PREDICTING SOUTH AFRICA'S TRUE MARINE BIODIVERSITY: A COMPARISON OF METHODS

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DECLARATION

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

Hannah B. Medd Date

This work is dedicated wholeheartedly to my parents, Randy and Cathie, --- thank you for guidance, strength, patience and love

Abstract

South Africa supports a high level of marine biodiversity, due largely to its diverse marine environment, which incorporates cool temperate West Coast, warm temperate South Coast and subtropical East Coast habitats. However, the recorded biodiversity reflects only a subset of the actual species present. The aims of this thesis are to estimate how many marine species remain to be described in this region and which areas are most in need of additional sampling effort.

Chapter 2 attempts to estimate unknown biodiversity by comparing the South African marine fauna with that of Europe, the world's best-researched region. South Africa has 10 916 reported marine species, against Europe's 23 460. Taxa were grouped in four categories: well-known, moderately-known, poorly-known and unrecorded, according to their state of knowledge in South Africa. Assuming groups that are well- known in both areas to provide a realistic ratio of true species richness there are 0.78 South African species for each European species. Assuming this ratio also applies to other taxa it is estimated that an additional 6 119 species, or 56% of the existing fauna, need to be described from the poorer known groups to raise the state of knowledge in South Africa to the equivalent of that in Europe (itself far from complete of course!).

In Chapter 3 published monographs were used to plot historical discovery curves of six South African marine taxa, in an attempt to see whether these could be extrapolated to predict unknown biodiversity to be described in the future. Dates of discovery were plotted for 968 species with discovery dates ranging from 1789 - 2001. Two sigmoidal curves, Logistic (5) and Weibull, were fitted to the data of each taxa and a predicted asymptote was estimated. The logictic curves estimated that a total of only 14 species remained to be identified in the six taxa examined, while the Weibull method estimated that 420 species remined to be described. Extrapolating these results to the fauna as a whole resulted in an estimated numbers of undescribed species of 157, using the Logictic curves, and 5 235 (48% more than the existing fauna) using Weibull curves. The former estimate is considered to be unrealistic, while the latter conforms well with the 6 119 undescrived species (56% of present fauna) estimated in Chapter 2. This method may not be well suited to South African fauna as the species lists still remain exponential and there have been relatively few taxonomists active in each group, which can introduce biases in the shapes of the discovery curves. The method did, however, reveal how incomplete the species lists are and the enormous biases introduced by the taxonomic specialisations chosen by the few local researchers present in developing countries, such as South Africa

Chapter 4 examines the biogeographic coverage of benthic sampling effort in southern Africa. A total of 428 benthic samples taken by the University of Cape Town Ecological Survey were analysed and grouped by region (Namibia, West, South and KwaZulu-Natal coasts). Regions were compared in terms of total number of samples taken, total number of species recorded and rates of species accumulation per sample. KwaZulu-Natal had the least samples, followed by Namibia and the West Coast, with the South Coast being the most sampled. Species accumulation curves were fitted to the randomized data and asymptotes estimated a total of 979 'missing' records, equivalent to a 62% rate of under-reporting of species. The shape of Namibian, South Coast and West Coast curves indicate that these regions are not nearly reaching an asymptote despite being relatively well sampled. KwaZulu-Natal's curve seems to be reaching a plateau, but has greatest diversity per sample and the smallest number of samples, so it is greatly under-sampled and in urgent need of further research.

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Chapter 1

Background and introduction

Marine vs. terrestrial biodiversity on a global scale

The Convention on Biological Diversity, held as part of the United Nation's 1992 Conference on the Environment and Development in Rio de Janeiro, Brazil, defined biological diversity as "The variability among living organisms form all sources including, *inter ali*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species and of ecosystems."

Several well-known global biodiversity patterns are apparent within the marine environment. Based on coral species richness, highest marine diversity occurs in the Indonesian archipelago and decreases radiating west across the Pacific Ocean. This is perhaps due to long periods of stable evolution and the large diversity of island types present of different sizes, their geological history and distance from sources of colonizing species (Stehli and Wells 1971). Marine organisms originated in the benthic sediment, therefore biodiversity levels are higher there compared to pelagic ecosystems (Angel 1993). The coasts demonstrate higher levels of biodiversity than the open ocean, due to their insularity and wider variety of habitats (Gray 1997). Also it is believed that temperate coastal marine systems are the most productive and most diverse systems (Suchanek 1994). As in terrestrial habitats, marine biodiversity increases from the Arctic to the tropics, however, in the Southern Hemisphere, this gradient is less clear (Clarke 1992). The Arctic is relatively young compared to the older system of the Antarctic and this is reflected in the Arctic's lower diversity and endemism (Dayton 1994).

Despite nearly 300 years of constant research, the number of species on Earth continues to be poorly-known (May 1988; Ray & Grassle 1991). Estimates of global species richness by May (1988) range from 5-50 million possible species, an order of magnitude of uncertainty! At the level of phylum, greater diversity of fundamental body plan and life histories exist in the marine system (Ray and Grassle 1991; Ray 1991). However, only approximately 11% of the total number of described global species are marine (Reaka-Kudla 1997). The description rate of new species of fish has remained linear for the last century, with ichthyologists describing approximately 600 new species per year (O'Dor 2003), far more than for any terrestrial vertebrate group (Ray 1991). Because of the extreme difficulties of sampling this habitat the number of extant deep-sea species remains particularly poorly-known, with estimates ranging from 500 000 (May 1994) to 10 million (Grassle and Maciolek 1992) and, including meiofauna, as many as 100 million (Lambshead 1993)! The discovery of the first living coelacanth, a group thought to have gone extinct 70 million years ago, in 1938, served as a reminder of how little is known about even very large species (Balon *et al.* 1998). A major novel group of ecosystems, hydrothermal vents, were only discovered in 1977, adding a further 20 new families, 50 new genera and over 100 species to marine species totals (Grassle 1989). One of the largest species of shark, *Megachasma pelagios*, the megamouth, was only discovered in 1976 (Taylor *et al.* 1983) and only recently were the endangered Kemp's Ridley marine turtle, *Lepidochelys kempii*, and the widespread olive Ridley, *Lepidochelys olivacea*, recognized as being separate species (Reaka-Kudla 1997).

In comparison to terrestrial ecosystems, marine environments are usually assumed to have low species richness, despite high phyletic diversity (Ray 1991; Gage 1996). To a large extent this derives from the virtual absence of beetles (Coleoptera), which include more than 400 000 described species (Gray 1997), from marine habitats. It is hypothesized that the higher-taxon diversity in marine systems results from the older age of oceanic biota (Gage 1996), that diversified more than 500 million years ago, as apposed to land colonization that occurred only 200-400 million years ago. This created longer marine lineages for a greater variety of body plans and functional and biochemical diversity (Reaka-Kudla 1997). The marine realm is also more benign than the terrestrial, since it is wet, osmotically non-stressful and has a greater heat capacity and hence smaller temperature range. Only a subset of the body plans that evolved in the sea are pre-adapted to survive in harsher terrestrial habitats. Gage (1996) estimated taxonomists have described only 160 000 metazoan marine species of approximately 1.8 million global species. This is despite the three-dimensional living space of the ocean, which provides almost 300 times the volume of suitable terrestrial living space (Gage 1996). Of the 33 animal phyla, 32 are marine and only 12 inhabit terrestrial ecosystems, with 64% marine endemism and only 5% terrestrial endemism within the animal phyla (Reaka-Kudla 1997). The total number of marine phyla and classes is about 20 times that found in terrestrial habitats (Ray 1991).

Ray and Grassle (1991) hypothesized discrepancies between marine and terrestrial biodiversity that accounts for these differences. These include: the marine systems' lack of physical extremes, lower likelihood of extinctions, reduced ability to respond to large-scale environmental changes, indistinct physical boundaries, greater genetic variety and higher importance of keystone species. Steele (1991) hypothesized that marine systems are more closely coupled to the physical environment than terrestrial systems, influencing differences in temporal scale of distribution shifts, reproduction cycles, trophic state of larger and longer lived organisms, functional responses to environmental fluctuations, recruitment timescales, and temporal response to climate shifts. Marine systems differ from terrestrial systems because boundaries are less distinct (Lasserre 1994), subtidal sampling is essentially blind, and marine systems are open, with large dispersal areas (Gray 2000). Marine biota are also less observable than terrestrial ones (Feral 2002).

Marine systems have also attracted less government and public research support than terrestrial ecosystems. This has been emphasized by the relative lack of environmental groups devoted solely to aquatic wildlife, the fact that endangered marine species were listed under the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) as food instead of wildlife, and that only 1.75% of all marine vertebrates have been evaluated by the IUCN's Red List of Threatened Species (Shumway 1999).

Global extinctions of marine fauna also occur far less frequently than terrestrial extinctions. Overexploitation is the main threat to marine species, and has resulted in the extinction of such species asthe Stellar's sea cow (*Hydrodamalis gigas*) (Vermeij 1993) and the Caribbean monk seal (*Monachus tropicalis*) (Knudston 1977; LeBoeuf *et al.* 1986; Vermeij 1993); the main threat to terrestrial life is habitat loss (Dulvy *et al.* 2003).

The ocean covers 71% of the earth and provides 99.5% of the liveable volume and the deep-sea, below 200 m, occupies an estimated 63.5% of Earth's surface, a vast, virtually untouched realm with no terrestrial counterpart (Grassle 2001). A deep-sea survey along the Eastern United States continental slope collected 707 polychaete species from 556 boxcore samples throughout six sampling periods covering an area of only 50 m^2; in comparison to 115 polychaete species identified from a similar survey along the shallow waters of the Lower Chesapeake Bay, further underscoring the inadequacy of knowledge of deep-sea fauna (Grassle 1991). In one of the first quantitative sampling surveys of the deep-sea, 233 30 x 30 cm samples at depths from 1 500 – 2 500 m along the coast of New Jersey and Delaware, U.S.A., Grassle and Maciolek (1992) recorded much higher species diversity than had been hypothesized, 798 species, 58% new to science, and their data suggest that there may be 10^7 or 10^8 undescribed deep-sea species, further demonstrating the enormous possibilities for future discoveries in the ocean.

State of knowledge of marine compared with terrestrial systems

Oceanic ecosystems are far less studied than terrestrial systems and the history of marine research tends to cover a shorter time period (Bianchi and Morri 2000). Even today marine systems remain neglected, receiving a disproportionately low amount of sampling attention (Ray and Grassle 1991; Patterson 2001). In a survey of papers published in the journal Conservation Biology, Irish and Norse (1996) showed that of 742 published papers only 5% were on marine topics, 9% freshwater related and 67% terrestrial based.

Winston and Metzger (1998) revealed that in 1991 only 13% of published taxonomic literature listed on the online database of Zoological Record Online pertained to marine ecosystems.

Marine biodiversity studies have been neglected for several reasons. Much of the marine realm is inaccessible without costly equipment and ship's time. Even shallow marginal seas are inaccessible to anyone but qualified divers. Because of the sea's vastness there is little common experience about natural events that occur in the ocean and most experiments are limited on a spatial and temporal scale (Ray and Grassle 1991). Schalk (1998) describes some of the reasons why the marine realm is less studied than the terrestrial realm, notably the difficulty of obtaining access the sea, especially extreme depths, the vagueness of three dimensional biogeographic borders, and the fact that the area of marine ecosystems is twice that of terrestrial environments. Another problem is the lack of distinct ownership of the open sea, making it difficult for governing bodies to give rights to research (Attwood *et al.* 1997).

Marine research has always been undervalued because of common misconceptions about the robustness of marine habitats. Despite evidence to the contrary, these include a perceived lower vulnerability, that fish stocks can never be overexploited because of their high fecundity, that large geographic ranges and wide dispersal make marine species less vulnerable to extinction, that economic extinction will occur before biological extinction, that marine populations will rapidly return to pre-exploitation densities, and that natural variability of marine populations makes them more resilient than terrestrial populations (Dulvy *et al.* 2003). Characteristics of the ocean, such as large volume, turbulence, and high flushing rates, have garnered a reputation of imperviousness to anthropogenic alterations. However, these effects are in fact being detected in coastal zones, as well as deep-sea environments (Attwood *et al.* 1997). The belief that the ocean is less impacted by anthropogenic effects may be one reason why marine biodiversity studies lag behind terrestrial investigations. Incomplete knowledge of the marine environment may also lead to underestimation of numbers of extinctions and extirpations (Powles *et al.* 2000).

To address this paucity of information, several international, regional and local organizations have joined together under a multitude of conventions and policies to create initiatives encouraging the proliferation of marine systematics research. One such organization is the Census of Marine Life (CoML) program. The CoML is a global consortium of researchers representing over 70 nations. The Census aims to answer questions about the past, present and future diversity, distribution, and abundance of marine species. To answer these questions, regions of key oceanic research capabilities across the globe have coordinated efforts with respect to field projects and data handling. The History of Marine Animal Populations, HMAP, a project incorporating knowledge from historians, anthropologists and other marine scientists, endeavours to determine what did live in the oceans. The Future of Marine Animal Populations, FMAP, uses mathematical models to predict what effect current environmental pressures will have on marine fauna in the future. The CoML also utilizes the Ocean Biographic Information System, OBIS, a massive database of marine species, to archive distributional data on all marine species.

Known and unknown biodiversity of South Africa

South Africa has been ranked as the third most biologically diverse country in the world, comprising only 2% of global land area, yet posessing 10% of global plant species, and

7% of global reptile bird and mammal species (Driver *et al.* 2004). There are also 11 130 described marine animal species, of which approximately 31% are endemic to the region (Gibbons *et al.* 1999).

One of the causes of high marine diversity of species in this region is the diversity of environmental conditions throughout the three main biogeographic provinces, which range from the cool temperate West Coast to warm temperate South Coast and subtropical East Coast (Gibbons *et al.* 1999; Turpie *et al.* 2000). The Benguela Current creates upwelling and high primary productivity on the West Coast, resulting in large stocks of pelagic and demersal fishes and rock lobster (Griffiths 2003). The warm Agulhas Current, flowing down South Africa's East Coast, is characterized by lower productivity and relatively high biodiversity (Bustamante and Branch 1996).

Apart from their intrinsic value, South Africa's living marine resources have considerable commercial value, generating potential income based on food, cosmetics, drugs and tourism (Arico 1995). The value of South African marine biodiversity in 1995, reflected by the commercial fishing sectors, totalled approximately R1.7 billion (Booth and Hecht 2000). The additional value of recreational shore anglers is estimated to be R671 million per year, that of spearfishing R19 million and the value of ecotourism activities ranges from R78 million per year for angling tourism to R7.3 million per year for whale watching, with comparable values for scuba diving and shark-viewing (Turpie *et al.* 2003).

South Africa has a relatively strong history of taxonomic research with the initial work, in what is called the "colonial phase", completed by well-known international taxonomists, such as Linnaeus, Bloch, Schnieder, Cuvier and Valenciennes, all of whom named fish from South Africa (Smith and Heemstra 1986). Also during this phase, Sir Andrew Smith, physician turned naturalist, headed the South African Museum in Cape Town from 1821 - 1837 (Linder and Griffiths 1999). He described 41 fish, among which were shark descriptions later used by Muller and Henle (1841) in their colossal work on elasmobranchs (Smith and Heemstra 1986).

The second phase of South Africa's systematic history involved the development of local expertise, led by the likes of John D.F. Gilchrist, the "father of South African ichthyology", who in his career as the first director of the Department of Sea Fisheries, publishing many papers from 1908 - 1924 (Smith and Heemstra 1986). Keppel H. Barnard compiled a massive two-part work on "Marine Fishes of South Africa" published in 1925 and 1927 (Smith and Heemstra 1986) and in a long and productive subsequent career also monographed a variety of other groups, including crustaceans, molluscs, and other minor taxa (Brown 1999). J.L.B. Smith, a chemist who had a penchant for fishing, published his first ichthyological paper in the Annals of the Albany Museum, and went on to become an enormously productive ichthyologist, whose work has most recently culminated in the monograph "Smiths Sea Fishes" (Smith and Heemstra 1986).

South African marine fishes demonstrate a relatively high level of endemism in comparison to other regions (Turpie *et al.* 2000). Approximately 83% of the world's fish families can be found in South Africa, a higher percentage than in the Philippines and Australia (Smith and Heemstra 1986). South Africa's described species of fish represents 16% of the total number of species known worldwide, with an incredible 100 new species being described during the past decade (Heemstra and Heemstra 2004). The variety of fish is attributed to the great diversity of habitats represented around the coast, including coral reefs, estuaries, sandy beaches, rocky shores, mud flats, mangroves, kelp beds, and ocean depths reaching 5 km; as well as to variability in abiotic factors, such as salinity, turbidity, substrate, and temperature (Heemstra and Heemstra 2004).

Southern Africa also supports one of the most diverse faunas of the Class Chondricthyes, cartilaginous fishes, with approximately 210 species, comparable to the United States or Australia, despite a coastline that is one third the length (Compagno 1999). Southern Africa has representatives of all 10 orders, 46 of 60 families, 115 of 185 genera and 210 of 1 164 global species of cartilaginous fishes and is a centre of endemism for catsharks, houndsharks, sawsharks, dogfish, skates, and chimeras (Compagno 1999).

