AN EVALUATION OF SAMPLING AND STATISTICAL METHODS FOR LONG-TERM MONITORING OF SUBTIDAL REEF FISHES: A CASE STUDY OF TSITSIKAMMA NATIONAL PARK MARINE PROTECTED AREA

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ABSTRACT

Tsitsikamma National Park (TNP) possesses the oldest (established 1954), and one of the largest (350 km^2) 'no-take' marine protected areas (MPA) in South Africa. A long-term monitoring (LTM) programme to observe the subtidal reef fishes in the TNP MPA was established in 2007. To date, 243 angling replicates have been completed, and a total of 2,751 fish belonging to 41 different species have been caught and released. In an era of unprecedented global biodiversity loss, data that can be used to monitor ecosystems and gauge changes in biodiversity through time are essential. This thesis aims to improve the methodological and statistical processes currently available for LTM of subtidal reef fish by providing an evaluation of the TNP MPA LTM programme.

Angling data revealed definitive spatial structuring, in the form of spatial autocorrelation, and a shift in viewing spatial dependency as a statistical obstacle to a source of ecological information created a new avenue of data inference. Species-specific distribution maps identified localized habitat as the main predictor variable for species abundance, emphasizing the need for accurate *a priori* bathymetric information for subtidal monitoring. 'Random forest' analyses confirmed spatial variables are more important than temporal variables in predicting species abundance. The effectiveness of Generalized Linear Mixed Models (GAMMs) to account for spatial autocorrelation was highlighted, and evidence that disregarding spatial dependencies in temporal analyses can produce erroneous results was illustrated in the case of dageraad (*Chrysoblephus cristiceps*). Correlograms indicated that the current sampling strategy produced spatially redundant data and the sampling unit size (150 m^2) could be doubled to optimize sampling.

Temporal analyses demonstrated that after 50 years of 'no take' protection the TNP MPA ichthyofauna exhibits a high level of stability. Species-specific size structure was also found to be highly stable. Dageraad was the only species to exhibit a definitive temporal trend in their size structure, which was attributed to recruitment variation and the possibility that large individuals may migrate out of the study area. The inadequacy of angling as a method for monitoring a broad spectrum of the fish species was highlighted, particularly due to its selectivity towards large predators. As a result, a new sampling technique known as Stereo Baited Remote Underwater Videos (stereo-BRUVs) was introduced to the LTM programme in 2013. Stereo-BRUVs enabled sampling of 2640 fish belonging to 52 different species, from 57 samples collected in less than two years. A comparison of the sampling methods concluded that, compared to angling, stereo-BRUVs provide a superior technique that can survey a significantly larger proportion of the ichthyofauna with minimal length-selectivity biases. In addition, stereo-BRUVs possess a higher statistical power to detect changes in population abundance. However, a potential bias in the form of ‘hyperstability’ in sites with unusually high fish densities was identified as a possible flaw when using stereo-BRUVs.

In an attempt to provide a more rigorous method evaluation, simulation testing was employed to assess the ability of angling and stereo-BRUVs to accurately describe a decreasing population. The advantage of this approach is that the simulated population abundances are known, so that each sampling method can be tested in terms of how well it tracks known abundance trends. The study established that stereo-BRUVs provided more accurate data when describing a distinct population decline of roman (*Chrysoblephus laticeps*) over 10- and 20-year periods. In addition, spawner-biomass was found to be a more accurate population estimate than relative abundance estimates (CPUE and MaxN) due to the inclusion of population size structure information, highlighting the importance of length-frequency data. The study illustrated that an evaluation framework that utilizes simulation testing has the potential to optimize LTM sampling procedures by addressing a number of methodological questions. This includes developing a procedure that aligns data collected from different sampling methods by applying correction factors, thus ensuring LTM programmes are able to adapt sampling strategies without losing data continuity.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES: FIGURES AND TABLES

LIST OF ACRONYMS AND ABBREVIATIONS

AIC	Akaike Information Criterion
ALK	Age-Length Conversion
ANOVA	Analysis of Variance
ASPM	Age-Structure Production Model
BRUVs	Baited Remote Underwater Video systems
CBD	Convention on Biological Diversity
CI	Confidence intervals
CITES	Convention on International Trade in Endangered Species
CN	Cape Nature
CPUE	Catch per unit effort
DAAD	German Academic Exchange Service
DAFF	Department of Agriculture, Forestry and Fisheries
DEA	Department of Environmental Affairs
DEAT	Department of Environmental Affairs & Tourism
DOVs	Diver Operated Video systems
EEZ	Exclusive economic zone
EBFM	Ecosystem-Based Fisheries Management
EKZNW	Ezemvelo KwaZulu-Natal Wildlife
FAO	Food and Agriculture Organisation (United Nations)
GAM	Generalized additive model
GAMM	Generalized additive mixed model
GLM	Generalized linear model
GIS	Geographical Information System
GPS	Global Positioning System
ICCAT	International Commission for the Conservation of Atlantic Tunas
KDE	Kernel Density Estimate
LTM	Long-term Monitoring
MaxN	Maximum number visible
MLRA	Marine Living Resources Act (South African)
MPA	Marine Protected Area
MRT	Multivariate Regression Tree
nMDS	Non-metric Multidimensional Scaling
NPAES	National Protected Area Expansion Strategy
ORI	Oceanographic Research Institute
PCA	Principle Component Analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
RAMSAR	Convention on Wetlands of International Importance
REML	Restricted maximum likelihood
RF	Random forest
RMSE	Root-mean-squared error
RUVs	(unbaited) Remote Underwater Video systems
SAEON	South African Environmental Observation Network
SANBI	South African National Biodiversity Institute
SANParks / SANP	South African National Parks
SSD	Sum of square Euclidean distances
SST	Sea surface temperature
TAE	Total allowable effort
TAPAS	Trawl and Acoustic Presence/Absence Survey
TNP	Tsitsikamma National Park
UCT	University of Cape Town
UNEP	United Nations Environment Programme
UNESCO	United Nations Educational, Scientific and Cultural Organization
UVC	Underwater Visual Census
VBGF	von Bertalanffy’s growth function
WA	Weighted Average

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[P]opular sentiment still holds that angling is basically noble, that common bonds bind the simple souls who seek solace and relaxation plumbing the essential nature and mystery of water. But I figure that the motivation that drives men to take pleasure in the pursuit and capture of a prey that is not required as food, and in many instances not even wanted, brands proponents with the vestigial mark of the predator beast. These are primal urges, older and stronger than family ties or human love: for popular sentiment, like law, is often an ass.

Yes indeed, too often is truth far removed from the romantic fictions. A taxonomy of fly-fishermen encompasses the broad diversity of order, class and species. And though I may be accused of posing answers to unasked questions, I will attempt a brief illustration of this esoteric fact. Our ancient forebears, in their seminal expression of raw emotion, set out to show that art imitates life. And so, by Jove, it did. Ancient Grecian flies must have been wondrous to behold, epitomising the ingenious use of natural material with infinite detail and no embellishment.

But the old civilisations flowered, then withered, as civilisations will. We have come a long way in the procession that followed. For now we live in an epoch where life has learned to imitate art, and the ideals that steered us here are adrift. We live at a time when not only do fly-fishermen have the gall to tie flies in preposterous shapes and outlandish colours, but the fish themselves are faithless enough to ingest these monstrosities with quite unseemly gusto. Even the fish, it seems, are adopting an anything goes attitude. And the Old World courtesy that once bound fly-fishermen to the cabal is now little more than a relic, existing like some endangered species only in isolated pockets, scattered here and there.

Wolf Avni (1997)

CHAPTER ONE

GENERAL INTRODUCTION

It is widely acknowledged that the current global ecological trend is one of biodiversity loss (UNEP 2002, Pereira and Cooper 2006, Hooper et al. 2012), with mitigation targets rarely being met (Butchart et al. 2010). Research highlighting the plight of the oceans after decades of misguided exploitation, particularly regarding fish and fisheries, is extensive (Jackson et al. 2001, Worm et al. 2006, Halpern et al. 2008, Norse et al. 2012, Worm and Branch 2012). Climate change and overexploitation of the oceans are global phenomena with global consequences, and coordinated research at all scales is imperative to providing effective mitigation strategies. To ensure coordination, addressing biodiversity information requirements has become a global priority in the field of marine conservation biology (Collen et al. 2013). To this end, this thesis aims to expand the current knowledge regarding sampling subtidal reef fish in Long-Term Monitoring (LTM) programmes. The overall intention of the thesis is to determine the necessary information requirements of LTM programmes to understand global marine ecosystems such that management strategies may provide the greatest impacts.

The significance of this thesis lies in its global application. However, the breadth of fisheries ecological research and its pace of development renders a truly comprehensive global review impractical. As such, the following brief review presents the management status of the South African linefishery to provide context for the local study. This review emphasizes the importance of LTM programmes within marine protected areas (MPAs) as a tool for managing subtidal reef fish biodiversity.

1.1 MANAGEMENT OF SOUTH AFRICAN LINEFISHERY

South Africa’s linefishery is defined as low to medium technology fisheries in which more than 200 fish species are caught by hand-line or rod and reel (long-line fisheries excluded) over a large geographical area (Branch et al. 2010, Solano-Fernández et al. 2012, Blamey et al. 2014). There are three recognized sectors within the linefishery: commercial, recreational, and small-scale (formerly termed subsistence). The linefishery is considered to be largely responsible for the depletion of many vulnerable endemic reef fish species (DAFF 2010), justifying Attwood and Farquhar’s (1999) statement that the management of linefisheries will be one of the greatest challenges for marine conservation in South Africa. Concerns regarding the overexploitation of some linefish species were voiced as early as the 1940s (Griffiths 2000). Unabated increases in fishing effort, in conjunction with technological advances and a thriving market, led to the serial overexploitation of many important linefish species towards the end of the 20th century (Griffiths 2000). In 2000 the Minister of Environmental Affairs and Tourism declared a state of emergency in the linefish sector, in terms of a provision in the Marine Living Resources Act (DEAT 1998); a decision most marine scientists today regard as a defining point in the history of South African fisheries management (Attwood et al. 2013). This step provided the Minister with extraordinary powers to regulate the linefishery. The total allowable effort (TAE) was reduced by 70% in 2000 (Blamey et al. 2014) and a Linefish Management Protocol (LMP) was drafted to define the procedures of monitoring, assessment and regulation, with the specific objective of rebuilding depleted stocks (Griffiths 2000).

In 2010 an initiative was set up to revise stock assessments for a number of important linefish species, many of which had not been updated in over a decade (Blamey et al. 2014). The initial results suggest that some commercially important linefish stocks appear to be recovering (DAFF 2012, Winker et al. 2013). Despite these first positive signals after a long history of severe overexploitation, effective management of South African linefisheries remains inconsistent with many populations considered overexploited or collapsed (DAFF 2012, Mann 2013).

Much of the mismanagement of linefish stocks is attributed to the accessibility of the resource to a wide range of user groups, including commercial, recreational, and small-scale fishers, as well as inshore trawl and longline fisheries (Attwood and Farquhar 1999, McCord and Zweig 2011, DAFF 2012). For example, South Africa's commercial linefisheries are managed with effort limitations (TAE) with additional output controls such as daily bag limits, size limits and closed seasons; there is no direct control over the total catch in this sector. Recreational anglers are also governed by the aforementioned output controls, but there are no effort limitations in this sector and the rates of fishing mortality have increased steadily along with the number of recreational fishers (Attwood and Farquhar 1999). In addition, the debacle regarding the small-scale fisher permit reallocation process (van Sittert et al. 2006) has severely decreased compliance within this sector, undermining the management strategies (Hauck 2008).

Equitable access for user groups to marine resources, as stated by the Marine Living Resources Act (DEAT 1998) is an ongoing and contentious debate to say the least (Branch and Clark 2006). The MLRA has proven problematic in practice due to the conflicting objectives of sustainability, stability and equity, all of which were not adequately defined or prioritized in the Act (van Sittert et al. 2006, Witbooi 2006). In addition, illegal fishing practices are common and seemingly continue to rise in South Africa, particularly with regard to coastal resources, which are systematically targeted (Hauck and Kroese 2006, DAFF 2012). Given the current status of South African linefisheries, there is an urgent need for appropriate management measures that allow for the implementation of rebuilding strategies (McCord and Zweig 2011).

1.2 THE ROLE OF MARINE PROTECTED AREAS IN LINEFISHERY MANAGEMENT

Although many linefishery resources are overexploited, management action can lead to stock recovery through robust stock assessments, effective data management and science-based management action grounded in the realities of resource abundance (Sink et al. 2012). Traditional single-species management practices are globally recognized as inadequate to ensure biodiversity conservation, and holistic approaches such as Ecosytem-Based Fisheries Management (Pikitch et al. 2004, Fletcher et al. 2010) and Ecosystem Approach to Fisheries (Jennings 2005) have consequently gained preference. The broad commitments of these conservation approaches include the planning, development and management of fisheries such that social and economic needs are met without jeopardizing the options for future generations to benefit from the full range of goods and services provided by marine ecosystems (FAO 2003). The underlying philosophy is that managers take full account of the range of fisheries impacts when setting objectives, and attempts to meet these objectives are to be based on and supported by reliable scientific advice (Pikitch et al. 2004, Jennings 2005). As traditional marine management strategies are failing to maintain the productivity and biodiversity of marine ecosystems, MPAs are being increasingly implemented to support commercially and ecologically important species (Attwood et al. 1997, Sink et al. 2012). Marine protected areas have long been advocated as a viable alternative to single species protection in fisheries management in South Africa and an effective tool in ecosytem-based management frameworks (Bennett and Attwood 1991, Attwood et al. 1997, Sink et al. 2012, Solano-Fernández et al. 2012, Kerwath et al. 2013a), because, by closing an area to exploitation, they rely on natural processes to restore and sustain fisheries resources.

The current MPA network in South Africa consists of 23 areas, many of which have multiple levels of protection (zoned) as seen in Table 1.1. Currently, only seven MPAs do not permit any form of extractive use and are therefore considered ‘no-take’ MPAs, equating to 0.17% of South Africa’s marine exclusive economic zone (EEZ) or 9.3 % of the coastline having complete protection (Sink et al. 2011). South Africa’s National Biodiversity Act (2004) and the Protected Areas Amendment Act (2004) call for a representative network of protected areas in the ocean, yet provide no operational definition of ‘representative’ (Solano-Fernández et al. 2012). The most recent biodiversity assessment indicates that 40% of marine and coastal habitat types are not represented at all in South Africa’s MPA network, of which 13 habitat types are both critically endangered and have no protection (Sink et al. 2012). Such statistics suggest that the current MPA network is inadequate, justifying the proposed National Protected Area Expansion Strategy (NPAES), which aims to protect 15% of the offshore shelf environment and 25% of the coastal or inshore environment by the year 2030 (DEA 2009). Initiatives such as the NPAES, and the recent marine orientated initiative, Operation Phakisa, imply that South Africa remains committed to ensuring MPAs play a central role in marine conservation. However, it must be acknowledged that actual protection depends on effective management and user compliance within protected areas (Sink et al. 2012), which remain fundamental issues in South Africa (Hauck and Kroese 2006, Tunley 2009).

Attwood et al. (2013) suggested the coastal MPAs provide the backbone of linefish sustainability in South Africa, citing Pinchot’s adaptation of the utilitarian principle for conservation: ‘*the greatest good to the greatest number- and that for the longest time*’. In essence MPAs are multispecies, effort control management tools that promote biodiversity and ecological integrity by providing refuge for less resilient species. Given the fickle history of linefishery management in South Africa, MPAs are undoubtedly the most plausible option for effective management of linefisheries because they offer scientists and managers an unprecedented level of ‘mandate’ consistency through which to operate. This is of particular importance in a country renowned for conservation management agendas ironically driven by the growing need to redress social-economic disparities (DEAT 1998) and thus subjected to constant political pressure (Branch and Clark 2006). That said, the application of MPAs in linefishery management remains controversial, with scepticism and contention amongst affected stakeholders (Tunley 2009). In particular the exclusion of subsistence and commercial fishers from MPAs such as Tsitsikamma and Langebaan is seemingly under continual review (Faasen and Watts 2007, Sunde and Isaacs 2008, Tunley 2009). The arguments of negatively impacted stakeholders mostly emanate from a perceived lack of empirical evidence illustrating that fishery closures in South Africa can increase yield without disadvantaging fishers (Sink et al. 2012). Literature highlighting the benefits of MPAs to fishers in South Africa is inadequate, with only two conclusive examples existing (Bennett and Attwood 1991, Kerwath et al. 2013a). This inability of scientists to translate MPA closures into direct yield benefits for fishers has left the effectiveness of MPAs as fisheries management tools open for debate. Here it must be reiterated that the objectives of MPAs extend further than simply enhancing fisheries: they broadly include maintaining biodiversity, ensuring ecological integrity and providing scientific reference sites for all marine organisms.

The scepticism around MPA efficacy will likely remain until irrefutable evidence, using local examples, is provided. To ensure the NPAES objectives are met, research institutes need to provide such evidence by improving the science base for MPAs through coordinated, standardized monitoring and research (Sink et al. 2012, Solano-Fernandez et al. 2012). Tunley (2009) identified the absence of a national monitoring program as a key weakness of MPA management in South Africa.

1.3 LONG-TERM MONITORING

Long-term monitoring programmes, in the context of ecology, aim to accumulate data on the abundance and distribution of species in space and time (Magurran et al. 2010). Their existence is largely attributed to the current global trend of biodiversity loss (UNEP 2002, Pereira and Cooper 2006, Hooper et al. 2012). Particularly, the ambiguity surrounding the effects of climate change and anthropogenic induced ecosystem degradation has thrust LTM programmes into the ecological research spotlight (Parr et al. 2003) as they are able to assess ecosystem dynamics and not just the current state of an ecosystem (Block et al. 2001). Thus, LTM datasets provide the information necessary to connect deviations from expected trends with their possible influential variables, promoting a better understanding of anthropogenic disturbances. Their extended temporal scale also enables a distinction between short-term natural variability and the prevailing ecological trend. Ecologists therefore endeavour to grow long-term datasets cumulatively so that the predictive power of models and their ability to provide accurate inferences increases to such an extent that future predictions become mere fractional extensions of long-term trends; as opposed to the current theme of over-extended estimations.

1.4 LONG-TERM MONITORING IN MARINE PROTECTED AREAS

Long-term monitoring studies within no-take MPAs provide an opportunity to assess and quantify natural variability, stability and persistence of resources in relatively undisturbed communities (Attwood et al. 1997, Vos et al. 2000, James et al. 2012) by essentially replicating large-scale ecological experiments that exclude direct human impacts (Hughes et al. 2005). The importance of this is twofold. Firstly, it allows for a better understanding of how climate change may influence the structure and functioning of marine ecosystems by removing the confounding effects of anthropogenic disturbance such as fishing (Bohnsack et al. 2004). Secondly, information collected from MPAs can be used to define the extent of change within exploited areas that lack natural baseline data (Pauly 1995, Barrett et al. 2007, James et al. 2012). In this regard, Barrett et al. (2007) emphasize the value of LTM programmes in MPAs as they provide reference areas critical for ‘understanding the effects of fishing on coastal species and systems, and placing these in the context of natural environmental change’. There is, however, a third quality of LTM programmes within MPAs that this thesis aims to take full advantage of: data consistency. Multiple influential variables and subsequent cascading ecosystem effects associated with exploited ecosystems drastically increase dataset complexity (Scheffer et al. 2005, Myers et al. 2007). In contrast, long-term data originating from well established ‘no-take’ MPAs possess relatively high consistency, quality and simplicity. These are assets that facilitate statistical testing and model formulation, providing researchers with the best opportunity to assess the performance of statistical techniques.

The Tsitsikamma National Park (TNP) MPA is the oldest (established in 1964) and one of the largest (320 km^2) no-take MPAs in Africa, situated in the centre of the warm temperate zone between the Indian and Atlantic Oceans. The primary motivation for the proclamation of the TNP MPA was to provide protection for commercially exploited reef fish species (Attwood et al. 1997, Tunley 2009) that are a critically depleted component of the South African linefishery (Griffiths 2000, DAFF 2012). To assess effectiveness of the MPA and to monitor the recovery of these fish populations, two LTM programmes were developed; the shore-angling and the subtidal (boat-angling) programmes. The former was established in 1998, while the latter was established in 2006 and provides the data on which this thesis is based.

The importance of the LTM programmes within the TNP MPA becomes apparent when the peer-reviewed outputs derived from both shore and boat angling data are collated. The programme has been instrumental in optimizing LTM methodology (Bennett et al. 2009, Bernard and Götz 2012, Götz et al. 2013, Bernard et al. 2014), as well as providing data for biological (Götz et al. 2008a), movement (Kerwath et al. 2007), genetic (Teske et al. 2010) and temporal variability studies (Hanekom et al. 1997, James et al. 2012) of fish. Data from the programmes have also been used to assess the effectiveness of MPAs on a national scale (Solano-Fernández et al. 2012) and to create an ichthyofaunal species list (Wood et al. 2000). These studies are in addition to research within the TNP MPA prior to the development of the current LTM programmes (Buxton and Smale 1984, 1989, Buxton and Allen 1989, Buxton 1990, 1993, Tilney et al. 1996, Brouwer and Buxton 2002).

Several other LTM programmes focusing on marine fish biodiversity are currently operational in South African MPAs (Table 1.1), which bears testament to the value of the information such programmes are able to provide.

Table 1.1: List of marine protected areas in South Africa and their associated long-term monitoring programmes.

Name	Year established	Size (km^2)	Zoned	% no-take	Monitoring programme Type
Malgas Island	2000	0.9	No	0	N/A
Marcus Island	2000	0.4	No	0	N/A
Jutten Island	2000	1.6	No	0	N/A
Langebaan	1985, revised in 2000	47.1	Yes	22	Boat angling
Sixteen Mile Beach	2000	107.1	No	0	N/A
Table Mountain	1977, revised in 1994	956	Yes	0.02	N/A
Helderberg	2000	2.4	No	100	N/A
Betty's Bay	1990	20.1	No	0	N/A
De Hoop	1985	288.9	No	100	Shore angling
Stilbaai	2008	31.9	Yes	62	N/A
Goukamma	1990	34	No	0	BRUVs^1
Robberg	1990	26.2	No	0	Shore angling
Tsitsikamma National Park	1964	264.4	No	100	Shore & boat angling, stereo-BRUVs
Sardinia Bay	1990	12.9	No	100	N/A
Bird Island	2004	70.6	No	100	N/A
Dwesa-Cebe	1975, revised in 2004	191.5	No	100	Shore angling
Amathole	2011	246.5	No	0	N/A
Hluleka	1991	40.9	No	100	N/A
Pondoland	1991, revised in 2004	1237.3	Yes	47.8	Boat angling, UVC^2, BRUVs
Trafalgar	1979	8.3	No	0	N/A
Aliwal Shoal	2004	124.7	Yes	1.7	N/A
St Lucia	1976	442	Yes	30.3	Shore angling
Maputaland	1987	384.5	Yes	33.8	N/A

^{1} BRUVs – Baited Remote Underwater Videos; ^{2} UVC – Underwater Visual Census

The absence of standardized sampling methods between LTM programmes is, however, a cause for concern (Bernard et al. 2014). This incompatibility confounds direct comparisons between programmes utilizing different sampling methods, preventing national or macroecological analyses (Murphy and Jenkins 2010) and inherently limiting the understanding of how MPAs improve fisheries and biodiversity conservation in South Africa.

1.5 THESIS OUTLINE

The overall aim of this thesis was to evaluate the subtidal reef fish LTM programme within the TNP MPA and to recommend the most appropriate sampling and statistical applications for development of a national standardized sampling strategy. The TNP MPA has been identified as an area of high strategic importance with regard to fisheries research (Tunley 2009, Sink et al. 2012), and extensive methodological studies have previously been carried out within the MPA (Bennett 2008, Bernard 2013). With the introduction of a novel, non-extractive video sampling method (Stereo Baited Remote Underwater Videos, from here on referred to as stereo-BRUVs) to South Africa, this thesis revisits the question of optimal sampling strategies within the TNP MPA with additional emphasis on investigating robust statistical techniques.

To achieve this, the thesis has been divided into seven chapters (Figure 1.1). After the general introduction (Chapter 1), Chapter 2 describes the study area, sampling strategy and a brief description of the TNP MPA ichthyofauna gathered from seven years of angling data. In a preliminary assessment it was apparent that the angling data possessed a high level of spatial autocorrelation, which was likely to

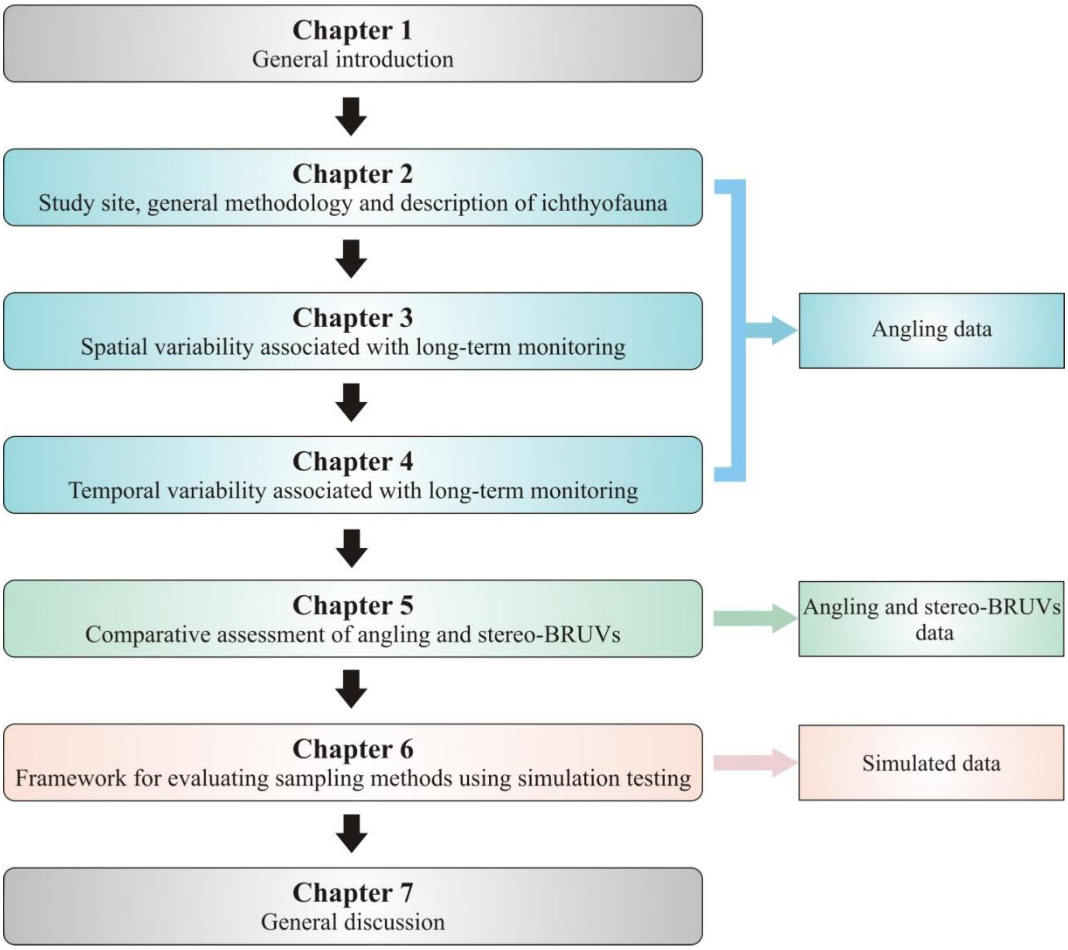


Figure 1.1: Flow diagram depicting thesis structure.

influence results of temporal analyses. As a result, a comprehensive investigation of the spatial variability within data from the LTM programme was conducted to ensure that all spatially explicit dependencies were accounted for in subsequent analyses (Chapter 3). Once these spatial dependencies were acknowledged, species-specific temporal abundance trends were modelled in Chapter 4. This chapter highlighted a significant disadvantage of angling data in the form of selectivity, to such an extent that sufficient data were only available to provide meaningful temporal analyses for five species. In an attempt to overcome the drawbacks associated with angling surveys, a new non-destructive sampling technique was introduced in 2013 in the form of stereo-BRUVs. This enabled comparisons between biodiversity, abundance estimates and size structure of the observed ichthyofauna derived from angling and stereo-BRUVs (Chapter 5).

