EFFECTS OF ENVIRONMENTAL VARIABILITY ON FISH DIVERSITY AND COMPOSITION ALONG THE SOUTHERN NAMIBIAN COASTLINE DURING SUMMER

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Biodiversity Management and Research at the University of Namibia and the Humboldt-Universität zu Berlin

By

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ABSTRACT

Species diversity, richness and composition of fish in bottom-trawling were investigated off the Namibian coast between Oranjemund and Henties Bay. Sampling followed a systematic transects design, along latitude gradients (28-22°S) at different seafloor depths (100-500m). In total 18 transects were sampled containing 105 stations. At each trawled station the whole catch was sorted into species type and the total body mass (kg) of each fish species was recorded. A total of 91 fish species were sampled in the study area. Environmental factors, in particular bottom water temperature, dissolved oxygen and salinity were recorded automatically by the CTD instrument. Results indicated significant differences in means of fish species diversity ($F = 14.01, df = 4, p < 0.001$) and richness ($df = 4, p < 0.001$) at different seafloor depths. Deeper areas were more diverse than shallower area. With regard to latitudinal transect gradients significant differences were observed in means of fish species richness ($df = 6, p < 0.05$) but not diversity ($F = 1.28, df = 6, p > 0.05$). The hierarchical cluster analysis on species presence/absence data separated the fish species composition into six groups, formed at 38% similarity level. Indirect gradient analyses indicated a complex interaction of gradients which have influenced the pattern of species composition. The direct gradient analysis indicates significant influence of water temperature ($F = 4.03, p < 0.05$) and salinity ($F = 1.55, p < 0.05$) on species composition at 100m and 200m seafloor depths. Differences in species diversity and richness of fish at seafloor depths might be a result of absence of disturbances by bottom-trawling at shallower depths. Insignificant differences in species diversity along latitudinal gradients indicate inconsequential effects of global latitudinal trends off the Namibian coast. It was concluded that environmental variabilities off the Namibian coast influence fish species composition.

Key words: Henties Bay, latitudinal gradient, marine environment, Namibia, Oranjemund, seafloor depths, species composition, species diversity.
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DECLARATION

I Festus Panduleni Nashima, declare hereby that this study is a true reflection of my own research, and that this work, or part thereof has not been submitted for a degree in any other institution of higher education.

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GLOSSARY

Analysis of Variance (ANOVA):

This procedure employs the F statistic to test the statistical significance of the differences among the obtained means of two or more random samples from a given population.

Benguela ‘El Niño’:

A southern oscillation event along the southwest coast of Africa that comprises of high sea surface temperature and a nutrient poor surface current that flows over the cold water masses and believed to be similar to El Niño events off the coast of Peru. This anomaly is accompanied by dramatic changes in coastal upwelling, species abundance
and distribution believed to cause massive deaths of fish. The opposite of El Niño is La Niña which is characterized by abnormally cold ocean water temperature in the eastern equatorial Pacific Ocean. Generally these climatic conditions are known as Niños event.

**Biological (biotic) data:**

These are data or measurements collected from biological sources, or simply data collected from living components (biotic) of the environment.

**Canonical Correspondence Analysis (CCA):**

Multivariate technique used for analyzing data on community composition and arranging them along environmental variables.

**Conductivity, Temperature and Depth (CTD) instrument:**

An instrument used to collect water samples at different depths within the water column. This instrument can also be used to determine conductivity, temperature, salinity and oxygen values within the water column through attached sensors.

**Confidence Interval (CI):**
The probability-based statistics that show a number to lie between an upper and a lower limit.

**Demersal fish species:**

These are fish species that live in close relation with the bottom of the ocean. Contrasts with pelagic fish species which live within the water column near the water’s surface.

**Detrended Correspondence Analysis (DCA):**

An indirect gradient analysis technique used to reveal a relationship among various species associations and underlining environmental gradient.

**Environmental (i.e. abiotic) data:**

Data or measurements that describe environmental conditions based on the state of the environment or simply data collected from physical or chemical components of the environment.

**Global Positioning Systems (GPS):**

An electronic device that uses positioning signals from satellites in order to locate precise latitude and longitude points. The GPS is important to locate sampling stations at sea.
Geographic Information Systems (GIS):

This is a system that allows automatic location of information suitable for mapping. Usually involves a software system that takes geographic position data and other data (example temperature) in order to create a map.

Hierarchical Cluster Analysis (HCA):

This is a multivariate analysis technique that involves the grouping of similar entities into classes. This analysis helps to determine if there exist similarities or differences in species composition along a gradient.

Hypoxia condition:

This is a condition of low oxygen concentration, below what is considered as aerobic. Water with oxygen concentrations less than 2ml/l is considered oxygen-deficient, while water with oxygen concentrations more than 5ml/l is considered oxygen-rich.

Kolmogorov-Smirnov test (K-S):

A statistical test used for testing data for normality. If data are normally distributed a parametric statistical test should be carried out, whereas if data are not normally distributed a non-parametric statistical test should be used for analysing data.
Mean (s):

An index of central tendency that statistician use to indicate the point on the scale of measures around which the population is centered. The mean is the most commonly-used type of average and is preferred in mathematics and statistics to distinguish it from other measures of central tendency such as the median and mode. For the comparison among several mean it can be referred to as ‘means’.

Monte-Carlo permutation test:

A statistical approach used to test for significance of relationship in environmental variables along canonical environmental axes.

Nautical miles (Nm):

International unit of distance measurement equal to 1,852 kilometers, mostly measured at sea.

Practical Salinity Unit (PSU):

This is a unit of measurement of salinity similar to parts per thousand (ppt). However, this measurement is based upon electrical conductivity of a sample relative to a reference standard of sea-water.

Shannon-Wiener Index of diversity ($H'$):
A biodiversity index which takes into account both the species richness (the number of species in the system) and evenness (the distribution of relative abundance among species), which are good indicators of species diversity.

**Species diversity:**

Species diversity refers to variabilities within living organisms describing in combination, the species richness and evenness.

**Species richness:**

A measure of the total number of species present at a particular area.

**Upwelling system:**

This is a process by which nutrient-rich water from the bottom of the ocean rises into surface nutrient-deficient waters. Areas with high upwelling intensity are characterized by high productivity which supports high biomass of fish species. The opposite of upwelling is down-welling, created by convergence of surface currents that causes surface waters to sink to lower depths.
CHAPTER 1
INTRODUCTION

1.1 Background

The national economy of Namibia is highly dependent on the extraction and use of natural resources. As a result, environmental factors are critical to sustaining in terms of production and yield. This also impacts on economic activities related to the use of marine resources. Namibian marine resources are dominated by hake species (*Merluccius capensis* and *Merluccius paradoxus*), which are caught by bottom trawling off the Namibian coast (NatMIRC, 2007). In the trawling catches, there are other fish species caught as by-catch, both in Namibian and South African waters. Although by-catch is a common side-effect of directed fisheries, the level depends upon the type of gear used and the amount of effort invested. But this might be associated with environmental variability within the ocean. As a result of environmental variability and fishing there are remarkable changes in distribution of fish species throughout the ocean water column (Gordoa *et al.*, 2006).

The Namibian marine environment falls entirely within the Benguela system, an eastern boundary current upwelling system in the south eastern Atlantic Ocean. The Benguela system extends from Cape Agulhas (35°S) along the southwest coast of Africa into Angolan waters (15°S). The Benguela is one of the four major eastern boundary current
upwelling systems of the world, characterised by the presence of cool surface waters and high biological productivity. The other upwelling systems include the Canary (including the Iberian Peninsula and North West Africa), the Humboldt located off the west coast of South America and the California, located off the west coast of North America. Conditions within the Benguela system changes continuously with regard to physical, chemical and biological conditions and these vary both in time and space (Sakko, 1998).

The changing character of the Benguela ecosystem results in a diversity of marine habitats, characterized by dynamic processes which can cause remarkable changes in distribution of fish species especially in the southern parts of the Atlantic Ocean. There are clear trends of decreasing species diversity from south to north as observed in the marine system off Namibia, which is in accord with global biodiversity trends. This anomaly effect might be a result of natural fluctuations in environmental conditions in the Benguela system. These environmental variabilities in turn may determine and influence the distribution of fish, implying that the catch composition of fish species can fluctuate highly and significant catch of non-targeted species could be made, posing a possible depletion of non-allocated fish species.

