson. 1995. The diet of Cape hake *Merluccius capensis* on the South coast of South Africa. S Afr J Mar Sci **15**: 225 - 239.

Pinnegar, J. K., Jennings, S., O'Brien, C. M., and N. V. C. Polunin. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market distribution. J Appl Ecol **39**: 377 – 390.

Platt, T and K. Denman. 1978. The structure of pelagic marine ecosystems. Rapp P.-v. Reun Cons Int Explor Mer **173**: 60 – 65.

Punt, A. E., and Leslie, R. W. 1991. Estimates of some biological parameters for the Cape hakes of the South African West coast. S Afr J Mar Sci **10**: 271–284.

Punt, A. E., and D. W. Japp. 1994. Stock assessment of the kingklip *Genypterus capensis* off South Africa. S Afr J Mar Sci **14**: 133 - 149.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologist. Cambridge University Press, Cambridge.

Rademeyer, R. A. 2003. Assessment and management procedures for the hake stocks off Southern Africa. MSc Thesis. University of Cape Town, Cape Town.

Rice, J. C. and H. Gislason. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in survey and models. ICES J Mar Sci **53**: 1214 – 1225.

Rice, J. C. 2000. Evaluating fishery impacts using metrics of community structure. ICES J Mar Sci **57**: 682 – 688.

Rice, J. C. 2003 – Environmental health indicators. Ocean Coast Manage **46**: 235 – 259.

Rice, J. C., and M.-J. Rochet. 2005. A framework for selecting a suite of indicators for fisheries management. ICES J Mar Sci **62**: 516 - 527.

Rijnsdrop, A. D., Van Leeuwen, P. I., Daan. N. and H. J. L. Heessen. 1996. Changes in abundance of demersal fish species in the North Sea between 1906 – 1909 and 1990 – 1995. ICES J Mar Sci **53**: 1054 – 1062.

Roberts, C. M., J. P. Hawkins, and F. R. Gell. 2005. The role of Marine reserves in achieving sustainable sustainable fisheries. Phil Trans R Soc B **360**: 123 - 132.

Rochet, M.-J. 1998. Short term effects of fishing on life history traits of fishes. ICES J Mar Sci **55**: 371 - 391.

Rochet, M.-J., and V. M. Trenkel. 2003. Which community indicator can measure the impact of fishing? a review and proposal. Can J Fish Aquat Sci **60**: 86 - 99.

Rogers, S. I., D. Maxwell, A. D. Rijnsdorp, U. Damm, and W. Vanhee. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. IV. Can comparisons of species diversity be used to assess human impacts on demersal fish faunas? Fish Res **40**: 135 - 152.

Sauer, W. H. H., and M. R. Lipinski. 1991. Food of squid *Loligo vulgraris reynaudii* (Cepahlopoda: Loliginidae) on their spawning grounds off the eastern cape, South Africa. S Afr J Mar Sci **10**: 193 - 201.

Schumann, E. H. 1987. The coastal ocean of the east coast of South Africa. Trans R Soc S Afr **46**: 215 – 228.

Shannon, L. V. and G. Nelson. 1996. The Benguela: large scale features and Processes and system variability. In the South Atlantic: present and past circulation. Wefer, G., Berger, W. H., Siedler, G. and D. J. Webb (Eds.). Berlin; Springer: 163 – 210.

Shannon, L. J., C. L. Moloney, A. Jarre, and J. G. Field. 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. J Mar Syst **39**: 83 - 116.

Shin, Y.-J., and P. Cury. 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquat Living Resour **14**: 65 - 80.

Shin, Y. –J. and P. Cury. 2004. Using an individual based model of fish assemblages to study of the response of size spectra to changes in fishing. Can J Fish Aquat Sci **61**: 414 – 431.

Shin, Y.-J., L. J. Shannon, and P. Cury. 2004. Simulations of fishing effects on the southern Benguela fish community using an individual-based model: learning from a comparison with ECOSIM. Afr J Mar Sci **26**: 95 - 114.