Institutions within South Africa have and still do support taxonomic work. The Iziko Museum in Cape Town, formerly the South African Museum, was one of the first museums established outside of Europe and holds a wealth of information, containing the largest collection of marine specimens in the region, dating back 150 years. These collections are supplemented by other collections, held mainly by the Natal Museum (Mollusca), South African Institute for Aquatic Biodiversity (fish) and the Port Elizabeth and East London Museums (Griffiths 2003).

Despite a relative strong taxonomic history, South Africa is currently facing a crisis in terms of taxonomic expertise and there are few permanent employment position for marine taxonomists (Griffiths 2003). South Africa's fish species have been relatively well documented, although Turpie *et al.* (2000) claim that the effort has been unevenly spread around the coastline. There has also been little research effort on surveying the deep-sea biota (Anderson and Hulley 2000). Gibbons (2000) also reveals that the majority of regional taxonomists will retire within the next decade and there is minimal interest among the upcoming generation of scientists to replace them.

The current situation is thus one in which the true biodiversity of South Africa's marine ecosystems remain unclear, because many species and indeed higher taxa still remain undescribed (Gibbons *et al.* 1999). Efforts within South Africa have been skewed so that they may represent an incomplete, or even misleading picture, of biodiversity for coastal fishes and invertebrates (Turpie *et al.* 2000; Awad *et al.* 2002). Description of the remaining undescribed biodiversity, using conventional methodologies, will take many decades and other innovative techniques, such as barcoding, are required in the interim to predict true species numbers.

Can we ever know how many species we have by conventional means?

Despite a growing interest in global biodiversity knowledge, a major factor limiting the absolute rate of species description is a diminishing taxonomic workforce. With some estimates at 13.6 million global species, only approximately 1.7 million have been described. Given a total of 2 000 working systematists globally, each would have to then describe 5 950 new species to describe the remaining biota in their lifetime (Blackmore 1996). Opportunities for recruitment of new taxonomists are waning, as the trend continues of concentration of systematic effort in specialized institutes, rather than in universities, where future taxonomists are more likely to be trained (Blackmore 1996). The decline can also be demonstrated by the decrease in systematic biology theses in Great Britain over the ten year period 1980 - 1990 (Winston and Metzger 1998). Resource availability and lack of job security have further driven the reduction of systematic biologists (Winston and Metzger 1998). New species may go undiscovered because no taxonomic expert is currently working on the group, or the species level taxonomy is considered satisfactorily understood (Vecchione *et al.* 2000). Catalogues of biodiversity have developed in a haphazard fashion, as taxonomists decide to work on particular taxa, based primarily on personal choice (Gaston and Spicer 1998). Generally, the groups that have been best described tend to be large-bodied, abundant, have wide distributions, occupy a vast array of habitats, and occur mostly in the temperature zones (Gaston and Spicer 1998). This is further supported by a review of approximately 150 years of research publications in Ireland, which revealed that the most comprehensively studied geographic areas and species continue to be those most studied today (Costello and Emblow 2000).

The most practical and commonly used indicator of biodiversity is the number of species within an area, habitat, or sample (Wilson and Costello 2005). However, at the current rate of description and with no increase in the number of working taxonomists, global biodiversity will take hundreds of years to record, even longer if funding for taxonomy continues to decrease (Oliver and Beattie 1993). New species of nematodes could total more than 1 million and even if the minuscule number of nematode taxonomists could work at the rate of the more numerous fish taxonomists, who total nearly 500, it would still take them thousands of years to catalogue the entire fauna (O'Dor 2003). On a fundamental level, arguments over what comprises a species still remain, further hampering progress (WCMC 1992). The accuracy of species lists presents a further complication. A recent review of fish species listed from Bermuda reported 55 misidentified species of the 499 listed, an 11% error rate for what is considered the best studied marine taxonomic group (Vecchione *et al.* 2000). With all of these restrictions, investigating total marine biodiversity by compiling an absolute species inventory by conventional means is time consuming and requires a lot of resources, in the form of money and taxonomic expertise, that are seldom available.

The general public's view of marine biodiversity is another stumbling block in the advancement of taxonomic knowledge. In a 1996 SeaWeb poll, more than half the respondents did not view scientific knowledge as a valid criterion for decision-making regarding marine issues (Brailovskaya 1998). The public's outlook of marine wildlife as only a food source, a disconnected view, can be an obstacle in finding support for marine conservation (Brailovskaya 1998).

Estimating biodiversity by non-conventional means

Describing every extant species by conventional means is impractical in the foreseeable future. Thus extrapolative techniques have been devised to optimize efficiencies (Magierowski and Johnson 2006) and are fast becoming the method of choice for many researchers, to avoid the protracted, labour-intensive method of counting all species.

Use of a subset of species from a community as a surrogate of total biodiversity, is commonly employed (Magierowski and Johnson 2006; Stork and Samways 1995). The choice of surrogate is usually based on a degree of familiarity with the taxa in an area (Rowden *et al.* 2004). The best surrogates reflect the ecological patterns of the local community, have a widespread distribution and are easily accessible, reducing field time and the need for taxonomic expertise (Smith 2005). Suitable biodiversity surrogates correlate with changes in biodiversity over spatial variability, succession, season, or disturbance (Colwell and Coddington 1994). Molluscs have been identified as good surrogates for the total biodiversity of rocky shores in New South Wales, Australia (Gladstone 2002) and polychaetes demonstrate good surrogacy for soft-sediment biodiversity (Olsgard and Sommerfield 2000; Olsgard *et al.* 2003). The validity of surrogacy in quantifying true species richness is debated (Clarke and Warwick 2001). Magierowski and Johnson (2006) investigated the robustness of potential surrogates for macrofauna communities inhabiting artificial kelp holdfasts and found that using a single higher taxon as a surrogate of total biodiversity in marine communities is suboptimal. Studies have shown that the presence of one species or taxon rarely correlates with the presence of many other species, but few alternatives exist and limited resources mean decisions must be made with incomplete data (Favreau *et al.* 2006).

Other commonly used substitute measures of biodiversity include the relationship between higher taxonomic levels and species richness, phylogenetic diversity, total number of species, or species richness combined with species occurrence (Richmond 2001). May (1988) describes other relationships to approximate species richness: food webs, relative abundance of species, number of species versus physical size, number of individuals versus physical size, abundance and body length, and commonness and rarity. Three approaches to discovering relative biodiversity identified by Gaston and Williams (1993) were the relationships between species richness and the number of higher taxa, environmental or habitat variable(s), and indicator taxa.

Another proxy of cataloguing total biodiversity is the application of rapid biodiversity assessment via the use of Recognizable Taxonomic Units (RTUs). Oliver and Beattie (1993) attempted to use RTUs to estimate species richness to determine whether a technician with little taxonomic knowledge could be used to produce accurate estimates equivalent to more time-consuming work of well-trained taxonomists.

There are also statistically rigorous estimation methods that can rapidly assess total species richness. Foggo *et al.* (2003) grouped over 20 techniques of species richness estimation into four categories: extrapolation of species-area curves, fitting of species-abundance distributions, non-parametric techniques and modelling species accumulation. Species accumulation curves are plots of cumulative number of species against some measure of sampling effort. As sampling effort increases, the curve approaches an asymptote that can be used to estimate the true species biodiversity at a location and the adequacy of sampling methods (Neigel 2003). The order in which samples are taken from the pool affects the shape of the curve, creating sampling bias, which can be avoided by repeatedly using random orders of samples and taking the average (Colwell and Coddington 1995; Walther and Morand 1998). Accumulation curves can create underestimations of true species richness, because of the tendency to assume equal detection probabilities for all species within an area. There will also be decreasing reliability under low sampling intensity (Brose and Martinez 2004). Logistic models are the best average fit for species accumulation curves and can afford a precise estimate with regards to future discoveries of new species (Costello and Emblow 2000).

Another approach to estimating species richness is the use of estimators. Estimators can be used in integration of the lognormal distribution and nonparametric estimators (Palmer 1990). Non-parametric estimators are based on the abundance or incidence of rare species and as the abundance and incidence of rare species changes with increasing sampling effort, there should be different richness as sampling effort increases (Walther and Morand 1998). The estimators described by Brose and Martinez (2004) are Jackknife 1, 2, 3, and the abundance-based versions, Chao1 (abundance-based) and Chao2 (incidence-based) and coverage estimators ACE (abundance-based) and ICE (incidence-based). PRESTON, an estimator using the lognormal distribution, bootstrap estimator, functions based on species/area relationships, and the number of observed species can also be used as estimators of species richness (Palmer 1990). Walther and Morand (1998) included the estimators Boot, MMMean, S_{obs}, and MMRuns. Foggo *et al.* (2003) also included estimators $S_{(infin)}$ and Lag $S_{(infin)}$. The estimators' performance is affected by sample coverage (Brose and Martinez 2004). Most estimators perform best in species-rich sampling communities with large populations whose individuals are aggregated among samples (Walther and Morand 1998).

The potential usefulness of the various indices of richness and diversity that have been developed is long established (Magierowski and Johnson 2006). Simpson's D and Shannon-Wiener H' indices are also widely used to reduce errors in sampling bias, but are subject to sampling effort effects (Foggo *et al.* 2003).

More high technology methods include the use of specifically designed models. Species abundance models are one way to represent diversity (Tsurumi 2003). Computer programs, such as EstiMateS, include two accumulation curve models and seven non-parametric estimators (Walther and Morand 1998). In the interest of saving time and resources, baseline data studies must be made to monitor changes and build dependable prediction models (Schalk 1998).

Thesis structure

This thesis will attempt to predict the true marine biodiversity of South Africa's marine macro-fauna, within available time and resource constraints, by applying three estimation methods to previously collected species data. This is done in the form of the following chapters:

Chapter 1 (this section) is a literature review and general introduction.

Chapter 2 attempts to estimate 'missing' biodiversity by using regional comparisons of species lists between well studied European waters, New Zealand, and the Western Indian Ocean with South Africa.

Chapter 3 investigates the ease of extrapolating true species numbers from species discovery curves for a variety of South African marine taxa.

Chapter 4 examines biogeographic sampling effort along the South African coast to estimate the adequacy of sampling effort in the various regions.

Chapter 5 concludes the thesis with a short synthesis.

General Methodology

This study will only consider marine macro-fauna. Protists and flora are not considered. The only definition of biodiversity in this thesis is that of species richness. When reference is made to South Africa, the definition used is the political borders from Namibia to Mozambique and offshore to the seaward boundary of the Exclusive Economic Zone (EEZ), unless otherwise noted. Numbers of species listed follow the published sources noted in later chapters. No attempt has been made to incorporate subsequent additions to the fauna, or taxonomic revisions made by later authors.

Chapter 2

Estimating marine biodiversity through regional comparisons

Introduction

One possible method of estimating the undescribed biodiversity of a region is to compare the composition of its biota with that of other, better researched, areas and to estimate which taxa are underrepresented or 'missing' from the region. This can be applied to many spatial scales, including areas as large as entire countries or regions. This chapter employs this method to compare the marine fauna of South Africa, Europe, New Zealand, and the Western Indian Ocean. Clearly, each region has specific characteristics that define the marine ecosystems, and differing biotic and abiotic factors determining the numbers and types of species present and their distributions. Other variables that affect the numbers of species on a regional list are the sampling effort and level of taxonomic expertise in that area, as well as the size and habitat diversity of the region. Each region also has variable resources available for sampling, processing, and identification. Obviously, there have been different levels of effort put into certain taxa in certain regions, the affect of which we hope to illustrate.

During the height of colonial expansion European scientists devoted their careers to collecting, cataloguing and naming novel species from newly explored regions of the world (Patterson 2001). However, once expeditions were concluded, the scientists usually returned to the northern Hemisphere. It is reported that approximately 80% of the world's ecological workforce is based in North America and Europe, with only 4-7% based in Sub-Saharan Africa and Latin America, despite the high biological diversity of these regions (May 1994). Therefore, South Africa, as well as the other two Southern Hemisphere regions in these analyses, are considered understudied in comparison to the European region.

South Africa's 2 600 km-coastline consists of three widely-accepted marine zoogeographic provinces; a cool temperate West Coast, warm temperate South Coast and subtropical East Coast (Emanuel *et al.* 1992). Each of these regions has different physiochemical conditions and supports a different array of marine species. The source used to document the South African marine fauna was Gibbons *et al.* (1999), which gives the total number of marine faunal species for South Africa as 11 130. Comparisons between regions are not a novel idea. Indeed, Gibbons *et al.* (1999) ascertain that the copepods of South Africa may be underrepresented, when compared to the richness in other areas, such as Europe.

The European region is considered the best studied of the areas in question. Historically, this area has had the benefit of a large number of taxonomists dedicated to an equally wide range of groups. The source of the European species list came from the European Register of Marine Species (ERMS). The overall objective of the ERMS was to create a register of European marine biodiversity, as well as taxonomic experts, and to make that information available in a user-friendly way to interested parties. The impressive effort involved many international organizations, including 800 scientists from 37 countries

(Costello 2000). The ERMS clearly defines the area covered, including the entire European continental shelf, the North Pole to the east coast of Greenland, Iceland, across the 26 degree parallel to the North West coast of Africa as well as the Baltic and Mediterranean Seas, including the islands of Madeira, Azores and Canaries. The checklist includes approximately 29 000 species from marine, intertidal and brackish waters (Costello 2000). Although we could not determine the exact measured area used in this survey, the coastline length of the European Union is 65 413 km. From a predictive model, Wilson and Costello (2005), calculated approximately 667 – 3 337 species, or one-twentieth to one-quarter of the current total, remain to be discovered in this region, despite the fact that it is the best studied marine area in the world.

Other comparisons can be made, to further illustrate South Africa's ranking in taxonomic knowledge among other Southern Hemisphere regions, by analyzing the relationship between New Zealand and the Western Indian Ocean marine fauna to that of Europe. The data covered a variety of areas with an array of taxonomic resolution, making it possible to compare only a few specific taxa.

New Zealand is hypothesized to be the second-best studied area used in this analysis. The International Union of Biological Sciences (IUBS) established Species2000 in 1996 with the objective of "enumerating all known species of organisms on Earth as the baseline dataset for studies of global biodiversity", motivating the creation of the New Zealand component, Sp2kNZ (Gordon 2000). Inventorying the marine environment was a formidable task, as New Zealand has the fifth largest Exclusive Economic Zone in the world (Rowden *et al.* 2004), with about 15 450 marine species identified and a further 3 550 that are known, but not officially described. The coastline of New Zealand stretches

5 134 km, longer than the combined countries of the Western Indian Ocean. New Zealand's marine environment spans 30° latitude (24° S to approximately 57° S), ranging from subtropics to the subantarctic and incorporating diverse habitats such as mudflats, mangroves, seagrass beds, kelp forests, rocky reefs, seamounts, canyons, open water pelagic systems and deep sea trenches (Arnold 2004). The 4.2 million km^2 EEZ area contains the highly productive Chatham Rise, incredible invertebrate diversity of Spirit's Bay, and is globally recognized for bird diversity on sub-Antarctic and Chatham Islands (Arnold 2004).

The Western Indian Ocean region was hypothesized to be more poorly studied than the other two Southern Hemisphere regions, which have a history of more intense taxonomic research and relative economic advantage (Gibbons *et al.*, 1999). The species list for this region was compiled by the Marine Species Database for Eastern Africa (MASDEA), a collaborative project started in 1996, with the objective of creating a database incorporating the species lists for the region, including the coasts of Somalia down the East Coast of Africa to Mozambique, the Red Sea, Eritrea, islands such as the Seychelles, Mauritius, Comoros, Reunion, and Madagascar (Berghe 2005). The coastlines that make up most of the sampled area include Somalia, Kenya, Tanzania, Mozambique and Madagascar, with a total combined coastline length of approximately 12 283 km, spanning 64° of latitude. This region is mostly considered to contain a tropical Indo-Pacific biota, this overlapping with the previously described subtropical East Coast Province of South Africa (Griffiths 2005). The main habitats include mangroves, seagrass beds, coral reefs, widespread sandy beaches and estuarine systems (Griffiths 2005).

Methods

The aim of this analysis is to use ratios of species richness to get some impression of how relatively well, or poorly, described the fauna of South Africa is. This requires the assumption that the relative proportions of species in groups that are well-described in both regions provide a true reflection of relative species richness. The ratios of species in taxa poorly studied outside of Europe then give some indication of how much work still needs to be done in the remaining regions to bring these up to European standards.

Comparisons were initially made between South African species numbers and those from Europe. The data for South Africa came from Gibbons *et al.* (1999) and the species list for Europe was extracted from the ERMS's interactive website (www.marbef.org/data). The numbers of comparable taxa were high between these regions, therefore the taxa could be broken down into four categories: well-known, moderately-known, poorly-known, and unrecorded (after Gibbons *et al.* 1999). I totalled the number of South African species and European species in each category and determined the ratio of each group. I then assumed the well-known group represented the true ratio between the regions and applied that corresponding ratio to the remaining South African totals. I then added the current number of well-known species to the altered totals of the other three categories, in order to ascertain the projected total of South African marine species. The expected total, minus the currently known species, gives an estimate of the overall number of species remaining to be described.