The effects of environmental variability on diversity and composition of deepwater fish species is not clearly understood, but could be substantial (Hampton et al., 2003). Thus, the Namibian fishing industry is constantly challenged by environmental influences that may detrimentally affect the catch composition of fish species. Although many studies
have been done, both by private and public initiatives, a greater emphasis has been placed on understanding the biology of the most valuable commercial fish species, in particular hake, Orange roughy, monkfish, horse mackerel, pilchard and large pelagic species (MFMR, 2001), there is an obvious lack of focus on other fish species caught together in trawling as by-catch. The present study emphasises the role of abiotic factors, in particular bottom water temperature, salinity and dissolved oxygen as part of the environmental variability off the Namibian coast.

1.2 Statement of the problem

The Ministry of Fisheries and Marine Resources (MFMR) has appropriate regulations in place for the management of marine resources, through the Namibian Marine Resources Act 2000 (Government Gazette, 2000). Often these regulations are being challenged by commercial fishing fleets assisted by environmental variabilities within the ocean. Environmental variabilities may in turn, determine and influence the distribution of fish species, resulting in significant catches of non-targeted species.

Most surveys favour certain fish species for studies, in particular valuable commercial fish species. This has resulted in a poor understanding of less valuable fish species and could lead to their eventual depletion. Thus, there is need for studies to incorporate the entire catch composition of fish species for better management and conservation of all fish species, regardless of their commercial status.
This study places greater emphasis on the entire catch composition of fish species caught in trawling catches and relates the catches to local factors within the ocean to provide a better understanding of how environmental aspects of the ocean influence the diversity and composition of fish species. In particular, the study aims at collecting relevant environmental data related to the composition of fish species in trawls conducted between Oranjemund and Henties Bay. Since it is presumed that environmental variabilities within the ocean strongly influences the diversity and composition of fish species, the findings from this study might be incorporated into management strategies for better conservation of many more marine resources.

1.3 General project objective

The primary objective of this study is to determine species diversity, richness and composition of fish in bottom-trawling and to relate these parameters to environmental factors of the ocean between Oranjemund and Henties Bay. The scope of the study is confined to fish species with body size greater than 10mm, which can be retained by trawling nets with inner-net mesh sizes of 10mm.
1.3.1 Specific objectives of the study are:

(a) To determine and compare diversity and richness of fish species at the seafloor, at horizontal distance from inshore to offshore.

(b) To determine and compare diversity and richness of fish species along latitudinal transect gradients, at 1 degree intervals between Oranjemund (28°S) and Henties Bay (22°S).

(c) To determine changes in fish species composition along a latitudinal gradient from Oranjemund (28°S) to Henties Bay (22°S) at different seafloor depths.

(d) To determine the influence of dissolved oxygen, water temperature and salinity on fish species composition.

1.3.2 Specific questions related to the research are:

(a) Are there differences in diversity and richness of fish species at the seafloor, at horizontal distance from inshore to offshore?

(b) Are there differences in diversity and richness of fish species along latitudinal transect gradients, at 1 degree intervals between Oranjemund (28°S) and Henties Bay (22°S)?
(c) How does fish species composition differ along a latitudinal gradient from Oranjemund (28°S) to Henties Bay (22°S) at different seafloor depths?

(d) How do dissolved oxygen, water temperature and salinity influence fish species composition?

1.3.3 The working hypotheses of the research could be formulated as follows:

(a) Diversity and richness of fish species are expected to increase along the seafloor, at horizontal distance from inshore to offshore due to high concentration of dissolved oxygen which is essential for fish respiration. This hypothesis is based on the assumption that dissolved oxygen concentration increases with increasing distance from the shore, influenced by decreases in water temperature.

(b) Diversity and richness of fish species are expected to decrease along the latitudinal transect gradients, at 1 degree intervals between Oranjemund (28°S) and Henties Bay (22°S). This is because of higher productivity toward the equator which positively influences diversity and richness of fish species.
(c) Species composition of fish is expected to differ along a latitudinal gradient from Oranjemund (28°S) to Henties Bay (22°S) at different seafloor depths. This is because the ocean is not uniform and is characterized by dynamic processes which can cause changes in microhabitats, which in turn influence fish species composition.

(a) Environmental factors (dissolved oxygen, water temperature and salinity) are expected to influence fish species composition. This is based on the assumption that some fish species may not be present at some trawled stations due to differences in adaptation and tolerance to environmental factors.
CHAPTER 2

LITERATURE REVIEW

2.1 The Namibian coastal area and its environment: An overview

The Namibian coastline stretches from the Orange River mouth (28°S) in the south to the Kunene River mouth (17°S) in the north, over an approximate distance of 1500 km (Van Zyl, 2000). The shore is dominated by sandy beaches with occasional rocky outcrops, which are exposed to heavy wave action. The continental shelf off the Namibia coast is generally narrow and believed to be one of the deepest in the world, with an average shelf edge depth of 350m (Shannon, 1985).

The Namibian coastal environment is dominated by the Benguela ecosystem, which has a decisive influence on Namibia’s marine resources. The system is continuous with an unusually intense cell of upwelling off Lüderitz, which effectively divides it into two parts – a southern Benguela system that extends to Lüderitz, and the northern Benguela system north of Lüderitz. The northern part is believed to constitute greater number of fish species due to increased productivity, but it might also be related to variabilities in temperature linked to changes in upwelling intensity (Stromme, 1995; Van Zyl, 2000).
2.2 Namibian marine biodiversity

The larger coastal environment of Namibia is associated with relatively low species richness. This is in accordance with the global trend of species richness that it is highest in equatorial regions and lowest at the poles. However, in Namibia the marine diversity provides an anomaly along this gradient since species richness is substantially lower than in the more southerly marine habitats off South Africa (Sakko, 1998). In addition, there is a clear trend of decreasing species richness from south to north in the marine system off Namibia (Van Zyl, 2000). This anomalous effect might be the result of natural fluctuations in environmental conditions in the Benguela system, which appears to be less pronounced in the north. According to Shannon (1985) these fluctuations are believed to be inherent in the functioning of the system, and could mean that most species that persist have evolved mechanisms for coping with such inherent variability.

According to Hampton et al., (2003) not much is known about the behaviour of fish in response to environmental variability within the Namibian ocean. However, it is believed that environmental variability can directly affect the species composition and abundance of fish species (Hampton et al., 2003). These environmental perturbations are also believed to be responsible for incidental catches of fish in trawling catches. The distribution of fish in response to environmental variability within the water column implies that indirectly fish could be subjected to both targeted and non-targeted catches.
An improved understanding of environmental variability in relation to catch composition of fish species in the Benguela ecosystem is very important and could be achieved through research. Better catches influence the livelihoods of many Namibians directly as well as indirectly, firstly in the form of employment as well as through cash remittances from those that are employed. In addition, an improved understanding of the interdependence between species of the Benguela ecosystem and an expected escalating environmental variability in response to climate change is highly relevant.

2.3 Environmental variabilities within the ocean

2.3.1 Temperature

Temperature of the ocean is generally subjected to changes at the surface and close to the shore, where water temperature varies seasonally and according to latitude zones (Buchheim, 2005). As a rule of thumb, ocean temperature increases towards the equator. On the western sides of the continents the tropical surface water turns increasingly warmer northwards. In Namibia, the ocean is surprisingly cool due to the influence of the cold Benguela Current, flowing from south to north (Gordoa et al., 2006).
It is well-known that temperature plays an important role in the physiology of fish species, which involves a multiple of processes such as metabolism, reproduction and distribution. Consequently, temperature determines what kinds of fish species can survive and how well the various species can function. Furthermore, it is believed that increases in temperature double the rate of chemical reactions and this may have some bearing on the activities of fish cells (Jobling, 1995). Notably, temperature has direct relation with the dissolved oxygen concentration. Warm water is relatively less oxygenated than cooler water. As a result, temperature is significant in determining fish abundance and distribution (Macpherson et al., 1991).