Method comparisons, however, are merely relative evaluations, which do not attempt to calculate the actual accuracy of each method; a more conclusive appraisal of data accuracy was deemed necessary for LTM programmes. Therefore, Chapter 6 assessed the ability of data derived from each sampling method to detect, and accurately quantify, a theoretical population decline in roman (*Chrysoblephus laticeps*) over long-term monitoring periods of 20 and 30 years using simulation testing. To achieve these aims, a stochastic age-structured production model was developed and used as an operating model to simulate a ‘true’ declining population, which was induced by sequential recruitment failures. Once a declining roman population had been generated, then sampling from it was simulated by generating relative abundance indices and size frequencies from each sampling method, which were fitted to an age-structured estimation model. Evaluating method accuracy was done by comparing the estimated abundance and spawner-biomass indices against the ‘true’ population trend. Finally, a synthesis of the thesis findings is provided in Chapter 7.

CHAPTER TWO

STUDY AREA, GENERAL METHODOLOGY AND A BRIEF DESCRIPTION OF THE ICHTHYOFAUNA OF THE TSITSIKAMMA NATIONAL PARK MARINE PROTECTED AREA

2.1 STUDY AREA

The Tsitsikamma National Park (TNP) marine protected area (MPA) is situated in the centre of the Agulhas Ecoregion (Figure 2.1). The region is alternatively known as the warm-temperate biogeographic region, which is a reference to the transition zone between the two oceans of South Africa (the warm Indian and cold Atlantic oceans). It is the oldest (established 1964), and one of the largest (320 km^2) ‘no-take’ MPAs in Africa. The MPA stretches along 72 km of coastline between the Groot River and Nature’s Valley, and extends 5 km offshore, effectively conserving 11% of South Africa’s temperate south-coast rocky shoreline and associated subtidal inshore habitats.

One of the primary ecological functions of the TNP MPA is to protect commercially exploited reef fish species (Attwood et al. 1997, Tunley 2009), as these are considered to be the most critically depleted component of the South African linefishery (Griffiths 2000, DAFF 2012). Reef fish, such as sparids, display a high degree of residency (Buxton and Allen 1989, Kerwath et al. 2007) and slow growth rates (Buxton 1993, Götz et al. 2008b), which make them vulnerable to over-exploitation.

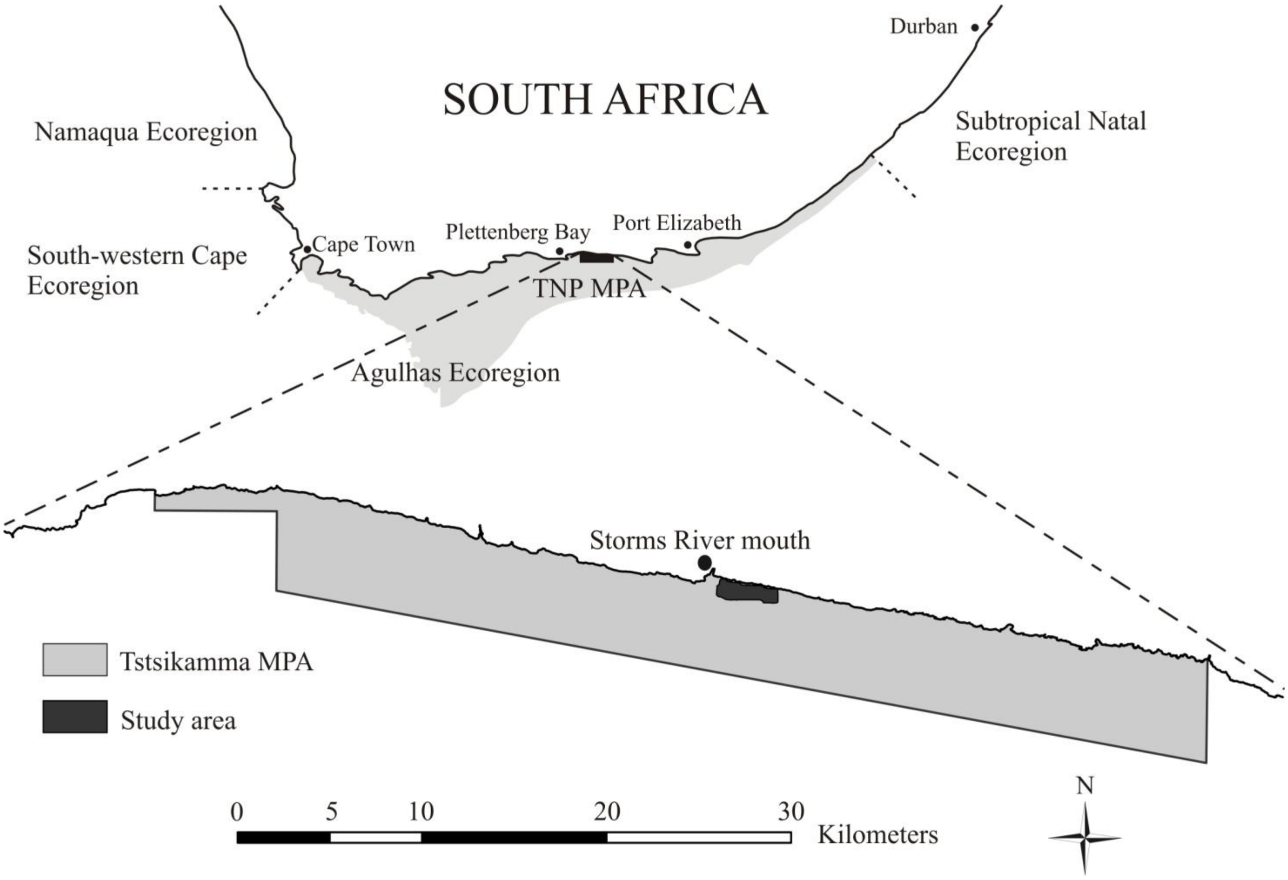


Figure 2.1: General study region showing the position of the Tsitsikamma National Park (TNP) marine protected area (MPA) within the Agulhas Ecoregion on the South African coastline. The expanded view depicts the extent of the TNP MPA as well as the study area on the Rheeders Reef complex.

After 50 years of protection from anthropogenic disturbances, the subtidal communities within the TNP MPA are considered stable and provide the best example of pre-exploitation inshore ecosystems available in South Africa today (Attwood et al. 1997). As such, the TNP MPA represents a unique site for fisheries baseline research (Watts and Faasen 2009).

2.1.1 RHEEDERS REEF

The study area lies to the east of Storms River mouth in the centre of the TNP MPA, an area locally known as Rheeders Reef (Figure 2.2). It is a large, diverse reef complex that is in close proximity (approx. 1 km) to the Storms River boat launch site and conservation offices. This location deters illegal exploitation of the subtidal area, and it is highly unlikely that the study area has been subjected to boat-based angling activities, with the exception of research angling, since proclamation of the MPA.

2.1.2 COASTLINE AND SUBSTRATE

The TNP MPA's physical characteristics include a high energy (Cowley et al. 2002, Götz et al. 2008a), steeply shelving coastline (Tilney et al. 1996) with several headlands and their associated bays (Martin and Flemming 1986, Götz et al. 2008a). Buxton and Smale (1984) describe the geology of the MPA as 'characterised by a large sandstone syncline with an east-west axis'. The subtidal structure is dominated by reefs formed by submerged aeolianite or sandstone dune cordons running parallel to the shore to depths of about 100 m at the offshore boundary of the TNP MPA. These reefs are separated by areas of low relief substrate that are periodically covered by unconsolidated sediments, mainly sand (Martin and Flemming 1986, Bernard and Götz 2012).

Buxton and Smale (1984) categorized the benthic habitat into three types of reef. The first occurs from the coastline to a depth of 10 m, and is characterized by low profile reef interspersed by extensive sandy flats. This reef type appears to be dominated by calcareous algae, with echinoderms, octocorals, poriferans and ascidians. The second reef type is characterized by rugged profile and depths of 10-25 m. This reef type is rich in ascidians, poriferans, octocorals, echinoderms and encrusting bryozoans. Microalgae are present at these depths, but the macroalgae associated with shallower areas are absent. The third type of reef, found at depths greater than 25 m, is similar to the second type of reef. There are, however, large stands of kelp (*Ecklonia radiata*) present and a notable lack of red bait (*Pyura stolonifera*).

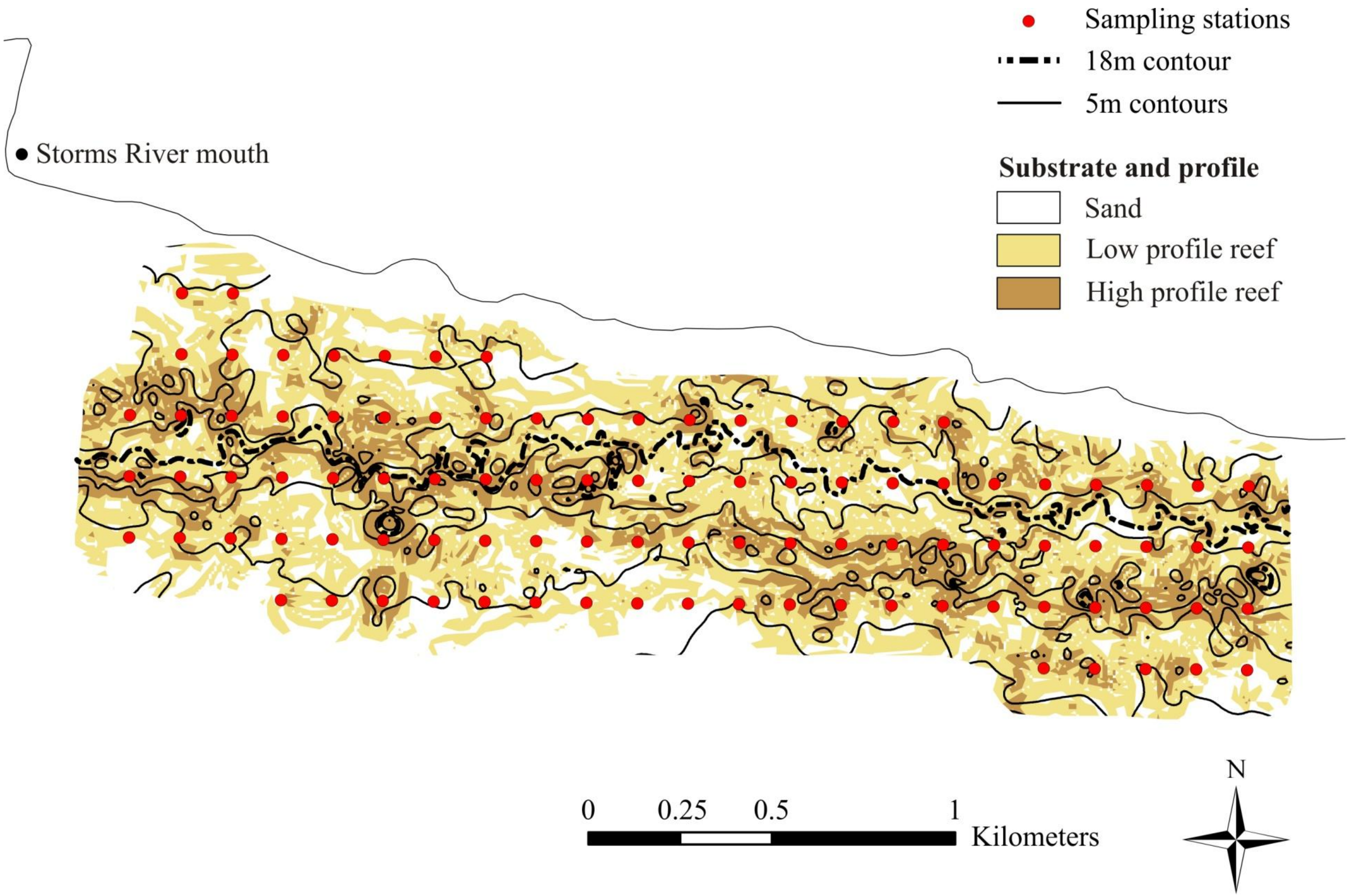


Figure 2.2: Bathymetric map of the study area on the Rheeders Reef complex. Positions of sampling sites are included.

2.1.3 CURRENTS, UPWELLING AND TEMPERATURE

Tilney et al. (1996) state that there are three factors that influence the currents in the TNP MPA: wind, tides and density stratification. Winds are predominantly alongshore, with westerly winds dominating throughout the year (Hanekom et al. 1989, Jury 1994). Similarly, currents are predominantly alongshore (Tilney et al. 1996, Attwood et al. 2002); the eastward current is a result of Agulhas counter currents, while the westward current is driven primarily by easterly winds (Götz 2006).

During the summer months the occurrence of easterly winds increases (Schumann and Martin 1991) and initiates cold upwelling along the TNP coastline through Ekman flux, which deflects water offshore (Schumann 1999). Upwelling events play a pivotal role in importing nutrients that drive primary production along the coast (Wieters 2005, Blanchette et al. 2009, Allan et al. 2010). Cold, dense, deep water is lifted up and towards the coast to compensate for the offshore loss, resulting in a rapid decrease in temperature of coastal waters. Schumann (1999) explains that upwelling along the south coast is somewhat unique in that it creates a temperature response at the coast itself. As a result, upwelling variability can subsequently be determined from coastal sea surface temperatures (SSTs).

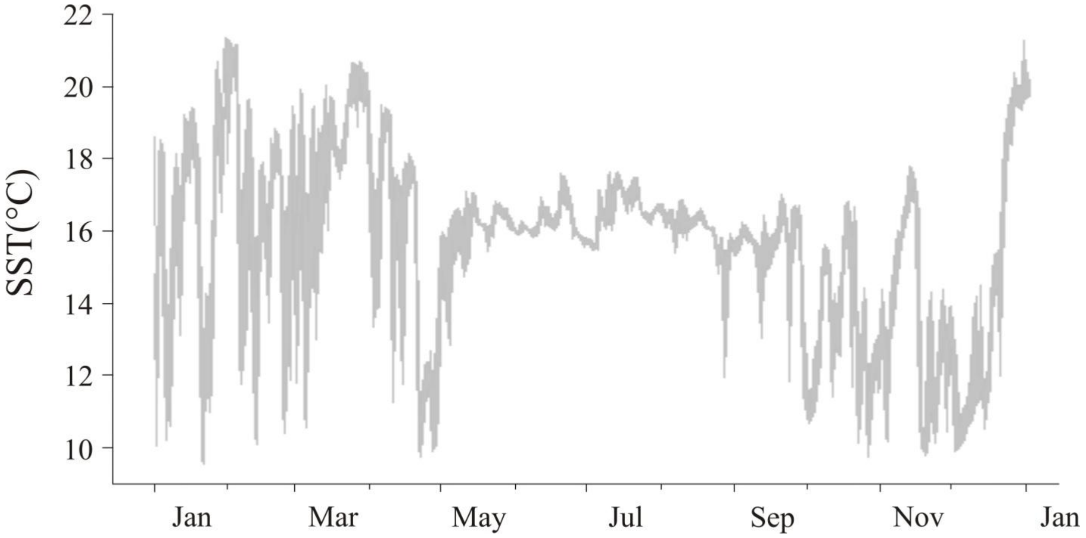


Figure 2.3: Daily sea surface temperatures (SST) for 2008 illustrating the high levels of variability in summer as a result of upwelling. In contrast, the winter period is stable with a relatively narrow SST range.

The TNP water column stratification intensifies in summer due to intermittent upwelling (Harris et al. 1978, Schumann 1999), which is often accompanied by the formation of distinct, prolonged thermoclines (Hanekom et al. 1989). Temperatures during this period range between 9 and 25°C (Hanekom et al. 1989) and differences of 8°C have been recorded between the surface and bottom at a depth of 30 m (pers. obs.). In contrast, winter produces regular longshore current oscillations with periods of two to four days (Tilney et al. 1996, Attwood et al. 2002), and nearshore water during winter is characterized by vertical stability (Figure 2.3) with a relatively isothermal water column. Sea temperatures typically fluctuate between 15 and 18°C during winter (Hanekom et al. 1989).

2.2 METHODS AND MATERIALS

2.2.1 DATA COLLECTION

Data collection commenced in 2007 as part as an initiative between the South African Environmental Observation Network (SAEON) and South African National Parks (SANParks) to provide long-term monitoring data for the subtidal ichthyofauna of the TNP MPA. To date, the dataset represents the longest and most comprehensive subtidal reef fish abundance estimate in southern Africa. Sampling took place biannually to account for seasonal variations, with summer (February) and winter (July-August) fieldtrips. The primary data collection method was based on angling. In addition to angling, a novel video sampling technique, in the form of Stereo-Baited Remote Underwater Videos (stereo-BRUVs), was introduced to the programme in 2013. These methods were supplemented with physical data in the form of water temperature profiles and bathymetry.

2.2.2 ANGLING METHOD

Angling was conducted with standardized hook-and-line tackle, which consisted of a single barbless 4/0 circle hook baited with pilchard (*Sardinops sagax*) and a 170 g sinker on each line. Circle hooks have been shown to decrease the probability of gut-hooking when compared to conventional J-shaped hooks (Cooke and Suski 2004, Cooke et al. 2005), with subsequent decrease in post-release mortality (Prince et al. 2002, Pacheco et al. 2011). In addition, the hook’s barb was flattened to facilitate hook removal (Schaeffer and Hoffman 2002), decreasing injuries to fish, reducing processing time and maximizing chances of fish survival.

Once at the surface, fish were handled using a PVC fish sling and wet cloth. The hook was removed, and the fish was identified, measured to the nearest millimetre (FL for teleost; TL for chondrichthyans) and sexed in the case of chondrichthyans. Swim bladders of fish exhibiting external signs of barotrauma were deflated by careful insertion of a 15-gauge hypodermic needle under a scale, through the body wall at a position where the swim bladder adheres to the abdominal wall (Bennett 2008). Emphasis was placed on minimizing processing time to avoid fish mortalities, and all mortalities that were detectable during handling and immediately after release were recorded.

To determine optimal angling site duration, full-day angling results from data collected during four preliminary fieldtrips in 2005/6 were broken up into half-hour periods. Each consecutive half-hour period was added cumulatively for each day to provide estimates of abundance for durations ranging between 0.5 and 8 hours. Results show that two angler-hours is the most cost-efficient compromise for long-term monitoring purposes (Bennett et al. 2009). The most logistically convenient sample unit comprised four people angling for 0.5 hours (two angler-hours) and was employed whenever possible. There were, however, a few occasions when only three anglers were available, in which case the time spent at each site was increased to ensure the standard two angler-hours per site was met.

2.2.3 STEREO BAITED REMOTE UNDERWATER VIDEOS METHOD

Stereo-BRUV systems were remotely deployed onto the sea floor to record the composition, abundance and size of the TNP MPA fish population. Each system consisted of 2 video cameras (Canon Legria HFM 506) mounted 70 cm apart on a horizontal centre bar within a stainless steel frame (Figure 2.4). On the centre bar, the camera housings were mounted on baseplates at an inwardly converged angle of 7 degrees to provide an overlapping field of view from the two cameras. A synchronizing diode was attached to the bait arm, and a bait container was positioned 1.2 m in front of the cameras within their field of view (Figure 2.4a). Approximately one kilogram of crushed pilchard was used as bait in each deployment, and the system was deployed by boat and left to film on the sea floor for a period of 1 hour. Previous research in temperate regions has found that >36 min is required to obtain measures of the majority of fish species, and that 60 min is advisable to include targeted fish species (Watson et al. 2005, Bernard and Götz 2012). With several systems available (usually four), stereo-BRUVs could be simultaneously deployed at multiple sites, maximizing sampling efficiency. Lights were not required in this study as the stereo-BRUVs were only deployed to a maximum depth of 30 m, which is well within the photic zone.

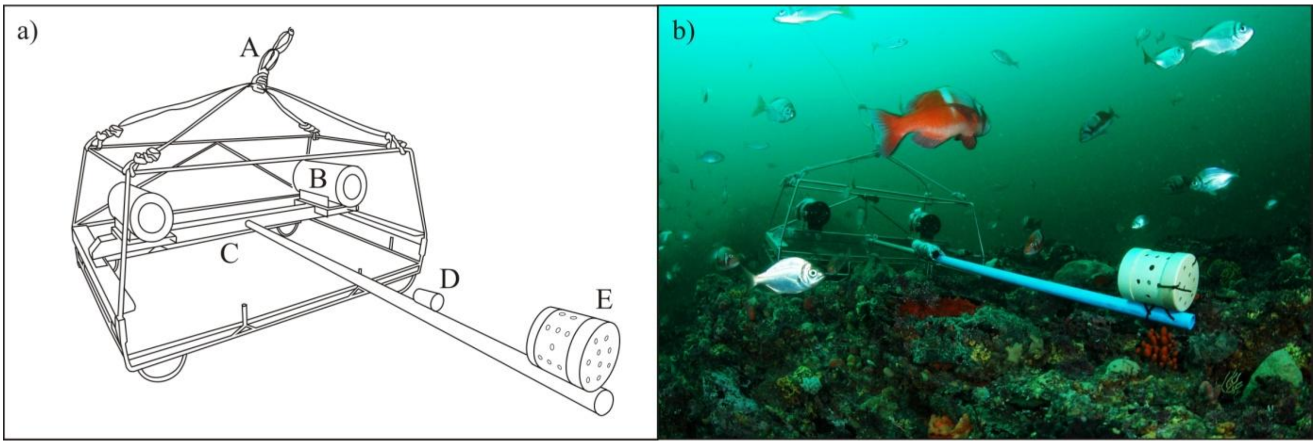


Figure 2.4: a) Schematic of a baited remote underwater stereo-video system (stereo-BRUVs). The system is linked to the surface by a buoy and rope that attaches to the stainless steel frame (A). A rigid centre bar (C) holds the housed digital high-definition cameras (B) on inward angled baseplates. Extending perpendicularly from the centre bar is a pole that holds the synchronizing diode (D) and the bait container (E). b) Stereo-BRUVs deployed at a depth of 20 m on Rheeders Reef in Tsitsikamma National Park marine protected area (photo: Steve Benjamin).

2.2.3.1 VIDEO ANALYSIS

Captured videos were in a MPEG Transport Stream (.mts) format and had to be concatenated into a single file before being converted into high definition Audio Video Interleave (.avi) file. This was done using the Xilisoft video converter ultimate v 6.5.5 software and allowed the videos to run at a much faster rate in the analysis software (EventMeasure).

The maximum number of any one species seen in a single frame during recording (MaxN) was taken as a measure of relative abundance (Cappo et al. 2003). This was done using the software EventMeasure (www.seagis.com.au), which facilitated capturing the MaxN value, species and time of MaxN (Appendix 2.1). The overlapping field of view allows for the size of fish visible in the synchronized video footage to be measured using EventMeasure. The video footage is synchronized using a synchronizing diode (Figure 2.4a: D) that is mounted on the bait arm and visible in both cameras. Length measurements of each fish (FL for teleost; TL for chondrichthyans) and their distance from the cameras (range) were made at the time of MaxN for each species (Appendix 2.2).

The EventMeasure software requires the cameras to be calibrated in their mounted position at the beginning and end of each sampling trip to ensure accuracy and precision (Appendix 2.3). This was done using a calibration cube and software called CAL (www.seagis.com.au) according to the procedures outlined by Harvey and Shortis (1998). The calibration procedure measures the base separation, camera orientations and lens distortions that are unique to each stereo camera pair. These parameters are uploaded to EventMeasure and incorporated in fish length and range calculations.

2.2.4 HABITAT MAPPING

The study area on the Rheeders Reef complex was bathymetrically mapped with a GPS linked echo-sounder by Bennett (2008) and Bernard (2013). The latitude, longitude and depth data were interpolated to create a bathymetric contour map using the geographic information systems (GIS) analysis package ArcMap (version 9.3). Interpolation of the data to a raster file was conducted using tension-splines with the spatial analyst package, following the recommendations of Götz (2006) and Bernard (2013).

The output cell size for the interpolation raster was set to 5 m^2 and reef profile was predicted using a five-level geometric interval classification scheme. This scheme employs an algorithm to create geometric intervals by minimizing the square sum of elements per class. In doing so, each class range has a similar number of values and the change between intervals is fairly consistent (ESRI 1996). This approach produces a comprehensive bathymetric map that isolates and categorizes areas of similar profile (ESRI 1996). Of the five levels selected, only three were represented in the data, and they were classified according to their slope values as (i) sand (very low profile bathymetry), (ii) low profile reef bathymetry and (iii) high profile reef bathymetry (Figure 2.2).

2.2.5 SITE STRATIFICATION

The Rheeders Reef study area was subdivided by a grid with cells of 150 m^2 (Figure 2.5), and the centre of each cell was taken as its target co-ordinates. Bennett (2008) initially advocated the use of 150×150 m cells to sample the TNP MPA subtidal ichthyofauna in an attempt to avoid pseudo-replication by taking into account GPS error and the swing of the boat at anchor at a depth of 30 m. Each cell was classified according to depth (shallow: <18 m; deep: 18–30 m) and bottom profile (high or low). Profile was classified as high or low according to the method described above (section 2.2.4). This approach produced four site classes: (i) shallow/high profile, (ii) shallow/low profile, (iii) deep/high profile and (iv) deep/low profile. Employing a power analysis, Bennett (2008) determined that a sample size of 32 angling sites per year was sufficient to detect a 10% change in abundance of the indicator species roman (*Chrysoblephus laticeps*). Therefore, 16 sample sites were randomly chosen for each biannual sampling trip, four from each stratified class. The sampling procedure was further randomized by the sequence with which the sites were sampled.