For further comparison of the relative status of South Africa's taxonomic knowledge, comparisons were also made between Europe, South Africa and the other southern Hemisphere regions of New Zealand and the Western Indian Ocean. The sources of data remained the same for Europe and South Africa, although at a broader taxonomic resolution. The datasets for the marine fauna of New Zealand were obtained from the outcome of the February Symposium of Species 2000 New Zealand, as presented at The XVIIIth (New) International Congress of Zoology by J. Buckeridge and D. Gordon, and the species totals for the Western Indian Ocean were gathered from the MASDEA website (www.vliz.be/vmdedata/masdea). Once the lists were obtained, I identified taxa in common between the regions so comparisons could be made. The list of taxa comparable between the regions is limited, as the sources were of varying taxonomic resolution.

Results

For illustrative purposes 68 different marine taxa for South Africa and Europe were subdivided into groupings, according to theit state of knowledge in South Africa, as listed by Gibbons *et al.* (1999). The total number of species used for this tabulation was 10 906 for South Africa and 22 042 for Europe. Overall, the level of taxonomic resolution differed greatly, as did the number of groups that fell into each category. Most groups fitted into the poorly-known category, which had 32 groups. There were 18 groups in the well-known category, 12 in the moderately-known and six in the unrecorded category, as set out in Table 2.1.

The ratios established for each taxonomic knowledge category for both South Africa and Europe are listed in Table 2.2. Including all the well-known species in both areas, South

Africa has 0.78 species for each European species. The proportion is smaller in the moderately-known category with 0.56 South Africa species to every European species. South Africa had only 0.21 species for each species recorded in Europe in the poorly-known category and of course had no representative species in the unrecorded category. Table 2.2 also shows the corrected numbers of species that would need to be described to raise the moderately, poorly-known and unrecorded groups, to the well-known category's ratio of 0.78:1, these being 711, 5 057, and 351 for the three groups respectively. The new South African estimated total number of species is 17 025, requiring the discovery of a further 6 119 new species.

Table 1.1. List of the number of South African and European marine species, categorized according to Gibbons *et al.* (1999).

Taxa	S.A.	Eur.
Well Known (n=18)		
Leptomedusae	380	389
Scleractinia	95	88
Polychaeta	760	1902
Gastropoda	2262	2875
Bivalvia	560	728
Cephalopoda	195	111
Gammaridea & Caprellidea	329	117
Asteroidea	91	565
Holothuroidea	122	413
Crinoidea	19	83
Ophiuroidea	119	351
Echinoidea	59	193
Osteichthyes	1821	1212
Chondrichthyes	179	145
Reptilia	6	5
Aves	222	85
Cetacea	37	42
Pinnipedia	6	7
TOTAL	7 262	9 311

Taxa	S.A.	Eur.
Moderately Known (n=12)		
Polyplacophora	29	63
Decapoda	750	704
Euphausiacea	49	41
Isopoda	300	673
Cumacea	98	195
Calanoidea	291	650
Cyclopoidea	14	181
Mormonilloida	2	2
Poecilostomatoida	37	353
Cirripedea	86	147
Pycnogonida	101	160
Echiura	21	19
TOTAL	1 778	3 188

Taxa	S.A.	Eur.
Poorly Known (n=32)		
Demospongia	245	2456
Hexactinellida	8	55
Scyphozoa	10	53
Cubozoa	2	1
Siphonophora	75	145
Octocorallia	204	136
Actinaria	43	211
Corallimorpharia	4	6
Ctenophora	11	46
Nematoda	338	1832
Polycladida	26	56
Tricladida (Maricola)	2	13
Kinorhyncha	1	53
Oligochaeta	3	345
Scaphopoda	16	51
Hyperiidea	125	15
Tanaidacea	19	279
Stomatopoda	35	22
Cladocera	5	10
Harpacticoida	10	1418
Myodocopina	19	44
Halocypridina	26	135
Halacaridae	14	279
Brachiopoda	31	18
Bryozoa	280	811
Entoprocta	6	47
Sipuncula	47	54
Pogonophora	1	23
Chaetognatha	28	58
Hemichordata	11	17
Cephalochordata	1	5
Ascidiacea	220	399
TOTAL	1 866	9 093

Taxa	S.A.	Eur.
Unrecorded (n=6)		
Placozoa	0	2
Rotifera	0	115
Tardigrada	0	86
Gastrotricha	0	240
Gnathostomula	0	5
Loricifera	0	2
TOTAL	0	450

Table 2.2. Ratios of South African marine species numbers to European species numbers for each category and extrapolated number of species still left to be described.

Knowledge Cluster	**S.A.:Eur.**	**Factor**	**Current S.A. species numbers**	**Corrected total**	**Total 'missing' S.A. species**
Well-known	0.78:1		7 262	7 262	0
Moderately-known	0.56:1	x 1.40	1 778	2 489	711
Poorly-known	0.21:1	x 3.71	1 866	6 923	5 057
Unrecorded	-	0.78 of European. number	0	351	351
Total				17 025	**6 119**

The differences in the ratios of described species in South Africa and Europe in all four taxonomic knowledge categories are also illustrated in Figure 2.1.

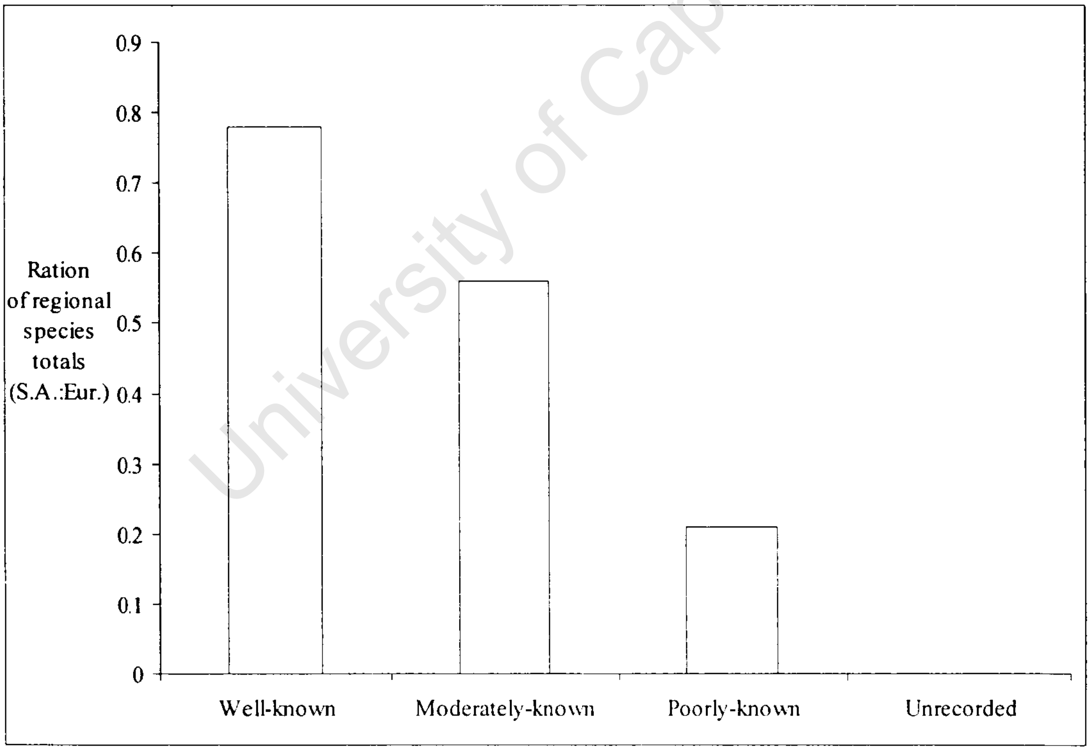

Figure 2.1. Ratio of South African species totals to European in four categories of taxonomic knowledge

A similar analysis can be carried out to compare states of knowledge in various Southern hemisphere regions, although comparable data are only available for a restricted group of taxa. As can be seen from Table 2.3 the chosen taxa for this analysis between Europe and the three Southern Hemisphere regions contain very different numbers of described species in each region. In this analysis, Europe had the highest number of total species records, with 21 700 species, 2.5 times the South African total of 8 486 recorded species. New Zealand ranked third with 6 683 species and the Western Indian Ocean had the fewest with 6 653 species. Europe had the highest number of species in every taxon except Pisces, which were most speciose in the Western Indian Ocean and South Africa.

Among the Southern Hemisphere regions, the numbers of species remained fairly consistent in groups such as Cnidaria, Annelida, Copepoda, and Echinodermata. In the Phylum Porifera, the Western Indian Ocean appeared to have a major lack of species, with only 44 listed, in comparison to 289 for South Africa and 440 for New Zealand. New Zealand had an unusually high number of Platyhelminthes species with 241, in comparison to the Western Indian Ocean with 37 and South Africa with only 28. South Africa listed 338 species of Nematoda, more than twice the New Zealand total of 129 and ten times the 32 species for the Western Indian Ocean. New Zealand demonstrates highest species numbers of Bryozoa, with 624 species, compared to South Africa with 280 species and the Western Indian Ocean with 120.

Table 2.3. List of the number of described species in various taxa for the four regions under consideration (WIO= Western Indian Ocean)

Taxa	Europe	S.A.	N.Z.	W.I.O.
Phylum Porifera	2 662	289	440	44
Phylum Cnidaria	1 500	842	714	789
Phylum Platyhelminthes	2 657	28	241	37
Phylum Nematoda	1 832	338	129	32
Phylum Annelida	2 292	766	502	646
Class Copepoda	3 010	429	304	452
Phylum Bryozoa	811	280	624	120
Phylum Brachiopoda	43	31	29	3
Phylum Mollusca	3 942	3 062	2 170	1 982
Phylum Echinodermata	1 605	410	531	538
Phylum Hemichordata	17	11	4	3
Superclass Pisces	1 357	2 000	995	2 007
Total	21 700	8 486	6 683	6 653

Discussion

The ratios established between well-known taxa in temperate regions and tropical environments and further comparisons of that relationship have been used to generate global species estimates (May 1994). Since Europe is the home of modern taxonomy, it was concluded that most research had been done there (Costello *et al.* 1996) and it remains one of the best known regions (Groombridge 1992). This analysis is based on the assumption that if a group of taxa is well studied in South Africa it should be well studied in Europe and so the resulting ratio of species numbers is a true reflection of the ratio of species richness between the two faunas.

The ratio of South African marine species to European ones among well-known groups was 0.78:1 and if this ratio is applied to the fauna as a whole the expected true species richness in South Africa is 17 025. Thus the calculated number of species remaining to be described is 6 119. This is more than half the overall South African total described to date. Since the first South African shells were named by Carl von Linne in 1758 (Day 1977), naturalists and researchers, foreign and native, have been describing South Africa's marine fauna and have reached an estimated 11 130 species (Gibbons *et al.* 1999). If it has taken approximately 231 years to describe these 11 130 species, at the current rate it could take more than 126 years to describe the remaining species, just to equal the current European state of knowledge, if effort remains constant and is not hampered by a diminishing workforce. It is well recognized, however, that even Europe's fauna remains incompletely described and indeed the rate of species description even there remains linear!

The comparison of the Europen fauna with that of various Southern Hemisphere regions helps to put South Africa into perspective with regards its level of taxonomic knowledge. The calculated totals indicate that for the taxa considered, Europe is the most biodiverse, followed by South Africa, New Zealand and lastly, the Western Indian Ocean. These totals are unconvincing as evidence that European seas contain higher biodiversity than the tropical Indian Ocean, but instead mirror a greater taxonomic effort in Europe (Griffiths 2005). However, closer comparisons of the table exhibits interesting details about states of knowledge in specific taxa and regions. Europe does maintain the highest number of species in each category except Pisces. The Pisces are among the most diverse vertebrates and best studied marine group, therefore the low number of European species may reflect biological reality. The uniformly low numbers of Brachiopoda may not be significant when South Africa is considered one of the most diverse areas with regards to the taxa with a total of only 31 species (Hiller 1994). The Hemichordata group showed unvaryingly low numbers, not surprisingly, considering the global number of species is only 85 (Gibbons *et al.* 1999).

Comparisons between Southern Hemisphere regions illustrate fascinating associations as well. Although notably lower than European totals, all three regions had similar numbers of Cnidaria, Annelida, Copepoda, and Echinodermata. These similarities may be due to biogeographic parallels between the regions, however, the number of described species in these regions should be interpreted with extreme caution, as inventories in some of these regions are likely very incomplete. The Western Indian Ocean has a noticeably low number of Porifera, this certainly being due to a lack of work done on that taxon (Richmond 2001). Many of the poorly represented taxa for the Western Indian Ocean can be explained by non-existent (Somalia) or very incomplete (Mozambique) biodiversity information (Griffiths 2005). Several typically diverse groups such as Bryozoa, Ascidia, Porifera and Annelida have no records for the region, or suspiciously low numbers (Griffiths 2005).

The seemingly high biodiversity of New Zealand Bryozoa can be attributed to a long history of research on the group, starting with the Challenger Expedition in 1874 and continuing mainly with the efforts of D.P. Gordon, who identified 798 species collected from 296 stations by hand, SCUBA, dredges, trawls, and sleds from varying depths (Rowden *et al.* 2004). New Zealand's biodiversity research is still in the early discovery stage, as sampling has almost entirely been restricted to depths less than 1 500 m and of specimens greater than 2 mm (Nelson and Gordon 1997). The total area of the seafloor sampled by the National Institute of Water and Atmospheric Research, universities and museums is less than 2 km^2 (Gordon 2000).

There are several reasons why two marine regions of comparable sizes might have different levels of biodiversity. These might include latitudinal range, bathymetry, geological and evolutionary history, as well as evenness and intensity of sampling and availability of taxonomic expertise (Rowden *et al.* 2004). The level of taxonomic effort between taxa can be influenced by the characteristics of the organisms, which make then either attractive or unattractive to taxonomists. Typical characteristics of taxa favoured by taxonomists include attractiveness, level of impact on humans, fashion, and ease of collection, preservation and classification (Groombridge 1992). Most marine biodiversity studies in the past have been random and opportunistic in distribution, focusing on easily-accessible locations and only identifying larger organisms (Thomas 1997).

Global location may be another factor influencing recorded biodiversity. Approximately 80% of the global taxonomic workforce is located in North American or European institutions and only 4 - 7% in Sub-Saharan Africa and Latin America (May 1994). Perhaps marine taxonomic studies are following a trend set by terrestrial biodiversity studies, where historically the initial work was undertaken by continental European scientists and Northern Hemisphere institutions (Patterson 2001), leaving southern workers untrained and unable to handle the curation of large amounts of type specimens. Insufficient funds or resources to maintain species collections are a common predicament, especially for those countries that have 50% or more of the population below the poverty line (Costello and Emblow 2000).

The effect of individual scientists on the trends of new marine species discoveries in Britain and Ireland were found to outweigh the effects of other influences, such as world wars and the development of new techniques (Costello *et al.* 1996). Therefore, the interests of the local taxonomists in developing countries of the Southern Hemisphere will have a significant impact on what taxa are studied. In the case of the Western Indian Ocean, consisting of many countries with very high populations and very low GDPs (Keesing and Irvine 2005), a lack of resources may also play a key role. Griffiths (2005) estimated that only half of the Western Indian Ocean's marine species have been described and with an absence of funding for work on taxa of little economic importance, the effect of the very few working taxonomists is evident (Richmond 2001).

Some of the current problems for South Africa are the fact that there are currently no taxonomists working on such speciose groups as crustaceans and there is a huge backlog of material that remains collected and yet unidentified (Griffiths 1999). In a recent review of the state of systematic study in South Africa many issues were voiced by those in the field, including the fact that many posts are not reopened after retirement, salaries are unattractive, some museums do not receive government funding, and there is a lack of taxonomy topics covered in school and university lectures (Adie *et al.* 2005). With the threat of alien species invasions, South Africa has a relatively low reported number compared to the better studied areas like Great Britain, but Robinson *et al.* (2005) claim that this may be due to the low sampling effort and poorly developed taxonomy, rather than resilience to invasion.

Southern Hemisphere regions appear to be lagging behind regions such as Europe, but there is evidence to support the fact that Southern Hemisphere regions may rival the

Northern Hemisphere in terms of biodiversity, despite lower recorded numbers. Indeed several studies of Antarctic marine biodiversity have claimed that the Southern Ocean and the surrounding areas have high species richness (Clarke 1992; Gray 2001b).

None of the species lists from either the Southern or the Northern hemisphere are near complete. Even the best studied ocean in the world still contains a significant number of undescribed marine species (Poore and Wilson 1993). Wilson and Costello (2005) suggested that in European seas, approximately 25% of the species still remain undescribed, a proportion that may be similar for the North-west Atlantic, but is estimated to be much greater elsewhere in the world. ERMS researchers originally extrapolated an estimate of 20 000 to 25 000 marine species in European waters, which was surpassed by the original collection of species names, totalling over 29 000 species, an underestimate, and a new forecast of more than 35 000 species has been predicted (Costello 2000). The situation does not seem to be changing.