Studies on the Namibian marine environment showed that several fish species, and in particular hake species have a positive correlation with seawater temperature, as observed in the years 1994 to 1995 (Boyer et al., 1998). During these periods, abnormal warm surface temperature of 2°C above the average were recorded in the upper 10m of the central shelf region off Walvis Bay that caused a southward shift in sardine population (Boyer et al., 1998). In contrast, in 1993 and 1997, a southward advection of oxygen-poor water on the shelf was observed which negatively affected fish species: this was associated with the intrusion of Benguela events known as Benguela Niños (Boyer et al., 1998).
2.3.2 Salinity

Salinity can be defined as the total weight (in grams) of organic salts dissolved in 1 kg of seawater, or simply the salt content of seawater (Lalli et al., 1997). The amount of dissolved salt or salinity varies between ocean zones as well as across oceans. The average salt content of the ocean is believed to be about 35 parts per thousand (ppt), but can vary at different latitudes depending on precipitation and evaporation rates. Salinity is believed to be lower near the equator than at middle latitudes due to a higher rainfall amounts at the equator (UCAR, 2000).

Different fish species are adapted to different salinity levels therefore low salinity water combined with hypoxic condition is believed to be detrimental to fish growth and survival. Generally, low salinity environments tend to cause stress to fish leading to high mortality due to reduced survival ability, poor feed intake, resulting in low productivity (Sarma et al., 2005). The overall effect is to affect species diversity and composition of fish species in the ocean.

In most cases, marine invertebrates and some fish species (in particular sharks and rays), have a blood salt content that is about the same as the average salinity of seawater. However, in bony fish (teleosts), the salt concentration of the blood is only about 30-50% of ambient salinity, and is believed to have several physiological consequences on
teleost fish (Lalli et al., 1997). Because there is a tendency for water to move across semi-permeable membrane from a zone of low salt concentration to one of high salt concentration (a process called osmosis), marine fish tend to lose water and increase their internal salt concentration. As a result, most fish have evolved various physiological mechanisms of osmoregulation that counteract this problem including the excretion of very small quantities of urine and secretion of salts across gills (Lalli et al., 1997). Such physiological mechanisms in teleost fish, enables them to withstand increased salt concentration in marine environments.

2.3.3 Dissolved oxygen

In the ocean dissolved oxygen is available as a by-product of photosynthesis, while also diffusing into the surface water from the atmosphere. Life below the sea surface depends on vertical circulation processes to replenish oxygen at depth (Scholes, 1982). This occurs through turbulent water mixing and the down-welling process which carries oxygenated water to greater depths. When oxygen supply is insufficient for the fish (i.e. to meet the minimal energy demands of essential functions), suffocation occurs. Therefore, dissolved oxygen is essential in marine ecosystems for respiration, and enabling fish to liberate energy from organic compounds (Kramer, 1987).
It is believed that most fish species have developed an alternative behavioural response to reduced dissolved oxygen concentration by changes in activity and understanding vertical or horizontal movements according to habitat changes (Kramer, 1987). The effects of reduced oxygen on activity are inevitable because of the coupling mechanisms between oxygen and energy budgets. More energy must be allocated to breathing when oxygen availability is reduced in order to maintain the same oxygen supply to tissues. With a reduced oxygen concentration several activities, such as feeding are strongly affected. Digestion and assimilation can not be met under hypoxic conditions (low oxygen concentration), as oxygen is a major components of energy budget for many fish species (Hoar et al., 1979).

Inducing habitat change is a very obvious behavioural response of fish to hypoxic conditions. While fish may not necessarily recognise hypoxic water per se, escape movements may be induced by respiratory distress. As a result, the affected species might move to sites of higher oxygen availability. Nevertheless, habitat shifts are likely to have cost implications in food availability, risk of predation and exposure to other physico-chemical conditions (Kramer, 1987). Several studies have shown instances where fish species migrate away from areas with hypoxic conditions. Hamukuaya et al., (1998) observed juveniles fish migrating away from inshore to offshore, avoiding oxygen-deficit water.
The occurrence of oxygen-depleted water in the Benguela ecosystem has been documented by Shannon and O’Toole (1999). It was recorded that water with oxygen concentrations of less than 2ml/l is oxygen-deficient, while water with more than 5ml/l is oxygen-rich with respect to fish of the Benguela ecosystem. The authors suggested that oxygen-deficient water might be a result of processes associated with underwater currents, characterized by higher temperatures. Warm-water flows southward along the Namibian coastal shelf at 200-400m depths and is responsible to reduce dissolved oxygen concentration to as low as < 2ml/l (Barnard 1998, p.191).

Hart and Curie (1960) have demonstrated the existence of an oxygen-deficient layer overlying the continental shelf north of Walvis Bay. Subsequent studies concluded that the central region (off Walvis Bay at about 23°S50’S) retained oxygen-deficient waters for most time of the year. Furthermore, low oxygen conditions can exist on the shelf further south as well, for example this is the case near the Orange River and around St Helena Bay (Hamukuaya et al., 1998). It can thus be concluded that oxygen-depleted subsurface water is a characteristic feature off the Namibian coast.

Another view on oxygen-deficits in the Namibian water is related to decaying organic matter from phytoplankton blooms, which leads to high accumulation of organic material in the water that eventually settles at the bottom of the ocean (Mann and Lazier,

2.3.4 Climatic changes and seasonality

There is evidence that the Benguela system has highly been impacted by climate change and environmental variability over the past half century (Hampton et al., 2003). It is concluded that significant changes in the global climate have a very strong impact on the Benguela system. Increases in ocean temperature and sea level (the latter is expected to increase by about 50cm by the end of the 21st century), through changes in wind. Coastal winds are likely to strengthen and thus upwelling events will intensify and are likely to expand the present upwelling areas. In turn this would have decisive effect on primary production in the Benguela Current Large Marine Ecosystems (Shannon and O’Toole, 1999).

Seasonal climatic changes may be reflected in benthic communities because of the differences in the amounts of detritus material reaching the sea-bed. This may provide food resources for bottom living organisms, some of which might be specialists (Summerhayes and Thorpe, 1996). However, if specialists are absent, bacterial organisms in the mud may multiply and take over the task of decomposition and use oxygen, resulting in hypoxic water. The decomposers might be less pronounced in upwelled areas.
Over the last 400 000 years the earth's climate has been unstable, with significant changes in environmental variabilities of the ocean (Bartholomae, 2008). It has been shown that environmental factors of the ocean are subjected to seasonal changes. Sea-surface temperature off the Namibian coast exhibits a strong seasonal signal with higher temperature in summer and autumn and cooler conditions during winter and spring (Bartholomae, 1996).

Salinity is observed to be at maximum during summer and autumn as a result of the annual southward movement of warm saline water into northern and central Namibia. Dissolved oxygen tends to be minimal in autumn and can be attributed to high water temperature which decreases the solubility of oxygen in water. In general, oxygen concentration in deeper layers is much lower than in surface water. During October there is a slight increase that could be attributed upwelling, which moves high oxygenated water into deeper water (Bartholomae, 1996).

According to Bartholomae (2008), several signals of changes in climate have been observed to affect the Benguela system. These include a reduction in coastal upwelling, increased frequency and severity of Benguela El Niño events and an increase in average summer wind stress. The likely consequences of these changes could, according to Bartholomae (2008), lead to a warm tropical low productive system, which would affect the entire ecosystem. Fish distributions, species composition and abundance would
change, making the fisheries flexible and adaptive to a changing system (Bartholomae, 2008).

In conclusion any change, in frequency, timing and spatial distribution of upwelling could create significant impacts on marine biodiversity (Castro and Huber, 1997). Although the tolerance level of most species in relation to physical features of the Benguela ecosystem is known, there is a lack of information on the distribution and abundance of species in response to environmental variability (Hampton et al., 2003). Investigations in this regard will provide helpful insight in the aggregation of non-targeted species in trawling catches.