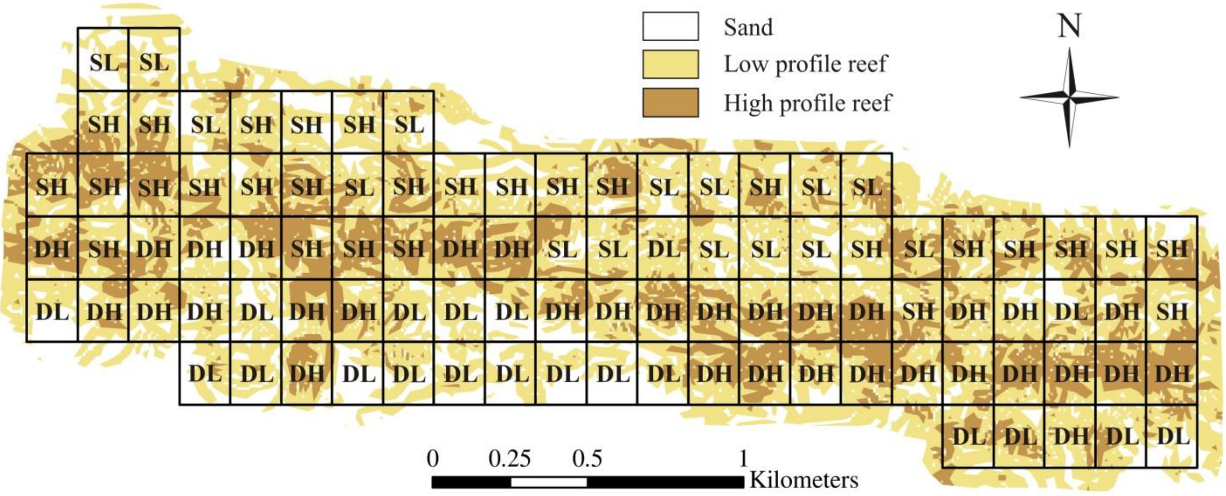


Figure 2.5: Stratified sampling strategy employed to select sites on Rheeders Reef. Four random sites from each category (SL - shallow/low profile; SH - shallow/high profile; DL - deep/low profile; DH - deep/high profile) were selected for each biannual sampling trip.

2.3 BRIEF DESCRIPTION OF THE ICHTHYOFAUNA OF THE TSITSIKAMMA NATIONAL PARK MARINE PROTECTED AREA

The ichthyofaunal composition of the TNP MPA has been well researched. The first guide to the fishes of the MPA was published in 1966 (Smith and Smith 1966), and several similar studies have subsequently been published (Buxton and Smale 1984, Burger 1991, Tilney et al. 1996, Hanekom et al. 1997, Wood et al. 2000, Smith 2006), which are all testimony to the ichthyofaunal diversity of the TNP MPA.

Table 2.1: Percentage frequencies per year for the ten most abundant species caught in the Tsitsikamma National Park marine protected area between 2007 and 2013.

Species	**Frequency (%)**						
	2007	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**
Chrysoblephus laticeps	65.43	57.72	62.03	56.65	62.07	60.67	68.02
Chrysoblephus cristiceps	17.77	10.89	5.64	5.06	10.63	11.27	8.50
Boopsoidea inornata	2.54	5.06	6.02	8.23	5.17	8.15	6.28
Mustelus mustelus	3.13	4.05	3.76	6.65	4.31	1.68	1.42
Spondyliosoma emarginatum	1.17	3.29	4.89	7.59	3.16	2.64	1.82
Galeichthys feliceps	0	0.25	3.01	1.27	0.57	4.56	0.81
Pomadasys olivaceum	0.39	4.05	0	2.22	0	1.68	0.20
Petrus rupestris	1.76	2.28	1.13	0.95	0.86	0.24	1.21
Pagellus natalensis	0.39	0.76	1.88	1.58	1.44	0.96	1.42
Pachymetopon aeneum	0.59	1.52	1.13	1.27	0.29	1.20	0.81

Wood et al. (2000) compiled an updated species checklist that summarized fisheries research in the TNP MPA over the last 20 years. The checklist recorded 202 species of fish from 84 families within the MPA, 75 (37.1%) of which are components of commercial or recreational fisheries. The methods included by Wood et al. (2000) were visual transects, rotenone collections, estuarine surveys, ichthyoplankton surveys and mark/recapture studies.

The current description of the TNP MPA ichthyofauna will add to the collection of research already compiled, and is based solely on angling data from 2007 to the end of 2013. During this period an angling effort of 486 angler-hours produced a total of 2,746 fish, belonging to 41 different species and 17 families (Appendix 2.4). Teleosts dominated the catch with 2,597 fish (95%), whereas a mere 145 of the fish caught (5%) were chondrichthyans. Biologically, the warm-temperate biogeographic region is characterized by high levels of endemism (Turpie et al. 2000, Branch et al. 2010), and 20 of the species caught (45%) are endemic to South Africa.

The larger ichthyofauna of TNP MPA is dominated by endemic and commercially important sea-bream (Sparidae) species, notably roman (*Chrysoblephus laticeps*) and dageraad (*Chrysoblephus cristiceps*) (Buxton and Smale 1984, Götz 2006, Bennett 2008, Branch et al. 2010, Bernard 2013). Sparids accounted for 88% of the total catch (Figure 2.6) and roman was outright the dominant species (Table 2.1) with 1,712 caught at an average catch-per-unit-effort (CPUE) of 3.5 fish per angler-hour. This was followed by dageraad (291), fransmadam (158), smooth-hound (92) and steentjie (87). The overall CPUE for all species was 5.6 fish per angler-hour.

Exploitation has been shown to alter the life history patterns of fish populations, particularly those of slow-growing sparids such as roman and dageraad (Buxton 1993, Götz et al. 2008b). Protection against exploitation has enabled roman populations to attain greater densities (Buxton and Smale 1989, Burger 1991, Smith 2006, Götz et al. 2008b), ages (Götz et al. 2008b) and sizes (Buxton 1988, Smith 2006, Götz et al. 2008b) inside the MPA than anywhere else currently recorded. The mean length of roman caught in Tsitsikamma was 323 mm, which is comparable to the findings of previous studies in the TNP MPA of 331 mm by Bennett (2008) and 313 mm by Smith (2006). However, the mean length of roman in TNP MPA is higher than that recorded in the younger and smaller Goukamma MPA, 302 mm (Götz et al. 2008b), and significantly higher than the 263 mm mean length found in Plettenberg Bay, a heavily exploited area (Smith 2006). The mean length of dageraad in this study (413 mm) was substantially higher when compared to a study done by Buxton (1993) in the TNP MPA of 317 mm. Literature regarding length-frequencies of fransmadam is limited; however, the mean length in this study was slightly higher than that found by James et al. (2012) in their assessment of shore angling data from the TNP MPA. These differences may be a result of sampling bias as Buxton (1993) employed visual transects, therefore limiting the depths sampled to shallow areas, and James et al. (2012) sampled using various hook sizes (2/0-8/0) and were able to select for smaller fish. Furthermore, Burger (1991) illustrated that the intertidal and subtidal ichthyofaunal communities of TNP MPA were significantly different with regard to species and size composition.

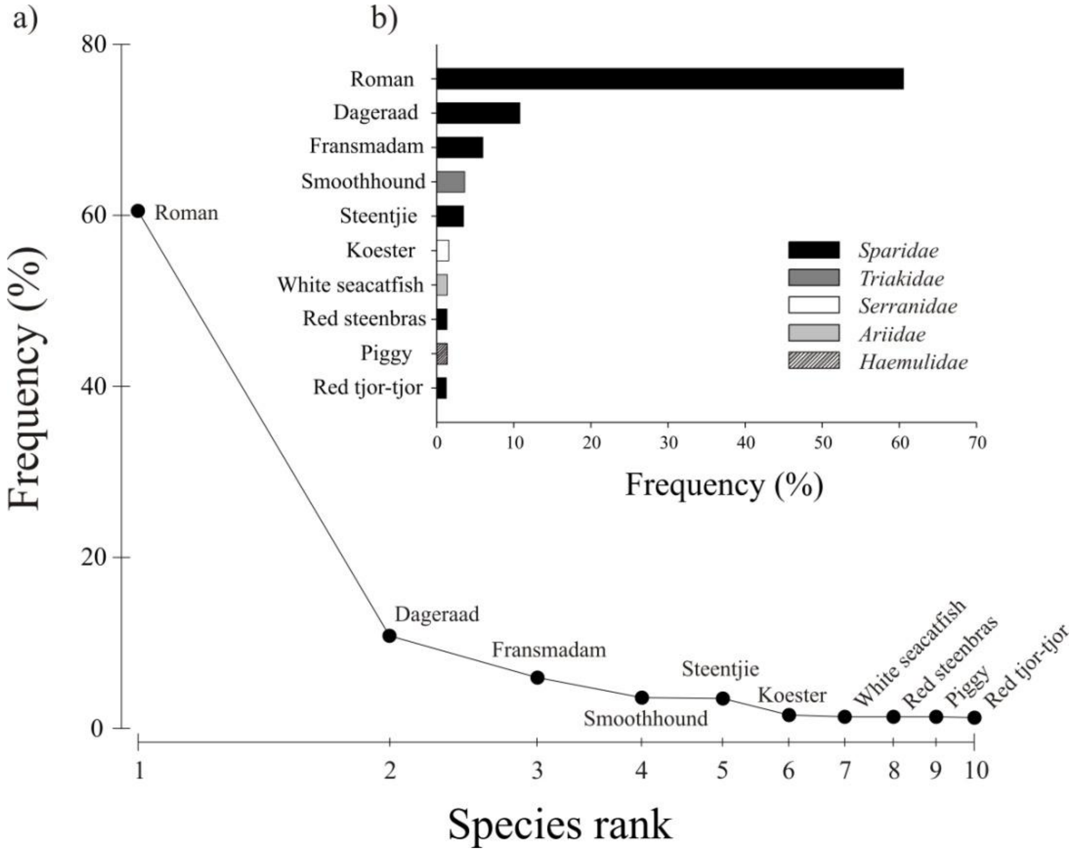


Figure 2.6: (a) Species dominance plot and (b) bar-graph showing the frequency of occurrence of the ten most abundant species caught in the Tsitsikamma National Park marine protected area between 2007 and 2013.

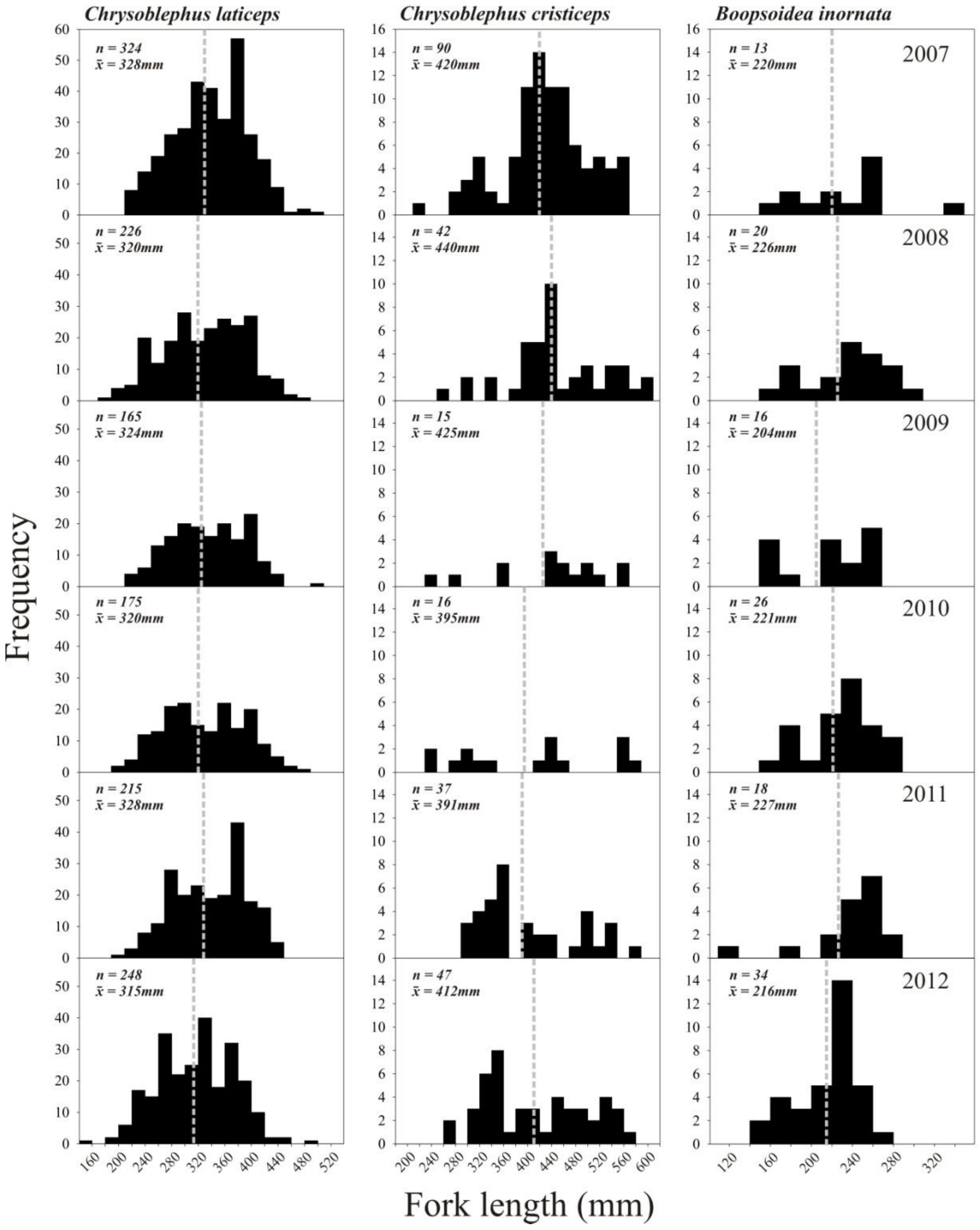
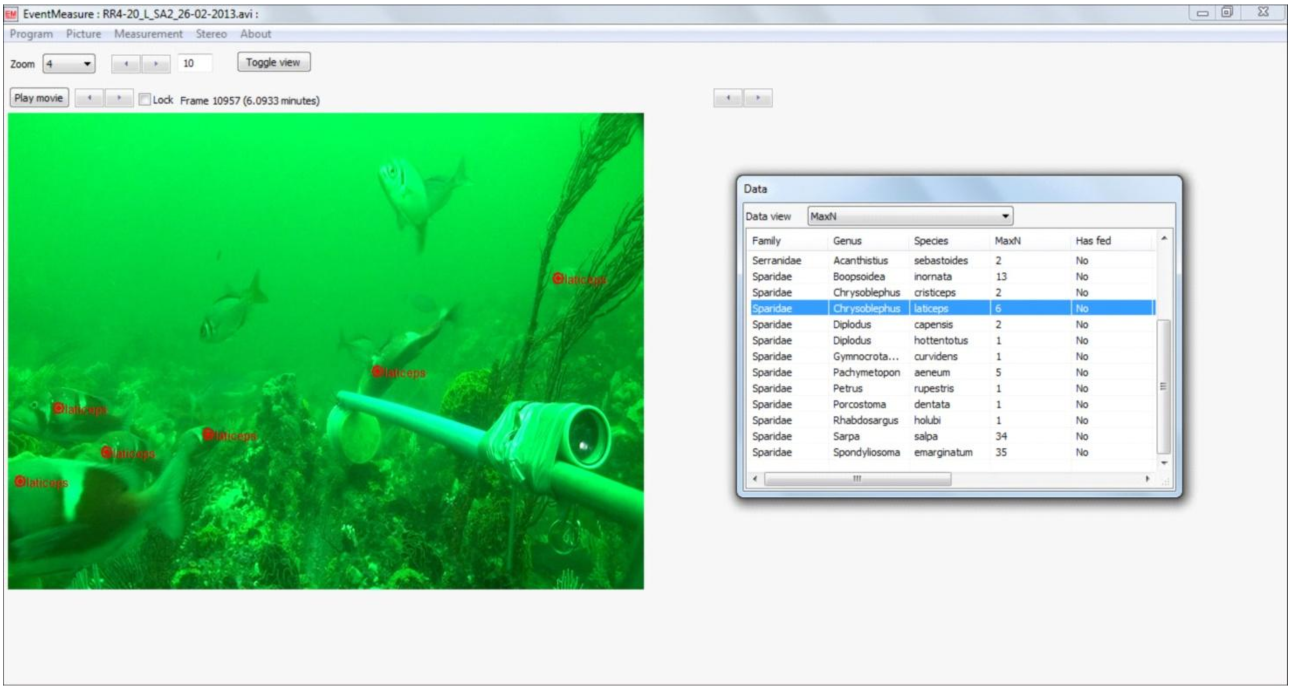


Figure 2.7: Length-frequency histograms for the three most abundant species caught in the Tsitsikamma National Park marine protected area between 2007 and 2012. The dashed lines represent the annual mean length (mm FL).

McClanahan et al. (2007) suggest that permanent closures to exploitation of over 37 years are required to maintain ichthyofaunal states that are representative of unexploited ecosystems. Because this study commenced after 42 years of protection against exploitation, the ichthyofaunal population structure of the TNP MPA could be considered stable. As expected, the mean size of the three most frequently caught species (roman, dageraad and fransmadam) remained relatively constant over the years of sampling (Figure 2.7).

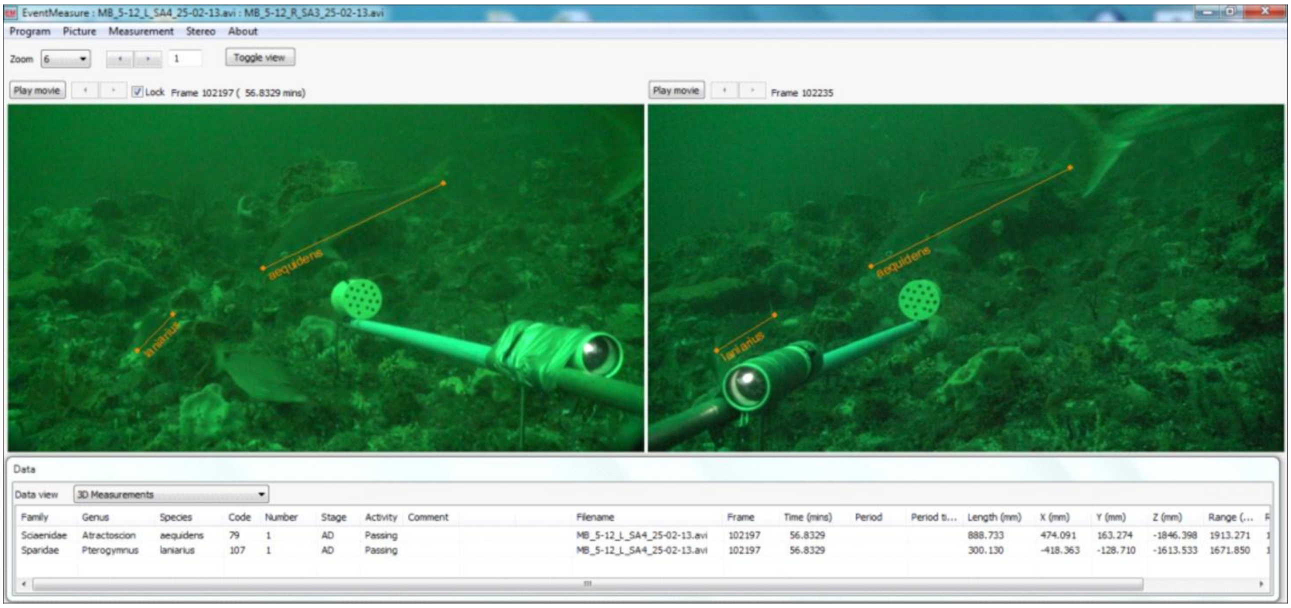
2.4 APPENDICES



Data view: MaxN

Family	Genus	Species	MaxN	Has fed
Serranidae	Acanthistius	sebastoides	2	No
Sparidae	Boopsoidea	inornata	13	No
Sparidae	Chrysoblephus	cristiceps	2	No
Sparidae	Chrysoblephus	laticeps	6	No
Sparidae	Diplodus	capensis	2	No
Sparidae	Diplodus	hottentotus	1	No
Sparidae	Gymnocrota...	curvidens	1	No
Sparidae	Pachymetopon	aeneum	5	No
Sparidae	Petrus	rupestris	1	No
Sparidae	Porcostoma	dentata	1	No
Sparidae	Rhabdosargus	holubi	1	No
Sparidae	Sarpa	salpa	34	No
Sparidae	Spondyliosoma	emarginatum	35	No

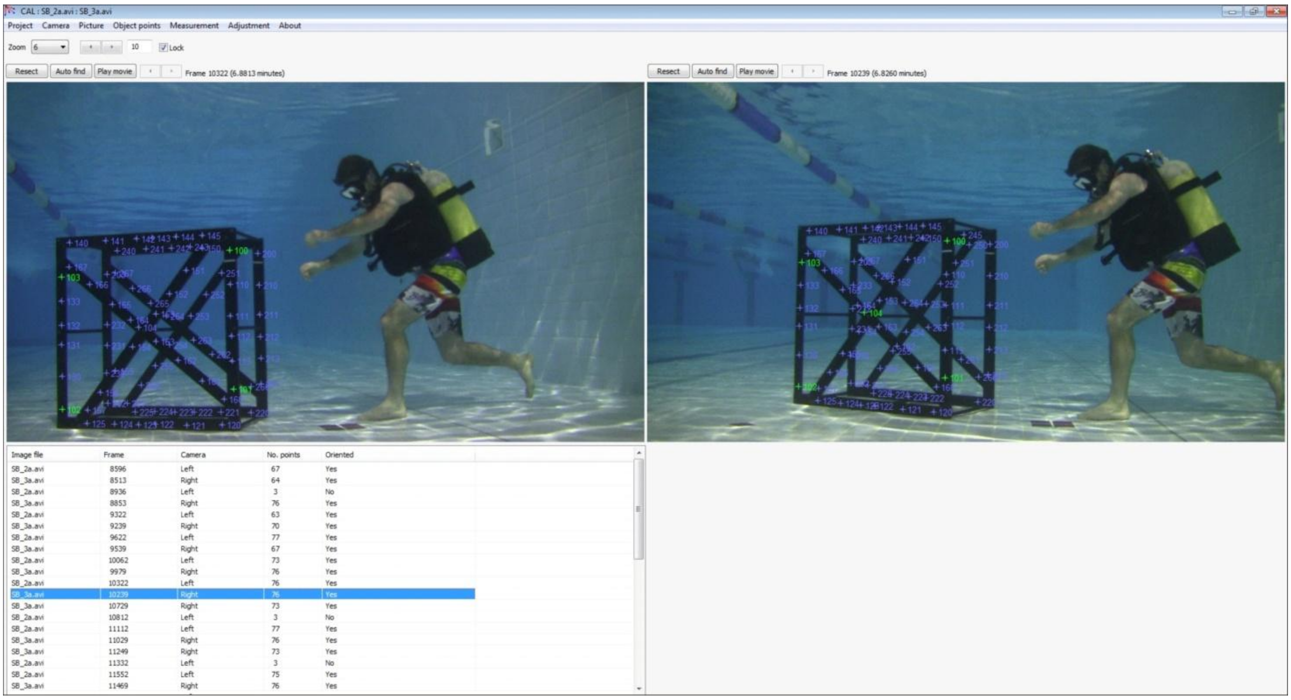
Appendix 2.1: Capturing MaxN data using the video analysis software EventMeasure (www.seagis.com.au).



Data view: 3D Measurements

Family	Genus	Species	Code	Number	Stage	Activity	Comment	Filename	Frame	Time (mins)	Period	Period ti...	Length (mm)	X (mm)	Y (mm)	Z (mm)	Range (...
Sciaenidae	Atractoscion	aequidens	79	1	AD	Passing		MB_5-12_L_SA4_25-02-13.avi	102197	56.8329			888.733	474.091	163.274	-1846.398	1913.271
Sparidae	Pterogymnus	laniarius	107	1	AD	Passing		MB_5-12_L_SA4_25-02-13.avi	102197	56.8329			300.130	-418.363	-128.710	-1613.533	1671.850

Appendix 2.2: Measuring the length of fish, and their range from the cameras, using the video analysis software EventMeasure (www.seagis.com.au).



Frame 10322 (6.8813 minutes)

Frame 10239 (6.8260 minutes)

Image file	Frame	Camera	No. points	Oriented
SB_2a.avi	8596	Left	67	Yes
SB_3a.avi	8513	Right	64	Yes
SB_2a.avi	8936	Left	3	No
SB_3a.avi	8853	Right	76	Yes
SB_2a.avi	9322	Left	63	Yes
SB_3a.avi	9239	Right	70	Yes
SB_2a.avi	9622	Left	77	Yes
SB_3a.avi	9539	Right	67	Yes
SB_2a.avi	10062	Left	73	Yes
SB_3a.avi	9979	Right	76	Yes
SB_2a.avi	10322	Left	76	Yes
SB_3a.avi	10239	Right	76	Yes
SB_3a.avi	10729	Right	73	Yes
SB_2a.avi	10812	Left	3	No
SB_2a.avi	11112	Left	77	Yes
SB_3a.avi	11029	Right	76	Yes
SB_3a.avi	11249	Right	73	Yes
SB_2a.avi	11332	Left	3	No
SB_2a.avi	11552	Left	75	Yes
SB_3a.avi	11469	Right	76	Yes

Appendix 2.3: Calibrating a stereo-BRUVs system using a calibration cube and the specific calibration software CAL (www.seagis.com.au).

Appendix 2.4: Mean annual CPUE for all species caught in the Tsitsikamma National Park marine protected area between 2007 and 2013 (n = 2,751).