Chapter 3

Estimating species richness of South African marine fauna utilizing species discovery curves

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Introduction

Many, perhaps even the majority, of marine species remain undescribed, yet the most commonly used indicator of biodiversity is the number of described species in an area (Wilson and Costello 2005). The historical rate of discovery of these species can, however, be used to create a species discovery curve, which can have predictive properties. Such curves are plots of the cumulative number of species discovered against time, with the curves tending to approach an asymptote, representing the total number of species in the areas, as taxonomic effort accumulates (Colwell and Coddington 1995; Walther and Morand 1998; Cam *et al.* 2002). The typical sigmoidal shape of such discovery curves begins with an initial period of a slow discovery as research begins, expertise is developed, and the first specimens are collected. This is followed by an increase in the rate of species description as expertise is established and then decreases again as the group becomes better known and the number of new species still to be found dwindles (Wilson and Costello 2005).

The S-shape is characteristic of discovery curves, but the details of the shape can be affected by many factors. Thompson and Withers (2003) utilized computer-generated simulations to determine the influence of species richness, relative abundance, and diversity on accumulation curves and found that situations with high proportions of rare species and few abundant species created a curve with a low shoulder and long upward slope to the asymptote, while simulations with high proportions of abundant species and few rare ones resulted in a curve with a steep initial slope, quickly reaching the asymptote.

Once the number of species has been plotted over time, the application of a predictive model can be used to provide information on future patterns of description. The choice of extrapolative model must be based on the particular collection situation (Soberon and Llorente 1993). Models must be evaluated in terms of the size of the area, the complexity of the fauna, how close the species list is to the actual total, as well as any yearly fluctuations the species undergo (Soberon and Llorente 1993). Predictive asymptotic models can provide a variety of information when applied to the species discovery curves. These include estimates of potential total species richness, status of the inventory, and the least effort required to reach an adequate level of completeness (Gaidet *et al.* 2005).

Several studies have analyzed the discovery rates of previously recorded marine species. Costello *et al.* (1996) investigated the rate of discovery of species recorded from British and Irish seas and showed that the rates were still very high for smaller-bodied organisms, even in these well-studied areas. Paxton (1998) analyzed a cumulative curve of open-water marine animals greater than two meters in length, between the years 1830

–1995, using a maximum likelihood method and found that a maximum of 47 species awaited description, at a rate of one species per 5.3 years. By comparing discovery rates of mysid crustaceans between different latitudes and regions, Wittman (1999) predicted the true species number to be as much as four times thai currently described. Wilson and Costello (2005) applied a non-homogenous point process to the discovery rates of European marine taxa and predicted, with 95% probability, that in this, the best-studied marine environment, there are between 667 and 3 337 species remaining to be discovered (excluding isopods due to high error), a proportion that is thought to be much higher in developing regions of the world.

There are several benefits to utilizing discovery curves and subsequent predictive models to forecast real biodiversity. At present, simple extrapolations from well-known groups are likely to provide the most secure estimates of the biodiversity of the large and poorly-known groups, given the current deficiency of more direct approaches (Groombridge 1992). Wilson and Costello (2005) found that past discovery rates were good indicators of future discoveries in the species-rich taxa, due to negligible fluctuations in rates of discovery, despite multiple authors, increased effort, or new technologies. Accumulation curves are affected by many factors, including the area's species richness, the overall abundance of certain species, and the evenness of species within a site and therefore can be useful in understanding species composition, as well as predicting the number of species (Thompson and Withers 2003). The calculated asymptote of the species accumulation curve can be used to estimate the actual number of species present, as well as to evaluate the adequacy of certain methods (Neigel 2003). Moreno and Halffter (2001) investigated bat species accumulation curves and found that 5-18 sampling nights were required to reach 90% of the inventory within seven habitat types, therefore establishing the methodology of least effort, another use of the accumulation curve. If the invested sampling effort has yet to reach the asymptote, predictive mathematical models can use the accumulation patterns for the effort to extrapolate the curve to the necessary effort to reach the asymptote (Moreno and Halffter 2001). In a study of large terrestrial mammals in an unprotected area of Zimbabwe, Gaidet *et al.* (2005) analyzed the direct sightings of large to medium-sized mammals along four transect counts and one water-point count and used species accumulation curves to analyze census completeness, to estimate the total number of resident species, and as a planning tool for further field work. Cam *et al.* (2002) used avian point count data from a spring roadside survey along nine routes through seven states collected by the North American Breeding Bird Survey, data repeatedly collected in the same period over a short period of time, and applied predictive models incorporating behaviour and heterogeneity elements.

As with all methodologies, there are several limitations to the analysis of discovery curves and associated models. When only a relatively small proportion of the assemblage has been sampled, extrapolating total species richness produces large errors (Willot 2001). The quality of the species counts can have a substantial influence on the results of extrapolative methods (Groombridge 1992). Species accumulation curves seem to be the most promising estimators of species richness for a range of conditions. However, uneven distributions may not be the same as the estimators' assumption of equal detection probabilities for all species, allowing the curves to underestimate true species richness (Brose and Martinez 2004). The shape of the accumulation curve is affected by the order in which samples are added to the total, either because of sample errors, or real heterogeneity (Colwell and Coddington 1995). Neigel (2003) claims that the species accumulation curves from a single location should not be used to extrapolate the species richness of diverse habitats. Linear dependence models (LDM) and Clench models have been used to estimate the lower and upper limits of the asymptotic total of species richness. However, these methods may only be useful where species accumulation curves have reached, or are close to reaching, an asymptote (Willot 2001). Some models cannot guarantee certainty about whether or not the peak rate has been reached for any taxa, resulting in lower predicted discovery rates in the immediate future (Wilson and Costello 2005).

Methods

South African marine taxa were placed into one of three categories as described by Gibbons *et al.* (1999), reflecting their state of taxonomic knowledge as being Good, Fair or Poor. Two representative groups were then chosen from each category for detailed analysis of species discovery rates, based on availablity of data. Chondricthyes and Cephalopoda were chosen from the well-known group, Isopoda and Amphipoda from the fairly-known group and Ascidiacea and sea anemones (cnidarians belonging to the orders Actiniaria and Corallimorpharia) from the poorly-known group.

Species lists for each group were derived from the appropriate monographs of South African marine fauna and the date of discovery of each species was recorded. The sources of data were Monniot *et al.* (2001) for ascidians, Acuna and Griffiths (2004) for sea anemones, Kensley (1978) for isopods, Griffiths (1976) for amphipods, Smith and Heemstra (1986) for chondrichthyes, and Roeleveld (1998) for cephalopods. The data consisted of the year of publication of the discovery of the species in South Africa. Although most of the dates were retrievable, some were not, due to the stipulation that the dates must be when the species was first identified in South Africa. A common problem with this method was that the only date that was included was when the type specimen was collected. In some instances that specimen came from a locality within South Africa and therefore that date could be used. It was easy to determine some references were from South Africa by the title, for example Barnard's (1955) "Additions to the fauna list of South African Crustacea". Similarly some were equally recognizable as being not South African, such as in "The marine fauna of the coast of Ireland". More difficult references referred to the origin of specimens as 'southern Africa' or documented decade-long global sea explorations, where the origin of the type specimen was hard to establish. Many reports were not in English or Afrikaans, or were impossible to locate with current resources. In other cases, the location within South Africa was listed in the species description, but not the date that the specimen was found. The only way to determine the date the species was described in South Africa was to search the literature backwards year by year, to discover when a South African specimen was first mentioned, a method that was not always possible with the time constraints of this project. Therefore, questionable references were eliminated to give a clearer picture of what we were focusing on, the date of description in South Africa.

For each group, a discovery curve was created by plotting the number of accumulating species over time. An analysis of 34 exponential and sigmoidal non-linear functions was carried out by FindGraph software (UniPhiz 2007). A table in order of lowest standard error was reported and the best fit curve was chosen and compared to the commonly used Weibull function (Weibull 1951).

Once the mean ratio of known compared to predicted species was calculated for the groups analysed, this same ratios were applied to the total numbers of species in the well-know, moderately-known and poorly-known groups. as listed in Table 2.1, in order to calculate the predicted numbers of undescribed species in the fauna as a whole. This method cannot be directly used to estimate species richness of taxa that are not represnted at all in South Africa.

Results

The data for each of the groups analyzed had very different characteristics. Of the species described in the sources, we were able to confirm South African dates of discovery for 71% of the isopods, 66% of the sea anemones, 83% of the ascidians, 98% of the chondrichthyans and only 25% of the cephalopods. The total number of species records used was thus 968. The sizes of the individual groups varied considerably, with the anemones having the fewest species at 31 and the amphipods the most records with 300 species. The earliest date of discovery was 1789 for the chondrichthyans and the most recent was 2001 for the ascidians. The discovery data were fitted with the two sigmoidal functions, Logistic (5) and Weibull, and plotted in Figure 3.1. The Logistic (5) function is defined as,

$$y = a + (b-a) /(1+((x-c)/d)^g)$$

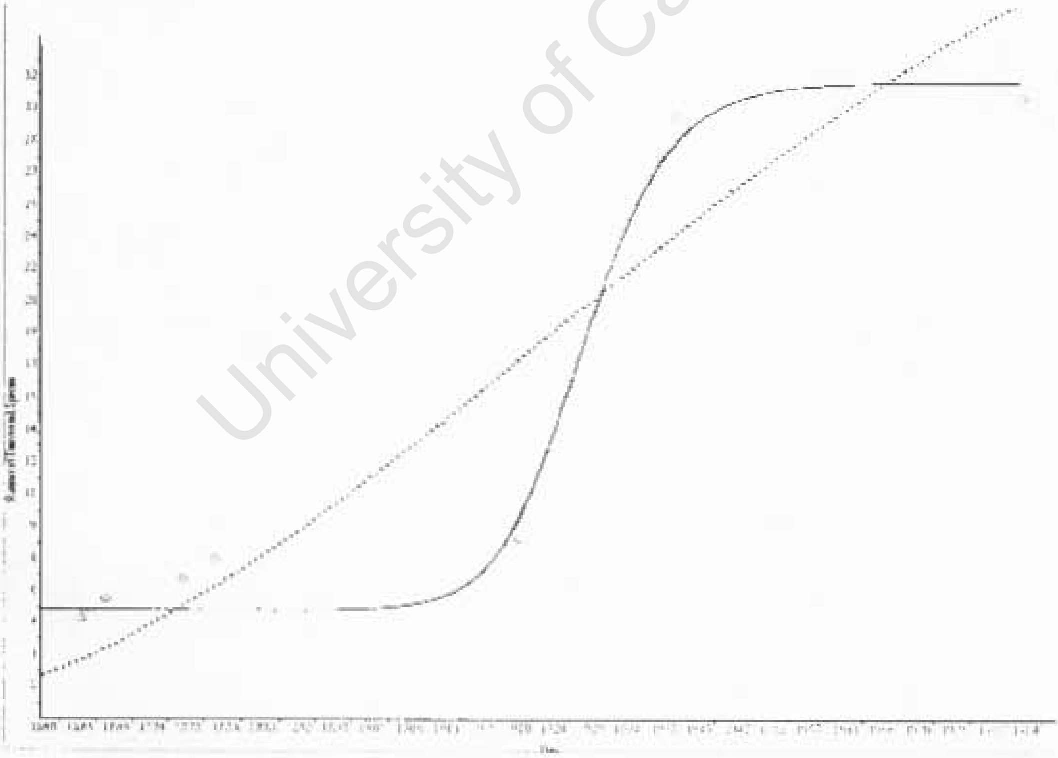
and the Weibull function as,

$$y = a * (1 - exp(-((b*(x-c))^d)))$$

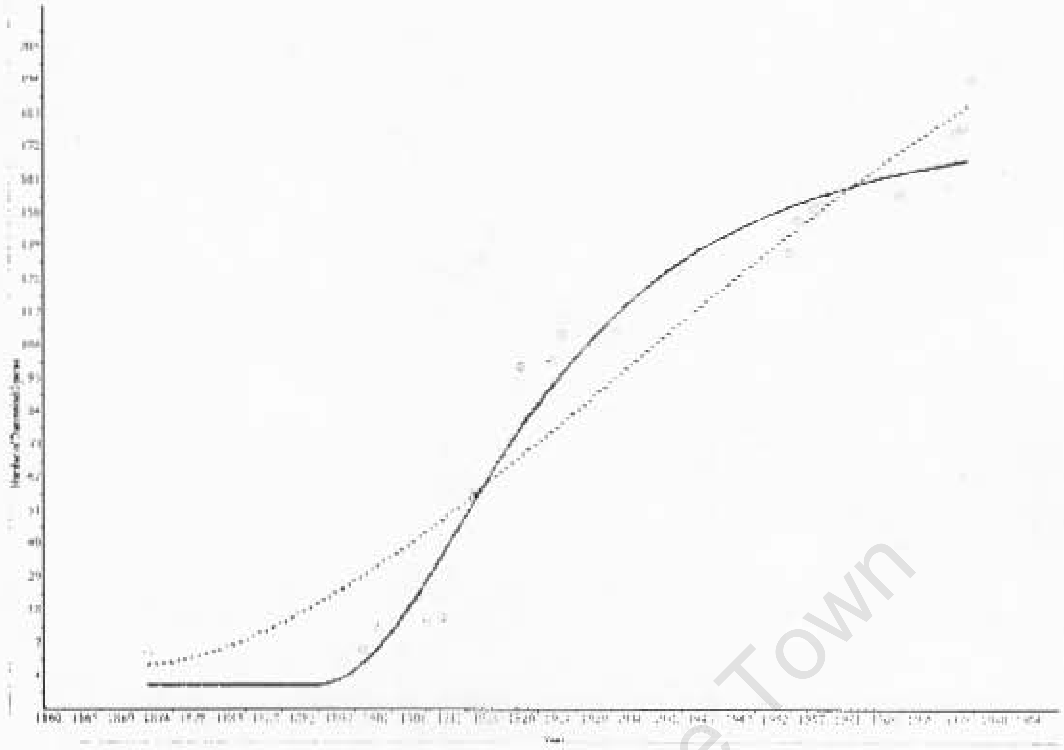
whereas a estimates an asymptote, b is the rate of species accumulation, the x-axis intercept is determined by c and d determines the shape.