2.4 Diversity measures in community studies

Complexity in community ecology requires a dualistic assessment of data to depict species and the abundance of species. The assessment is normally conducted using diversity indices which can group data into a single evaluation index for each sample to allow inference from the data in a statistical sense. Many diversity indices have been developed and the most common one in use concern species diversity and richness (Clarke and Warwick, 2001). These diversity indices have been developed by ecologists interested in understanding patterns of spatial and temporal variation in diversity, and are regarded as indicators of the well-being of ecological systems (Magurran, 1988).
Species diversity indices determine the equitability components of diversity to varying degrees. The most commonly used index to measure species diversity is the Shannon-Wiener Index of diversity which takes into account both the species richness and evenness, and therefore qualifies as a good indicator of species diversity. Species richness is simply referred to as the total numbers of species present (Krebs, 1989). In Namibia, several authors (Hamukuaya, Bianchi and Baird, 2001) in marine research have shown great interests in the use of diversity indices as means of environmental monitoring and depicting patterns in marine species.

2.5 Analysis of species composition and environmental relationships

The Hierarchical Cluster Analysis (HCA) is a type of analysis that classifies sites or variables and helps to find structure in species data. This analysis involves the grouping of similar entities together into several groups (Everitt, 1993; Gauch, 1982). The results of hierarchical clustering are represented by dendrogram with the x-axis representing the full set of samples and the y-axis defining a similarity or dissimilarity level at which two samples or groups are considered to have fused (Clarke and Warwick, 2001). This classification method has been developed by ecologists and is in use, both in terrestrial and marine studies. The classification gives information on the occurrence of species and detects relationships between communities and their environment by analysis of groups formed by the clustering process (Van Tongeren, 1986).
The inferring of species composition to known environmental variables becomes vital to an understanding of the complexity of community ecology (Ter Braak, 1986). Several multivariate techniques have been developed to relate community composition to known environmental variables. The most used technique is the ordination analysis that helps arrange sites along axes on the basis of data on species composition. The term ordination was introduced by Goodall (1954) and stems from the German word ‘Ordnung’ which was used by Ramensky (1930) to describe this approach (Ter Braak, 1995).

The result of the ordination along two dimensions (two axes) is a diagram in which sites or species are represented by points while vectors (arrows) represent environmental variables. These points are arranged so that points that are close together correspond to sites that are similar in species composition and vice versa (Jongman et al., 1995). The head of the arrow for an environmental variable depends on the correlations of such environmental variable with the axes and the sites or species correlated with them (Ter Braak, 1986).

Both the classification and ordination methods are currently in use in research done by various multidiscipline’s around the world. Hamukuaya, Bianchi and Baird (2001), are among marine researchers in Namibia interested in the application of such methods (Hamukuaya et al., 2001).
CHAPTER 3

METHODS AND MATERIALS

3.1 Study area

The study area is located between Oranjemund (28°S) and Henties Bay (22°S) in an area perpendicular to the coastline of Namibia on the southwest coast of Africa (Figure 1). Namibia is situated in the southwest of the African continent and it is bordered by the Atlantic Ocean on the west, Angola to the north, Botswana to the east, Zambia and Zimbabwe to the northeast and South Africa to the south.

Figure 1: The study area off the Namibian coast.
The study area falls within Namibia’s 200 Nautical miles (Nm) Exclusive Economic Zone (EEZ) over which Namibia have sovereign rights within its EEZ to control the use and exploitation of marine resources in a sustainable way, as stated in the Sea Fishery Act (29 of 1992) (Government Gazette, 2000). The darkened points in Figure 1 represent one-hundred and five (105) sampling stations off the Namibian coast.

3.2 Study design

Sampling followed a systematic transect design, with a semi-random distribution of stations along transects, selected in such a way that each 100m seafloor depth has at least one station. The study was designed in such a way that latitudinal lines (i.e. 28°S, 27°S, 26°S, 25°S, 24°S, 23°S and 22°S) between Oranjemund and Henties Bay each consists of at least three transect lines (as replicates). In total 18 transects were sampled. Transects were about 20-25 Nautical miles (Nm) apart, with transect lengths of about 80 Nm.

3.3 Collection of abiotic and biotic data

Data collection was conducted during the period 10 January – 30 February on-board the *FV Blue Sea 1* vessel during the annual National Marine Information and Research Centre (NatMIRC) fish survey. These types of surveys are aimed to determine fish
biomass off the Namibian coast. Sampling was conducted throughout the day from 06h00 until 24h00.

Biological data were sampled at all stopover stations (105 stations in total) within the study area but environmental data were only sampled at 58 stations due to time limitation, and this was roughly done depending on the distance between stations. The *FV Blue Sea 1* vessel (research vessel) was used for the survey and a *Gisund Super two-panel* bottom trawl net was used for trawling (net towed behind a vessel). The outer lining of the cod-end mesh size was 20mm while the inner-net was 10mm.

3.3.1 Collection of abiotic data

Spatial information, in particular trawling seafloor-depth, bottom water temperature, dissolved oxygen and salinity were monitored and recorded automatically by the Conductivity, Temperature and Depth (CTD) instrument. The CTD instrument collects measurements at 1-meter interval but for the purpose of this study, dissolved oxygen (ml/l), temperature (°C) and salinity (PSU) were selected for bottom depths (m) of each station. Information recorded by the CTD instrument can directly be imported into the computer on board of the vessel. An automated vessel GPS (Global Positioning Systems) was used to record the coordinates at each trawling station and were plotted using *ArcView GIS 3.2* software programme to indicate the trawled stations and the relevant sets of information.
3.3.2 Collection of biotic data

At each trawled station, the whole catch was brought on deck and sorted into species type. Sorting was done manually by fishery scientists from the National Marine and Information Research Centre with student assistance from the University of Namibia. After sorting, fish numbers were counted for determination of fish species richness. A scale instrument was used to determine measurements of the total body mass (kg) of each fish species. Measurements of total body mass (kg) of fish species were used for calculating biodiversity indices. After completion of measurements, sampled fish were packed in boxes for the National Marine Aquarium of Namibia to be used as fish feed.

3.4 Data manipulation and analysis

The statistical packages SPSS 14.0, Primer 5.0 and CANOCO 4.5 for Windows were used to analyze the data pertaining to species diversity, richness and composition of fish in relation to environmental parameters. The Kolmogorov-Smirnov (K-S) test was used to test whether data for fish species diversity, richness and environmental variables (i.e. bottom water temperature, oxygen and salinity) follows a normal distribution.
The total body mass (kg) of fish species caught at each trawled station was used as surrogate for proportional abundance of fish species:

\[ p_i = \frac{n_i}{N} \]

- Where \( p_i \) is the relative proportional abundance (Kg) of fish belonging to the \( i^{th} \) species \( (n_i) \), \( N \) is the total body mass (kg) of all fish species in the trawled sample at \( i^{th} \) station (Brower and Zar, 1984).

3.4.1 Species diversity and richness of fish

The Shannon-Wiener Index of diversity \((H')\) was calculated for each trawled station using the proportional abundance (kg) of fish species caught by the net:

\[ H' = -\sum (p_i) \cdot (\ln p_i) \]

- Where \( H' \) is the information content of sample (value of Shannon-Wiener Index of diversity); \( \ln \) is the natural logarithm (in particular a natural logarithm to the base of \( e \) is preferred and commonly used), while \( p_i \) is the proportion of total sample belonging to \( i^{th} \) species (Mfune, 2007; Magurran, 1998).
To determine species diversity of fish at 100m, 200m, 300m, 400m and 500m seafloor depths and along latitudinal transect gradients at 28°S, 27°S, 26°S, 25°S, 24°S, 23°S and 22°S, proportional abundance of fish species caught per trawled station was used to calculate species diversity applying the Shannon-Wiener Index of diversity. The species richness of fish was calculated as the number of fish species caught at each trawled station.

The One-way Analysis of Variance (ANOVA) was used to test for significant differences in species diversity of fish at different seafloor depths and along latitudinal transect gradient. Seafloor depths and latitudinal gradient were analysed separately. The ANOVA is a parametric equivalent that analyses one-factor (i.e. seafloor depths or latitude) that affect a response variables (i.e. species diversity) (Dytham, 2006). To determine which means differs, Bonferroni (equality of variance assumed equal) or Dunnet’s post-hoc (equality of variance assumed not equal) tests were performed on SPSS 14.0 for Windows statistical programme (Webstat, 2000).