Species	Common name	CPUE fish.angler^{-1}hr^{-1}						
		2007	2008	2009	2010	2011	2012	2013
Ariidae								
Galeichthys feliceps	White seacatfish	0	0.031	0.125	0.063	0.031	0.232	0.060
Callorhinchidae								
Callorhinchus capensis	Elephantfish	0	0	0	0	0.016	0	0
Carangidae								
Trachurus trachurus	Maasbanker	0.031	0	0.047	0	0	0.012	0
Carcharhinidae								
Carcharhinus brachyurus	Bronze whaler	0.016	0.078	0.031	0.094	0	0.037	0
Carcharhinus obscurus	Dusky shark	0	0.016	0	0	0	0	0
Haemulidae								
Pomadasys olivaceum	Piggy	0.031	0.250	0	0.109	0	0.085	0.020
Hexanchidae								
Notorynchus cepedianus	Spotted sevengill shark	0	0	0	0	0	0	0.020
Pomatomidae								
Pomatomus saltatrix	Elf	0.016	0.188	0	0	0	0.024	0
Rajidae								
Raja straeleni	Biscuit skate	0	0	0	0.016	0	0	0
Sciaenidae								
Argyrosomus japonicus	Dusky kob	0	0.031	0	0.016	0	0	0
Atractoscion aequidens	Geelbek	0.250	0.047	0.016	0.016	0	0	0
Scyliorhinidae								
Haploblepharus edwardsii	Puffadder shyshark	0	0.016	0.031	0.031	0	0.012	0.020
Poroderma africanum	Striped catshark	0	0	0	0.016	0	0	0.100
Halaelurus natalensis	Tiger catshark	0	0	0	0	0.016	0	0
Serranidae								
Serranus knysnaensis	African seabass	0	0	0	0	0	0.012	0
Acanthistius sebastoides	Koester	0.078	0.047	0.047	0.063	0.031	0.037	0.380
Epinephelus marginatus	Yellowbelly rockcod	0	0	0	0	0	0.012	0
Sparidae								
Diplodus capensis	Blacktail	0.016	0.063	0.031	0.047	0	0.061	0
Pachymetopon aeneum	Blue hottentot	0.047	0.094	0.047	0.063	0.016	0.061	0.040
Rhabdosargus holubi	Cape stumpnose	0	0	0	0.016	0	0	0.020
Argyrozona argyrozona	Carpenter	0.094	0	0	0.016	0.109	0.049	0

Chrysoblephus cristiceps	Dageraad	1.422	0.672	0.234	0.250	0.578	0.573	0.360
Boopsoidea inornata	Fransmadam	0.203	0.313	0.250	0.406	0.281	0.415	0.420
Pterogymnus laniarius	Panga	0	0.016	0.047	0.016	0.063	0.024	0
Petrus repestris	Red steenbras	0.141	0.141	0.047	0.047	0.047	0.012	0.100
Chrysoblephus gibbiceps	Red stumpnose	0.016	0	0	0	0.031	0	0.020
Pagellus natalensis	Red tjor-tjor	0.031	0.047	0.078	0.078	0.078	0.049	0.140
Chrysoblephus laticeps	Roman	5.234	3.563	2.578	2.797	3.375	3.085	2.440
Lithognathus mormyrus	Sand steenbras	0	0	0	0.016	0.016	0	0
Cheimerius nufar	Santer	0	0	0.078	0.016	0.016	0	0.020
Spondyliosoma emarginatum	Steentjie	0.094	0.203	0.203	0.375	0.172	0.134	0.160
Sarpa salpa	Strepie	0	0.016	0.063	0	0	0	0
Sparodon durbanensis	White musselcracker	0	0	0.016	0	0	0	0
Sphyrnidae								
Sphyrna zygaena	Smooth hammerhead	0.016	0	0.016	0.016	0	0	0
Tetraodontidae								
Amblyrhynchotes honkenii	Evileye puffer	0	0	0.016	0	0	0	0
Triakidae								
Mustelus mustelus	Smooth-hound	0.250	0.250	0.156	0.328	0.234	0.085	0.100
Galeorhinus galeus	Soupfin shark	0	0.063	0	0	0.016	0.037	0.020
Triakis megalopterus	Spotted gullyshark	0	0	0	0	0	0.012	0
Triglidae								
Chelidonichthys kumu	Bluefin gurnard	0.016	0.031	0	0	0.313	0	0.020

CHAPTER THREE

SPATIAL VARIABILITY ASSOCIATED WITH LONG-TERM MONITORING OF THE SUBTIDAL ICHTHYOFAUNA IN TSITSIKAMMA NATIONAL PARK MARINE PROTECTED AREA

3.1 INTRODUCTION

Tobler's (1970) First Law of Geography states 'everything is related to everything else, but near things are more related than distant things'. This law describes a fundamental property of most ecological datasets, that of spatial dependence. Spatial dependence is a phenomenon that results from both exogenous (induced) and endogenous (inherent) processes acting on spatial distribution of a species (Figure 3.1), creating dependencies amongst individuals, which manifest in distributional patterns (Fortin and Dale 2005, Planque et al. 2011). A major component of spatial dependence is autocorrelation of these processes. The term 'autocorrelation' refers to the degree of correlation of a variable with itself, hence the prefix 'auto' (Fortin and Dale 2005, Plant 2012). Autocorrelation is scale or distance dependent; the values of a particular variable or observation may be more similar than expected (positive autocorrelation) or less similar than expected (negative autocorrelation) (Fortin and Dale 2005). 'Spatial autocorrelation' therefore implies that the relationship amongst values of a given variable is a function of the distances between them or their location in space (Fortin and Dale 2005, Beale et al. 2010, Plant 2012). Anselin and Bera (1998, p241, as cited by Fortin and Dale 2005) loosely define spatial autocorrelation as 'the coincidence of value similarity with locational similarity'. Hence, the notion of spatial dependence implies that there is a lack of independence among data from nearby locations.

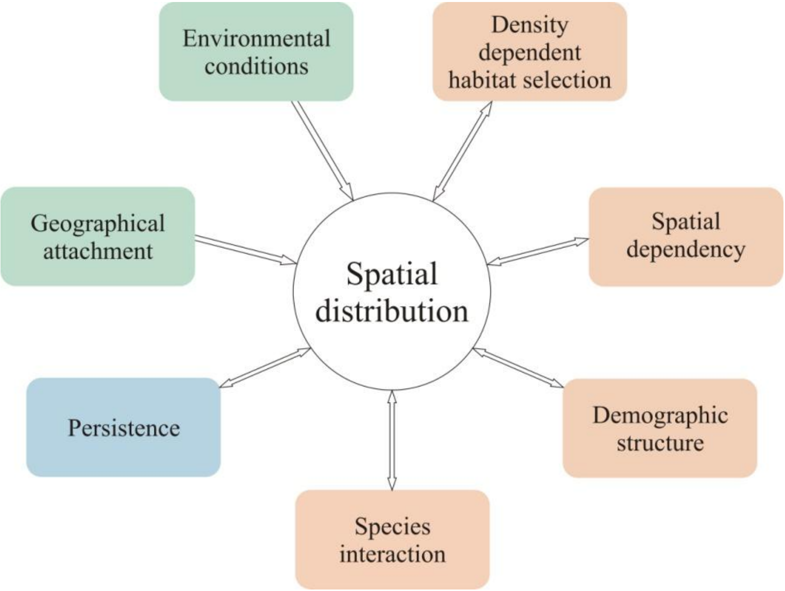


Figure 3.1: Conceptual schematic illustrating the processes of spatial distribution of fish. Exogenous controls are in green, endogenous controls are in red and blue is a controlling parameter that is dependent on the current and past state of the population. Adapted from Planque et al. 2011.

3.1.1 INDEPENDENCE AND STATISTICAL INFERENCE

The presence of spatial dependency in the form of autocorrelation introduces numerous deviations from the assumptions of classical statistics that warrant attention (Hamylton 2013), particularly the violation of independence of observations (sample units) (Legendre 1993). If proximate observations are not independent of each other they cannot be freely permuted at random to create the reference (null) distribution of the test statistic (Hamylton 2013). The result of this is the effective decrease in the number of degrees of freedom in the sample to less than that estimated from the number of observations (Legendre 1993, Fortin and Dale 2005, Zuur et al. 2009, Borcard et al. 2011, Hamylton 2013). Consequently, statistical tests of model significance generate artificially narrow confidence limits thereby increasing the likelihood of a Type I error (incorrect rejection of the null hypothesis) and inflating the goodness of fit measure. Furthermore, the model standard error may be underestimated due to allocating some of its effect to interactions in the existing dependent variables (Legendre 1993, Dray et al. 2012, Hamylton 2013). As such, spatial dependence in ecological data can obscure relationships between biological response variables and explanatory variables due to spatial structuring within the residuals overpowering these relationships. These statistical deviations can be addressed through maintaining a clear association between quantitative data and the spatial coordinates that locate them (Dray et al. 2012, Hamylton 2013).

3.1.2 INCORPORATING SPATIAL DEPENDENCE

Animal and plant populations are rarely distributed randomly in space but rather exhibit spatial patterns, and fish populations are no exception (Planque et al. 2011). Autocorrelation is inherent in natural systems in the form of patchiness or gradients, both of which can occur over a wide range of spatial scales (Fortin and Dale 2005). In his paper titled ‘Spatial autocorrelation: trouble or new paradigm?’ Legendre (1993) insists that autocorrelation is simply a ‘fact of life’ for ecologists. As the title suggests, the author believes that autocorrelation can be viewed in two ways: a nuisance during statistical testing, or as a source of ecological information that can enhance our understanding of the spatial structure of ecological processes (Legendre 1993, Fortin and Dale 2005). As fisheries management policies shift from single species assessments to the more holistic Ecosystem-Based Fisheries Management (EBFM) (Hall and Mainprize 2004, Pikitch et al. 2004, Branch and Clark 2006), the need to understand the influence of spatial structures on ecological processes continues to grow. This, along with the technological advances in computational power and geographical information systems (GIS), has led to the emergence of a field that quantitatively examines spatially explicit data in ecology, referred to as ‘spatial analysis’ (Liebhold and Gurevitch 2002). This field of study fully embraces Legendre’s (1993) new paradigm and aims to explicitly understand, measure and model spatial patterns in ecological data (Liebhold and Gurevitch 2002).

Recently, McIntire and Fajardo (2009) expanded the concept of spatial analysis further by proposing the use of space as a surrogate for uncovering unmeasured and/or immeasurable ecological variables or processes through the analysis of spatial patterns and their residuals. The rationale behind the conceptual framework was that ecologists often fail to draw clear links between patterns and processes as a result of ‘missing’ variables. Spatially structured residuals usually indicate either that the model may be misspecified, in the sense that important variables predictors may be missing from the model, or that other processes are important besides the effects of the measured environmental variables (Fortin and Dale 2005, Wagner and Fortin 2005, McIntire and Fajardo 2009, Dray et al. 2012). Given that the majority of ecological processes are spatially structured, the introduction of a spatial component as a proxy or ‘substitute variable’ acknowledges the presence of such potentially underlying processes that may be difficult to measure directly in field studies, but may be important predictors, e.g., missing environmental variables or biotic interactions (Liebhold and Gurevitch 2002, McIntire and Fajardo 2009, Dray et al. 2012). Although these missing ‘variables’ may not be identified, their combined influence can be quantified through spatial analysis and incorporated into mixed models as random effects (Zuur et al. 2009, Dray et al. 2012, Hamylton 2013), thereby enhancing model performance.

3.1.3 IMPORTANCE OF SPATIAL ANALYSES IN LONG-TERM MONITORING

A primary focus within ecology is the study of population fluctuations over time and space (Koenig 1999, Lindenmayer and Likens 2010). Whereas much of the emphasis in long-term monitoring (LTM) is placed on the temporal abundance trends, spatial aspects are often poorly investigated or completely neglected (Legendre 1993, Zuur et al. 2009). This is reflected in the various methods that have been devised for eliminating or avoiding the effects of spatial dependence when measuring biotic responses over time (Liebhold and Gurevitch 2002). For example, the estimation of temporal abundance indices often involves averaging samples across space and/or stratifying to specifically exclude particular conditions, which emphasizes the willingness to ignore the influence of space on population dynamics. In doing so, ecologists accept a high level of variability within a temporal dataset, resulting in low precision of the predicted abundance trend. To fully comprehend long-term population variability depends, however, on a firm understanding of each sampling point’s ‘instantaneous’ variability resulting from the *in situ* environmental conditions. By understanding and accounting for this instantaneous variability, the analyst will be able to standardize spatially explicit abundance data, making temporal abundance estimates more precise and reliable.

Acknowledging the importance of spatial aspects in assessing temporal trends will benefit LTM through the development of new statistical methods and conceptual frameworks, which can be applied to provide decision makers with the most accurate information possible. Furthermore, investigating spatial autocorrelation can identify and quantify the extent of redundant information in survey datasets. Spatial analysis can therefore be applied to optimize the dimension of sample units (Hamylton 2013) and refine existing sampling protocols. This would also ensure the optimal use of resources, which is essential to the persistence of LTM programmes.

3.1.4 STUDY AIM

The overall aim of this study was to assess the importance of spatial component of LTM in the Tsitsikamma National Park (TNP) marine protected area (MPA). Multivariate analyses were used to provide an overview of species distribution throughout the sampling area and the spatial and temporal variables linked to these distributions were then ranked using ‘random forest’ (RF) analyses. The degree of spatial autocorrelation within the data was investigated for the five most abundant species by using Moran’s *I* statistic (Moran 1950), and by analysis of residual structures of spatially explicit GAMs (generalized additive models). Mixed models (GAMMs) were introduced to account for the violation of independence, and predictive species abundance estimates were calculated. The outcomes of the study include a detailed description of the ichthyofauna, species-specific spatial structure and the extent of spatial dependence and autocorrelation within the TNP LTM angling dataset. Furthermore, the study identifies the most appropriate statistical techniques to be incorporated into a spatial analyses protocol, which can be applied to other LTM programmes.

3.1.5 STUDY OBJECTIVES

The objectives of this study include:

- Describe ichthyofaunal distribution patterns within the sampling area in the TNP MPA
- Describe species-specific distribution patterns within the TNP MPA
- Quantify species-specific spatial autocorrelation
- Compare performance of predictive models that include a spatial component with those without a spatial component
- Assess the importance of specific environmental variables on species distribution
- Assess possible data redundancy due to inadequate sampling unit size

3.2 METHODS AND MATERIALS

3.2.1 DATA COLLECTION

The research was conducted on Rheeders reef complex within the TNP MPA (Section 2.1). Sample site selection was based on a stratified random scheme described in Sections 2.2.5. The sampling method employed was angling, which is described fully in Section 2.2.2. Catch-per-unit-effort (CPUE) was calculated as the number of fish per angler per hour (fish.angler^{-1}hour^{-1}) in all cases.

3.2.1.1 ENVIRONMENTAL VARIABLES

Water *temperature* (average bottom temperature recorded during angling at a site) was recorded using a submersible temperature logger (HOBO Temperature Logger - Onset Computer Corporation) attached to the anchor line a meter above the anchor chain. Site *depth* was recorded off the boat's echo sounder. *Substrate* and reef *profile* were inferred from a bathymetric map (Figure 2.4).

3.2.2 DATA ANALYSIS

3.2.2.1 NON PARAMETRIC ABUNDANCE ANALYSES

First, the categorical variables *substrate* and *profile* were combined to form three categorical spatial predictors for fish distributions: *reef-high profile* (RHP), *reef-low profile* (RLP) and *sand* (S). Non-parametric Kruskal–Wallis tests, followed by Tukey's comparison tests, were conducted to determine if the combined catch-per-unit-effort (CPUE) and number of species caught at various *substrate* and *profile* categories differed significantly.

3.2.2.2 MULTIVARIATE REGRESSION TREE

Multivariate Regression Trees (MRTs) were used in exploratory analyses to describe the relationship between spatial variables and community distribution. The MRT approach was chosen because it is considered a robust method that can handle non-linear relationships and higher order interactions between multivariate response variables and environmental predictors (De'ath 2002). The process employs binary recursive portioning of data to cluster sampling sites according to species similarity (De'ath 2002). The portioning of the data is realized through a series of binary splits of the predictor variables and the highest within group species similarity is achieved by minimizing the sum of square Euclidean distances (SSD) within each resultant group. The regression tree starts with a single binary split at the top and 'grows' with each subsequent split, with each split resulting in two new nodes. The terminal unsplit nodes of the tree represent the final groups termed 'leaves' (De'ath 2002).

In the MRT analysis, the species composition of each sample site was related to the spatial variables *substrate*, *latitude* and *longitude* with the aim of objectively grouping the sampling sites into spatial units of high species similarity. The percentage contribution of each species (>3% frequency of occurrence) to the ichthyofaunal composition of each terminal group was calculated. All MRT analyses were carried out in the R statistical programming environment, version 3.1.0 (R Development Core Team 2014) using the 'mvpart' library (De'ath 2002).

3.2.2.3 VARIABLE IMPORTANCE

Classification procedures are among the most widely employed statistical methods in ecology, with numerous applications in species distribution modelling (Guisan and Zimmermann 2000, Cutler et al.

2007). The ensemble method ‘random forests’ (RF; Breiman 2001) is an extension of the Classification and Regression Tree approach (CART; Breiman et al. 1984), whereby a large number of classification trees are constructed from randomly selected subsets of the original data and grouped to form a ‘forest’ algorithm (Lawler et al. 2006, Lennert-Cody et al. 2008). One of the by-products of RF calculations is a measure of variable importance. Although most multivariate statistical procedures measure variable importance indirectly through selection criteria, such as statistical significance and Akaike’s Information Criterion (Cutler et al. 2007), RF quantitatively estimates the importance of each variable based on cross-validation, allowing for direct comparisons of importance between variables. In this study RF was employed as a data exploration tool to isolate meaningful predictor variables, as well as to illustrate the relative importance of spatial variables over their temporal counterparts with regard to predictive power. The RF analyses were carried out in the R statistical programming environment using the package ‘RandomForest’ (Cutler et al. 2007).

3.2.2.4 SPECIES-SPECIFIC DISTRIBUTION

Species distribution was mapped on the assumption that CPUE is an adequate measure of relative abundance (Hilborn and Walters 1992, Maunder and Punt 2004). Exploratory analysis revealed non-linearity between the response variable (CPUE) and the continuous predictor variables (*year, season, position*) for the five most abundant species. As a result Generalized Additive Models (GAMs), which are semi-parametric extensions of generalized linear models (GLMs) where the linear predictor incorporates smoothing functions of the variables (Wood 2006), were used. Generalized additive models are particularly useful when dealing with non-linear and non-monotonic relationships between the response and the predictor variables (Wood 2006, Zuur et al. 2009), and therefore offer benefits beyond those of GLMs when constructing ecological models. Predictor variables considered in the model included *year, season,* and *position* (*latitude; longitude*). The full GAM for each species was formulated as:

$$CPUE = year + season + s(lat, long) + \varepsilon \qquad \text{(Eq. 3.1)}$$

where *s*() denotes the smoother function and ε the associated model residuals. Models were run on the Poisson family distribution with a log-link and smoothing of the continuous variable (*lat,long*) was realized by thin plate regression spline functions (Wood 2006). All analyses were carried out within the R programming environment and the GAMs fitted using the ‘mgcv’ library package (Wood and Augustin 2002).

3.2.2.5 SPATIAL AUTOCORRELATION

Moran’s *I* statistic (Moran 1950) was used to capture the extent to which the environmental variables *depth* and *temperature,* as well as combined and species-specific CPUE, covaried with themselves across space. This measure was calculated as the cross product for a given variable of interest, z_i, at location i:

$$I(d) = \frac{N}{\sum_i \sum_j W_{i,j}} \frac{\sum_i \sum_j W_{i,j}(z_i - \hat{z})(z_j - \hat{z})}{\sum_i (z_i - \hat{z})^2} \qquad \text{(Eq. 3.2)}$$

where d is the distance class for which Moran's I is calculated, N is the total number of sampling sites within the study area, z is the variable of interest (e.g., CPUE) and $\hat{z}$ is its mean value, and $W_{\mathrm{i,j}}$ is a proximity matrix of spatial weights. The variable $W_{\mathrm{i,j}}$ takes the value of 1 when sites i and j are at or within a distance interval d, and 0 otherwise. In this way, only the pairs of sites (i,j) within the stated distance interval (d) of each point location were taken into account (Hamylton 2013).

Moran's I statistic may vary between -1.0 and +1.0, with values close to 0 suggesting the spatial distribution is random. Positive and negative spatial dependences are indicated by larger positive and negative $I(d)$ values, respectively (Cheal et al. 2007, Borcard et al. 2011, Hamylton 2013).

Moran's I statistic was calculated for all variables of interest at a local and global scale. Global Moran's I provides a single value of autocorrelation for the variable of interest throughout the entire sampling area; an area average of sorts. In contrast, local Moran's I calculates an autocorrelation value for each observation unit based on similarities of neighbouring sampling units within specified distance interval (d). For local calculations, a distance interval of 150 m was predefined as this was the distance between the neighbouring sample sites (Figure 2.4). Local spatial autocorrelation was estimated using Moran's I correlograms, and significance was assessed using a Monte Carlo simulation method with 1000 permutations (Kühn 2006, Bivand et al. 2013). These analyses were performed in the R programming environment using the 'spdep' library package (Kühn 2006, Bivand et al. 2013)

Global spatial autocorrelation for all variables of interest was estimated employing the *Global Moran's I* tool in ArcGIS version 10.1 (ESRI 1996). This tool calculates Moran's I index as well as an expected value. Significance of spatial autocorrelation was calculated using the number of features in the dataset (n) and the residual variance, and was expressed in the form of a *z-score* and *p-value*.

3.2.2.6 COVARIATE PREDICTORS

The effects that *depth* and *temperature* had on CPUE of the five most abundant species were non-linear, and were therefore estimated using GAMs of the following form:

$$CPUE = year + season + s(temperature) + s(depth) + s(temperature \times depth) + \varepsilon \qquad \text{(Eq. 3.3)}$$

where $s()$ denotes the smoother functions and ε the associated model residuals. For all GAMs the discrete variables (*year* and *season*) were included as parametric coefficients, while the continuous variables (*temperature* and *depth*) were fitted with a tensor product smoother (Wood 2006). Models were run on the Poisson family distribution with the log-link and the smoothness selection criterion based on restricted maximum likelihood (REML). When analysing roman (*Chrysoblephus laticeps*) and dageraad (*Chrysoblephus cristiceps*) the data were subsetted to only contain samples where the substrate was reef in an attempt to avoid zero-inflation due to excessive zero counts from unsuitable habitat, as these species are known to be reef associated (Heemstra and Heemstra 2004). Ignoring excessive zeros (zero inflation) within a Poisson distribution can lead to biases in parameter and standard error estimations, as well as causing model overdispersion (Zuur et al. 2009).

With the exception of fransmadam (*Boopsoidea inornata*), analysis of model residuals revealed definitive spatial structuring, which corresponded to the Moran's *I* spatial autocorrelation statistics. As a result, Generalized Additive Mixed Models (GAMMs) were applied with a correlation structure embedded in the model residuals (Zuur et al. 2009) to account for spatial autocorrelation. The configuration of the residual correlation structure was based on experimental variograms, assuming one of the following theoretical forms: exponential, spherical or Gaussian (Fortin and Dale 2005, Zuur et al. 2009). The fixed variables of the GAMMs were formulated as before (Eq. 3.3), with an additional correlation structure applied to the residuals. The most appropriate correlation structure was selected by minimizing the Akaike Information Criterion (AIC) for each species model (Zuur et al. 2009), which assumed one of the following forms:

Exponential:

$$\gamma(h) = c_0 + c_1\left[1 - \exp\left(\frac{h}{a}\right)\right] \qquad \text{(Eq. 3.4)}$$

Spherical:

$$\gamma(h) = \begin{cases} c_0 + c_1\left[\frac{3h}{2a} - \frac{1}{2}\left(\frac{h}{a}\right)^3\right], \text{for } 0 < h < a \\ c_0 + c_1 \qquad , \text{for } h \geq a \end{cases} \qquad \text{(Eq. 3.5)}$$

Gaussian:

$$\gamma(h) = c_0 + c_1\left[1 - \exp\left(-3\frac{h^2}{a^2}\right)\right] \qquad \text{(Eq. 3.6)}$$

where h is the distance between the sampling points (also known as spatial lag), a is the spatial range, c_0 is the nugget effect and c_1 the sill of the experimental variogram (Fortin and Dale 2005). The residuals of the models that incorporated correlation structure were plotted to ensure the spatial structuring had been sufficiently accounted for. Predictions for the effects of *temperature* and *depth* on the expected CPUE (± 95% CI) for each species were calculated.

3.3 RESULTS

3.3.1 INFLUENCE OF HABITAT ON ABUNDANCE AND DIVERSITY

Significant differences were found in CPUE ($\chi^2 = 36.7$; df = 2, $p < 0.001$) and number of fish species ($\chi^2 = 28.5$; df = 2, $p < 0.001$) sampled between the different habitat-profiles (Figure 3.2). Subsequent Tukey's test revealed that sand was significantly different to RHP and RLP in both cases, while no differences were found between RHP and RLP.

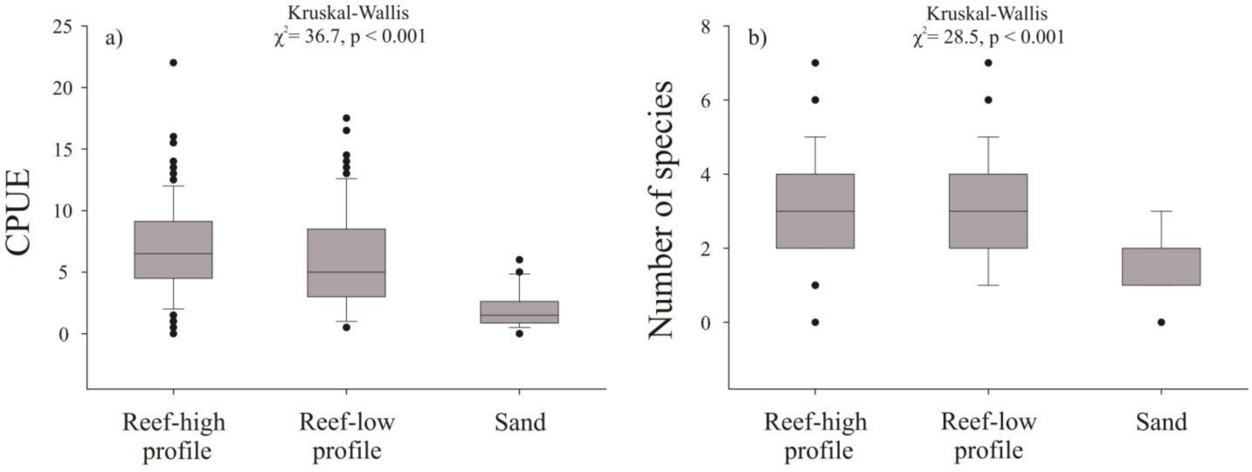


Figure 3.2: Box and whisker plots comparing the effects of the variables *substrate* and *profile* on (a) catch-per-unit-effort (CPUE; fish.angler^{-1}hr^{-1}) and (b) the number of species caught per site. The plots depict the data median, 10th, 25th, 75th and 90th percentiles as vertical boxes with error bars and outliers as shaded circles.