(a) Ascidians

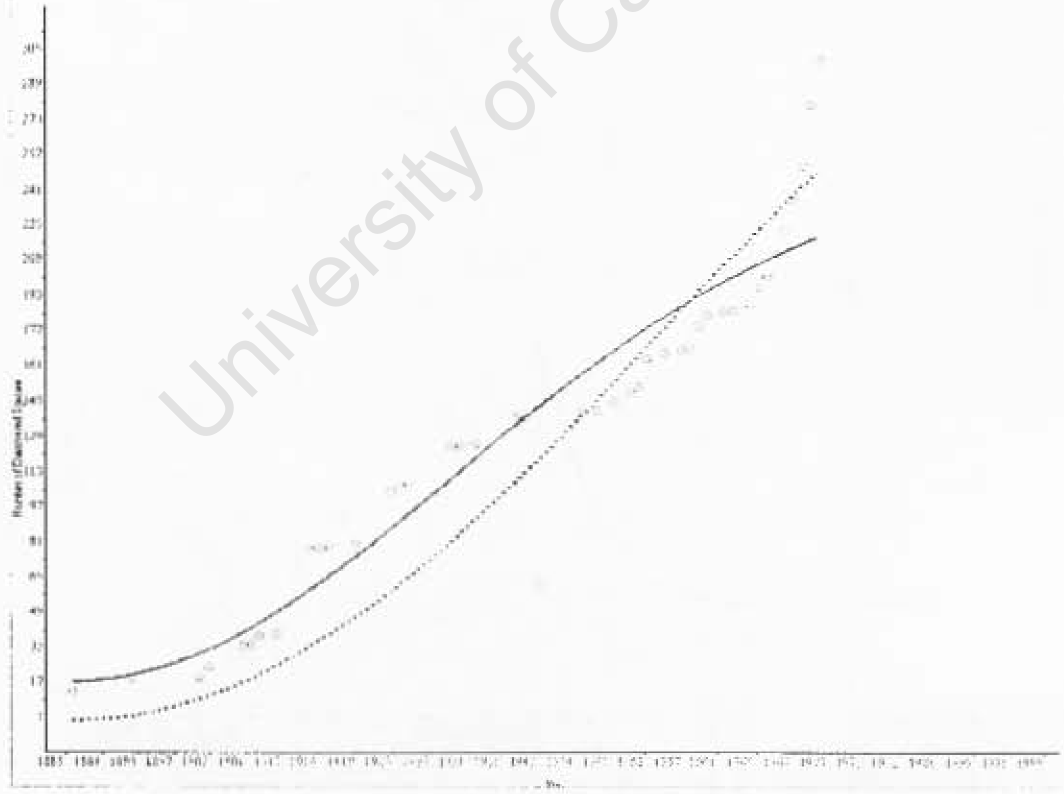
(b) Anemones



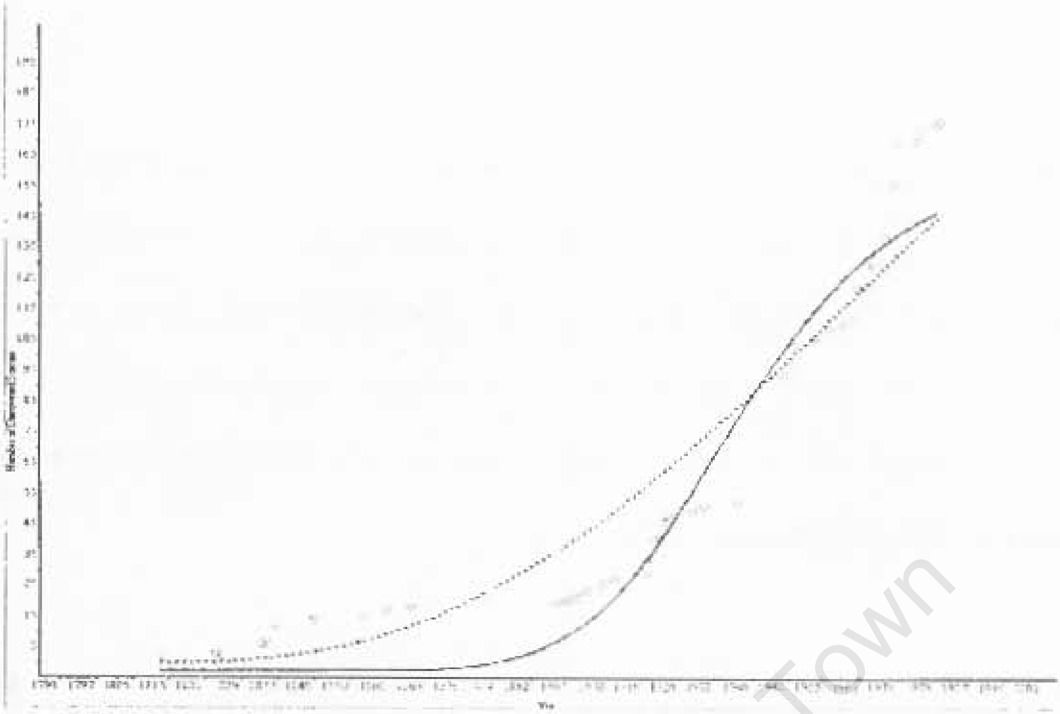
(c) Isopods



(d) Amphipods



(e) Chondricthyes



(f) Cephalopods

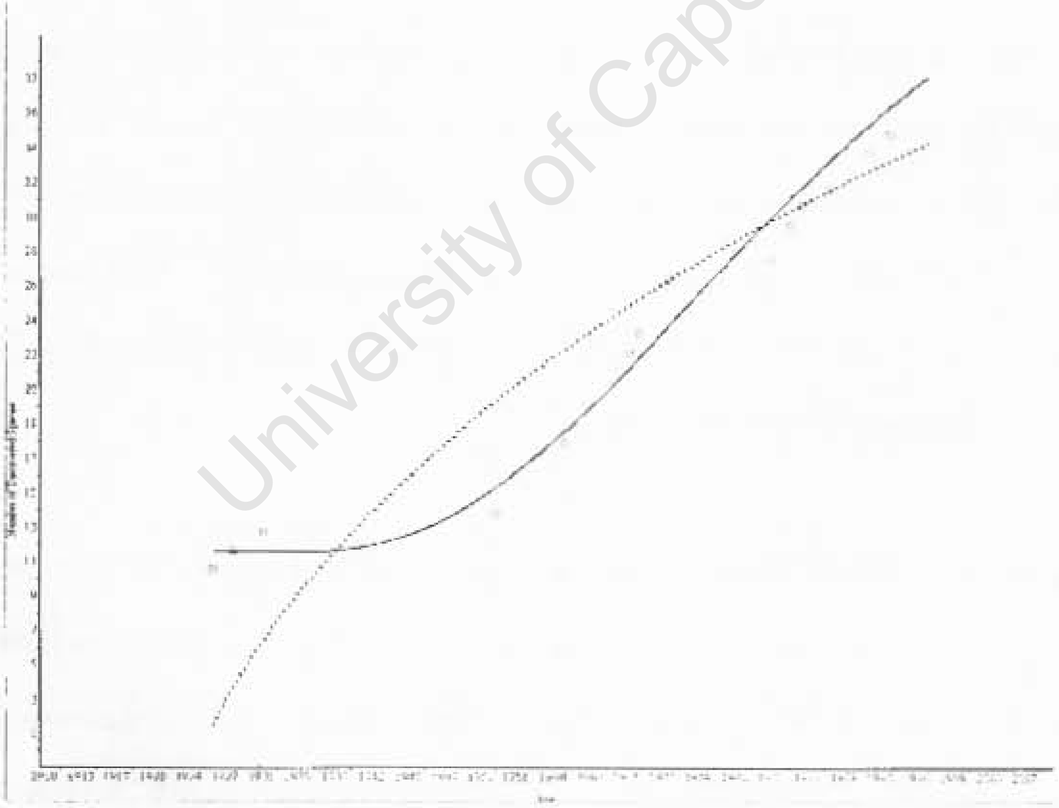


Figure 3.1. South African species discovery data for six taxa: (a) ascidians; (b) sea anemones; (c) isopods; (d) amphipods; (e) chondricthyes; (f) cephalopods. Each set of

data has been fitted to the non-linear, sigmoidal Logistic (5) function (solid line) and Weibull (dotted line) (FindGraph 2007).

The patterns of discovery differed greatly between groups. Ascidians reached 90% of their currently recorded species only in 2001, cephalopods by 1998, while the anemones reached that point by 1938 and the amphipods, isopods and chondrichthyans by the mid-1970s. Over 60% of the ascidians, amphipods, chondrichthyans and cephalopods were described between 1950 -- 2000. The other groups had the majority of the descriptions take place in the period between 1900 -1950.

The curve for the ascidians incorporated a total of 122 species recorded over 121 years with an average rate of description of approximately one species per year. However, the curve does not appear smooth, as there were only 19 description events. The curve shows a relatively late start, with the first significant work, describing 23 species, published in 1898. The curve remains steady for a time until another slight increase from 1911 to 1912 with 13 further species added. Over the 10 year period 1954 - 1964 there was a relatively steady addition of 43 species. The final major increase occurs only in 2001, with the addition of 23 newly described species.

The anemones had the smallest numbers of species, 31, and had the fewest taxonomic papers, with only 11 over 154 years, giving an average rate of 0.2 species described per year, the slowest of all the groups analysed. Approximately 74% of the species were described in the 1900's and 71% between 1900 -1950. There were two long periods of no discoveries, the first over the 38 years 1882 - 1920 and the second of 44 years 1940 -

1984. The shape thus looks as though it might be approaching an asymptote, but has a very small number of erratic data points.

The South African amphipod fauna included 300 species described over 95 years. This group has the highest average description rate of nearly 3.2 species per year. Over 82% of the species were described in the 20th century, with over half in the second half of that century. The discovery curve still appears to be advancing exponentially, with no indication of reaching an asymptote, despite the relatively high number of species already described.

The isopods are represented by 195 species, almost the same number of amphipods, but there is only half the number of contributing publications. The description took place over 122 years, resulting in an average rate of 2.4 species identified per year. Over 97% of the species were described in the 1900's and over 65% in the first half of that century. Major contributions occurred in 1914 and 1920, with contributions of 41 and 42 species respectively.

There were 47 papers describing new chondrichthyans, the highest number for all the groups. The description of these species took place over 196 years and resulted in a total of 176 species, or 0.9 species described per year. More than 89% of the species were described in the 20th century and 66% of those after 1950. Despite the earliest recorded of 1789, the discovery curve has a very slow start, and included a long period of 32 years of no discoveries between 1870 and 1902. A steady increase from 1921-1926 added 21 species and a major contribution in 1949 a further 41, this being followed by a steady climb from 1967 - 1976.

The cephalopods have the second smallest number of species, 44, and only 17 validated South African references ranging from 1924 - 1998. The average rate of species description is 0.6 per year. All of the species were described in the 20th century and 70% were described between 1950 and 2000. This is the only group not to have any descriptions before 1900, so the curve only starts after 1920 and shows no sign of reaching an asymptote. Between 1932 and 1955 there was no description of new cephalopods in the South African area for 23 years.

Table 3.1 gives summary information on the predictions given by the two sigmoidal functions best fitted to the discovery data by the best fit option of the FindGraph software. The ranking of all 34 functions for each taxa can be found in Appendix A. Of the 34 exponential and sigmoidal functions, ExpGauss and Exp 2-4 returned the lowest standard error. However, since we were interested mainly in the asymptote, these were not plotted. The Logistic (5) function consistently resulted in a lowest standard error for sigmoidal curves and it was compared to the well-referenced Weibull function, which reported higher standard errors. The Logistic (5) function also returned inappropriate asymptote predictions, less than the observed total, for the isopods and the chondrichthyes.

Table 3.1. Comparison information of the two sigmoidal curves fitted to the data.

Taxa	**Function**	**Standard Error**	**Predicted Asymptote**	**Percent increase over present fauna**
Ascidians	*Logistic (5)*	10.23	130	6
	Weibull	18.91	183	50
Sea Anemones	*Logistic (5)*	1.43	32	3
	Weibull	4.28	47	52
Isopods	*Logistic (5)*	11.76	188	-4
	Weibull	17.70	293	50
Amphipods	*Logistic (5)*	21.68	308	3
	Weibull	26.42	450	50
Chondrichthyes	*Logistic (5)*	13.94	168	-5
	Weibull	17.96	264	50
Cephalopods	*Logistic (5)*	1.97	57	30
	Weibull	4.69	67	52

Overall, there were an estimated 14 more species left to be described for these six taxa analysed according to the Logistic (5) function and a possible 420 species remaining to be described according to the Weibull function.

These figures can be used to estimate the total numbers of predicted and hence undescribed species in the fauna as a whole. In making this estimate I have assumed that the ratio of descrived to prediceted species in the groups plotted is representative of the well-, moderately- and poorly- known taxa in the fauna as a whole, as shown in Table 3.1. The predicted revised estimates of biodiversiy are shown in Table 3.2.

Table 3.2. Ratios of the known South African marine species numbers to predicted numbers generated by two functions fit to the data for each knowledge category and extrapolated number of species still left to be described.

	Knowledge Cluster	**Known:Predicted (from Table 3.1)**	**Factor**	**Current S.A. species**	**Corrected total**	**'missing' S.A. species**
Logistic (5)						
	Well-known	1:1.02	1.02	7262	7407	145
	Moderately-known	1:1.00	1.00	1778	1778	0
	Poorly-known	1: 1.06	1.06	1866	1978	12
					Total=	157
Weibull						
	Well-known	1:1.47	1.47	7262	10675	3413
	Moderately-known	1: 1.50	1.50	1778	2667	889
	Poorly-known	1: 1.50	1.50	1866	2799	933
					Total=	5235

Discussion

This analysis looked at the rates of discovery of several South African taxa and investigates whether these provide data that can be utilised to determine projected future rates of description, and to estimate the region's true species richness.

South Africa has a relatively sporadic taxonomic history. Linder and Griffiths (1999) identified three phases of systematic history, starting in the colonial phase, when early expeditions visited the region, but repatriated the samples to Europe for analysis. This was followed by the descriptive phases, when some work was completed locally, ending with the modern phase, when effort shifts to biological and phylogenetic focuses. These phases may influence the trends in dates of discovery for South African marine species. The 968 species used in this analysis are only a fraction of the known marine biodiversity for South Africa, but the relatively low number of description events recorded, 159 data points, indicates that work is done mostly in the form of large monographs, usually by one or two taxonomists dedicated to each group.

The species discovery curves described for European marine fauna demonstrated a rapid increase in the late 19th century (Costello and Emblow 2000). By contrast, most of the curves for South African species showed a slower start, with more than half of the species described during the second half of the 20th century, lagging well behind the European trend. Linder and Griffiths (1999) claim the second half of the 19th century was the start of the descriptive phase in South Africa, when locals started to become involved in species descriptions. Therefore, approximately 100 years after the start of the descriptive phase, over half of the described species have been catalogued.

South African ascidians have a relatively high number of species described. The significant contributions to the list were due to the work of only three taxonomists. Sluiter contributed 17 species in one published work (1898). Millar published work spanning 1953 – 1964, with large species numbers added to the total in 1955 and 1962. Monniot *et al.* (2001) was the source of the monograph used to compile the species list and in one year added a further 23 species.

The majority of the descriptions of anemone species come from a single publication by Carlgren (1938), who described 19 species in one published work, over 61% of the total species described for the area! England and Robson contributed the only species after 1940, 46 years later in 1984. There were thus two long time lags with no published works on this group, between 1882 and 1920 and between 1940 and 1984. This is simply due to a lack of taxonomists interested in this particular group.

The exponential shape of the amphipod graph indicates that the group is definitely not reaching an asymptote, even with the high number of described species. There are several large contributions by single authors. The exponential shape of the curve is due to a steady increase in the late 1900's, with 98 species added to the list by Griffiths in five years 1970 and 1975. Wilson and Costello (2005) found that taxa with smaller body size and high dispersion rates maintain a high rate of description in Europe and that relationship should be the case for less studied regions, like South Africa.

The species list for isopods had a relatively high total number of species, but most of the taxa were added by just two taxonomists. Barnard - the director of the South African Museum - recorded 103 new isopod species in three publications in 1914, 1920 and 1940. Kensley added a further 34 in works published in 1975 and 1977. Barnard is the only influential taxonomists in this analysis who contributed to several groups, describing numerous amphipods, many chondrichthyans and producing the "Marine Fishes of South Africa" in 1925 and 1927. The isopods discovery curve does not look as if it is approaching an asymptote. This is also true in Europe, which still has a large predicted number of undiscovered isopod species (Wilson and Costello 2005).

The dates of description for chondrichthyans look unlike any of the other graphs. There is a long time gap in description at the end of the 19th century, possibly because some chondrichthyan taxonomists, like Regan and von Bonde (Smith and Heemstra 1986) were also working on marine bony fishes at the time. In 1949, Smith made a contribution of 41 species and Bass identified 30 species in 1975 and 1976. Thus the graph does not indicate any approach of an asymptote, despite the large size and high profile of these species.

The cephalopod description curve demonstrates a difficulty of this method. The checklist used for tabulating South African species listed 173 species, but we were only able to validate 44 dates of description for this area. This graph only represents the latter half of the description effort for this group. Over half of the species were described by Robson in the first half of the 1900's and Roeleveld in the second half of the 1900's. Southern African species constitute 20-30% of the global total and a large number of specimens at the Iziko Museum in Cape Town indicate the true species richness of this group should be relatively high.

Extrapolating the results obtained for these selected taxa to the fauna as a whole, we can estimate the total numbers of species left to be described in South Africa. These calculations are shown in Table 3.2 The two functions used returned very different results.

The Logistic (5) predictions estimate very low numbers of undescrives species, indeed the estimated asymtote was in some cases lower that the currently described number of species, indicating that this is an inappropriate curve to use. Morover, suprisingly, the largest numbers of undescribed species (145) were predicted to come from the 'well-known' group, which is contrary to logic and to the results from Chapter 2. The overall number of undescribed species returned by this method was only 157. Even given that this method does not estimate the 'unknown' taxa (see Chapter 2), this is an extremely unlikely result, given the very poor state of knowledge of many speciose taxa (eg Namatoda, Copepoda) in this region.

The estimated total using the Weibull function is that 5 235 species remain to be described. Given that this excludes the 'unknown' groups (which account for possible another 300-400 species) this estimate is close to that of 6119 undescribed species obtained in Chapter 2. It is , however, suprising that the bulk of the 'undescribed ' species (3413) are predicted to come from the 'well-known' groups, rather than from those that are thought to be less well known.

Sampling from a large collection of species, new species are initially encountered rapidly and as samples accumulate, the rate should decline as the total number of species approaches an asymptote (Flather 1996; Soberon and Llorente 1993). The asymptote is then an estimate of species numbers (Palmer 1990; Bunge and Fitzpatrick 1993; Soberon and Llorente 1993). Fitting a non-linear curve to species discovery data commonly present complications, like unreasonable results from data anomalies, and even a good fit does not guarantee a legitimate extrapolation (Baker *et al.* 2006). Another downfall is that several functions can fit the same data well, but with varying estimations of asymptotes (Cam *et al.* 2002). Of the two functions used in these analyses, the Logistic (5) function resulted in the lowest values for standard errors for all taxa. The performance of the Weibull function has been evaluated and found to be a suitable formulation for computing species-accumulation curves and is the most versatile sigmoid model (Flather 1996; Tjorve 2003). In this analysis, however, the function reported high standard error values, but more realistic values (those predicted values equal to or higher than the observed value) for the predicted asymptote than the Logistic (5). It is beyond the scope of this thesis to evaluate the performance of these functions, however, there is further work to be done in finding a better fit to these data. Another limitation to the method is that it only predicts species to be discovered in groups that already have a significant number of species described, neglecting not only the taxa with very few described species but those groups of taxa with no current representation in South Africa.