Species richness data were not normally distributed. Consequently, a Kruskal–Wallis test (a non-parametric statistical test as alternative for ANOVA, when the assumption of normality is not met) was used to test for significant differences in fish species richness at the seafloor depths and along latitude transect gradients. Mann-Whitney U tests was used to determine which means differs.
3.4.2 Determinants of fish species composition

The Hierarchical Cluster Analysis (HCA) using average linkage method was performed on species-transect matrix data from 105 stations and containing 91 fish species for presence or absence data. This test was carried out using Primer 5.0 for Windows to produce a classification identifying similarities among seafloor depths and latitudinal gradient based on species composition.

For ordination, a Detrended Correspondence Analysis (DCA) was applied to presence/absence species data analyzed using CANOCO 4.5 for Windows. The DCA is an indirect gradient analysis widely used in the exploration of ecological data. DCA provides a non-linear rescaling of the ordination axes in units of mean standard deviation of the species turnover (Dytham, 2006).

The Canonical Correspondence Analysis (CCA) was used to relate fish species composition to measured explanatory variables consisted of bottom water temperature, dissolved oxygen and salinity. The CCA is a direct gradient technique which identifies an environmental basis for community ordination by detecting the patterns of variation in community composition that can be best explained by the environmental variables (Jongman et al., 1995). Monte-Carlo permutation test was used to test for significant influence of each environmental variable on species composition.
4.1 Species diversity and richness of fish at the seafloor depths

A total of 91 fish species were investigated during the present study. Observed fish species comprises of varieties of fish species of different body sizes and lengths. The diversity of fish species were investigated at various localities within the study area as characterized by their physiological and behavioural adaptation. No ‘new’ fish species were recorded during this study.

The results indicated differences in means of species diversity and richness of fish off Namibian coast as observed at different seafloor depths. It was observed from Figure 2 that inshore areas (100-200m seafloor depths) are less diverse than offshore area (300m, 400m and 500m seafloor depths). Species diversity tends to increase from inshore to offshore within the study area and was observed to be lower at 100m and 200m seafloor but higher at 300m, 400m and 500m seafloor depths (Figure 2).
Fish species diversity at 100m and 200m was $H' = 0.87$ whereas at 300m, 400m and 500m seafloor depths were the value of $H' = 1.25, 1.36$ and 1.46 respectively. The comparison of means in fish species diversity indicated significant differences among seafloor depths ($F = 14.018, df = 4, p < 0.001$) as indicated by dissimilar asterisks above error bars (Figure 2). The Leven’s test of homogeneity of variance assumed was not equal ($t = 7.98, df = 4, p < 0.01$). *Dunnett’s post-hoc* test indicated significant differences among the following groups: (a) 100m and 200m and (b) 300m, 400m and 500m seafloor depths ($p \leq 0.05$).

**Figure 2**: Comparison of means species diversity at the seafloor depths (m). Error bars indicate 95% confidence interval of the mean.
Similar trends observed in fish species diversity (Figure 2) was also found in species richness. The means of fish species richness increased from inshore to offshore. With regard to horizontal distance, minimum species richness was found at 100m seafloor depth and maximum at 500m seafloor depth (Figure 3).

**Figure 3**: Comparison of means species richness at the seafloor depths (m). Error bars indicate 95% confidence interval of the mean.

The general trends compares means of fish species richness indicates an increase from inshore to offshore seafloor depths. The lowest mean observed species richness (S = 7) was recorded at 100m seafloor depth and the highest (S = 13) at 500m seafloor depth (Figure 3). The means species richness of fish at 100m, 200m, 300m, 400m and 500m seafloor depths were 7, 11, 12 and 13 respectively. Significant differences were observed in means of species richness among seafloor depths ($df = 4$, $p < 0.001$). The
Mann-Whitney U test indicated that significant differences were found among the following groups: (a) 100 and 200m and (b) 300m, 400m and 500m seafloor depths ($p < 0.05$).

4.2 Species diversity and richness of fish along latitudinal transect gradient

Means of fish species diversity fluctuated along latitudinal gradient. A comparison of means in fish species diversity indicated that species diversity was relatively high at 28°S and low at 26°S latitude (Figure 4).

![Figure 4: Comparison of means in species diversity of fish along latitudinal transect gradient between Oranjemund (28°S) and Henties Bay (22°S). Error bars indicate 95% confidence interval of the mean.](image)
An analysis of variance (ANOVA) indicated non-significant differences in means of species diversity along latitudinal transect gradient ($F = 1.281, df = 6, p > 0.05$). Although there were no significant differences observed in means of fish species diversity (Figure 4) it was observed that the means in fish species diversity was relatively high ($H’ = 1.66$) around Oranjemund (28°S) and lower ($H’ = 1.08$) at Lüderitz (26°S) area.

Results on the comparison of means in fish species richness varies slightly from fish species diversity shown in Figure 4. The means of fish species richness are depicted in Figure 5.

**Figure 5**: Comparison of means in species richness of fish along latitudinal transect gradient between Oranjemund (28°S) and Henties Bay (22°S). Error bars indicate 95% confidence interval of the mean.
Significant differences in means of fish species richness were observed along latitudinal transect gradient ($df = 6$, $p < 0.05$). The Mann-Whitney U test indicated that significant differences in means of fish species richness exist between 26°S and 28°S latitudes ($p < 0.05$) as indicated by dissimilar asterisks above error bars (Figure 5). Noteworthy, fish species richness was lower ($S = 9$) around Lüderitz (26°S) than around Oranjemund (28°S) ($S = 14$).

4.3 Determinants of fish species composition

4.3.1 Classification of fish species composition

The HCA dendrogram separated the fish species composition into six main distinct groups, formed at 38% similarity level (Figure 6). Clusters were generated using absence and presence of data containing 91 fish species collected in the study area. The HCA revealed a classification of several fish species into similar groups with regard to seafloor depths and latitudinal gradient (Figure 6).
Figure 6: Hierarchical Cluster Analysis (HCA) dendrogram showing similarity of fish species composition at the seafloor depths along latitudinal gradient from Oranjemund (28°S) to Henties Bay (22°S) based on presence/absence of data. *Cluster coding: S - station number, L – latitudinal position, D - seafloor depth.
Cluster 1 was dominated by the MELANOSTOMITIDAE (family name; Table I) and was predominant south of 28°S latitude, (i.e. at Oranjemund area) with an average seafloor depth of 100m. Cluster 2 was formed by species from stations found at 22°S latitude where the seafloor depth is 200m (except station 100 (S1)) and was dominated by *Merluccius capensis*. In cluster 3, there were two sub-clusters (1 and 2) be identified. It is clear from sub-cluster 1 that stations 34, 35, 46, 47, 56 and 57 sampled at the 100m depth had a 100% similarity in fish species composition. Sub-cluster 2 was formed by species from stations at varying latitudes, at 100m and 200m seafloor depths. Cluster 3 was dominated by both *Merluccius capensis* and *Merluccius paradoxus* (Figure 6).

Cluster 4 was formed by species found at 22°S latitude except for one station sampled at 28°S latitude. Cluster 5 was formed by species from stations at 28°S latitude inshore, showing a 60% similarity level in species composition, dominated by *Nezumia micronychodon*. Cluster 6 was generally dominated by the *Merluccius capensis* (Table I) in which three sub-clusters (1, 2 and 3) can be observed. The sub-cluster 1 was formed by species from stations at 23°S latitude and 300m seafloor depth. Sub-cluster 2 contains species assemblage sampled at 300m and 400m seafloor depths while sub-cluster 3 was sampled at 500m recording a 50% similarity level in species composition (Figure 6). Sub-clusters 2 and 3 were formed by species from stations found at varying latitudes.
Clusters formed by HCA dendrogram contained numerous fish species with *Merluccius paradoxus* commonly found at each cluster. *Merluccius capensis* was the dominant fish species among clusters and dominated two of the six clusters (cluster 2 and 6; Table I).