3.3.2 ICHTHYOFAUNAL DISTRIBUTION

The recursive partitioning procedure employed by the MRT analysis for *substrate*, *latitude* and *longitude* as spatial variables produced a tree with four 'groups' explaining 22.8% of the variance in the species distribution (Figure 3.3a). *Substrate* was found to be the most important 'spatial' variable and explained 14.5% of the variance in the species distribution, followed by *latitude* (5.0%) and finally *longitude* (3.3%).

Group one contained only sand substrate sites and consisted of four species, two of which were elasmobranchs; copper shark (*Carcharhinus brachyurus*; 5.8%), smooth-hound (*Mustelus mustelus*; 41.9%), bluefin gurnard (*Chelidonichthys kumu*; 25.6%) and red tjor-tjor (*Pagellus natalensis*; 5.8%). Group two consisted of reef species found adjacent to the shoreline (*latitude* >-34.03 degrees) and accounted for the majority of the sites within the sampling area. The group was made up exclusively of sparids with roman (66.8%) being the dominant species, followed by dageraad (7.6%), fransmadam (6.8%) and steentjie (*Spondyliosoma emarginatum*; 4.1%). Group three had the highest number of species (seven species), all of which occurred in similar proportions: soupfin shark (*Galeorhinus galeus*;

17.7%), smooth-hound (11.8%), carpenter (*Argyrozona argyrozona*; 11.8%), copper shark (5.9%), red tjor-tjor (5.9%), spotted gully shark (*Triakis megalopterus*; 5.9%) and maasbanker (*Trachurus trachurus*; 5.9%). This group only consisted of four sites and is a geographically defined transition zone between the sand sites in group one and the RHP sites of group four. As a result a multitude of species, which were either sand or reef associated were sampled, and four of the seven species (carpenter, maasbanker, soupfin shark and spotted gully shark) were unique to the group. Group four is the least diverse and consisted of only three species: roman (57.5%), dageraad (23.4%) and koester (3.4%).

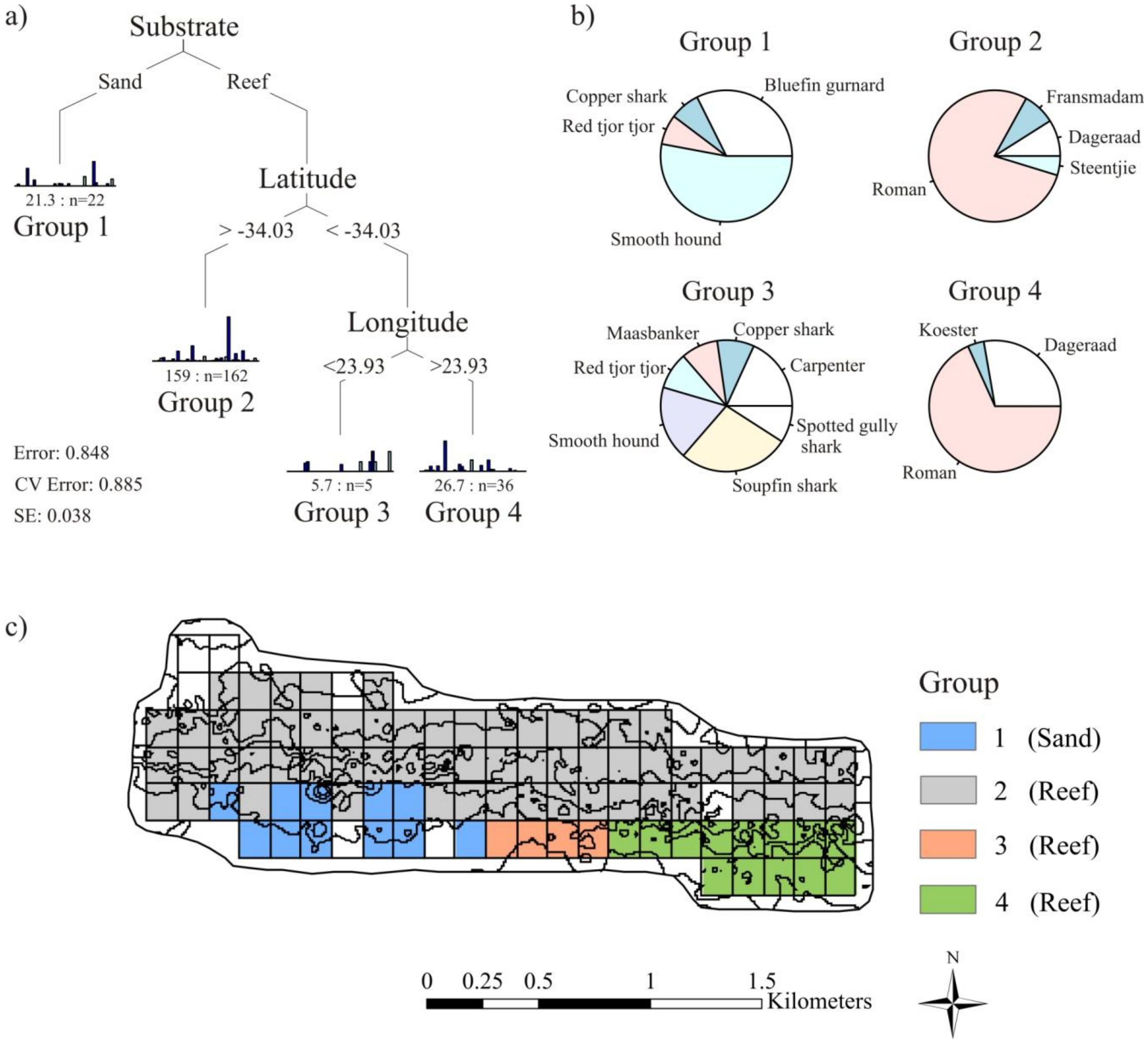


Figure 3.3: Analysis of the Tsitsikamma National Park marine protected area ichthyofaunal distribution using (a) a multivariate regression tree (MRT) depicting the four terminal groups, the sample size for each group and value at which the split occurred for each variable; (b) the ichthyofaunal groups and their relative species proportions (>3%) within each group; (c) a map showing the geographical locations of the ichthyofaunal groups assigned to each sample site.

3.3.3 SPECIES-SPECIFIC DISTRIBUTIONS

The GAM-predicted distributions for the 5 most abundant species were variable and exhibited unique and predominantly irregular spatial patterns (Figures 3.4 and 3.5). However, the combined species distribution was similar to the distribution of roman, which was a result of roman's dominance. A summary of relevant species-specific GAM statistics, such as variable significance, is provided in Appendix 3.1.

3.3.3.1 ROMAN

The GAM for roman was able to explain 46% of the null deviance in the data. The variables *season* and *lat,long* were both significant; however, the variable *year* was not significant. Roman had a semi-regular distribution that was confined to sites with reef substrate, and very low abundance estimates were exhited at sandy sites in the south-west edge of the study area (Figure 3.4b).

3.3.3.2 DAGERAAD

For dageraad, the GAM was able to explain 61.7% of the spatial variance and the variables *year, season* and *lat,long* were all significant. Dageraad distribution revealed the highest spatial variablity (Figure 3.4c), which manifested in three distinct zones of high CPUE and a notable absence in the centre of the study area (*latitude*: 23.9121 – 23.9256 E).

3.3.3.3 FRANSMADAM

The GAM for fransmadam was able to explain 20.5% of the spatial variance in fransmadam distribution. The variable *lat,long* was the only significant variable; however, the variables *year* and *season* were retained in the model. Like roman, fransmadam distribution was restricted to sites with reef substrate and was found to be most prevalent in shallow areas and near to the shore (Figure 3.5a).

3.3.3.4 SMOOTH-HOUND

The GAM for smooth-hound explained 38% of the null deviance and *lat, long* was the only significant variable. The smooth-hound distribution pattern suggested that the species was most prevalent in sandy areas, both shallow and deep, on the edge of the Rheeder's reef complex (Figure 3.5b).

3.3.3.5 STEENTJIE

For steentjie the GAM accounted for 29.9% of the spatial variability in the data, with *lat, long* once again being the only significant variable. Steentjie distribution was clustered around three areas of high abundance; however, these areas showed no discernable link to specific habitat (Figure 3.5c).

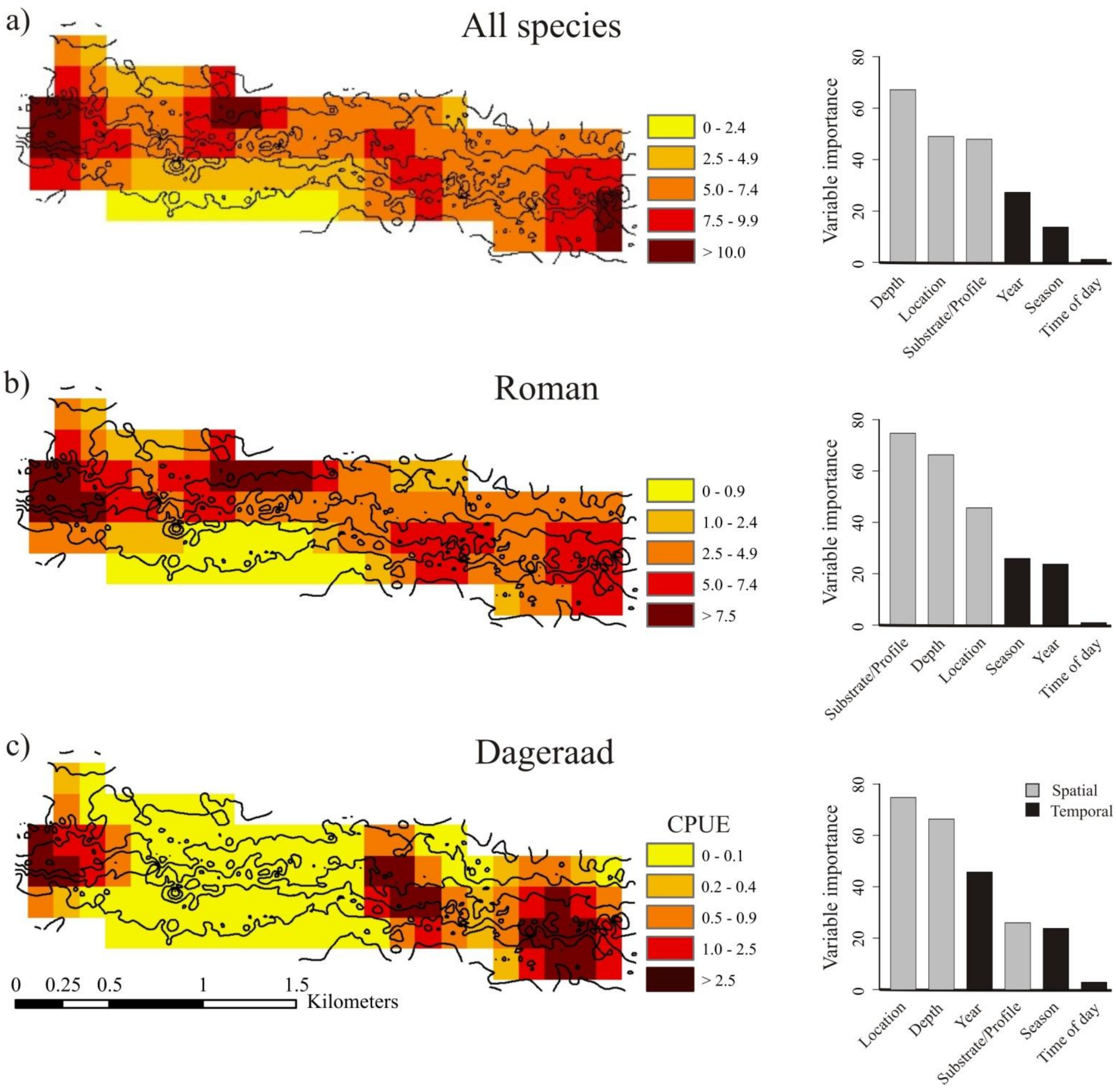


Figure 3.4: Bathymetric map of the Tsitsikamma National Park marine protected area study area (5 m contour) overlayed with species distribution maps of (a) all species combined, (b) roman and (c) dageraad. In all cases CPUE is regarded as a proxy for abundance. The maps are combined with barplots depicting the importance of individual variables in predicting the distribution of species throughout the study area, categorized as spatial or temporal.

3.3.4 RANDOM FOREST

The RF analysis suggested that the three spatial variables *location*, *depth* and *substrate/profile* had a far greater influence on the ability to predict species abundance than their temporal counterparts *year*, *season* and *time of day*. With the exception of one species (dageraad), the spatial variables were the three highest ranked according to their importance on all occasions (Figures 3.4 and 3.5)

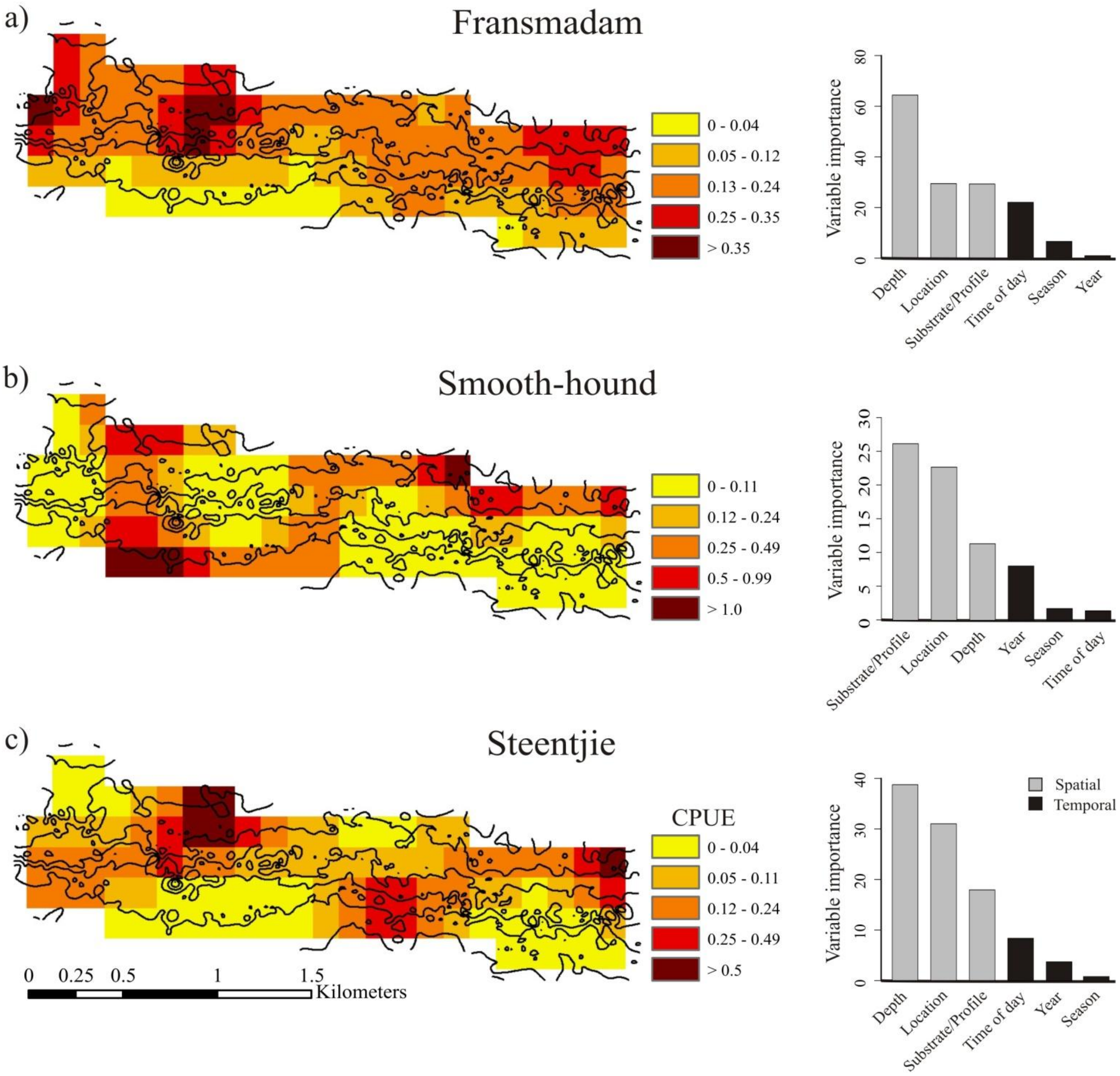


Figure 3.5: Bathymetric map of the Tsitsikamma National Park marine protected area study area (5 m contour) overlayed with species distribution maps of (a) fransmadam, (b) smooth-hound and (c) steentjie. In all cases CPUE is regarded as a proxy for abundance. The maps are combined with barplots depicting the importance of individual variables in predicting the distribution of species throughout the study area, categorized as spatial or temporal.

The variable *year* played a slightly more important role in predicting abundance than *substrate/profile* in the case of dageraad. The importance of each variable within their spatial and temporal classifications varied according to species.

3.3.5 SPATIAL AUTOCORRELATION

The variable *depth* showed significant spatial autocorrelation within the study area (Figure 3.6a and Table 3.1) and local Moran's *I* indices suggested strong positive autocorrelation at a distance of up to 300 m, the equivalent of two adjacent sampling sites. Conversely, strong negative autocorrelation was detected between 600–900 m from the site of comparison. Positive autocorrelation indicate similarities, while negative autocorrelation indicate differences between sites. No autocorrelation was evident at lag distances larger than 900 m. In contrast, the variable *temperature* showed no signs of spatial autocorrelation at any lag distance (Figure 3.6b).

Significant spatial autocorrelation in abundance was exhibited in all examined species, with the exception of fransmadam (Table 3.1). The combined species correlogram (Figure 3.7a) shows significant autocorrelation up to a lag distance of 300 m, which is consistent with both roman and dageraad (Figure 3.7b and c, respectively). At lag distances greater than 300 m the correlation index of roman remains within the expected values of a random distribution, suggesting no discernable patterns. In contrast, the correlation index of dageraad deviates from the expected values both positively and negatively, suggesting a 'patchy' distribution pattern. The local Moran's correlation index for fransmadam (Figure 3.7d) corroborates the lack of spatial autocorrelation in the global analysis. The global and local Moran's *I* indices indicate a general lack of spatial independence in the data, in both the predictor and response variables. This violation of independence introduces a number of deviations from basic statistical assumptions, which need to be addressed.

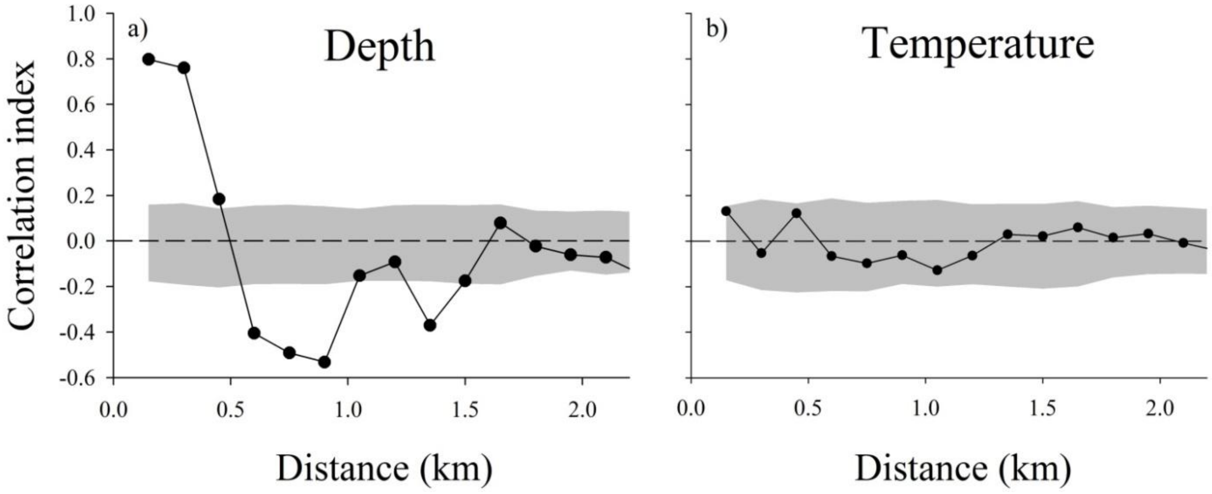
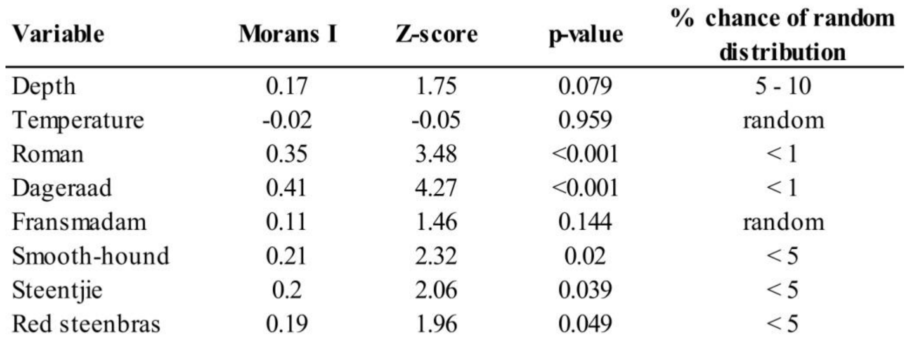


Figure 3.6: Correlograms depicting local Moran's *I* correlation indices for the variables (a) *depth* and (b) *temperature* at varying lag distances. Each point indicates the distance between sampling sites. The grey area indicates a Monte Carlo simulation of the range of expected correlation index values in the absence of autocorrelation.

Table 3.1: Global Moran's *I* values, and associated levels of significance, illustrating the average spatial autocorrelation of two environmental variables (*depth* and *temperature*) and the six most abundant species in the Tsitsikamma National Park marine protected area.



Variable	Morans I	Z-score	p-value	% chance of random distribution
Depth	0.17	1.75	0.079	5 - 10
Temperature	-0.02	-0.05	0.959	random
Roman	0.35	3.48	<0.001	< 1
Dageraad	0.41	4.27	<0.001	< 1
Fransmadam	0.11	1.46	0.144	random
Smooth-hound	0.21	2.32	0.02	< 5
Steentjie	0.2	2.06	0.039	< 5
Red steenbras	0.19	1.96	0.049	< 5

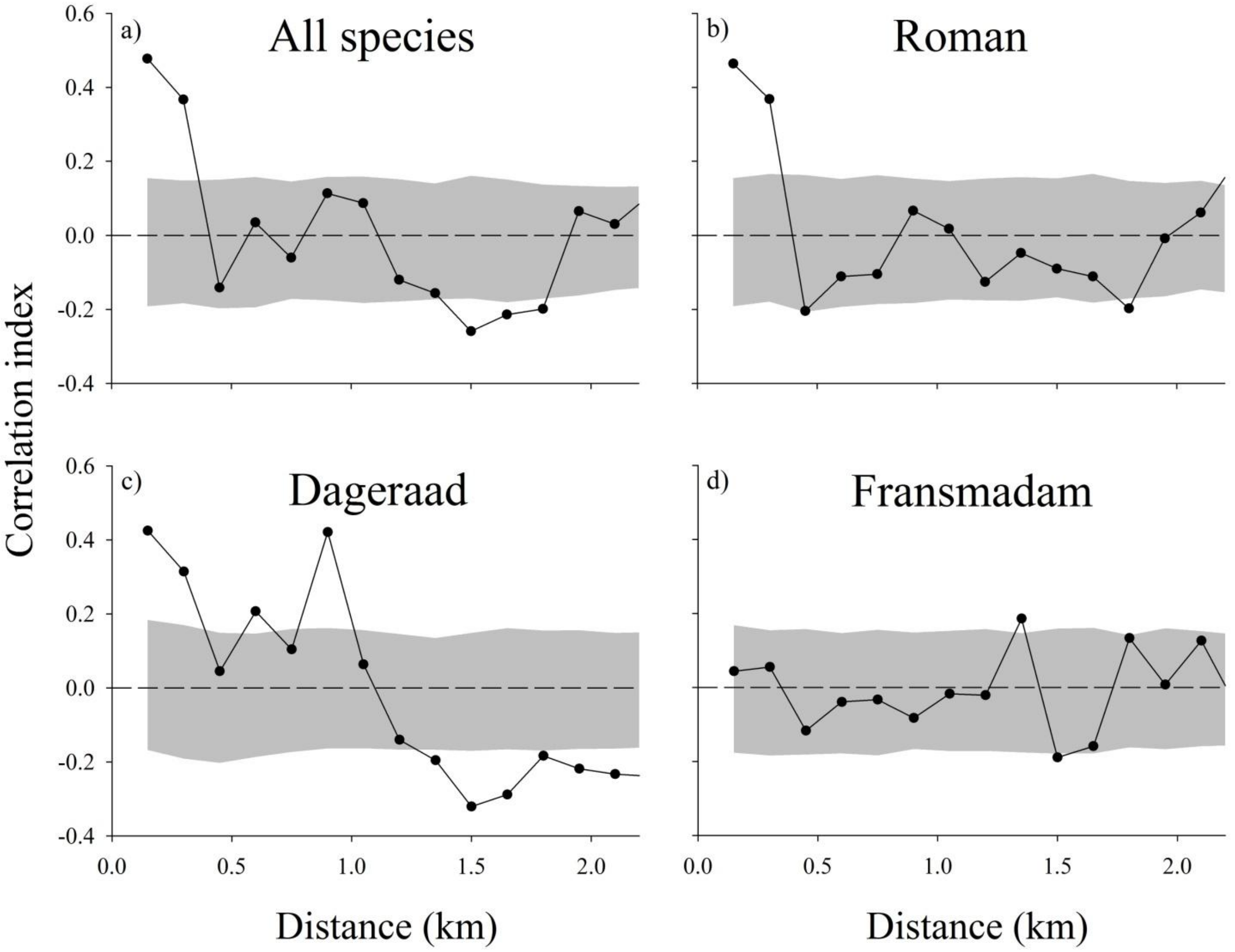


Figure 3.7: Correlograms depicting local Moran's *I* correlation indices for observed CPUE of (a) all species combined, (b) roman, (c) dageraad and (d) fransmadam at varying lag distances. Each point indicates the distance between compared sample sites. The grey area indicates a Monte Carlo simulation of the range of expected correlation indices in the absence of autocorrelation.

3.3.6 ACCOUNTING FOR SPATIAL AUTOCORRELATION

Dageraad data were found to have the highest degree of spatial autocorrelation of all the species analysed, and were therefore chosen as an example to display the effects of violating independence in predicitve models. Figure 3.8a illustrates dageraad CPUE predictions over the depth range based on a model that does not account for spatial depedence (GAM). Figure 3.8b illustrates the same data, but is based on a model that accounts for spatial dependence (GAMM). The GAM is clearly overfitted, as each high abundance area on the distribution map can be connected to the peaks in the predictive model at the corresponding depths. In contrast, the GAMM that accounts for spatial autocorrelation produces predictive estimates that are more indicative of a continuous variable such as *depth*.