With the biases introduced by these data (i.e. low number of data points) the predicted asymptotes should be evaluated with caution. These curves may be telling a different story. The shapes of the curves in fact probably reveal more about the careers and taxonomic interests of local scientists than the actual numbers of new taxa remaining to be described in each group. It is expected that as the sampling effort increases, the number of new species recorded will tend to decrease and flatten out to an asymptote (Cam *et al.* 2002). The discovery curves for many South African taxa, like the amphipods and cephalopods, do not seem to be reaching an asymptote, indicating that large numbers of species remain to be described.

In conclusion then, the trends in the discovery of new species of most groups in South Africa are derived from the work of only a very few systematists. The species discovery curves thus reflect this stochastic effect, instead of the true remaining undiscovered biodiversity of the area. In places such as Europe, where the task force of taxonomists is much larger, with several to many taxonomists working on each group at any one time, it is much more likely that the curves will be a true reflection of the proportion of undescribed species remaining in the fauna and this have better predictive validity.

This method of estimating true species richness is considered the weakest of the three methods attempted in this thesis. Determination of date of discovery specifically in South Africa can be time-consuming, making it impractical for rapid assessment of species richness. Another disappointing aspect of the method is that the fitting of a representative function was difficult and resulted in impractical values for an asymptote, or high standard error values. This indicates that the description of South African marine fauna is still in its initial stage and that predicted biodiversity estimated by this method is likely to be subject to considerable error. Clearly, however, all the groups examined are far from being fully described.

Chapter 4

The effect of biogeographic distribution of sampling effort on South Africa's recorded species richness

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Introduction

Emanuel *et al.* (1992) divided the coastline of southern Africa into 48 sections, each 100 km long, and analysed the distribution patterns of more than 2 000 marine coastal invertebrate species in each of these. A cluster analysis revealed four major zoogeographical provinces in the region, a Cool Temperate North-West Coast (Namibian) Province, a Cool Temperate South-West Coast (Namaqua) Province, a Warm Temperate South Coast (Agulhas) Province and a Subtropical East Coast (Natal) Province. There was a general increase in species richness across these provinces from West to East.

Several subsequent studies have further examined biogeographic patterns of biodiversity of specific taxa in the region. Turpie *et al.* (2000) investigated the distribution of 1 239 species of fish around the South African coast and showed that species richness increased progressively from West to East. Awad *et al.* (2002) examined the geographic diversity patterns of 11 different invertebrate groups. Each groups showed a different pattern, some increasing progressively from West to East, and others showing peak species richness in the South West Cape. Bolton and Stegenga (2002) surveyed 803 seaweed species and found that these showed peak species richness at the Cape Peninsula.

The main constraint in all of the above analyses was that sampling effort in each of the 50 or 100 km zones analysed was known to be inconsistent. Thus it is difficult to distinguish true differences in species richness from differences in numbers of recorded species resulting from differential sampling effort. This chapter attempts to engage this problem by examining the rate of species accumulation in a series of benthic samples collected from various regions around South Africa by the University of Cape Town Ecological Survey. This is an extensive series of samples collected by Professors T. A. Stephenson and J. H. Day of the Zoology Department of the University of Cape Town between approximately 1940 and 1970. The advantages of this data set are that all samples were collected by the same group of researchers, using the same gear (primarily a 0.1m^2 van Veen grab and standard benthic dredge) and vessels, and were identified by the same taxonomists, thus presumably to the same degree of resolution. The samples thus represent a remarkable uniform sample set that can be used to compare biogeographic trends in species richness, based on an accurately known sampling effort. The UCT Ecological Survey benthic catalogues, and samples, are currently deposited at Iziko Museums in Cape Town and are categorised and catalogued by broad geographic regions, namely South West Africa (now Namibia), West Coast, South Coast and Natal (now KwaZulu-Natal). The catalogues list the samples taken in a chronological sequence and give the date, the coordinates, the sampling technique, the bottom type, the depth and the substratum for each, plus a list of species collected and the abundance of each. Even today these still remain by far the most comprehensive collections of benthic marine invertebrates available from South Africa.

In this chapter an attempt is made to utilise the rates of species accumulation in these samples to investigate the state of knowledge of the benthic invertebrate fauna in various geographic regions around southern Africa, and to evaluate the veracity of previous conclusions with regard to biogeographic patterns in species richness.

Methods

All data analyzed were extracted from the benthic catalogues of the University of Cape Town Ecological Survey, currently housed at Iziko Museums in Cape Town, formerly the South African Museum, and initially collected by Professor T. A. Stephenson, Professor J. H. Day and co-workers. For each region, there are two catalogues, numeric and systematic, the former listing each sample in chronological order, with all species found in each sample, while the latter lists all species found in the region in systematic order and the samples from which each was recorded.

Samples were originally assigned to specific catalogues according to region of collection, the catalogues being named as follows: South West dredge (SWD), West Coast dredge (WCD), South Coast dredge (SCD), & Natal dredge (NAD), these are referred to below by the current regional names of Namibia, and West, South, and KwaZulu-Natal Coasts of South Africa. Despite the catalogues titles of 'dredge' the samples in fact consist of both dredge and grab samples (usually taken in parallel at each location) plus a small number of dive or trawl-collected samples. The areas covered by the catalogues are shown in Figure 4.1 and in fact correspond well to the recognized biogeographic provinces in the region.

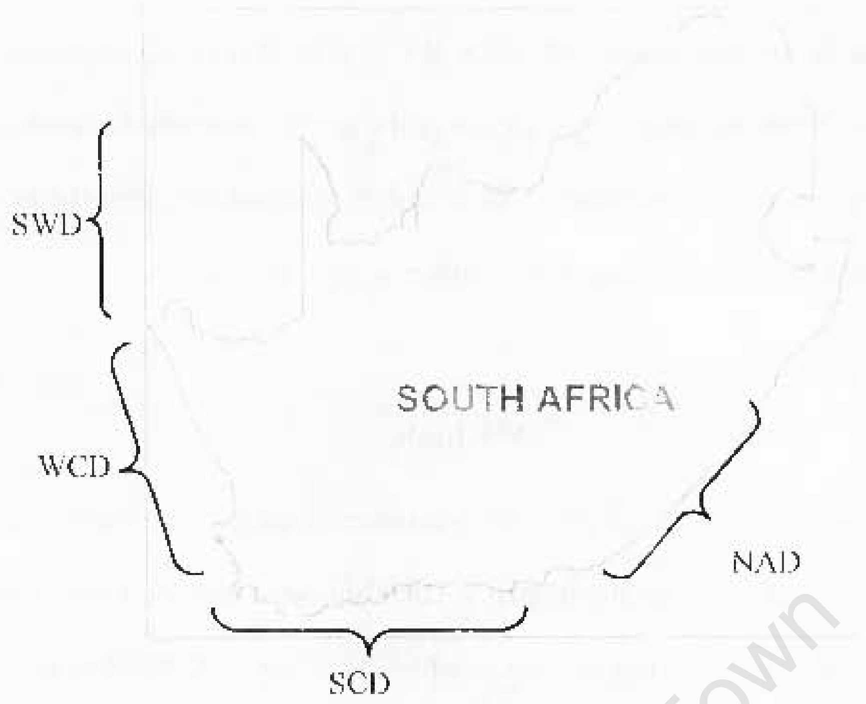


Figure 4.1 Map of southern Africa showing the regions covered by the various catalogues of the University of Cape Town Ecological Survey.

Information was compiled from the catalogues on the number of samples taken in each region, the number of species identified, the techniques used, and the depths reached. Some information could not be employed as the notes containing the needed information were indecipherable, therefore reducing the actual number of samples and species used in this analysis. The data were randomized using Primer 7.1 through 999 iterations and accumulation curves of species against number of samples taken were then plotted for each region. The data were fitted to accumulation curves and plotted in Statistica 7, from which asymptotes for each region could be estimated. The ratio of the two predominant sampling techniques, grabs and dredges, was calculated for each region, as well as the number of new species collected per sample in each region by both techniques.

Results

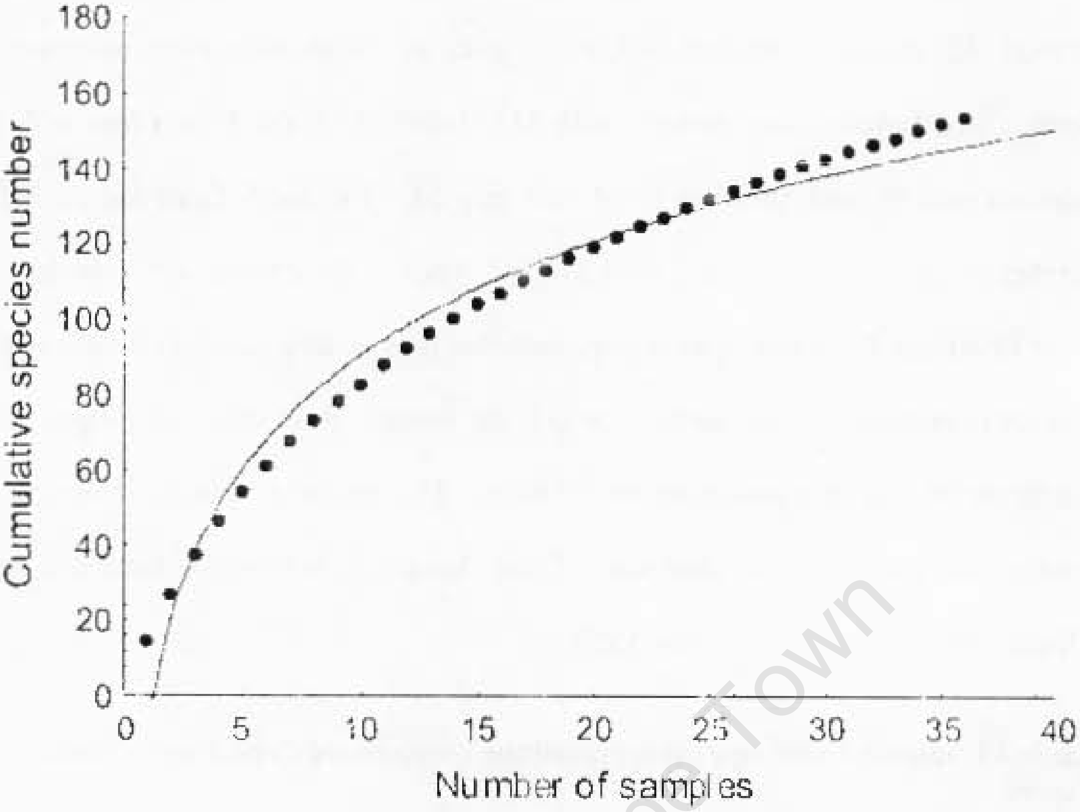
In total, 428 samples were included in this analysis. When subdivided by region, the South Coast had the most samples with 115, followed by the West Coast with 104, Namibia with 36, and KwaZulu-Natal with only 24. The South Coast had the highest number of accumulated species, with 744 and Namibia the lowest, with only 154. The West Coast and KwaZulu-Natal regions recorded intermediate numbers of 503 and 214 species respectively. The depths at which the samples were collected ranged from a minimum of 5 m to a maximum of 1 240 m. The sampling techniques were mostly dredges and grabs, but included some diving, sampling on shore by hand and trawls. This information is summarized in Table 4.1.

Table 4.1 Information on four catalogues of the University of Cape Town's Ecological Survey

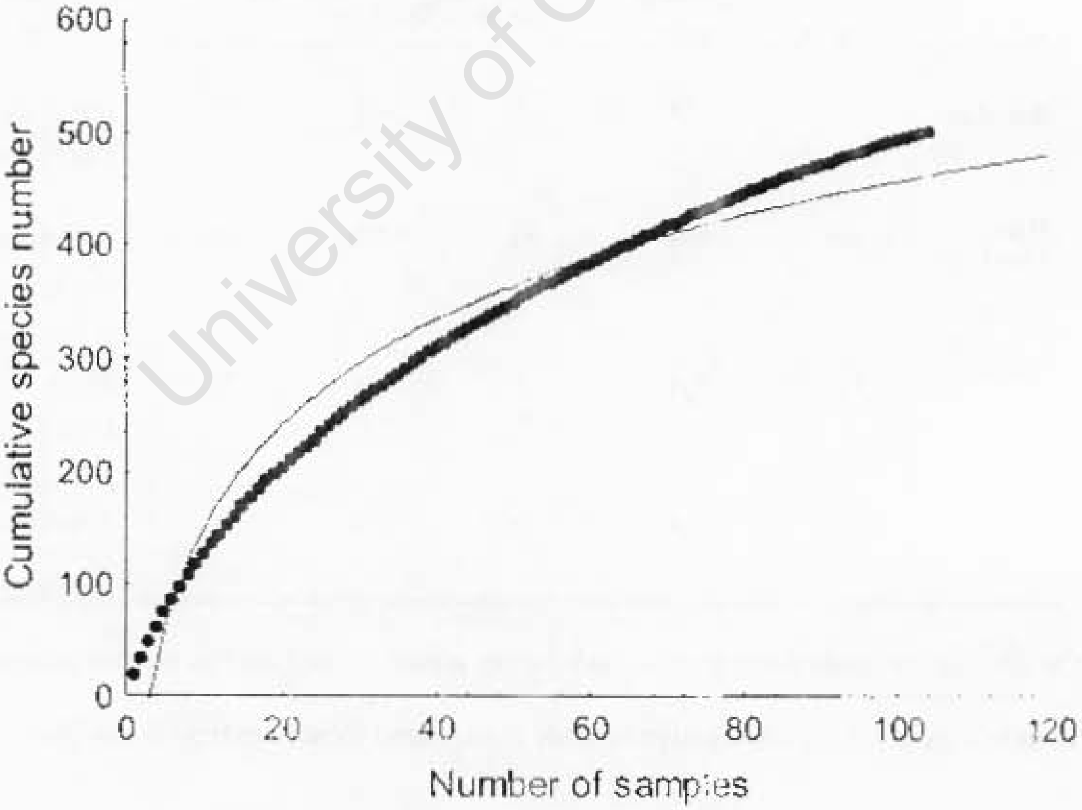
	Number of Samples	Cumulative Number of Species	Min. Depth (m)	Max. Depth (m)	Avg. Depth (m)	Major Techniques Utilized
Namibia	36	154	5	180	45	*39% Grabs* *26% Dredges*
West Coast	104	503	11	1 240	121	*38% Dredges* *36% Grabs*
South Coast	115	744	7	325	79	*36% Dredges* *32% Grabs*
KwaZulu-Natal	24	214	15	200	75	*40% Grabs* *21% Dredges*

The species accumulation curve for each survey area is plotted against number of samples taken in Figure 4.2. No distinction is made with respect to sample type in this plot.