**Table I**: The proportional abundance and percentage contribution of fish species in each cluster.

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Species Name</th>
<th>Common Name</th>
<th>Proportional abundance (kg)</th>
<th>Percentage contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Paracallionymus costatus</em></td>
<td>Cape dragonet</td>
<td>0.232</td>
<td>7.74</td>
</tr>
<tr>
<td></td>
<td><em>Triplophos hemingi</em></td>
<td></td>
<td>0.170</td>
<td>5.68</td>
</tr>
<tr>
<td></td>
<td>MELANOSTOMITIDAE (family name)</td>
<td>Scaleless black dragon fishes</td>
<td>0.648</td>
<td>21.60</td>
</tr>
<tr>
<td></td>
<td><em>Merluccius paradoxus</em></td>
<td>Deepwater Cape hake</td>
<td>0.441</td>
<td>14.70</td>
</tr>
<tr>
<td></td>
<td><em>Maulisia microlepis</em></td>
<td></td>
<td>0.196</td>
<td>6.54</td>
</tr>
<tr>
<td></td>
<td><em>Trachipterus trachypterus</em></td>
<td>Peregrine ribbonfish</td>
<td>0.247</td>
<td>8.23</td>
</tr>
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<td></td>
<td><em>Chelidonichthys capensis</em></td>
<td>Cape gurnard</td>
<td>0.304</td>
<td>10.14</td>
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<td></td>
<td><em>Hoplostethus melanopus</em></td>
<td>Small scale slime head</td>
<td>0.177</td>
<td>5.90</td>
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<td>Cape gurnard</td>
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<td>6.26</td>
</tr>
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<td>3</td>
<td><em>Sufflogobius bibarbatus</em></td>
<td>Pelagic goby</td>
<td>1.954</td>
<td>6.30</td>
</tr>
<tr>
<td></td>
<td><em>Caelorinchus simorhynchus</em></td>
<td>Banded whiptail</td>
<td>2.193</td>
<td>7.08</td>
</tr>
<tr>
<td></td>
<td><em>Nezumia micronychodon</em></td>
<td>Small tooth grenadier</td>
<td>1.781</td>
<td>5.75</td>
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<td>Cape hake</td>
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4.3.2 Indirect gradient analysis of fish species composition

The results of the DCA applied to 58 stations and 91 fish species indicate a division of fish species composition into five groups along variable latitudinal gradient at different seafloor depths (Figure 7).
Figure 7: Detrended Correspondence Analysis (DCA) ordination diagram showing the separation of fish species composition along latitudinal gradient at different seafloor depths. * Roman numerals denote seafloor depths (i.e. I - 100m, II – 200m, III – 300m, IV – 400m and V – 500m), while symbols represent latitudes (i.e. ● - 22°S, ◊ - 23°S, ♦ - 24°S, □ - 25°S, ○ - 26°S, ■ - 27°S and ∆ - 28°S).

Group 1 is associated with species composition sampled at 100m seafloor depth. The 100m seafloor depth is characterized by continuous changes in environmental conditions as influenced by atmospheric weather. Groups 2, 3 and 4 are formed by species composition sampled at 200m, 300m and 400m seafloor depths, respectively. Group 5 contains assemblages collected at 500m seafloor depth.
The observed patterns of grouping indicate a complex interaction of gradients which might have influenced species composition especially along DCA 2 axes. The gradient along DCA axis 1 is mainly associated with increasing seafloor depths which can influence fish species composition. The results of the DCA (Figure 7) indicate that Axis 1 accounts for 55.5% of the variation in species data whereas Axes 2, 3 and 4 have account for 42.0, 24.9 and 16.4% species variation respectively. The groups’ separation was greater along axis 1 which has a longer gradient than along Axis 2. There are about 100% species turn-over from the left-most (latitude 25°S, seafloor depth 100m) station in group 1 and right-most station in group 5 (latitude 24°S, seafloor depth 500m).

4.3.3 Species composition and environmental variables

Bottom water temperature, dissolved oxygen and salinity recorded by the CTD-instrument were plotted for each station to determine the variation in environmental differences along the Namibian coastal shelf. Slight changes observed in environmental factors were not significant.
(a) Seafloor depths (m)

Seafloor depths tend to increase with increasing distance from inshore to offshore along the Namibian coastal shelf as indicated in Figure 8.

![Figure 8](image_url)

**Figure 8**: Comparison of changes in seafloor depths (m) along the Namibian coastal shelf. Inshore areas are characterized by shallower seafloor depths of about 100m and tend to increase with distance from the shore. In the study area the seafloor depths ranges between 100-500m.

(b) Dissolved oxygen concentration (ml/l)
The changes in the amounts of dissolved oxygen concentration along the Namibian coastline are indicated in Figure 9.

**Figure 9**: Comparison of changes in the amount of dissolved oxygen concentration (ml/l) along the Namibian coastal shelf.

The amounts of dissolved oxygen concentration increase from inshore to offshore, but several observations could be made in addition. There is a tendency for higher amounts of dissolved oxygen concentration being found in the south (Oranjemund area) and declining towards the Henties Bay area. Noteworthy is the amount of dissolved oxygen
concentration that shows an increase around the shore of the Lüderitz area, indicating the existence of an anomaly in the general pattern.

(c) Salinity (PSU)

Changes in salinity levels (PSU) between Oranjemund and Henties Bay are indicated in Figure 10.
Salinity levels are characterized by slight changes along the Namibian coastline which ranges between 34.34 and 35.38 PSU. Noteworthy, was the fact that salinity levels were relatively high inshore (~35 PSU) than offshore (~34 PSU). This might be due to higher inshore temperatures, which would increase the rate of evaporation.

(d) Temperature (°C)
Changes in water temperature along the Namibian coastal shelf are shown in Figure 11.

Figure 11: Comparison of changes in water temperature (°C) along the Namibian coastal shelf.

Temperature of the water is generally higher inshore than offshore and also tends to increase towards the Henties Bay area. As depicted in Figure 11 temperature of the water fluctuates between 5.7 and 13.8°C. This pattern correlates negatively with the dissolved oxygen concentration, shown in Figure 10.

4.3.4 Relationship between species composition and environmental variables
The CCA diagram (Figure 12) displays the station points along each of the environmental factors.

**Figure 12:** The Canonical Correspondence Analysis (CCA) diagram showing the relationship between sampling sites and environmental factors. * Roman numerals denote seafloor depths (i.e. I -100m, II – 200m, III – 300m, IV – 400m and V – 500m), while symbols represent latitudes (i.e. ● - 22ºS, ◊ - 23ºS, ♦ - 24ºS, □ - 25ºS, ○ - 26ºS, ■ - 27ºS and ∆ - 28ºS).

The site–environment biplots produced by the CCA diagram display the assemblages and the environmental variables correlated with them. Temperature and salinity were highly correlated with each other ($r = 0.74$) but negatively correlated with oxygen ($r = -0.17$ and $r = -0.14$, respectively). Sampling sites at 100m and 200m seafloor depths were associated with higher salinity and temperature while those found at 300m were associated with higher oxygen concentration.
There is a clear gradient formed along CCA axis 1 characterized by seafloor depths while there is no clear gradient formed with CCA axis 2. Environmental factors appear less important with regards to latitudes. The first CCA axis was positively correlated with temperature and salinity. The second CCA axis was positively correlated with oxygen. The results observed in Figure 12 indicate that higher temperature and salinity were observed in inshore than offshore water while oxygen seems to be relatively high in-between inshore and offshore.

The explanatory variables which significantly affected species composition were bottom water temperature \((F = 4.03, p < 0.05)\) and salinity \((F = 1.55, p < 0.05)\). 11.2% of the total variation in species data was explained by the environmental variables. The influences of oxygen concentration on species composition was insignificant \((F = 1.05, p > 0.05)\). A Monte-Carlo permutation test for the first canonical axis of CCA revealed that sites and species composition (Figure 12 and 13) were significantly correlated with environmental variables \((F = 3.917, p < 0.05)\) while the tests of all canonical axes was also significant \((F = 2.228, p < 0.05)\). Interaction between seafloor depths and latitude gradient was insignificant \((F = 1.03, p > 0.05)\).

The CCA diagram (Figure 13) displays fish species and the environmental variables, which jointly reflects the species distributions along each of the explanatory variables.
Figure 13: The Canonical Correspondence Analysis (CCA) diagram showing fish species (Δ), in relation to environmental variables. The actual names of fish species represented by letters in the CCA diagram are given in Table II.