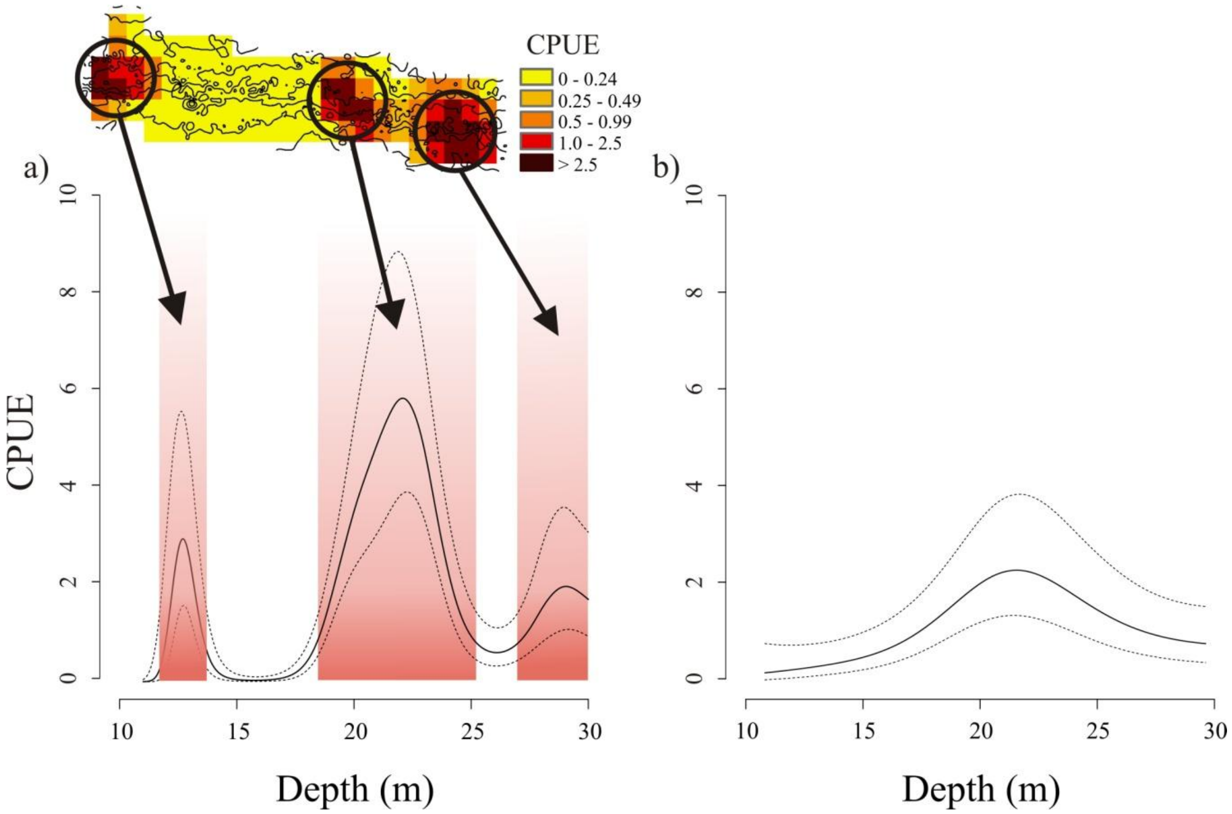


Figure 3.8: A comparison of predicted dageraad catch-per-unit-effort (CPUE) by *depth* based on two different models. The first model (a) is a GAM without a correlation structure, while the second model (b) is a GAMM with a spatial correlation structure incorporated as a random effect. The three areas of high dageraad CPUE in the distribution map (a) correspond to the peaks in predicted CPUE at those depths.

3.3.7 EFFECTS OF DEPTH AND TEMPERATURE ON ABUNDANCE

The effects of depth on fish abundance differed amongst the studied species (Figure 3.9), whereas an increase in temperature resulted in a linear increase in CPUE for all species analysed (Figure 3.10). The magnitude of the temperature effect on CPUE did, however, vary amongst species.

3.3.7.1 ROMAN

Temperature explained a significant proportion of the variation in roman CPUE data (*temperature*: $\chi^2 = 7.28$, $p = 0.007$), with mamixum CPUE predicted around 20°C. Roman CPUE was influenced by depth and peaked at 22 m; however, this was not significant (*depth:* $\chi^2 = 0.77$, $p = 0.38$). The interaction between temperature and depth was found to have a significant influence on CPUE, and more roman were caught in shallow water during periods of low temperature (*temperature~depth*: $\chi^2 = 0.53$, $p = 0.03$). Catch rates varied seasonally, with significantly more roman caught in winter than summer (*season*: $\chi^2 = 17.73$, $p < 0.0001$), however, the year in which sampling took place had no significant effect on roman CPUE (*year*: $\chi^2 = 0.77$, $p = 0.99$).

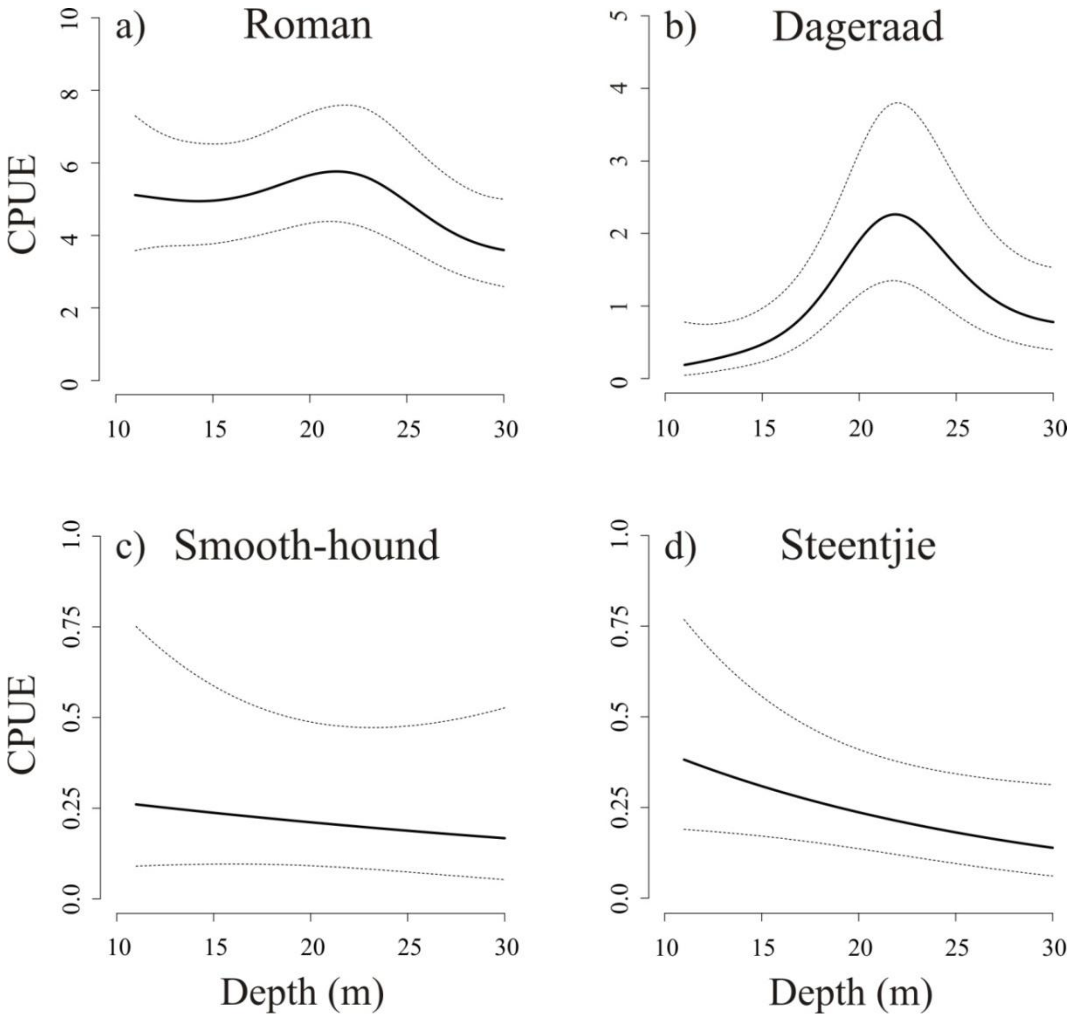


Figure 3.9: Predicted effects of the variable *depth* on catch-per-unit-effort (CPUE) for the four most abundant species; (a) roman, (b) dageraad, (c) smooth-hound and (d) steentjie. The dashed lines indicate the 95% confidence interval.

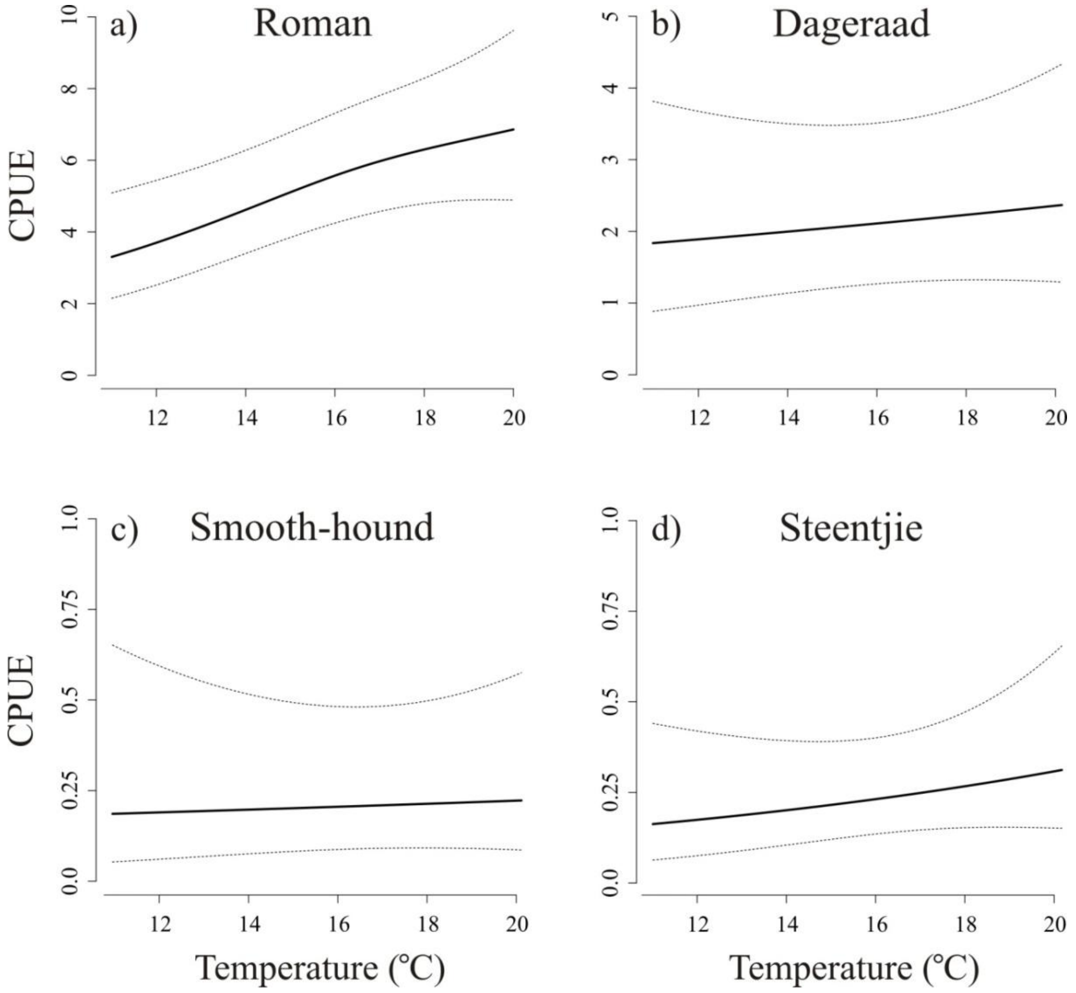


Figure 3.10: Predicted effects of the variable *temperature* (°C) on catch-per-unit-effort (CPUE) for the four most abundant species; (a) roman, (b) dageraad, (c) smooth-hound and (d) steentjie. The dashed lines indicate the 95% confidence interval.

3.3.7.2 DAGERAAD

Dageraad CPUE was significantly influenced by depth (*depth*:$\chi^2 = 5.23$, $p < 0.001$) with the maximum CPUE recorded at 22 m, declining rapidly at depths above or below this value. In contrast, temperature only had a minor positive influence on dageraad CPUE, which was linear but not significant (*temperature*: $\chi^2 = 0.35$, $p = 0.55$). Additionally, dageraad CPUE was higher in winter than summer but *season* remained an insignificant variable (*season*: $\chi^2 = 2.53$, $p = 0.11$). Surprisingly, dageraad CPUE had declined consistently since sampling started in 2007 at a level that was approximately significant (*year*: $\chi^2 = 3.18$, $p = 0.07$) as seen in Appendix 2.4.

3.3.7.3 SMOOTH-HOUND

Smooth-hound catch rates were positively correlated with temperature and negatively correlated with depth. Both of these relationships were linear in nature, but neither of them was significant (*depth*: $\chi^2 = 0.38$, $p = 0.54$; *temperature*: $\chi^2 = 0.07$, $p = 0.80$). Catch rates of smooth-hound were, however, significantly influenced by substrate, as sandy sites provided significantly higher CPUE than reef sites (*profile/class: sand*: $\chi^2 = 3.69$, $p = 0.001$). More smooth-hounds were caught in summer than winter, but this was not significant (*season*: $\chi^2 = 0.17$, $p = 0.86$). Annual trends suggest a decrease in the number of fish caught per year, but this again was not significant (*year*: $\chi^2 = 1.11$, $p = 0.27$).

3.3.7.4 STEENTJIE

Steentjie CPUE showed a positive linear correlation with temperature that was not significant (*temperature*: $\chi^2 = 0.96$, $p = 0.34$) and a negative correlation with depth that was approximately significant (*depth*: $\chi^2 = 3.88$, $p = 0.052$). Catch rates for steentjie were higher in winter than summer, but this was not significant (*season*: $\chi^2 = 1.39$, $p = 0.17$) and no significant annual trend was observed (*year*: $\chi^2 = 0.14$, $p = 0.89$).

3.4 DISCUSSION

3.4.1 SPATIAL DISTRIBUTION OF THE OBSERVED ICHTHYOFAUNA

Literature regarding the distribution of marine fishes in South Africa is largely restricted to three themes; the distribution of juveniles or larvae in the surf zone and estuarine environments (Harris et al. 1999, Vorwerk et al. 2003, Næsje et al. 2007), movement and geographical range studies based on tagging (Brouwer 2002, Cowley et al. 2002, Griffiths and Wilke 2002, Kerwath et al. 2007, Watt-Pringle et al. 2013, Maggs et al. 2013) and the use of fisheries-dependent data to describe the distribution of commercially important species (Badenhorst and Smale 1991; Barange et al. 1999; Cockcroft et al. 2008, Winker et al. 2013). Information on fish distribution within the TNP MPA is scarce (Buxton and Smale 1989), despite the numerous publications describing the area’s ichthyofaunal composition (Burger 1991; Buxton and Smale 1984; Hanekom 2011; Smith and Smith 1966; Smith 2006; Tilney et al. 1996; Wood et al. 2000; Bennett et al. 2009). This is also the first study in South Africa to utilize data from a LTM programme to describe the finer scale distribution of fish species employing CPUE as opposed to mark-recapture data. A standardized sampling approach that allowed for repetitive sampling of sites (Section 2.2.5) over eight years facilitated the description of the ichthyofaunal distribution within the study area of the TNP MPA. Additionally, a detailed understanding of the benthic profile and substrate is paramount in these types of analyses, and bathymetric data collection should be prioritized in subtidal LTM programmes. The data requirements for such a spatial study are large, and despite several years of data, detailed analyses were only possible for the five most abundant species.

Observed species distribution patterns in the study area were not random. This is expected as randomness implies an absence of behaviour, which is unlikely according to fundamental evolutionary principles (Fortin and Dale 2005, Planque et al. 2011, Hamylton 2013). Evidence of the non-random distribution was presented in the form of the categorization (MRT analysis) of communities into four geographically unique groups, as well as the significant species-specific autocorrelation tests. The high degree of spatial structuring within the MPA's ichthyofauna is illustrated by the fact that the most prolific and widespread species, roman, was found to have significant spatial dependence (Moran's *I*, $p<0.001$) despite constituting 61% of the total catch and being caught at 74% of the sites sampled.

Multivariate regression trees split the sampling area into four distinct geographical groups. Group two contained the majority of the sample sites and was dominated by four sparid species, namely roman, dageraad, fransmadam and steentjie. This group comprised sites with a depth of less than 20 m and embodies the 'typical' ichthyofauna of the TNP study area. A clear community shift occurred at latitudes greater than 34.03 degrees south, which is undoubtedly a result of the co-linear variable *depth*. At depths greater than 25 m the ichthyofauna diversified, and the prevalence of elasmobranchs increased. Despite the higher diversity at deeper sites, overall CPUE decreased at depths greater than 22 m, with the exception of group four, which was unique in that it had the lowest diversity yet consistently produced the highest catch rates due to the dominance of 'highly catchable' roman and dageraad. This area consisted of deep (>20 m) high profile reef around which the large sparids congregated. Red steenbras (*Petrus rupestris*) and red stumpnose (*Chrysoblephus gibbiceps*) were often caught here, but their presence was overshadowed by the other two prolific sparids, roman and dageraad. Group three consisted of only four sampling sites yet possessed the highest group diversity (seven species). The portrayed high fish diversity in this area is misleading, as the observed 'diversity' is a result of low catch rates at these sites, whereby any fish caught contributed to a high proportion (greater than the stipulated 3% in the analysis) of the overall catch. Group one consisted entirely of sandy sites and was dominated by species such as smooth-hound and bluefin gurnard. Unsurprisingly, sites in this group had the lowest average catch rates of the entire sampling area.

3.4.2 THE ROLE OF HABITAT IN ICHTHYOFAUNAL DISTRIBUTION

Ecologists study spatial patterns to infer the existence of underlying processes that influence species distributions, such as movement or responses to environmental heterogeneity. Spatial structure may indicate intraspecific and interspecific interactions such as competition, predation, and reproduction, or be driven by environmental heterogeneity of variables such as food availability (Fortin and Dale 2005). Understanding the role of each of these possible variables on species distribution would require an exceptionally in-depth study that is far beyond the scope of this thesis. As such, this study was limited to two fundamental questions: (i) what is the role of habitat in species distribution, and (ii) can fine scale spatial analysis explain the influence that 'missing variables' have on species distribution? The latter question will be addressed later in the discussion.

The measurements of benthic habitat were relatively rudimentary and were confined to substrate type and profile. These were combined with *in situ* depth and temperature measurements, which have been shown to influence the species-specific fish abundance in the Tsitsikamma MPA (Buxton and Smale 1989, Smith 2006, Bennett 2008) and were therefore considered 'habitat' variables. Substrate type had the most influence on species distribution. Specifically, sparids were found exclusively on reef whereas smooth-hounds were predominantly caught on sand. Proximity to reef seemingly played a role in prevalence of elasmobranchs, as sandy sites that were adjacent to reef were favoured. This is presumably due to sharks making foraging excursions onto the reef, as their general diet preferences would suggest (Heemstra and Heemstra 2004, Mann 2013). Substrate type does, however, lack stability in areas of reef-sand transition or in close proximity to rivers, as sediment deposition is a dynamic process. This was noted at sites in the south-eastern section of the sampling area that were categorized as 'sand', but produced abnormally large positive residuals when modelling reef associated species. Ground-truthing these sites using stereo-BRUVs camera systems (Section 2.2.3) revealed them as hard substrate sites, which were presumably once covered by sediment, originating from the nearby Storms River. Caution must therefore be applied when using substrate type from historic maps as a categorical predictor in LTM, and regular ground-truthing of sample sites is recommended.

Depth undoubtedly had an effect on fish community structure, but in most cases its influence was found to be exaggerated by spatial autocorrelation (Appendix 3.2). Once autocorrelation was accounted for, depth remained a significant predictor only for dageraad. The fairly narrow depth range of 10–30 m in the study area is likely to represent suitable habitat for the majority of the abundant subtidal species in the TNP MPA and therefore influence of depth on distribution was less when compared to other variables. However, a distinct contrast is noticeable when analysing shore angling (<10 m) data collected from a different site within the TNP MPA by researchers between 1998–2005 (James et al. 2012). In their study the five most abundant species, in order, were blacktail (*Diplodus capensis*), galjoen (*Dichistius capensis*), fransmadam, black musselcracker (*Cymatoceps nasutus*) and roman. Neither galjoen nor black musselcracker were ever caught in my study, suggesting a complete shift in dominant species over a surprisingly short depth range (0–10 m). Consequently, it must be noted that the optimal predicted depth for species analysed in my study is limited to the depth within the sampling area (10–30 m), and species such as dageraad may have optimal depths greater than 30 m.

In contrast to depth, an increase in temperature generally resulted in an increase in roman CPUE once autocorrelation had been taken into account. In addition, the effect of the interaction term *depth-temperature* on roman CPUE was significant. This could be related to frequently occurring upwelling events, which cause sudden and drastic decreases in water temperature leading to the formation of distinct thermoclines (Schumann 1999). Sampling during such an event produces significantly lower roman catch rates, particularly at depths below the thermocline where the water is colder. These findings are comparable to those of Buxton and Smale (1989), who noted that during upwelling events in the TNP MPA high concentrations of fish can be found around pinnacles that protrude above the thermocline.

The TNP is regarded as the transition zone between the warm Indian Ocean and cold Atlantic Ocean, and species that are endemic to the area generally have a wide temperature tolerance range (Heemstra and Heemstra 2004). However, sampling rarely occurred beyond the 10–20°C range to avoid biases caused by extreme temperature conditions.

3.4.3 USING SPATIAL STRUCTURE AS A SOURCE OF ECOLOGICAL INFORMATION

Models relating habitat characteristics to community structure are generally limited to answering two questions: (i) how well is the distribution of a species explained by a set of predictor variables and, (ii) which predictor variables are irrelevant in the sense that they fail to strengthen the explanatory power of the model? In this study reef profile had little effect on the distribution and catch rate of dageraad. However, analysis of model residuals for dageraad revealed a high level of spatial structuring, indicating that the model may either be 'missing' an important predictor variable or that processes other than the measured environmental factors may influence distribution (Fortin and Dale 2005, McIntire and Fajardo 2009, Dray et al. 2012). Here, the 'missing' variable is likely due to the inability to accurately define profile as an environmental variable as it is limited to two broad categories within the reef subset: high and low (Section 2.2.3). This grouping is presumably too rudimentary and therefore inappropriate to accurately describe species-specific associations with reef profile, if they were to exist. In the case of dageraad, the 'random forest' analysis indicated location to be the most important variable in predicting species distribution. Clearly, latitude and longitude coordinates have no direct influence on fish within the small spatial extent of this study area, and therefore are a proxy for a combination of unmeasured environmental effects at that point in time and space. In the case of dageraad, the co-ordinates corresponded to areas of very high profile when superimposed with bathymetry data. The constraint is that the category 'high profile' is too broad and possibly includes areas that would have been better described as 'medium profile'. As a result, the variable *profile* was not a significant predictor of dageraad CPUE. This inability to accurately measure all environmental variables highlights two fundamental outcomes of this study. The first is to reiterate the value of obtaining accurate bathymetric information of a study area prior to analyses, and the second defines the crux of this study by emphasizing the importance of spatial analysis as source of ecological information in LTM programmes. In accordance, Dray et al. (2012) state that 'beyond the standard nuisance viewpoint, an alternative and more promising perspective is that describing spatial structures in data can help us challenge our models and improve our understanding of species and community distributions'. Without spatial structure the ecological character of any community would exhibit a limited geographic expression and appear completely random; with it communities exhibit spatial patterns, which provide the fundamental information from which ecologists gather knowledge (Hamylton 2013).

3.4.4 ACCOUNTING FOR SPATIAL DEPENDENCE WHEN MODELLING DISTRIBUTION

The need to integrate ecological concepts and statistical theory is one of the most challenging issues facing ecologists (Fortin and Dale 2005). The majority of statistical methods assume spatial stationarity, i.e., spatial autocorrelation and the effects of environmental variables are taken to be constant across the sampled area (Osborne et al. 2007). Yet this is rarely the case in ecological field studies. Acknowledging the presence of interactions between communities of neighbouring sample sites, or non-stationarity, advocates a need for a model with a spatially dependent covariance structure within the residuals (Cliff and Ord 1981). Results from this study reiterate this need, as model predictions and the hierarchy of parameter importance differed significantly between models with and without a spatial covariance structure (Appendix 3.2).

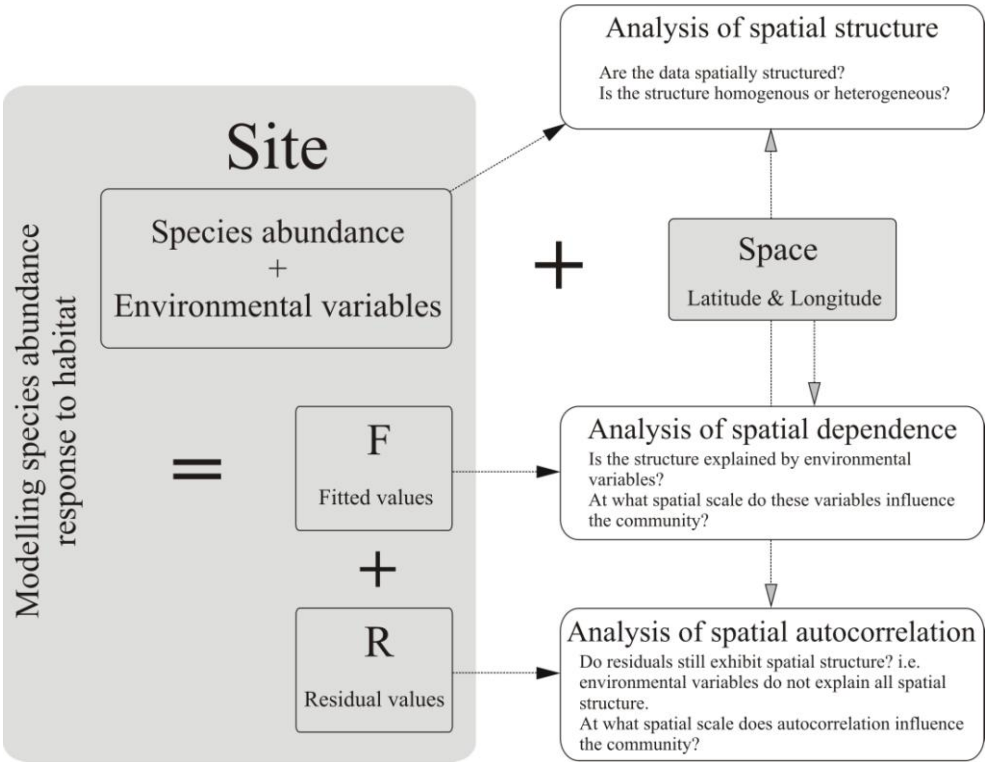


Figure 3.11: A conceptual diagram illustrating the steps followed when investigating spatial structure in ecological community data. The diagram highlights the relationships between data, questions and statistical models applied (Adapted from Dray et al. 2012).