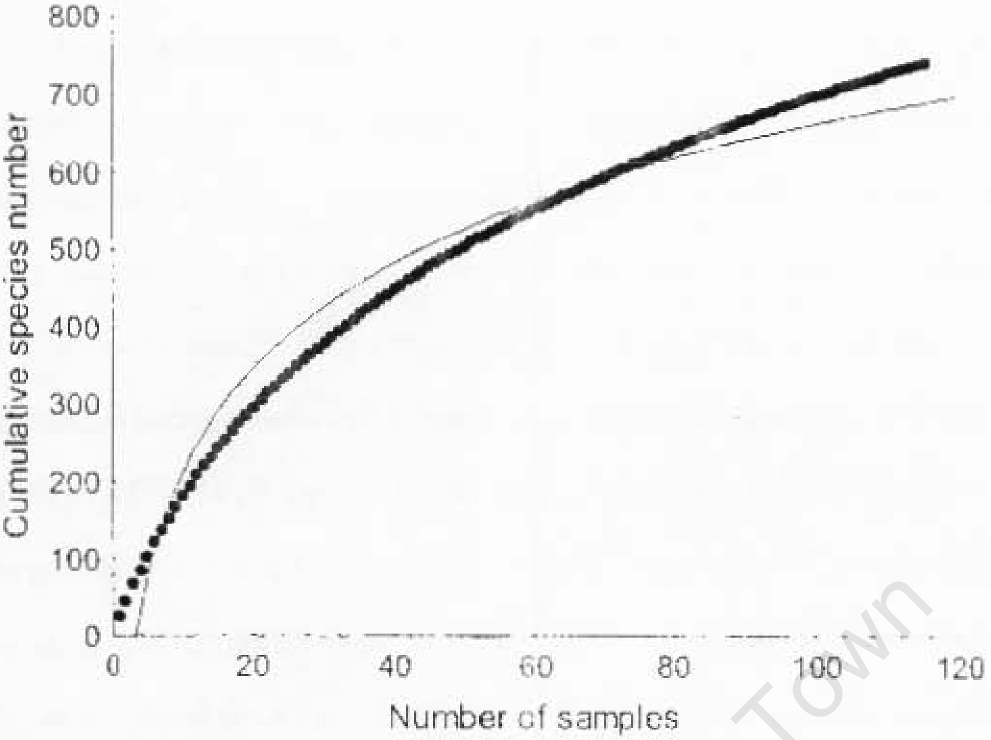
(a) **Namibia**



(b) **West Coast**



(c) South Coast



(d) KwaZulu-Natal

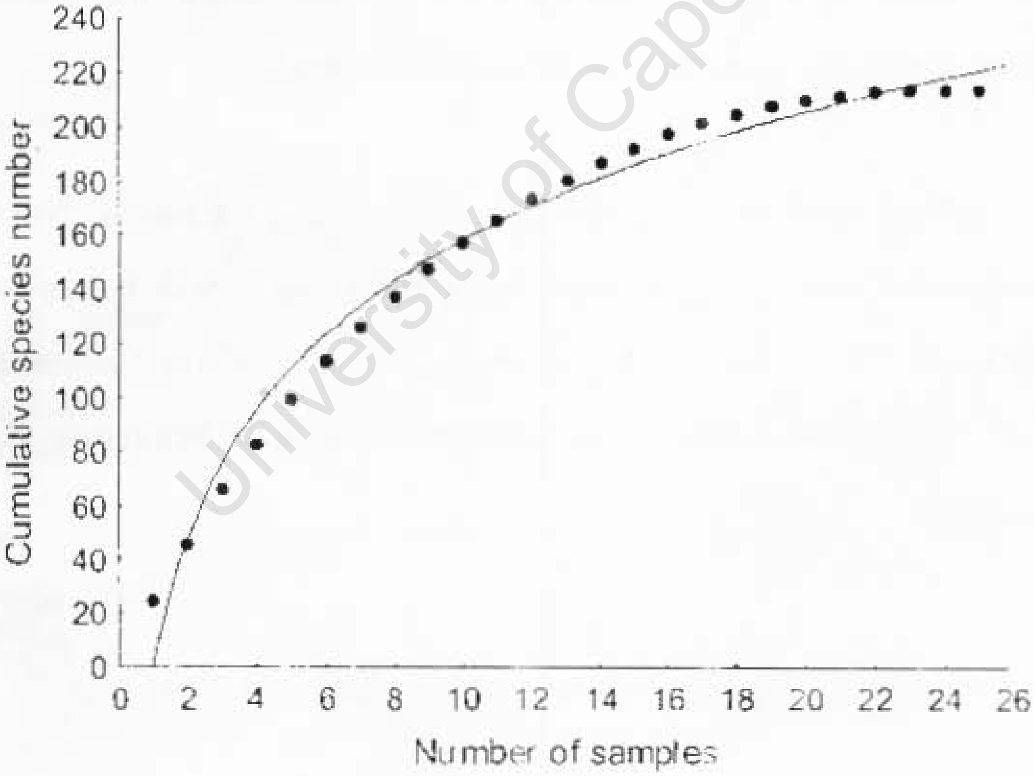


Figure 4.2. Species accumulation curves for marine benthos of (a) Namibia, (b) West Coast, (c) South Coast and (d) KwaZulu-Natal.

Several characteristics of this graph stand out. The fitted curves after randomization demonstrate the typical shape of rapid initial description, while only the KwaZulu-Natal curve seems to be approching a plateau. The Namibia curve reaches the lowest total number of species of 154, after a total of 36 samples taken. The West Coast curve shows a much more rapid initial accumulation, and only appears to be heading towards a plateau after 104 samples, but with far more species at 503.. The South Coast curve has a similar rate of species accumulation, but the shape shows a less obvious plateau despite having the highest number of samples taken in any of the regions, 115. The total number of species recorded, 744, is by far the largest of the regions, yet the curve still appears to be undergoing a steady increase, implying that not nearly all the species in the region have yet been adequately sampled. The KwaZulu-Natal region has the fewest samples at 24, yet a relatively high number of species, with 214; the species accumulation curve has by far the most rapidly increasing slope but appears to asymptote.

The South Coast's predicted asymptote was the highest at about 1 083 species. The West Coast region had the second highest asymptote at 995 species, with the KwaZulu-Natal not far behind with 362 species. The Namibian region had the lowest asymptote at 148 species. The best fit equations for the data are listed in Table 4.2 as well as the asymptote for each region.

Table 4.2. Best fit function for each of the four region's data as well as estimated asymptote.

Region	Equation	R^2	Asymptote
Namibia	$y = -10.04 + 100.37 \log10(x)$	0.97	148
West Coast	$y = -161.68 + 309.37 \log10(x)$	0.97	995
South Coast	$y = -241.97 + 452.79 \log10(x)$	0.96	1 083
KwaZulu-Natal	$y = 0.14 + 158.20 \log10(x)$	0.94	362

The average number of new species added per sample was lowest for Namibia, with only approximately 3.3 new species, followed by 9.1 new species added per sample in the South Coast region, 9.7 species in the West Coast region and the highest average in the KwaZulu-Natal region with 11.3 new species per sample. The average number of new species added per sample was calculated for each of the four regions of the survey and is given in Table 4.3.

Table 4.3 Average number of new species per sample for the four regions of the southern African coast.

Area	Avg. num. of new species per sample	Avg. num. of new species per sample after ~ 40 samples
Namibia	2.7	3.3
West Coast	3.8	9.7
South Coast	5.1	9.1
KwaZulu-Natal	11.3	11.3

The ratio of grab samples to dredge samples was calculated to analyze any bias introduced by the sporadic nature of sampling techniques between the regions. KwaZulu-Natal's ratio was greater than one with 2.00. Namibian sampling struck a balance with a ratio of exactly one to one. The South Coast and West coast were slightly under one with 0.95 and 0.89 respectively. This information for each region is demonstrated in Table 4.4.

Table 4.4 Ratio of grabs to dredges and the average number of new species collected per sample in each region by Grab or Dredge for each of the four southern African regions.

	Ratio *G:D*
Namibia	1.00
West Coast	0.89
South Coast	0.95
KwaZulu-Natal	2.00

Discussion

On the basis of current total reported species richness it might appear that Namibia has the least biodiverse invertebrate benthos of the four regions, followed by KwaZulu-Natal, the West Coast and finally the South Coast, which has the most species recorded. However, it is clear that there is a large discrepancy between the sampling efforts across the biogeographical provinces, as based on the University of Cape Town's Ecological Survey. The numbers of samples are inconsistent throughout the region as well as the depth investigated. Even the sampling techniques were of differing ratios. Each of these issues has a dramatic effect on reported species richness.

The accumulation curves of the four catalogues display this effect clearly. The appearance of the Namibian curve is misleading. Although the curve does not seem to be levelling off, the predicted asymptote is actually less than the observed species total, indicating the areas have been adequately sampled and the data provide a fair representation of the true regional biodiversity, which is relatively low in this region, as indeed has been reported by previous authors (Emmanuel *et al.* 1992; Turpie *et al.* 2000, Awad *et al.* 2002). Surprisingly, the difference between the observed and the predicted species totals is greatest for the West Coast region, perhaps due to the large number of samples taken.

The South Coast does not appear to be reaching an asymptote, despite being the most intensely sampled of all the regions. However, from the accumulation curve, the South Coast is estimated to reach an asymptote at 1 083 species, an additional 339 species. This suggests that the region has a much greater benthic invertebrate biodiversity than regions to the West – a contention again supported by evidence from other previous studies on other taxa and habitats (Emmanuel *et al.* 1992; Turpie *et al.* 2000) and especially by Awad *et al.* (2002), who found the South Coast region to be the area of maximum diversity for several invertebrate taxa.

The KwaZulu-Natal situation is even more extreme, the curve showing a high initial slope, but containing so few samples that the asymptote is estimated at 362 species, an addition of 148 species. This suggests that KwaZulu-Natal has a very high benthic biodiversity, but remains severely under-sampled. Biological evidence and results from other studies also suggest this to be the region with highest species richness, both in the case of coastal fish (Turpie *et al.* 2000) and several invertebrate groups (Awad *et al.*

2002). The latter authors also suspected that true diversity has been under-represented in this region due to inadequate sampling.

This method results in an estimate that an additional 979 benthic macrofaunal records are required before these four regions are completely sampled (note that this does not imply that 979 additional species need to be recorded, since there is large overlap between the species recorded in the four regions). This estimate cannot be directly compared with those in Chapters 2 and 3, of course, since the analysis here is based only on those species of benthic macrofauna that are sampled by grab and dredge – techniques that are used only in deeper water and on soft substrata. By contrast the analyses in earlier chapters consider all species collected from a wide range of habitats and by a wide variety of sampling techniques. The analysis nevertheless provides a good indication of which areas have been adequately sampled and which are under-sampled – the conclusion clearly being that future sampling effort needs to be concentrated on the east coast. It is also meaningful to calculate that the extrapolation of the existing species lists to asymptote would require, on average, the addition of 41% more species to existing lists. The ratio of underreporting is similar to that calculated in earlier chapters which suggest that between 47% (Chapter 3) and 55% (Chapter 2) of all macrofaunal species are yet to be described.

Biases could have been introduced to the data analysis if all sampling techniques are considered. The number of replicates of sampling types was not uniform in each region as demonstrated by the differing ratios of grabs to dredges. The Namibian ratio of grabs to dredges showed equal usage of both sampling techniques. The West Coast and South Coast sampling techniques seem only slightly skewed in favour of dredges. KwaZulu-

Natal catalogues show the other extreme with a large bias towards grabs, as much as twice as many were taken. A grab is defined by Holme and McIntyre (1971) as an instrument that is lowered on a vertical warp from a stationary ship to take a deposit sample of any given surface area, typically sampling slow-moving and sedentary members of the epifauna and infauna. There are several shortcomings of the grab technique. Grabs only scrape the surface of hard-packed sand, sometimes inadequately sampling animals in the top 10 cm, scarcer species, and faster moving organisms. Because grabs were the dominant sampling technique in KwaZulu-Natal, benthic fauna with patchy distribution and low abundance may be inadequately sampled. This region was sampled by a proportionately lower number of dredges, half the amount of grabs. In each region, dredges consistently reported higher numbers of new species per sample, so a bias towards grabs may reflect lower recorded biodiversity of Namibia and KwaZulu-Natal. Our data clearly demonstrate that KwaZulu-Natal has the largest number of species reported per sample and the low absolute number of species currently recorded is merely a reflection of the relatively low absolute number of samples taken in this region. The number of samples taken needs to be increased in regions such as KwaZulu-Natal but also the sampling techniques should be varied to increase the possibility of sampling species with more diverse distributions.

Similar biases caused by differing levels of sampling effort have an affect on all of the previous reported patterns of species richness along the coast. Awad *et al.* (2002), for example, noted peaks in species richness at localities such as False Bay, Port Elizabeth and Durban, the locations of the main coastal marine laboratories in South Africa and they attributed these to increased sampling effort at these sites. Turpie *et al.* (2000) also observed stepped increases in the number of fish species corresponding to well-studied and often-fished areas along the South African coast. Bolton and Stegenga (2002) also identified KwaZulu-Natal as the area most lacking in data on the distributional and ecology of regional algal species.

Such problems are inherent to comparisons of species inventories in regions where there is no indication of how complete the survey is (Willot 2001). However, if there is solid information on sampling effort, as is the case here, the rate of species accumulation per sample probably provides a much better indicator of total species richness than the actual regions species list. In this case the rapid species accumulation curve in KwaZulu-Natal provided convincing evidence that this is indeed the most species rich of the regions, but has simply been under-sampled to date.

The UCT Ecological Survey has much more information to offer towards an in-depth investigation of species richness patterns. The exact coordinates of the surveys' boundaries can be derived from the catalogues and can be used to investigate finer-scale patterns of species distributions. The depth of each sample is also recorded, allowing for analysis of the pattern of sampling effort and species richness with respect to depth and distance off-shore (Griffiths 2005). Grassle and Maciolek (1992) concluded that there was a continual increase in the number of species with depth and even greater rates of species accumulation across the depth contours. Wilson and Costello (2005) used a predictive model on the dates of discovery of isopod crustaceans and found the groups had a large number of undiscovered species and proposed that because of their prevalence in deeper waters, the advent of deep sea exploration will only increase the rates of discovery. Further analysis of the UCT catalogues is likely to demonstrate similar trends and that deeper water taxa are greatly under-represented in the South African fauna list and an obvious target area for future biodiversity research. This will be the topic of a future study.

Chapter 5

Synthesis

This thesis has attempted to estimate the current state of knowledge of marine biodiversity in South Africa. Three methods were used to approach this question, with varying results. All three methods were based on analysis of previously collected data over a large temporal and spatial scale, making standardization difficult. Although the resulting analyses were more descriptive than statistically rigorous, interesting results were obtained and new insights acquired.

Method 1 compared the taxonomic state of knowledge of South Africa's marine species to that from other global regions. Europe was chosen to set the standard, due to its long history of taxonomic research, which makes it without doubt the area with the best documented marine biota in the world. The described marine fauna of South Africa used in this analysis consists of 10 906 species, while the species list used for Europe comprises 22 042 species. The fauna of South Africa was tabulated into well-known, moderately-known, poorly-known and unrecorded groups, based on the status of taxonomic knowledge within each taxon. An assumption was made that the ratio between well-known groups in South Africa and Europe gave a true reflection of the relative species richness of the two faunas. Based on this ratio (of 0.78:1 between South African and Europe) it was possible to calculate how many species needed to be described in other taxa in order to bring the South African state of knowledge up to the current European level. It was concluded that a further 6 119 species (56% of the current total fauna) await such description, 711 from the moderately-known group, 5 057 from the poorly-known group and 351 from the unrecorded group. This method has several advantages, as the data were easily acquired from previously published studies. However, an assumption had to be made that there is a constant predictable ratio between the species richness of different taxa between the two regions. Given the different geographic centres of origin and diversity of the different taxa, as well as the different habitat conditions in Europe and South Africa, this is unlikely to be accurate for all group, although, when averaged across all groups, we still have confidence in our estimate. It should also be borne in mind that even in Europe, the marine area that is considered the most thoroughly studied in the world, many species still remain undiscovered and indeed the rate of species discovery remains linear. This the estimate given here simply reflects what is required to raise the South African state of knowledge to European levels, not what is required to completely describe the fauna! Not surprisingly it was also noted that the 'missing' fauna in South Africa is largely in 'difficult' groups for which taxonomic expertise is not present in this region.

Method 2 analyzed the historical rates of species discovery in six groups of South African marine taxa. Assuming that the form of the plotted data would follow the typical sigmoid shape, the aim of the chapter was to predict the asymptotes of these curves and therefore find out how far along that curve the process was. The results showed that it was difficult to fit curves to the data, largely because of the stochastic nature of the discovery curves in this region (in turn an effect of the small total number of taxonomists and the particular specialisation pursued by each). Two types of curve were fitted to the data, logistic and Weibull. The logistic curves appeared to underestimate biodiversity, in some cases predicting asymptotes that we in fact lower than the currently described numbers of species. When extrapolated to the fauna as a whole this method predicted that only 157 species remain to be discovered – an unrealistic estimate, given the know lack of taxonomic knowledge in several speciose taxa in this region.

The Weibull curves gave more credible results. When extrapolated to the fauna as a whole this method predicted that 5 235 species remain to be discovered. This represents a 48% increase over the existing described fauna – a result close to the 56% predicted in Chapter 2.

Method 3 used benthic data collected as part of UCT's Ecological Survey to illustrate the distribution of benthic sampling effort around the South African coast. These catalogues are the most comprehensive sources of compiled survey information for the region, spanning a considerable amount of time and endeavour. The existing data sets can be used to calculate the numbers of recorded benthic invertebrate species in each region, which totalled 154 for Namibia, 503 for the West Coast, 744 for the South Coast, and 214 for KwaZulu-Natal. These figures are certainly strongly biased by differences in sampling effort – the total numbers of benthic samples from this series in each region being very different, at 36 for Namibia, 104 for the West Coast, 115 for the South Coast and only 24 for KwaZulu-Natal. The data were randomized and fitted with accumulation curves and an asymptote was predicted for each region. The total number of additional records required (species x regions for which they were unreported) was 979, the largest addition predicted in the West Coast area. This corresponds to a 62% increase over existing species records, a level of under-description similar to those estimated in earlier chapters. Perceived benthic biodiversity hotspots within South Africa may thus be more a reflection of hotspots of sampling effort than of true species richness. This analysis attempted to resole this issue by instead examining the number of new species recorded per sample and the rate of species accumulation with increasing samples number in the various regions. The KwaZulu-Natal regions in fact showed the largest mean number of species per sample at 11.3, higher than the South Coast with only 9.1 species per sample, the West Coast with 9.7 species per sample and Namibia with only 3.3 species per sample. Similarly a plot of accumulated species against number of samples showed that the accumulation curves for KwaZulu-Natal reaches a plateau, while that for the other regions are still increasing, despite a larger number of samples taken. The curve for KwaZulu-Natal may appear this way because of the lowest numbers of samples taken and a bias towards the grab sampling technique. This indicated that the highest benthic diversity in fact lies in the East, but this fact has been hidden by inadequate sample effort off the KwaZulu-Natal coast.