The species-environment biplots produced by the CCA diagram display the species assemblages and the environmental variables correlated with them. Fish species were strongly correlated with temperature and salinity for the first axis and oxygen for the second axis. The *Merluccius capensis*, *Lophius vomerinus*, *Beryx splendes* and *Caelorinchus simorhynchus* were distinct fish species observed, unrelated to the ordination axes as they were centered in the ordination diagram (Figure 13).
Raja leopardus, Hoplostethus melanopus, Callorhinichus capensis, Allocyttus verrucosus, Gadella imberbis and Galeorhinus galeus were associated with high temperature while Austroglossus pectoralis, Congiopodus spinifer, Mustelus higmani and Holohalaelurus regain were associated with high dissolved oxygen concentration in the water. Galeorhinus galeus, Brama brama, Chlorophthalmus atlanticus and Beryx decadatylus were associated with high salinity.

Table II: The names of fish species as represented by letters in the CCA-diagram (Figure 13). Name given in capital letters represent family name.

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<tr>
<th>Letters</th>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Letters</th>
<th>Scientific Name</th>
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CHAPTER 5

DISCUSSION

5.1 Species diversity and richness of fish

The present study investigated several patterns in fish species diversity and richness between the Oranjemund and Henties Bay area. These patterns might be related to
environmental conditions off the Namibian coast. As a result, depending on the physiology and biological adaptation of fish species, these environmental conditions determine fish occurrence and distribution within the ocean.

5.1.1 Seafloor depth

The observed trends show that fish species diversity and richness shows a relatively increase from inshore to offshore, with significant differences observed between shallow (i.e. 100-200m) and deep seafloor depths (i.e. 300-500m). This might be associated with natural fluctuations in environmental conditions in the Benguela system. Similarly, a low diversity level at 100m and 200m depth might be accompanied by high abundance of fish species (Sakko, 1998).

Temperature is one of the most important physical properties of the marine environment which exerts an influence on many physical, chemical, geochemical and biological events. Water temperature determines the concentration of dissolved oxygen in the water, which profoundly relate to biological processes. Generally ocean water temperature is higher inshore than offshore (Figure 11), resulting in relative low amounts of dissolved oxygen inshore (Figure 9). The observed differences in both diversity and richness might be a direct result of a decline in dissolved oxygen concentration from inshore to offshore. This observation has been supported by a
number of authors who pointed out that oxygen unavailability in the water can limit fish distribution. Temperature could thus be regarded as a limiting factor for fish occurrences (Kramer, 1987).

According to Figures 2 and 3, the 200m-seafloor depth tends to be the cut-off region for significant changes in both diversity and richness of fish. This might be due to greater variations in environmental conditions, which may have direct effects on the occurrence and abundance of fish.

It is also well-known that several fish species were restricted to certain seafloor depth conditions, which might be associated with their biological adaptation. Although *Merluccius capensis* and *Merluccius paradoxus* were the dominant fish species, it is clear that greater numbers of fish species were absent at 100-200m depths and only a few species were entirely absent at 300-500m seafloor depths. The latter included *Chlorophthalmus atlanticus, Emmelichthys nitidus, Raja straeleni, Cruriraja parcomaculata, Callorhinchus capensis, Galeorhinus galeus, Allocyttus verrucosus* and *Zeus capensis*. This might be related to their tolerance ranges or adaptation to several environmental conditions within the ocean.

Another important complexity in community ecology is to explain low and high diversity on the ocean seafloor, which might be associated with the level of disturbances. The Namibian marine environment is governed by several management regulations,
aimed at fisheries resources sustainability. Among these management options are restrictions on fishing at depths shallower than 200m imposed on all commercial fishing vessel operating within Namibian water for conservation purposes and to safeguard illegal landing by mid-water trawlers (Oelofsen, 1999).

The level of disturbance would be minimal if the restrictions were to be enforced in the respective area. Ecologists point out that when disturbances are rare, the system hardly create new niches for new species colonization, whereas frequent disturbances may have detrimental impacts. Species with a low reproduction capacity may even go extinct. In-between there is an intermediate level of disturbance (an ideal called the ‘intermediate disturbance hypothesis’), which maximizes biodiversity (Krebs, 1989). As a result absence of disturbances by bottom-trawling at shallower depths might be the reason for low species diversity at those localities.

It was hypothesised that diversity and richness of fish species will increase along the seafloor depths, at horizontal distance from inshore to offshore. This hypothesis will be accepted due to results observed in both fish species richness and diversity. The results indicated similar trends of increasing species diversity and richness from inshore to offshore. These trends might be associated with changes in the environmental conditions of the ocean.
Temperature of the water was higher inshore than offshore and this correlates negatively with the dissolved oxygen concentration in the water. These changes might negatively influence the occurrence and distribution of fish species. On the other hand, lower species diversity and richness at 100m and 200m seafloor depths might be associated with the lack of disturbances (in particular from bottom fishing), believed to create new niches for new species colonization.

5.1.2 Latitudinal gradient

In general there is an increase in species diversity and richness towards the equator (Sakko, 1998). In the case of Namibia, several authors have indicated that there is a clear decrease in species diversity from south to north, which seems to be influenced by instability of the Benguela system. This instability is regarded as more important than the latitudinal gradient when predicting species diversity in Namibia’s marine environment (Sakko, 1998).

It is surprisingly that significant differences were only observed in fish species richness but not species diversity. The Mann-Whitney U test indicated a significant difference in fish species richness between Lüderitz (26°S) and Oranjemund (28°S) area (Figure 5). The observed significant differences in species richness might be due to differences in productivity and environmental conditions between the two locations. The average, both in fish species diversity and richness, were lower at Lüderitz area (Figure 4 and 5) than at Oranjemund.
A decline in means both in species diversity and richness around Lüderitz area might be associated with upwelling. Upwelling systems are in general are more extreme in cases of unstable environments. Such systems, predictably, support a low diversity of species. At the same time they are among the most productive habitats of the world (McNaughton and Wolf, 1970). It is believed that the upwelling cells around Lüderitz are intense and perennial, which leads to anomalies in temperature, salinity and oxygen concentration. This upwelling cells provide nutrients to support high primary production, which contribute to extreme oxygen depletion in the water column (Bruchert et al., 2006), and this might also be the reason for a decline in diversity and richness of fish species.

In conclusion, while it was hypothesised (hypothesis b) that diversity and richness of fish will decrease along latitudinal transect gradient from Oranjemund to Henties Bay, this was apparently not the observed pattern. Significant differences were only observed in means of fish species richness, but not species diversity. Such an observation indicates that global latitudinal trends in species diversity are less important in Namibian water but rather characteristic of Benguela system. Significant differences in species richness between Lüderitz and Oranjemund area might be explained by differences in environmental conditions and productivity within those areas.
5.2 Determinants of fish species composition

The classification and ordination using the HCA and DCA has aggregated fish species composition into several groups. It was observed the HCA and the ordination diagrams that related to latitudinal gradient were less important in the classification of fish species composition. It is rather the seafloor depth that tends to highly influence fish species composition. The influence of fluctuating environmental changes in the Benguela system might be responsible for fish species composition to even out distribution along the latitudinal gradient without any clear groupings.

It was hypothesised (hypothesis c) that fish species composition is expected to differ along latitudinal gradient at different seafloor depths between Oranjemund and Henties Bay. Several groupings of species composition were observed with regard to seafloor depths but not between latitudes.

It is clear that several fish species (regarded as being deep water fish or shallow water fish) have been found in mixed combinations at the seafloor. The *Merluccius paradoxus* is usually regarded as the most common deep-sea fish while *Merluccius capensis* is regarded as a shallow water fish. This pattern was however not the observed. This might be due to fluctuation in environmental conditions which might have caused changes in the distribution of fish species.
The 100% similarity observed in the HCA indicated equality in species richness (S = 2) at those given sites. In the Namibian waters, latitudinal gradient does not necessarily influence species composition, but environmental fluctuations might be important in explaining fish species composition. Other explanatory variables off the Namibian coast between Oranjemund and Henties Bay area might be essential to depict patterns in species composition along the latitudinal gradient.

Temperature and salinity were highly correlated with each other and both were negatively correlated with oxygen. The general trends observed in changes in environmental variables along the Namibian coastal shelf between Oranjemund and Henties Bay area indicated that bottom water temperature and salinity decreases relatively fast from inshore (< 200m) to offshore (> 300), contrary to observed trends in oxygen concentration.