Depth, which was highly autocorrelated, had far less influence on CPUE when spatial autocorrelation was incorporated into the model. In contrast, the importance of temperature, which was not autocorrelated, increased substantially for roman. This is the consequence of a type I error, which manifests in a tendency to indicate significant habitat affinities even if the environmental variable in question is not actually a significant driver of species abundance (Dormann et al. 2007, Dray et al. 2012). By introducing a covariance structure to a model (Figure 3.11), this error is accounted for to some extent, increasing the ability of the model to filter out 'noise' and describe actual environmental-biotic relationships.

3.4.5 IMPORTANCE OF SPATIAL ANALYSES IN THE TSITSIKAMMA NATIONAL PARK LONG-TERM MONITORING PROGRAMME

The motivations for spatial analyses are diverse, but the common thread is the quantification of spatial patterns (Dungan et al. 2002, Fortin and Dale 2005, Dray et al. 2012, Hamylton 2013). This study revealed the TNP MPA ichthyofaunal distribution to be patchy yet ‘locationally’ consistent over time. Additionally, ‘random forest’ analyses confirmed that spatial variables were significantly more influential than temporal variables in predictive abundance models. It therefore seems intuitive that a complete understanding of species-specific distribution is fundamental *a priori* information when assessing population variability over time, which is the primary objective of LTM in the TNP MPA. The species distribution maps will form part of the integral baseline information against which future assessments can be compared. It is hoped this study will contribute to the increasingly emergent field of spatial analysis in ecology (Beale et al. 2010) by emphasizing its application in LTM programmes.

A fundamental challenge of LTM programmes around the world is their sustainability. These programmes are expensive (Bernard 2013) and generally experience funding limitations, especially in developing countries such as South Africa. It is vitally important that managers and scientists optimize available time and money, which can be done by streamlining the sampling protocol. In the case of the TNP MPA LTM, the spatial analysis identified that there may be redundant data due to the sample site dimensions being too small (150 × 150 m), essentially creating pseudo-replicates amongst adjacent sites. Without previous spatial data, selecting an optimal sampling site size when implementing the LTM programme was merely an estimate, and the precautionary approach should be applied. These dimensions were initially implemented so as to provide the finest scale analysis possible, and were based on accounting for GPS error and ‘play’ on the anchor line so as to ensure sampling never occurred in adjacent sites through human error. Local Moran I indices for roman and dageraad reveal that strong autocorrelation occurred within two adjacent cells (375 m radius) of the chosen sample site, and the dataset therefore contains redundant data. In retrospect, these site dimensions were too small, and based on species-specific local autocorrelation indices, could be at least doubled in size (300 × 300 m). This would mean a two-fold increase in the number of site replications possible with the same amount of effort, further optimizing time and money allocated to the LTM programme. This finding emphasizes a key premise of this thesis, which is the recognition that flexibility is the key to the sustainability of LTM programmes. Such methodological adjustments are essential to all LTM programmes to ensure the optimal use of resources while constantly improving data quality.

3.5 CONCLUSIONS

This study illustrated the potential of fine scale spatial analyses to provide insight to subtidal ichthyofaunal ecology. The shift in viewing spatial dependency as a statistical obstacle to a source of ecological information has created a new avenue of data inference, which has been shown to be effective in assessing the influence of environmental variables and habitat on fish abundance. The statistical methods explored to account for spatial autocorrelation are applicable to a wide range of LTM programmes in the marine environment, and elsewhere, and it is recommended that they are applied wherever spatial dependencies exist. The study emphasized the need for accurate *a priori* bathymetric information for LTM programmes in subtidal habitats, as fish communities are undoubtedly linked to localized habitat. Analysing spatial autocorrelation was shown to be important for optimizing sampling strategies by quantifying the area in which redundant data occurs, which then can be used to reassess the optimal size of sample sites. As monitoring continues to move toward ecosystem-based models, future work should focus on the spatial analysis of invertebrate communities as this is likely to influence ichthyofaunal distributions.

3.6 APPENDICES

Appendix 3.1: Summary of species distribution GAMs for the five most abundant species, as well as a GAM containing all the species pooled together.

	All species		Roman		Dageraad		Fransmadam		Smooth-hound		Steentjie	
	df/edf[1]	χ^2	*df/edf*	χ^2	*df/edf*	χ^2	*df/edf*	χ^2	*df/edf*	χ^2	*df/edf*	χ^2
Year	6	1.30	6	0.38	6	3.03**	6	1.64	6	1.85	6	0.69
Season	1	2.15*	1	3.65***	1	2.53*	1	1.27	1	0.33	1	1.44
s(Lat,Long)	13.69	5.97***	13.91	6.39***	13.92	7.75***	13.28	2.46**	12.85	6.96***	13.51	4.22***
% explained by model	37.6		46.0		61.7		20.5		38.0		29.9	
Phi (ϕ) [3]	3.78		3.75		2.41		1.91		1.80		1.63	

1: df/edf = degrees of freedom for the parametric coefficients and estimated degrees of freedom for the smooth terms [s(covariate)]
2: χ^2, significance level: "***"<0.001, "**"<0.01, "*"<0.05
3: Phi (ϕ) = overdisersion parameter

Appendix 3.2: Summary of the effects of environmental variables on species-specific catch-per-unit-effort (CPUE). Shaded columns contain results from GAMs without spatial components, and unshaded columns contain results from GAMMs with spatial autocorrelation accounted for by applying a correlation structure to the model residuals.

	Roman				Dageraad				Smooth-hound				Steentjie			
	df/edf[1]	χ^2	*df/edf*	F[3]	*df/edf*	χ^2	*df/edf*	F	*df/edf*	χ^2	*df/edf*	F	*df/edf*	χ^2	*df/edf*	F
Year	1	11.13***	1	<0.01	1	52.21***	1	3.18	1	1.23	1	1.23	1	0.38	1	0.02
Season	1	18.12***	1	17.73***	1	1.58	1	2.53	1	0.02	1	0.03	1	0.98	1	1.93
Depth	8.89	102***	1	0.77	8.99	62.87***	3.61	5.23***	8.95	41.84***	1	0.38	8.94	22.04**	1	3.82*
Temperature	1	0.92	1	7.28**	3.79	25.07***	1	0.35	4	40.17***	1	0.07	3.97	4.33	1	0.96
Depth~temperature	12	112.77***	12	0.53*	12	83.14***	12	<0.01	12	45.74***	12	<0.01	12	7.47	12	<0.01
Profile~substrate	-	-	-	-	-	-	-	-	2	23.37***	2	6.9***	-	-	-	-
% explained by model	28.4		-		43.5		-		46.9		-		24.4		-	

1: df/edf = degrees of freedom for the parametric coefficients and estimated degrees of freedom for the smooth terms [s(covariate)]
2: χ^2, significance level: "***"<0.001, "**"<0.01, "*"<0.05
3: F-statistic, significance level: "***"<0.001, "**"<0.01, "*"<0.05

CHAPTER FOUR

TEMPORAL TRENDS IN THE SUBTIDAL ICHTHYOFAUNA OF THE TSITSIKAMMA NATIONAL PARK MARINE PROTECTED AREA

4.1 INTRODUCTION

4.1.1 LONG-TERM MONITORING EMERGES FROM GLOBAL BIODIVERSITY LOSS

It is widely acknowledged that the current global ecological trend is one of biodiversity loss (UNEP 2002, Pereira and Cooper 2006, Hooper et al. 2012), with mitigation targets rarely being met (Butchart et al. 2010). Studies suggest that biodiversity loss is altering key processes on which the global ecosystem depends (Cardinale et al. 2012, Hooper et al. 2012), and that further species loss will accelerate ecosystem degradation (Hooper et al. 2012). Amongst these claims lies an intrinsic vagueness that often borders on complete uncertainty (Araújo et al. 2005, Araújo and Rahbek 2006, Botkin et al. 2007, Cardinale et al. 2012). Regrettably, this is the nature of long-term predictions based on data with a temporal scale that is a fraction of the forecasted prediction. However ecology, and subsequent ecological monitoring, is a relatively young discipline and these predictions are likely to gain precision over time. Paramount to striving for predictive accuracy is the global implementation of long-term monitoring (LTM) programmes (Parr et al. 2003, Lindenmayer and Likens 2009, Magurran et al. 2010), to accumulate data on the abundance and distribution of species in space and time (Magurran et al. 2010). Ideally, such data will be used to track ecological changes indefinitely, such that future predictions will become mere fractional extensions of long-term trends as opposed to the current theme of over-extended estimations.

Lindenmayer and Likens (2009) define LTM as a process where ‘repeated field-based empirical measurements are collected continuously for at least 10 years’. This definition seems inadequately broad and the specific temporal scale of 10 years is abitrary as this timeframe should be heavily dependant on the longevity of the organisms of interest. However, the definition does highlight the need for ‘repeated field-based empirical measurements’, which provide the cornerstone of ecological monitoring. Generally, the objective of LTM is to determine trends in resource characteristics over the largest permissible temporal scale. As such, LTM assesses the dynamics of the resource and not just the current state (Block et al. 2001), linking deviations from expected trends to possible influential variables. As long-term datasets grow cumulatively, so do their predictive power and ability to provide accurate inferences.

Testament to the current concerns over global biodiversity trends lies in the international commitment to ecological LTM programmes. Several international agreements (CBD, CITES, RAMSAR, ICCAT, UNESCO, etc.) have been signed by numerous countries as a commitment to biodiversity and species conservation, with the majority of nations insisting on quantitative accountability through LTM programmes. Nationally, South African National Parks (SANParks) is obligated to monitor marine protected areas (MPAs) as specified in the National Environmental Management: Protected Areas Act (DEA 2004b), and requirements for biodiversity management are set out in the National Environmental

Management: Biodiversity Act (DEA 2004a). Under these acts, South Africa has created initiatives such as the National Biodiversity Strategy and Action Plan and the National Biodiversity Framework (DEAT 2006). These initiatives are fulfilled through dedicated research institutes, such as the South African Environmental Observation Network (SAEON) and the South African National Biodiversity Institute (SANBI), whose mandates focus on assessing temporal biodiversity trends through LTM.

4.1.2 IMPORTANCE OF LONG-TERM MONITORING IN MARINE PROTECTED AREAS

Magurran et al. (2010) suggest there are two key questions concerning the temporal component of ecological LTM. The first question is invariably linked to the total measurable change in the observed ecosystem over the monitoring period. The second question, however, is more complex and involves partitioning this observed change by causal effect, i.e., natural variability or anthropogenic impact/experimental treatment (Magurran et al. 2010). The separation of these causal effects depends highly on the ability to define baseline conditions and natural variability (Parr et al. 2003). Long-term monitoring studies in MPAs partially alleviate this difficulty as they provide an opportunity to assess and quantify natural variability, stability and persistence of resources in relatively undisturbed communities (Attwood et al. 1997, Vos et al. 2000, James et al. 2012). This information can be used to define the extent of change in exploited areas that lack natural baseline data (Pauly 1995, Barrett et al. 2007, James et al. 2012). Barrett et al. (2007) emphasize the value of LTM in MPAs as they provide ‘reference areas for understanding the effects of fishing on coastal species and systems, and placing these in the context of natural environmental change’.

In addition to providing baseline data, well established MPAs provide researchers with a unique opportunity to study ecosystems that are fairly free of anthropogenic influences. Fishing and its knock-on effects (such as indirect effects and habitat destruction) are widely recognized as the most significant anthropogenic influences on marine systems (Jackson et al. 2001, Halpern et al. 2008), with their obvious impact being the reduction in abundance of target species (Pauly et al. 1998, 2002, Jennings 1999). However, there are cascading ecosystem effects (Scheffer et al. 2005, Myers et al. 2007), which are far less obvious, and drastically increase the complexity of direct comparisons. Varying magnitudes of fishing effort over a range of spatial and temporal scales add further variability and data complexity (Barrett et al. 2007). In contrast, long-term data originating from established MPAs possesses relative consistency, quality and simplicity. These are assets that also compel statistical testing and model formulation, providing researchers with the best opportunity to assess the performance of statistical techniques.

4.1.3 IMPLICATIONS OF LONG-TERM MONITORING ON FISHERIES MANAGEMENT

The importance of translating information gathered from LTM programmes into tangible improvements in management strategies is emphasized in Elzinga et al.'s (2001) definition of monitoring: ‘the collection and analysis of repeated observations or measurements to evaluate changes in condition and progress toward meeting a conservation or management objective’. Ideally, scientific knowledge should be considered provisional and management a process of continuous learning through experimentation and subsequent adaptation (Grumbine 1994). Lindenmayer and Likens (2009) strongly oppose the implementation of LTM programmes that are not driven by management needs, stating monitoring ‘should elicit greater engagement by resource managers by ensuring that the questions posed pass the test of management relevance’. However, the importance of LTM data in providing context for short-term experiments and observations should not be overlooked (Lovett et al. 2007). In reality these two approaches to gathering ecological information cannot be considered mutually exclusive under an adaptive management framework, as both play important roles in biodiversity conservation. Ideally, long- and short-term approaches should be standardized and complementary to increase depth of insight and efficiency.

4.1.4 STUDY AIM

This study was conducted as part of SAEON and SANPark’s mandate to implement a LTM programme in the Tsitsikamma National Park (TNP) MPA, focusing on the subtidal ichthyofauna. The study had three primary aims: (i) the analysis of several years of data to assess temporal trends in diversity, abundance and size distribution, (ii) to provide baseline data from a well-established MPA (established in 1964; 320 km^2), and (iii) to optimize statistical methods for analysing LTM data. To realize these aims, the influence of time on the ichthyofauna was assessed thoroughly, as this is the cornerstone of LTM. Multivariate analyses provided insight into annual variability in community structure mainly through the use of graphics, ordination and PERMANOVA (Permutational Multivariate Analysis of Variance) tests. Analyses in Chapter 3 indicated a high level of spatial autocorrelation within the data. As such, predictions of annual catch-per-unit-effort (CPUE) generated from Generalized Additive Models (GAMs) and Mixed Models (GAMMs) were compared to quantify spatial autocorrelation’s influence on temporal data. Additionally, a novel Kernel Density Estimate (KDE) technique was applied to assess annual length-frequency variability in an attempt to overcome the limitations of mean length comparisons.

4.1.5 STUDY OBJECTIVES

The objectives of this study include:

- Quantify temporal variability in the TNP MPA’s ichthyofauna
- Illustrate which species have the most influence on ichthyofauna variability
- Describe species-specific temporal abundance (CPUE) trends
- Quantify the influence of spatial autocorrelation on temporal trends
- Investigate annual variability in length-frequency distributions of abundant species

4.2 METHODS AND MATERIALS

4.2.1 DATA COLLECTION

The research was conducted in the TNP MPA (Section 2.1) using angling as the method of data collection (Section 2.2.2). Sample site selection was based on a stratified random scheme described in Section 2.2.5. In brief, it involved sampling 32 sites per year (16 per biannual sampling trip), spread equally among the four stratified habitats.

4.2.1.1 ENVIRONMENTAL VARIABLES

Water *temperature* (average bottom temperature recorded during angling at a site) was recorded using a submersible temperature logger (HOBO Temperature Logger - Onset Computer Cooperation) attached to the anchor line a meter above a three meter anchor chain. Site *depth* was recorded off the boat's echo sounder. Bottom type and reef *substrate/profile* were inferred from a bathymetric map and the echo sounder colour display (Figure 2.4).

4.2.2 DATA ANALYSIS

4.2.2.1 MULTIVARIATE COMMUNITY ANALYSIS

To visualize seasonal and diurnal differences in community structure, ranked species abundance (dominance) curves were produced for the categorical temporal variables *season* (summer/winter) and *time of day* (morning/midday/afternoon), respectively. Species were ranked in decreasing order of abundance expressed as a percentage of the total abundance of all taxa. Log-transformation of the x-axis enabled a better visualization of the more common species (Clarke and Warwick 1994). One-way ANOVAs were performed to determine if there were any differences in mean Shannon–Wiener index (Shannon 2001) and mean CPUE (fish.angler^{-1}hour^{-1}), respectively, with regard to *season* and *time of day*. Irregular distribution of samples within the categorical variable *time of day* rendered a two-way ANOVA inappropriate.

Non-metric Multidimensional Scaling (nMDS) based on Bray–Curtis log-transformed data (Field et al. 1982, Clarke and Ainsworth 1993) was used to evaluate the annual variability in community assemblage, where distances between points are directly proportional to assemblage dissimilarity. To condense community variability into fewer dimensions for ease of analysis, a Principle Component Analysis (PCA) was derived from the Bray–Curtis log-transformed data. This enabled the identification of species that had the most influence on community assemblage annual variability.

Anderson's (2001) Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to assess the response of community composition to multiple simultaneous temporal variables, including *year*, *season* and *time of day*. In addition, the spatial variable (*profile/substrate*) was included to quantify its influence on community composition. PERMANOVA is a multi-level routine that first calculates the distances between each pair of sampling units, which are then stored in a distance matrix. The matrix is used to calculate the between group Euclidean sum of squares (SS_T) using:

$$SS_T = \frac{1}{N}\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} d_{ij}^2 \qquad \text{(Eq. 4.1)}$$

and the within group Euclidean sum of squares (SS_W) using:

$$SS_W = \frac{1}{n}\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} d_{ij}^2 \varepsilon_{ij} \qquad \text{(Eq. 4.2)}$$

where d_{ij} is the distance between observations i and j, N is the total number of observations between groups and n is the total number of observations within a group. Finally, the among group sum of squares (SS_A) is calculated through simple arithmetic as $SS_A = SS_T - SS_W$ (Anderson 2001). Significance is calculated using a permutation test with the following F-statistic:

$$F = \frac{SS_A/(a-1)}{SS_W/(N-a)} \qquad \text{(Eq. 4.3)}$$

where (a-1) are the degrees of freedom associated with the variable and (N-a) are the residual degrees of freedom (Anderson 2001).

The permutation test randomly shuffles treatment labels on the observed data points n_{boot} times and calculates a new F-statistic value for each reshuffle, denoted as F^π. The underlying assumption is that if treatment effects were negligible, the actual F-statistic would be similar to average F^π value obtained through random shuffling of treatment labels (Anderson and Legendre 1999, Anderson 2001). If, however, the effect of treatment was significant then the value of the actual F-statistic would appear large relative to the distribution of F^π values obtained under permutation. The calculation of a p-value is based on the ratio of F^π values that are greater than or equal to the value of the actual F-statistic as a proportion of the number of permutations executed (n_{boot}), such that:

$$p = \frac{No.of\, F^{\pi} \geq F}{n_{boot}} \qquad \text{(Eq. 4.4)}$$

The PERMANOVA routine was run in the R programming environment using the ‘adonis’ function in the ‘vegan’ package.

4.2.2.2 TEMPORAL ABUNDANCE PREDICTORS

Exploratory analysis of the effects that the two main temporal variables (*year* and *season*) had on CPUE of the five most abundant species (roman, dageraad, fransmadam, steentjie and smooth-hound) revealed these relationships to be non-linear. Subsequently, Generalized Additive Models (GAMs) of the following form were fitted:

$$CPUE = year + season + s(temperature) + \varepsilon \qquad \text{(Eq. 4.5)}$$

where *s*() denotes the smoother functions and ε the associated model residuals. For all GAMs the discrete variables (*year* and *season*) were included as parametric coefficients, while the continuous variable (*temperature*) was fitted using a 'thin plate regression spline' smoother (Wood 2006). *Time of day* was excluded in this analysis as the number of samples collected in the afternoon were disproportionally small. As the response CPUE was expressed in counts, models were run using a Poisson distribution with a log-link function. Each model was assessed for over-dispersion, and where applicable quasi-Poisson distributions were applied. The smoothness selection criterion was based on restricted maximum likelihood (REML).

The exploratory GAM framework ignores the strong spatial structuring identified in Chapter 3, Section 3.3.4. To account for this, Generalized Additive Mixed Models (GAMMs) of the following form were applied:

$$CPUE = year + season + s(temperature) + s(lat, long) + \varepsilon \qquad \text{(Eq. 4.6)}$$

with a correlation structure embedded in the model residuals (Zuur et al. 2009). The models' correlation structure assumed one of three forms (exponential, spherical or Gaussian) describe by Equations 3.4 – 3.6 (Section 3.2.2.6), which was determined by minimizing the Akaike Information Criterion (AIC) for each species model (Zuur et al. 2009). Predictions for the effects of the temporal variables *year* and *season* on the expected CPUE (± 95% CI) were calculated for the five most abundant species.

4.2.2.3 SIZE COMPOSITION

Kernel density estimates (KDEs) were performed on length-frequency data to assess annual length variability for each species. A KDE is a non-parametric density estimator of a random variable that, unlike conventional density estimates, overcomes the problem of assigning frequency data into discrete bins by smoothing out the contribution of each observed data point over the local neighbourhood of that data point (Silverman 1986, Hwang et al. 1994). It does this through estimating the shape of the distribution *f(x)* using the following:

$$\hat{f}(x) = \frac{1}{nh}\sum_{i=1}^{n} K\left(\frac{\hat{x} - x_i}{h}\right) \qquad \text{(Eq. 4.7)}$$

where *K* is the kernel, *h* is the smoothing parameter called the bandwidth and *n* is the number of observations. The bandwidth of the kernel is a free parameter ($h > 0$) that exhibits a strong influence of the resulting estimate (Sheather and Jones 1991, Liao et al. 2010). In this case, the optimal bandwidths for each year were calculated using the ‘plug in’ method proposed by Shearer and Jones (1991) from the ‘dpik’ function in the R package ‘Kernsmooth’ (Wand 2014). Kernel densities were fitted using the ‘sm.density’ function in the R package ‘sm’ (Bowman and Azzalini 2010).

Significance of annual variability was tested by comparing KDEs for each year against a null model using a permutation test, as described by Langlois et al. (2012a). Firstly, the geometric mean of each year’s KDE bandwidth was calculated for each species to avoid any ‘weighting’ effect on any particular year due to differences in sample sizes between the years (Langlois et al. 2012a). This mean bandwidth was then used as the null model, which is a KDE representation of the length-frequency distribution from all the years combined. The difference between the observed KDEs of each year to the expected KDE of null model was calculated using sum-of-squares, such that:

$$\mathrm{SSQ}_y = \sum_i (\mathrm{KDE}_{i,y} - \mathrm{KDE}_{i,\bar{y}})^2 \qquad \text{(Eq. 4.8)}$$

where $\mathrm{KDE}_{i,y}$ is the kernel density estimate for length bin *i* and year *y* and $\mathrm{KDE}_{i,\bar{y}}$ is the corresponding representation of kernel density estimates in length bin *i* averaged across all years ($\bar{y}$).

To enable a permutation test, an iteration process was employed that randomly resampled length-frequency observations without replacement and subsequently assigned the resampled data to a year. Kernel densities were then fitted to each resampled year and the KDEs compared to the KDE of null model for a total of 10,000 iterations (n_{boot} = 10,000) to provide a total of 10,000 permuted sum-of-square values (SSQ_y^{π}) using Equation 4.8.

The *p*-values for each year were calculated analogously to Equation 4.4, such that:

$$p_y = \frac{\text{No.of } \mathrm{SSQ}_y^{\pi} \geq \mathrm{SSQ}_y}{n_{boot}} \qquad \text{(Eq. 4.9)}$$

where SSQ_y^{π} is the multiple permutations of SSQ_y calculated during each of n_{boot} iterations. Again, the underlying assumption of the permutation test is that if the effect of year on size structure was negligible, the observed sum-of-squares of KDEs (SSQ_y) would be similar to average sum-of-squares value (SSQ_y^{π}) obtained through random shuffling of annual length-frequency data.

Significant annual deviations from the null model were indicated through *p*-values; however, the length ‘regions’ within each length-frequency distribution that were responsible for these significant deviations could only be represented visually. This was done by producing a plot of the null model (± SE) using the ‘sm.density.compare’ function, upon which the observed KDEs were overlaid (Langlois et al. 2012a). These results were compared to one-way ANOVAs and subsequent Tukey’s posthoc, as well as Kolmogorov–Smirnov tests, which are traditional methods of assessing length variability. These traditional methods treat fish length as a normal response to the categorical variable *year*.

4.3 RESULTS

4.3.1 ICHTHYOFAUNA COMPOSITION

There was negligible seasonal effect on both ichthyofaunal diversity (Figure 4.1a) and community composition (Table 4.1), with the exception that more roman were caught in winter than summer (species rank 1: summer - 55%, winter - 68%). This influenced overall CPUE considerably (Appendix 4.2), resulting in winter sampling having a significantly higher CPUE than sampling during summer (t = 6.32, df = 1, p = 0.013). Results from the PERMANOVA demonstrate that grouping of samples by *season* was significant (Table 4.1); however, the low R^2 value indicates that only 1.3% of the variability in community composition can be explained by the seasonal grouping. *Time of day* was not a significant grouping variable in the PERMANOVA, and was found to have little effect on diversity or community composition (Figure 4.1b) or overall CPUE (F = 0.91, df = 2, p = 0.41).

Table 4.1: Results of PERMANOVA tests on the influence of categorical predictors *year, season, time of day* and *substrate/profile* on ichthyofaunal composition. The *p-value* depicts significance while the R^2 value is a quantitative indicator of the extent of predictor influence on the community.

Categorical predictor	df	R^2	*p-value*
Year	6	0.042	0.01**
Season	1	0.013	0.05*
Time of day	2	0.007	0.517
Substrate/profile	2	0.149	0.001***

The nMDS plot (Figure 4.2a) shows low annual variability in community composition. This was substantiated by PERMANOVA results, which indicate that annual groupings only explain 4.2% of the variability in community composition. S*ubstrate/profile* was the most influential grouping variable as it was able to explain 14.9% of the variability in community composition.