Shin, Y.-J., M.-J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J Mar Sci **62**: 384 - 396.

Smale, M. J. 1991. Occurrence and feeding of three shark species, *Carcharhinus brachyrus, C. obscurus* and *Sphyrna zygnea*, on the Eastern cape coast of South Africa. S Afr J Mar Sci **11**: 31 - 42.

Smale, M. J. 1992. Predatory fish and their prey - An overview of trophic interactions in the fish communities of the West and South coast of South Africa. S Afr J Mar Sci **12**: 803 - 821.

Smale, M. J., B. A. Roel, A. Badenhorst, and J. G. Field. 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. J Fish Biol **43**: 169 - 191.

Stefansson, G., and A. A. Rosenberg. 2005. Combining control measures for more effective management of fisheries under uncertainty: quotas, effort limitation, and protected areas. Phil Trans R Soc B **360**: 133 - 146.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science **277**: 1300 - 1302.

Travers, M., Y.-J. Shin, L. Shannon, and P. Cury. 2006. Simulating and testing the sensitivity of ecosystem-based indicators to fishing in the Southen Benguela. Can J Fish Aquat Sci **63**: 943 - 956.

Traverse, M., Y. Shin, L. Shannon, and P. Cury. 2004. Evaluation of the sensitivity of ecological indicators to fishing using a simulation approach: application to the southern Benguela upwelling ecosystem. ICES CM 2004/ FF:17, 34p.

Trenkel, V. M., and M.-J. Rochet. 2003. Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community. Can J Fish Aquat Sci **60**: 67 - 85.

Trenkel, V. M., J. K. Pinnegar, M.-J. Rochet, and B. D. Rackham. 2004. Different surveys provide similar pictures of trends in a marine fish community but not of individual fish populations. ICES Journal of Marine Sicence **61**:351 - 362.

Versmisse, D., R. Duboz, E. Ramat, Y. Shin, and M. Traverse. Application of an evolutionary algorithm to the calibration of an individual-based model. Ecol Model (submitted).

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. Science **277**: 494 - 499.

Walmsley, S. A., R. W. Leslie, and W. H. H. Sauer. 2006. Managing South Africa's bycatch. ICES J Mar Sci **64**:

Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on the efficacy of marine protected areas: how large should protected areas be? Bull Mar Sci **66**: 745 - 757.

Walters, C., and J. F. Kitchel. 2001. Cultivation/Depensation effects on juvenile survival and recruitment: implication for the theory of fishing. Can J Fish Aquat Sci **58**: 39 - 50.

Warwick, R. M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. Mar Biol **92**: 557 – 562.

Warwick, R. M., Pearson, T. H., and Ruswahyuni. 1987. Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. Mar Biol **95** 193 – 200.

Warwick, R. M., and K. R. Clarke. 1994. Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. Mar Biol **118**: 739 – 744.

Warwick, R. M., and K. R. Clarke. 1995. New 'biodiversity'measures reveal a decrease in taxonomic distinctness with increasing stress. Mar Ecol Prog Ser **129**: 301 - 305.

Wilderbuer, T. K., A. B. Hollowed, W. J. j. Ingraham, P. D. Spencer, M. E. Conners, N. A. Bond, and G. E. Walters. 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Berring Sea. Prog Oceanogr **55**: 235 - 247.

Williams, A., J. A. Koslow, and P. R. Last. 2001. Diversity, density and community structure of the demersal fish fauna of the continental slope off western Australia (20 to 35° S). Mar Ecol Prog Ser **212**: 247 - 263.

Worm, B., and J. E. Duffy. 2003. Biodiversity, productivity and stability in real food webs. Trends Ecol Evol **18**: 628 - 632.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, New Jersey.

Zwanenburg, K. C. T. 2000. The effects of fishing on demersal fish communities of the Scotian Shelf. ICES J Mar Sci **57**: 503 - 509.