The CCA diagrams have demonstrated a clear influence of environmental factors on fish species composition. Temperature and salinity (i.e. CCA axis 1) were the most important environmental variables influencing fish species composition. Surprisingly, dissolved oxygen influence on fish species composition was insignificant. Temperature at shallow seafloor depths (i.e. 100-200m) is mostly subjected to continuous change as influenced by surface weather. These continuous changes in temperature, in turn, may influence other physical components of the ocean such as the amount of dissolved oxygen concentration posing greater influences on fish species composition. Several authors
have reported that temperature influence fish distribution and determine what kinds of fish species can survive and function in fluctuating environmental conditions (Buchheim, 2005).

As depicted on the CCA diagram (Figure 12), temperature and salinity tend to influence fish species composition more in shallower seafloor depth than at deeper seafloor. It has been reported that different fish species are adapted to different salinity levels and the condition may be more drastic when combined with hypoxic condition (Sarma et al., 2005). Thus, with continuous changes in increased ocean water temperature at shallower depths, the amount of dissolved oxygen may decline, exerting greater influence on fish species composition.

The analysis of Variance (ANOVA) indicated insignificant influence of dissolved oxygen concentration on species composition although fluctuations at different localities were observed. Dissolved oxygen availability in marine environment is essential to fish for respiration, enabling fish to liberate energy from organic compounds (Kramer, 1987). The influence of oxygen concentration on species composition is insignificant suggesting fish species have developed coping behavioural responses to changes in dissolved oxygen concentration.
It is evident that dissolved oxygen concentrations were low (<2ml/l) at several shallow seafloor depths (<200m) implying that fish easily undergo vertical or horizontal habitat changes to sites of higher oxygen availability. Although it has been documented that dissolved oxygen concentration lower than <2ml/l is renders the water oxygen deficient to fish (Barnard 1998, p. 191), it may be possible that some fish species have developed adaptations to minimal oxygen concentration. For this reason specific studies may be required to test/demonstrate this hypothesis. On the other hand, the Benguela system is characterized by inherent continuous water mixing. As a result, upwelling signifies that oxygen-deficient water in the Namibian waters occurs frequently to which fish species have to adapt.

The ordination interpretation (Figure 13) suggests that fish species at the edge of the ordination diagrams are often rare, lying there either because they prefer extreme conditions or by chance (Jongman et al., 1995). Most fish species located at the edge of the CCA diagram (Figure 13) were rare according to their total proportional abundance except for Mustelus higmani. The distribution of this species (i.e. Mustelus higmani) seems to be highly influenced by the relatively high oxygen concentration in the water.
In conclusion, it was hypothesised (hypothesis d) that environmental factors (temperature, salinity and oxygen) influenced fish species composition. The bottom water temperature and salinity significantly influenced fish species composition but not oxygen. The influences of temperature and salinity on fish species composition were significant at 100m and 200m seafloor depths.

The insignificant influence of oxygen on species composition might be associated with behavioural adaptation of fish. On the other hand, it might be that oxygen-deficient conditions in the water are fluctuating so fast that they are insignificant to fish species. A number of fish species were correlated with environmental variables sampled but some were not latter indicates that other explanatory variables (not sampled in this study) might be important in describing the spatial distribution of fish species.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study highlighted several trends in fish species diversity and richness off the Namibian coast between Oranjemund and Henties Bay area. Biodiversity (or fish diversity) within Namibian water varies with habitats (in particular with seafloor depths)
and systematically increases from inshore to offshore. These trends might be associated with inherent fluctuating environmental conditions within the ocean. Bottom Ocean water temperature was higher inshore and declines toward offshore which correlates negatively with the amount of dissolved oxygen concentration.

Low dissolved oxygen concentration in the water inhibit the rate of respiration of fish which may result in suffocation of some fish, hence the remaining fish may have developed mechanism of avoiding area with poor conditions. These might be responsible for a decline in fish species diversity and richness. Apart from the environmental influences on fish diversity, disturbances from fishing, especially bottom trawling is believed to disrupt and displace benthic communities and causes high diversity in offshore (> 300m) than inshore (< 200m seafloor depth) areas. In Namibian waters, commercial bottom-trawling is restricted to areas below 200m seafloor depth, thus displacement of local species are rare with no new niche being created for new fish species invasion that would increase biodiversity.

The Namibian marine environment is associated with the Benguela system characterized by changes in environmental conditions. The fluctuations in environmental conditions created local trends in fish species diversity living off the Namibian coast. This trend is not in accordance with the global increase in species diversity toward the equator. Such observation indicates that global latitudinal trends in species diversity are less important
in Namibian water and is rather characteristic of Benguela ecosystem. With regard to latitudinal gradient, significant differences were only recorded in species richness but not in diversity and were observed between Lüderitz and Oranjemund area. These differences were due to local environmental conditions and productivity within those areas.

Changes in environmental factors (in particular bottom water temperature and salinity) off the Namibian coast influence fish species composition and are more pronounced between seafloor depths. This is not the case with latitudes gradient as observed between Oranjemund and Henties Bay. These observations are attributed to the ability of fish species to withstand or adapt to environmental fluctuation within the Benguela ecosystem.

The bottom water temperature and salinity sampled off the Namibian coast between Oranjemund and Henties Bay were positively correlated with each other but negatively correlated with oxygen concentration in the water. The general pattern observed in environmental variables along the Namibian coastal shelf shows temperature and salinity to be relatively high inshore than in offshore waters.

Accordingly, the bottom water temperature, salinity and oxygen were hypothesized to influence fish species composition (hypothesis d). Temperature and salinity significantly influence fish species composition at 100m and 200m seafloor depths. There was
insignificant influence of oxygen on species composition as indicated through behavioural adaptations of fish to cope in such conditions. The influence of sampled environmental variables was restricted to certain fish species and this indicates that other explanatory variables might be significant in explaining the spatial distribution of fish.

6.2 Recommendations

To test the reliability of these results, sampling needs to be done at the same period either during the day or night. This is because some fish species are believed to undergo vertical migration as a mechanism for behavioural adaptation and some may either be diurnal or nocturnal at some point in time; thus not prone to being caught. This might better explain the spatial distribution of several fish species with regard to time and thereby increase the efficiency of commercial fishing. At the same time this might help reduce the catch of untargeted fish species.
To better understand the dynamics of Namibian biodiversity, a complete biodiversity inventory is necessary for the whole Namibian coastline. Moreover, there is a need to conduct more studies of similar kind targeting vast amount of explanatory variables, because some fish species sampled in this study were unrelated to the sampled environmental variables. Sampling at varying seasons will help to draw comparison of changes in fish species composition over time. Conditions within the marine environment change with season which is likely to influence fish behaviour within the ocean water column. Finally, a similar study focusing on pelagic areas of the oceans would be necessary for comparison between pelagic and demersal fish species composition. This may help give better insight into possible changes in fish behavioural distribution within the marine environment as influenced by climatic changes known to occur within the ocean.

REFERENCES

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### APPENDICES

**Appendix 1**: Geographical location of all stations sampled off the Namibian coast between Oranjemund and Henties Bay.

| Station no. | Latitude (°S) | Longitude (°E) | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 |
### Appendix 2: Environmental variables recorded off the Namibian coast between Oranjemund and Henties Bay.

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### Appendix 3: The species matrix based on proportional abundance (kg) of fish species collected between Oranjemund and Henties Bay off the Namibian coast.

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The table above lists the frequency distribution of various species.
<p>| Callorhinchus capensis | 0.069 | 0.000 | 0.126 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
|------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Neoharriotta pinnata   | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.015 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Hydrologus sp.         | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Heptranchias perlo     | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Hexanchus griseus      | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Scyllorhinus capensis   | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Galeus polli           | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Holohalaeurus regani   | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Deania profundorum     | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.014 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Etmopterus brachyurus  | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Centroscyllium fabricii| 0.000 | 0.043 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Squalus megalops        | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.050 | 0.002 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.012 |
| Mustelus higmani        | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.036 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Galeorhinus galeus      | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Austroglossus microlepis| 0.000 | 0.000 | 0.000 | 0.000 | 0.026 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Austroglossus pectoralis| 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Stomias boa boa         | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |</p>
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