The criteria of comparing the three methods used in this thesis are ease of use and reliability of results. The ease of use includes time taken for data collection and interpretation. The first method did not require extensive time or resources, except for the location of some of the poorly-known regions species lists. Despite some assumptions in this method, the estimated number of remaining species results is probably the most reliable of the three methods attempted here. The species discovery curves required the most amount of work, as researching the date of description was complicated and a good working knowledge of curve-fitting was essential. The limited number of data points and assumptions in this method cast some doubt on the results, but the overall estimate of under-reporting of species (48%) is similar to that estimated in Chapter2 (56%). Compiling the data for the third method was not arduous and the accumulation curve-fitting to the data to obtain an asymptote was straightforward. The results are based on a large set of data from the UCT Ecological survey and a finer resolution method could be implemented, however, the results seem satisfactory. Extrapolation of the results form this one habitat type and sampling method indicate that some 62% of the fauna remains un-described, again a similar estimate to those obtained above.

A major conclusion of these methods was that there is a variety of biases present in the collection and analysis of the taxonomic samples that have been used to determine the amount of recorded biodiversity in South Africa. There are far fewer working taxonomists in South Africa than in Europe and therefore the taxa of interest of those few taxonomists have receive an unbalanced amount of attention in comparison to other groups, skewing the recorded amount of biodiversity. Similar effects are evident in the fauna lists of other smaller countries, like New Zealand. At the current rate of description it could take that region a further 100-400 years to describe the unknown species there (Gordon 2004). This study similarly concludes it will take South Africa as long as 144 years to reach the current European state of taxonomic coverage at the current rate of effort.

This situation poses a problem for managers. As threats to marine ecosystems continue, taxonomic knowledge will be the basis of many important conservation and management decisions, such as the location of marine protected areas. Such decisions have in the past been made on insufficient information, as some of the more conspicuous, better known taxa in the best studied region of the world still have many species left to be described (Costello *et al.* 1996). Choosing sites for future protected areas needs to ensure all targeted species are included and well established marine reserves in South Africa such as De Hoop, Tsitsikamma and St. Lucia-Maputaland still contain a large proportion of undescribed species (Turpie *et al.* 2000). To be able to make well-informed conservation decisions, the authorities need information about what species are present and the level of biodiversity. The current knowledge of marine species richness is comprehensive in comparison to that in other African countries, but not to well-studied regions like Europe.

There is not enough time, funding or resources to support a large scale all-inclusive marine survey, therefore, it becomes imperative to consolidate the work by gathering new information quickly, cheaply, and with a small workforce. Rapid-assessment techniques can serve as surrogates for full species inventories (Gray 2001a). This can be accomplished by training parataxonomists to swiftly identify only key species that have been chosen as a proxy to the area's species richness to augment survey and inventory capabilities (Thomas 1997). Other methods using surrogates, such as the use of Recognizable Taxonomic Units (RTU's), can also be implemented (Oliver and Beattie 1993). Another approach is to utilize any information that has already been collected, as was done in this thesis. Museum and other collections are a reservoir of material that could allow researchers to capitalize on centuries of collection effort (Blackmore 1996). South Africa has the advantage of retaining a very large amount of information in the collections of several established institutes, but with the disadvantage of lacking available resources to fully catalogue and identify much of what is preserved. There is a relatively large amount of data in South African institutions that has been backlogged and remains to be identified (Griffiths 1999).

The irony remains that, as the opportunities to discover species and understand marine biodiversity advance with the technological age, so fewer trained taxonomists exist to take advantage of such progress (Gibbons *et al.* 1999). Decline in systematists is short-sighted, as taxonomy is the basis of all biology and ecology (Brown 1999). If the description of new species continues at the same rate with an unchanging number of taxonomists, the cataloguing of the global species richness will take several hundred years to complete and as the funding for taxonomy declines, coupled with a declining workforce, the task seems impossible (Oliver and Beattie 1993). If the trend of the taxonomic workforce shifting to specialized private institutes and away from academia elsewhere continues, perhaps South Africa's attention and funding should be concentrated on academia, ensuring the training of future systematists, and creating the incentive of job prospects. Becoming a taxonomic expert takes years of training, access to extensive specimen collections, type material and specialized literature, an intricate and lengthy process that is not always practical in certain regions of the world, or in the time crunch created by the current biodiversity crisis (Richmond 2001). Of the marine specimen collections within Europe surveyed by Costello and Emblow (2000), as part of the development of the European Register of Marine Species database, 64% were incompletely catalogued due to insufficient funds and resources.

Following the CoML's global example, South Africa needs to coordinate what is known, including summarizing the information contained in the country's museums, collating current research projects conducted by universities and other institutes, and any other valuable resources of information within the country. Finding out what is unknown at a regional scale is also recommended by identifying specimens housed in museums and other collections that are unnamed and need taxonomic attention, diverting attention to those sections of the biota that has received the least attention but may be highly diverse, as well as focusing attention on what geographic areas require more research. This thesis can serve as a very initial source in addressing the last two concerns.

Certain programs are underway to facilitate future analysis of this kind. AFROBIS, the African component of the CoML's Ocean Biogeographic Information System, is a database that has been created to assist potential investigations by pooling all the regional data into a readily accessible form.

Approximately 50% of humanity lives within 50 km of the coast, which only comprises 2% of the oceans area, but is reported to contain more than 6% of the described species, suggesting either high biodiversity or intense sampling effort (O'Dor 2003). As technologies become more available, the deep-sea, very little studied in South Africa, should become another research priority because the potential for undiscovered biodiversity there is high and, despite the perceived remoteness of the environment, toxic compounds have been found to accumulate in deep-sea sediments, exemplifying detrimental anthropogenic influences that need to be monitored (Grassle 1991). The depth distribution of past sampling effort can be investigated using the University of Cape Town's Ecological surveys and other benthic sources.

Although South Africa has a rich history of marine research covering many diverse taxa and biogeographic regions, this analysis has revealed gaps that, if closed, would greatly enhance the country's recorded marine biodiversity. In terms of taxa, taxonomic effort devoted to those falling into the poorly-known category, as established in Chapter 2, would contribute greatly to the overall species richness. The moderately-known category could contribute 1 013 species, or 45% of the calculated 'missing' fauna, to South Africa's marine biodiversity. Despite biodiversity research like that of Sink *et al.* (2005) and the work carried out at the Oceanicographic Research Institute, like that of Schcleyer *et al.* (2006), the KwaZulu-Natal region is an area that has lacked sampling effort relative to other parts of the country and it is apparent that additional research endeavours in this biologically diverse area have the potential to augment the nation's species richness. In a study of distribution, Awad *et al.* (2002) found certain groups of marine invertebrate demonstrate species richness increasing from West to East along the South African coast, but over half of the groups investigated showed highest richness along the South Coast. The information revealed in this thesis could have influenced those results, by providing evidence for higher species richness along the East Coast. With future research focusing on this region, the marine biodiversity of South Africa will increase and true species distributions may become more evident.

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Appendix : Order of performance (ranked by standard error) of 34 sigmoidal and exponential functions (FindGraph ver. 1.77) for six South African taxa.

Ascidians		**Sea Anemones**		**Isopods**	
Std. Error	*Function*	*Std. Error*	*Function*	*Std. Error*	*Function*
1.000000	Exponential: ExpGauss	1.000000	Exponential: ExpGauss	1.000000	Exponential: ExpGauss
1.000000	Exponential: Exponential 2-4	1.000000	Exponential: Exponential 2-4	1.000000	Exponential: Exponential 2-4
9.793826	Exponential: ExpGrowth 4	**1.437071**	**Sigmoidal: Logistic 5**	**11.763276**	**Sigmoidal: Logistic 5**
10.234766	**Sigmoidal: Logistic 5**	3.596347	Exponential: Phased Bi-Exp	**17.697663**	**Sigmoidal: Weibull**
11.405600	Exponential: Exp2Growth 5-2	**4.283910**	**Sigmoidal: Weibull**	25.339464	Exponential: ExpGrowth 4
11.950979	Sigmoidal: Richards Model	4.458715	Exponential: ExpGrowth 4	31.241146	Exponential: Exp2Growth 5-2
13.066604	Sigmoidal: Hill	4.657741	Sigmoidal: Hill	37.391701	Sigmoidal: Hill
18.910372	**Sigmoidal: Weibull**	4.841490	Exponential: Exp2Growth 5-2	42.716920	Sigmoidal: Logistic General
19.452005	Sigmoidal: Logistic General	5.857782	Sigmoidal: Boltzmann	48.501926	Sigmoidal: Boltzmann
21.332846	Sigmoidal: Boltzmann	7.199643	Exponential: Exp2Decay 5	53.268123	Sigmoidal: Logistic Model
25.314262	Exponential: Exponential 1	8.356883	Sigmoidal: Logistic General	54.064332	Exponential: Exponential 1
26.953456	Sigmoidal: Logistic Model	8.672485	Exponential: ExpDecay 4	56.057921	Sigmoidal: Gompertz Model
27.271862	Exponential: ExpGrowth 3	10.206237	Exponential: ExpGrowth 3	56.288410	Sigmoidal: Richards Model
27.781107	Exponential: Shah	10.234756	Exponential: Exponential 1	59.342089	Exponential: ExpGrowth 3
27.781108	Exponential: Exp and Linear	10.781066	Exponential: Exponential 2-1	59.660118	Exponential: Exponential 2-1
27.835649	Exponential: Exponential 2-1	10.783823	Exponential: Shah	59.847933	Exponential: Shah
28.528522	Exponential: Stirling	10.783828	Exponential: Exp and Linear	59.847933	Exponential: Exp and Linear
28.553868	Sigmoidal: Logistic 4	10.994999	Sigmoidal: Dose Response	61.304487	Sigmoidal: Logistic 4
28.576630	Exponential: ExpDecay 7	10.994999	Sigmoidal: MMF Model	61.344441	Exponential: Stirling
28.576651	Exponential: ExpDecay 5	10.994999	Exponential: Stirling	62.071712	Exponential: Modified Exponential 3
28.901149	Exponential: Modified Exponential 3	10.994999	Exponential: Yeild-fertilizer	62.590680	Exponential: Vapor Pressure Model
29.179568	Exponential: Vapor Pressure Model	10.995269	Exponential: ExpDecay 7	62.691385	Exponential: Exponential3
29.300148	Exponential: Modified Exponential 2	10.995520	Exponential: ExpDecay 5	62.747787	Exponential: Exponential 2-2
29.364256	Exponential: Exponential3	11.012121	Sigmoidal: Logistic 4	62.883633	Exponential: Modified Exponential 2
29.390787	Exponential: Exponential 2-2	11.132708	Exponential: Modified Exponential 3	62.898367	Exponential: Exponential 2-3
29.395964	Exponential: Exponential 2-3	11.253283	Exponential: Vapor Pressure Model	72.219304	Sigmoidal: MMF Model
30.813675	Sigmoidal: Gompertz Model	11.270016	Exponential: Modified Exponential 2	81.712987	Exponential: ExpDecay 5
30.946005	Sigmoidal: Dose Response	11.279080	Exponential: Exponential3	81.713034	Exponential: ExpDecay 7
33.397400	Sigmoidal: MMF Model	11.337736	Sigmoidal: Logistic Model	86.502561	Exponential: Phased Bi-Exp
33.862784	Exponential: Yeild-fertilizer	11.344816	Exponential: Exponential 2-2	86.542634	Exponential: Exp2Decay 5
35.865458	Exponential: Phased Bi-Exp	11.346647	Exponential: Exponential 2-3	88.160952	Exponential: ExpDecay 4
41.078142	Exponential: Exp2Decay 5	11.443164	Sigmoidal: Gompertz Model	93.501501	Sigmoidal: Dose Response
45.410861	Exponential: ExpDecay 4	11.893058	Sigmoidal: Richards Model	93.502902	Exponential: Yeild-fertilizer
146722.771	Exponential: Exp2Growth 5-1	4324.46360	Exponential: Exp2Growth 5-1	472844.996	Exponential: Exp2Growth 5-1

Amphipods		**Chondrichthyes**		**Cephalopods**	
Std. Error	*Function*	*Std. Error*	*Function*	*Std. Error*	*Function*
1.000000	Exponential: ExpGauss	1.000000	Exponential: ExpGauss	1.000000	Exponential: ExpGauss
1.000000	Exponential: Exponential 2-4	1.000000	Exponential: Exponential 2-4	1.000000	Exponential: Exponential 2-4
18.716708	Exponential: ExpGrowth 4	**13.938012**	**Sigmoidal: Logistic 5**	1.774932	Exponential: Exp2Growth 5-2
21.679755	**Sigmoidal: Logistic 5**	**17.694201**	**Sigmoidal: Weibull**	1.843048	Exponential: ExpGrowth 4
26.415538	**Sigmoidal: Weibull**	28.263777	Exponential: ExpGrowth 4	**1.974989**	**Sigmoidal: Logistic 5**
35.495414	Exponential: Exp2Growth 5-2	32.531401	Sigmoidal: Hill	2.791995	Exponential: Phased Bi-Exp
39.279516	Sigmoidal: Hill	46.991317	Sigmoidal: Boltzmann	3.281231	Sigmoidal: Boltzmann
53.195246	Sigmoidal: Boltzmann	49.177812	Exponential: Exponential 1	3.954988	Sigmoidal: Hill
59.969605	Sigmoidal: Logistic General	51.671884	Exponential: Exp2Growth 5-2	**4.686759**	**Sigmoidal: Weibull**
64.953324	Exponential: Exponential 1	53.810201	Sigmoidal: Logistic General	5.606193	Sigmoidal: Logistic General
71.545761	Exponential: ExpGrowth 3	54.142419	Exponential: ExpGrowth 3	7.855316	Exponential: ExpDecay 4
71.880421	Exponential: Shah	54.255611	Exponential: Exp and Linear	7.987233	Sigmoidal: Gompertz Model
71.880421	Exponential: Exp and Linear	54.270993	Exponential: Shah	8.356055	Exponential: Exponential 1
71.954089	Exponential: Exponential 2-1	54.541846	Exponential: Exponential 2-1	8.664562	Exponential: Exp2Decay 5
73.435618	Exponential: Stirling	55.752461	Exponential: Stirling	8.962184	Exponential: Exp and Linear
73.501501	Sigmoidal: Logistic 4	55.867682	Sigmoidal: Logistic 4	8.968111	Exponential: Shah
74.271443	Exponential: Modified Exponential 3	56.508344	Exponential: Modified Exponential 3	8.972189	Exponential: Exponential 2-1
74.829538	Exponential: Vapor Pressure Model	57.014536	Exponential: Vapor Pressure Model	9.008146	Exponential: ExpGrowth 3
75.148646	Exponential: Modified Exponential 2	57.265653	Exponential: Modified Exponential 2	9.211881	Sigmoidal: Logistic 4
75.224639	Exponential: Exponential3	57.574644	Exponential: Exponential3	9.211915	Sigmoidal: Dose Response
75.228174	Sigmoidal: Logistic Model	57.614707	Exponential: Exponential 2-2	9.211915	Exponential: Stirling
75.386130	Exponential: Exponential 2-2	57.624991	Exponential: Exponential 2-3	9.211915	Exponential: ExpDecay 7
75.397667	Exponential: Exponential 2-3	58.351183	Sigmoidal: Logistic Model	9.211915	Sigmoidal: MMF Model
78.193894	Sigmoidal: Richards Model	58.611516	Exponential: ExpDecay 5	9.211915	Exponential: ExpDecay 5
79.070503	Sigmoidal: Gompertz Model	58.613650	Exponential: ExpDecay 7	9.211915	Exponential: Yeild-fertilizer
102.727909	Exponential: ExpDecay 5	60.106919	Sigmoidal: Richards Model	9.345735	Exponential: Modified Exponential 3
102.727914	Exponential: ExpDecay 7	62.584424	Sigmoidal: Dose Response	9.354344	Sigmoidal: Logistic Model
108.143911	Exponential: Phased Bi-Exp	65.661682	Exponential: Yeild-fertilizer	9.386976	Exponential: Exponential3
110.201956	Sigmoidal: Dose Response	72.737435	Exponential: Phased Bi-Exp	9.455166	Exponential: Vapor Pressure Model
114.939363	Exponential: Yeild-fertilizer	78.298173	Sigmoidal: MMF Model	9.480427	Exponential: Modified Exponential 2
119.312597	Exponential: ExpDecay 4	83.414408	Exponential: Exp2Decay 5	9.505712	Exponential: Exponential 2-2
121.821846	Exponential: Exp2Decay 5	86.259811	Exponential: ExpDecay 4	9.507516	Exponential: Exponential 2-3
145.279778	Sigmoidal: MMF Model	90.666973	Sigmoidal: Gompertz Model	9.795074	Sigmoidal: Richards Model
100000000.	Exponential: Exp2Growth 5-1	5202.33880	Exponential: Exp2Growth 5-1	77067567.6	Exponential: Exp2Growth 5-1