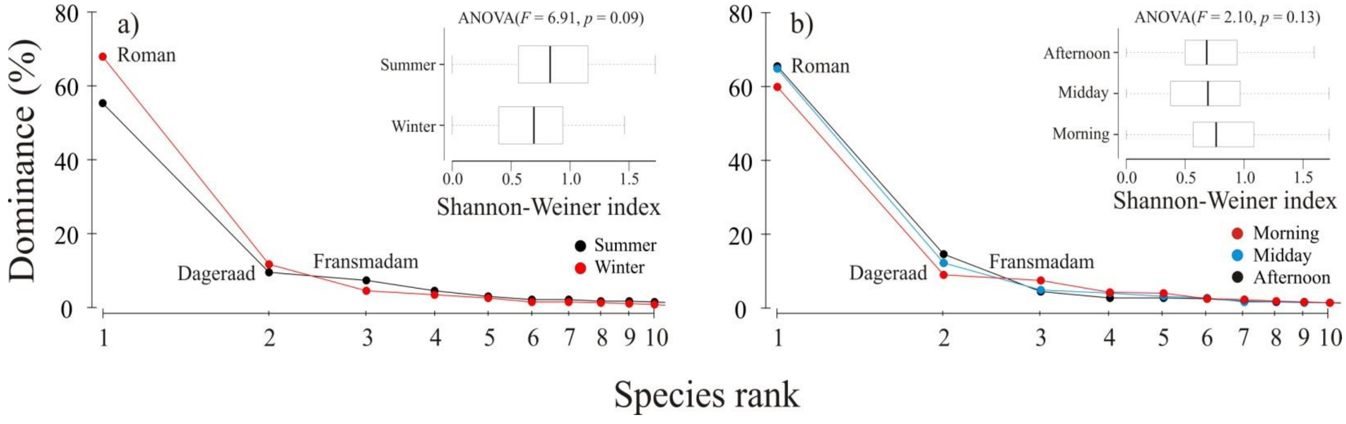


Figure 4.1: Species dominance plot and the mean site diversity (Shannon–Weiner index) in the Tsitsikamma National Park marine protected area between 2007 and 2014 for (a) *season* and (b) *time of day*. The box and whisker plots depict the data median, 10th, 25th, 75th and 90th percentiles as horizontal boxes with error bars.

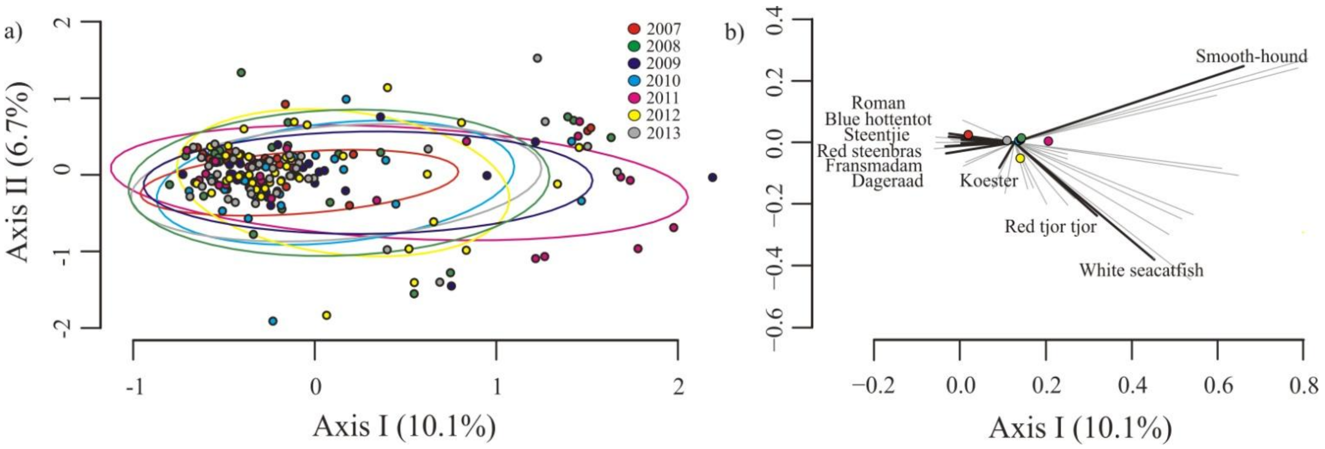


Figure 4.2: (a) Non-metric Multidimensional Scaling (nMDS) and associated 90% confidence interval ellipses depicting the annual ichthyofaunal composition overlap. (b) Principle component analysis (PCA) showing the influence of each species on annual ichthyofaunal composition.

The species that had the most influence on ichthyofaunal composition variability are illustrated in the form of a PCA (Figure 4.2b), with further details provided in Appendix 4.1. Primary and secondary components cumulatively explain 16.7% of the variability in the data, which indicate no substantial species compositional trend. The explained variability can be mainly attributed to *substrate* preference, which is noticeable by a distinct separation between smooth-hound and white seacatfish (sand orientated) and reef associated species along the first PC axis. Within the reef associated species a gradient is noticeable along the second PC axis, which is likely linked to *depth* preferences. Roman, steentjie and blue hottentot are generally found in higher abundances in shallower water, while the abundance of red steenbras, fransmadam, dageraad and koester generally increases with depth.

4.3.2 TEMPORAL TRENDS IN SPECIES ABUNDANCE

Standardized annual CPUE estimates of the five most common species indicate stable populations, with few common trends noticeable over the seven-year sampling period (Figure 4.3). Once again, the combined species CPUE was similar to that of roman, which is a result of roman's dominance in the angling survey samples. Additionally, roman and dageraad followed similar temporal trends of high and low catch rates. Confidence intervals varied widely amongst species as well as between the models applied (GAMs and GAMMs with spatial component). Abundant species had smaller confidence intervals than their scarcer counterparts, as expected, but this was further affected by the degree of spatial autocorrelation in the species catch rate. Significance of spatial autocorrelation for each species was assessed using correlograms and subsequent AIC in Chapter 3. Spatial autocorrelation had implications for the significance of the temporal variable *year* with regard to CPUE, which will be further discussed using dageraad as an example. A summary of species-specific models can be found in the deviance tables of Appendix 4.4.

4.3.2.1 ROMAN

Analysis of deviance together with sequential χ^2-tests showed that *year* explained a significant proportion of the variability in roman CPUE ($\chi^2 = 2.56$, $p = 0.02$). Both 2009 and 2010 produced low CPUE values, while 2007 and 2013 had the highest values. Roman CPUE was also influenced by *season* ($\chi^2 = 16.59$, $p < 0.01$) with significantly more roman caught in winter than summer.

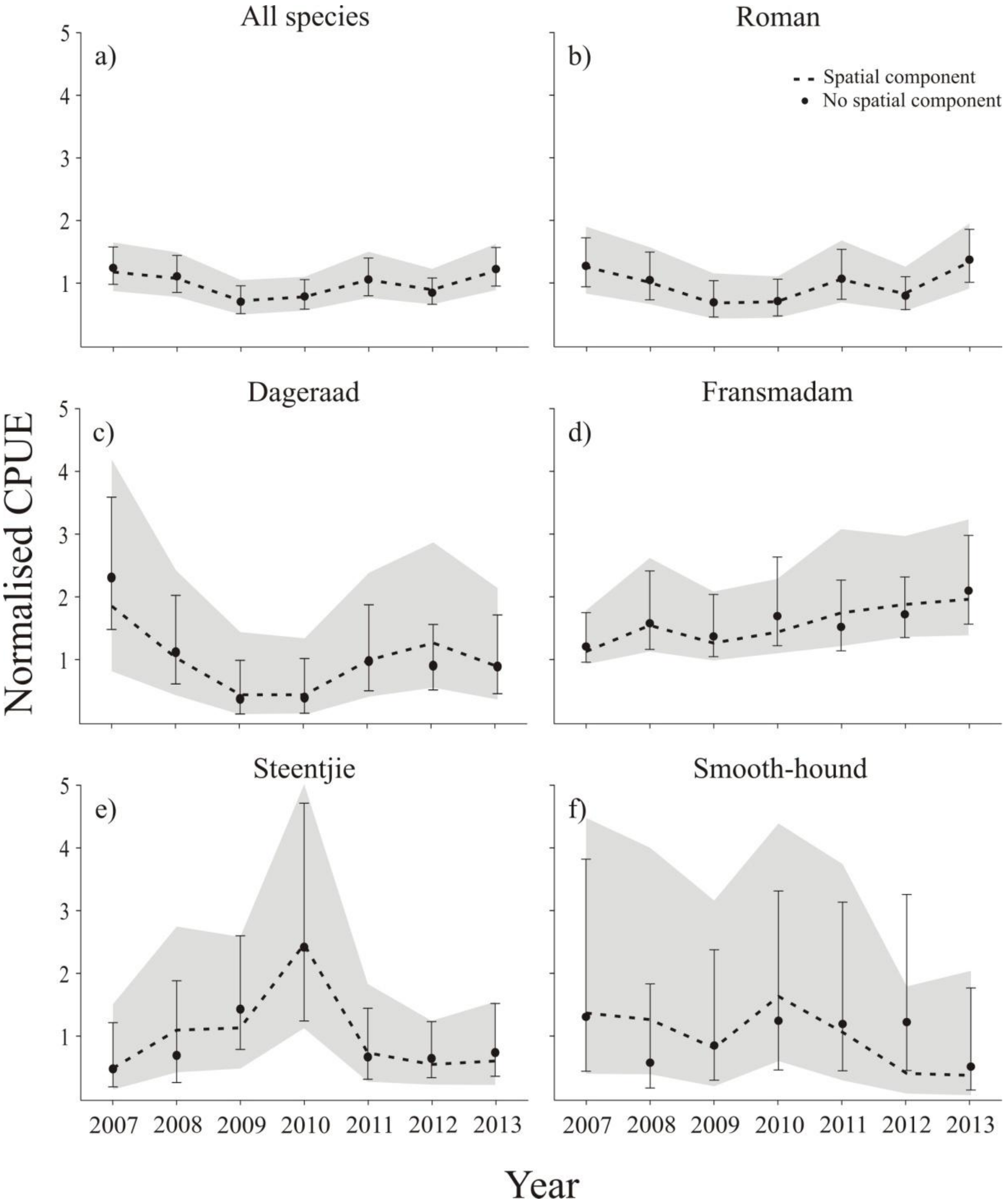


Figure 4.3: Predicted annual normalized catch-per-unit-effort (CPUE), and confidence intervals (CI) of (a) all species, (b) roman, (c) dageraad, (d) fransmadam, (e) steentjie and (f) smooth-hound. The data was normalized to aid comparisons between species. The points and error bars represent the GAMs fitted without a spatial component while the dashed line and shaded area represent the GAMMs fitted with a spatial component.

4.3.2.2 DAGERAAD

A significant proportion of variability in dageraad CPUE was explained by the temporal variable *year* ($\chi^2 = 2.27$, $p = 0.04$). As with roman, the years 2009 and 2010 had the lowest CPUE values, and 2007 had a distinctively high number of dageraad caught. S*eason* had little effect on dageraad catch rate ($\chi^2 = 1.09$, $p = 0.30$) although slightly more were caught in winter.

4.3.2.3 FRANSMADAM

The temporal variables *year* and *season* could not explain a significant proportion of the variability in fransmadam CPUE ($\chi^2 = 1.32$, $p = 0.25$; $\chi^2 = 0.11$, $p = 0.74$, respectively). Fransmadam CPUE was annually inconsistent, with 2010 and 2013 producing higher values and 2007 the lowest. Marginally more fransmadam were caught in summer than winter.

4.3.2.4 STEENTJIE

Year was able to explain a significant proportion of variability in steentjie catch rates ($\chi^2 = 2.46$, $p = 0.03$), but *season* was not ($\chi^2 = 0.04$, $p = 0.84$). Steentjie exhibited a relatively stable annual CPUE with the exception of two years, 2009 and 2010. CPUE was distinctively high in 2010, reaching a level approximately three times that of the average year. Steentjie CPUE was marginally higher in summer than winter.

4.3.2.5 SMOOTH-HOUND

Neither *year* nor *season* was able to explain a significant proportion of variability in smooth-hound CPUE ($\chi^2 = 0.90$, $p = 0.50$; $\chi^2 = 0.60$, $p = 0.44$, respectively) and annual CPUE was relatively consistent throughout the study. Marginally more smooth-hounds were caught in summer, although this too was not significant. These ambiguous temporal trends are likely a result of the high variability within the data, coupled with a small sample size, for the species.

4.3.3 INFLUENCE OF SPATIAL AUTOCORRELATION ON HYPOTHESIS TESTING

Dageraad CPUE was found to have a high degree of spatial dependency and autocorrelation (Section 3.3.4) and will be used as an example here to illustrate the potential consequences of disregarding residual structuring in models. The GAM fitted without any spatial component revealed that every *year* was significantly different from the model intercept. In contrast, the GAMM with the spatial component (fixed and random) indicated only years 2009 and 2010 were significantly different from the intercept. The explanation behind the differences in levels of significance is twofold: firstly, the model without fixed spatial component is misspecified: *lat,long* has previously been shown to be a significant predictor of dageraad abundance and therefore must be included in the model as a fixed variable. Secondly, and more important, the ‘understated’ confidence intervals of the GAM without any spatial component (Figure 4.3c) increase the likelihood of a Type I error and obscure relationships (Table 4.2).

Table 4.2: Comparison of the significance of the temporal variable *year* on the normalized CPUE of dageraad using a GAM without any spatial component against a GAMM with spatial components.

	GAM No spatial component		**GAMM With Spatial component**	
	t-value	*p-value*	*t-value*	*p-value*
2007	2.856	0.004**	0.201	0.841
2008	-1.986	0.048*	-1.616	0.107
2009	-3.445	<0.001***	-2.735	0.007**
2010	-3.458	<0.001***	-2.750	0.006**
2011	-2.148	0.033*	-1.565	0.119
2012	-2.736	0.006**	-1.098	0.273
2013	-2.382	0.018*	-1.777	0.077

4.3.4 SIZE COMPOSITION

4.3.4.1 ROMAN

ANOVA results for roman mean length revealed the population to be consistent in size structure over the seven-year sampling period (F = 1.68, df = 6, p = 0.12). This is in agreement with the permutation test on KDEs, which found that none of the annual length-frequency data differed significantly from the null distribution (Table 4.3). These results indicate the roman population is stable and has a consistent length-frequency distribution (Figure 4.4a).

4.3.4.2 DAGERAAD

Analysis of annual length-frequency data for dageraad produced contrasting results. An ANOVA shows no significant difference in the annual mean lengths (F = 1.94, df = 6, p = 0.07), which is likely result of high, but comparable, within year variability (Bartlett's K-squared = 9.53, df = 6, p = 0.1461). However, a visual assessment of mean lengths suggests an annual trend (Appendix 4.3), which is corroborated by the strong departures of annual KDEs from the null distribution (Figure 4.4b). The KDE shows a relatively high abundance of large fish in the population in 2007 and 2008, which increases further in size until 2009. The abundance of large fish then decreases sharply, leading to a significantly smaller size-structure in 2010, followed by a steady increase in size until 2013. Permutation tests on the length-frequency KDEs found that dageraad had the most inconsistent length-frequency distribution of all the species, with the years 2007, 2008, 2011 and 2013 having KDEs that differed significantly from the null distribution (Table 4.3).

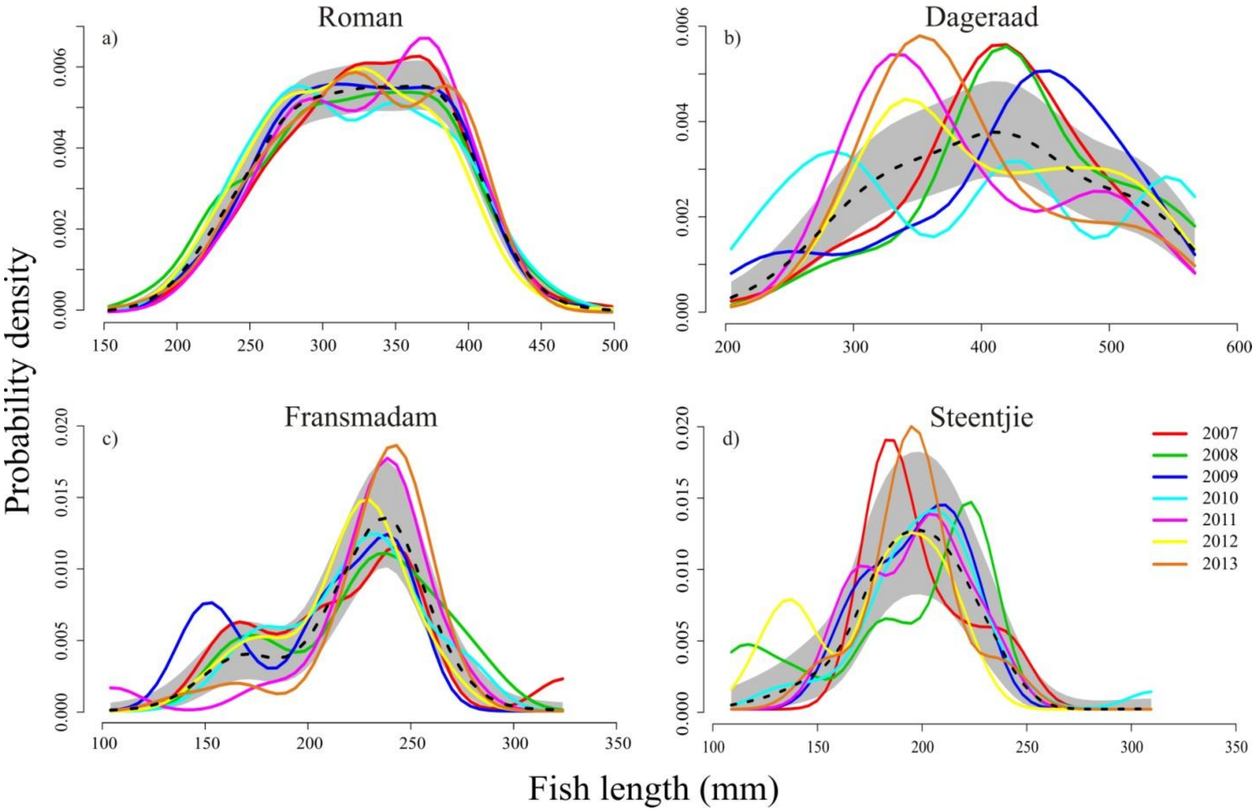


Figure 4.4: Comparisons of annual length-frequencies and kernel density estimate (KDE) probability functions of the four most abundant species; (a) roman, (b) dageraad, (c) fransmadam, (d) steentjie in the Tsitsikamma National Park (TNP) marine protected area. The dashed lines and shaded areas represent the null models and their respective standard errors.

4.3.4.3 FRANSMADAM

ANOVA results for fransmadam revealed that annual mean length did not differ significantly ($F = 1.31$, df = 6, $p = 0.26$), whereas permutation tests on annual KDEs identified that the length-frequency distribution in 2013 was significantly different to the null distribution. This is evident in the boxplot depicting annual length variability (Appendix 4.3), which shows considerably fewer smaller fish in 2013 despite the ANOVA suggesting otherwise. Additionally, visual assessments of annual KDEs show a high level of variability in small fish (<200 mm).

Table 4.3: Results from annual length-frequency distribution comparisons using permutation tests and kernel density estimates (KDEs).

Species	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**
Roman	0.14	0.66	0.98	0.25	0.16	0.22	0.32
Dageraad	0.01*	0.05*	0.27	0.07	0.01*	0.11	0.02*
Fransmadam	0.72	0.49	0.35	0.84	0.09	0.54	0.02*
Steentjie	0.37	0.07	0.85	0.79	0.90	0.24	0.37
Smooth-hound	0.18	0.55	0.04*	0.40	0.02*	0.22	0.07

* indicates significance at 5% level

4.3.4.4 STEENTJIE

Observed annual steentjie length-frequency revealed a high level of stability in size structure. ANOVA results show that mean annual length ($F = 0.87$, df = 6, $p = 0.52$) did not differ significantly, nor did KDE permutation tests on length-frequency distributions show any significant deviations from the null distribution. Visual examination of the KDEs revealed there were slight annual deviations from the null distribution, particularly for 2008, however these were not significant (*p* = 0.07). This is likely influenced by the large confidence intervals in the KDE null distribution (Figure 4.4d), which is a consequence of small annual sample sizes. Similar to fransmadam, steentjie KDEs depict a relatively high level of variability in small fish.

4.4 DISCUSSION

4.4.1 TEMPORAL TRENDS IN TSITSIKAMMA NATIONAL PARK ICHTHYOFAUNA

Established in 1964, by 2014 the TNP MPA had been a 'no take' sanctuary for 50 years. It is therefore unsurprising to have found a high degree of temporal stability in the ichthyofauna of the TNP MPA throughout the seven-year study period. Dageraad was the only species to exhibit a definitive temporal trend in terms relative abundance and size structure. This was attributed to recruitment, and possible adult movement behaviour independent of exploitation, based on the observed annual length distribution patterns and the fact that the population is within an unexploited MPA. The details of this hypothesis are discussed further in Section 4.4.3. With the exception of Dageraad, all analyses point to an established community that exhibits little temporal variation in species abundance and size structure. However, here it must be reiterated that this stability is limited to the highly resident species within the TNP MPA. The reason for this is twofold: firstly, the random stratified sampling protocol does not actively target migrating species and so catches of such species were both sporadic and negligible; secondly, migrant species cannot be equated to resident species with regard to protection status as 'no take' MPAs only afford temporary protection to migrant species, and these species will likely be exposed to exploitation beyond the boundaries of the MPA.

There has been much debate around the rates of recovery of exploited populations within no-take MPAs (Russ et al. 2005, Babcock et al. 2010), which range from rapid (1-3 years [Halpern and Warner 2002]) to extending over four decades (Russ and Alcala 2004). The longevity of the TNP MPA far exceeds any time frame suggested for a full recovery of fish populations, bolstering the view that it currently possesses a fish community that is near to pristine. Correspondingly, the overall temporal trend in diversity and ichthyofaunal composition was stable. Here it must be mentioned that poaching within the chosen study area of the TNP MPA is negligible to non-existent. This is due to the study area's proximity to the tourist accommodation, SANParks offices and the patrol vessel launch site (Section 2.1.1), which ensures any intruding vessel would undoubtedly be noticed and investigated. Indeed, poaching from the shore is a well documented problem in much of the TNP MPA (Hauck and Kroese

2006, Tunley 2009), but there is evidence that a clear disconnection exists between this nearshore ichthyofaunal community and the offshore subtidal community investigated here (James et al. 2012) .

Despite the simple yet intuitively logical finding that the 50 year old ‘no-take’ MPA possesses a near pristine subtidal ichthyofaunal assemblage, the results must be interpreted with some caution. Bennett and Attwood (1991) suggest that although angling is a practical method of assessing stock recoveries, its applications in ‘holistic’ ecology are limited and any CPUE data should be carefully interpreted. Smith et al. (2007) failed to record an effect of exploitation on species diversity inside and outside the TNP MPA using boat based angling, as did Götz et al. (2009) in the nearby Goukamma MPA. This inability to identify community changes across a distinct exploitation boundary does not inspire confidence when attempting to detect changes within a well established MPA over several years. Selectivity of dominant, large predator species was cited as a disadvantage of angling as a sampling method in assessing community variation (Götz et al. 2009). Indeed, the dominance of species such as roman and dageraad is likely to overpower variation in less abundant species, despite accounting for this through data transformation (Clarke and Warwick 1994, De’ath 2002). Such problems of sampling accuracy confound estimates of change (Stewart-Oaten et al. 1995). For example, Solano-Fernández et al. (2012) found that boat-angling data showed an increasing biodiversity trend from west to east in MPAs along the South African coast, which was interrupted by a local minimum between Tsitsikamma and Port Elizabeth. In contrast, several studies describing the ichthyofauna of the TNP MPA using a variety of sampling methods reveal the area holds a high level of ichthyofaunal diversity (Buxton and Smale 1984, Burger 1991, Tilney et al. 1996, Hanekom et al. 1997, Wood et al. 2000, Smith 2006). Furthermore, Wood et al. (2000) recorded 202 species of fishes from 84 families within the MPA using a number of sampling techniques. These conflicting biodiversity estimates of the TNP area are a direct result of different sampling methods, and confirm the selective nature of angling. This selectivity is particularly apparent in the TNP MPA due to the abundance of two aggressive and highly ‘catchable’ sparids: roman and dageraad.

4.4.2 TEMPORAL TRENDS IN ABUNDANCE

Due to angling selectivity, species-specific abundance estimates were only possible for the five most abundant species, after which confidence decreased to such an extent that predictions were no longer meaningful. However, the rigorous sampling design and large numbers of spatial and temporal replicates in this study allowed for a comprehensive examination of the results for plausible biological explanations with regard to the observed variability within these species (Götz et al. 2009). Roman CPUE was significantly higher in winter, which is likely linked to early summer spawning (Götz et al. 2009) and the prior build-up of energy reserves in winter (Buxton 1990, Götz et al. 2009). The high residency of roman (Kerwath et al. 2007) negates any spawning/seasonal migration as a possible explanation. Due to their dominance, roman's higher CPUE in winter influenced overall CPUE between seasons, which was significant.

The increased abundance of steentjie in 2009 and 2010 correlates directly with the years when roman and dageraad CPUE were lowest, suggesting that the 'spike' in steentjie CPUE is merely an artefact of sampling. Götz (2006) categorized roman and steentjie as a single functional group based on a ichthyofaunal composition study of nearby Goukamma MPA, indicating that the two species co-inhabit the same areas and ruling out the possibility of sampling biases due to habitat segregation (i.e., sampling one habitat type more than another). The influence of environmental variables on CPUE was then assessed, specifically temperature. Intense localized upwelling events were experienced in both the summer sampling trip of 2009 and the winter trip of 2010 (range: 10.0–21.2°C and 11.5–18.0°C, respectively). Temperature has been shown to influence roman catch rates (Section 3.3.6), with a decrease in temperature significantly lowering CPUE. Buxton and Smale (1989) also found a significant decrease in roman CPUE in the TNP MPA at low water temperatures. It is hypothesized that the increase in steentjie CPUE is the direct result of decreased competition from the more aggressive roman due to intense localized upwelling during sampling events. This effect was particularly pronounced in 2010 as the upwelling unusually occurred in winter (Schumann 1999) when roman CPUE is usually highest. Such results highlight the disproportionate effect of extreme environmental conditions on species abundance estimates, and the inability of models to accurately account for these unusual events. Although collecting data during such events is important in gaining species-specific biological information, if the temporal objectives of LTM programmes are to be met it is advisable to define a set of environmental boundary parameters prior to assessing temporal trends.

Changes in abundance and mean size of targeted species are the most noticeable effects of fishing (McClanahan et al. 1999, Barrett et al. 2007, Götz et al. 2009), and therefore consistency in these indices are characteristics of an unexploited, stable population (Leaman 1991). Accurately defining variation in both indices over time is statistically complex and direct comparisons of temporal trends in population densities and community composition are likely to be inaccurate in datasets that contain high spatial variation (Stewart-Oaten et al. 1995, McClanahan 1998, Thompson and Mapstone 2002). Using dageraad as an example, the influence of spatial dependency and autocorrelation in temporal analyses was highlighted in this study. To account for spatial dependency, the spatial variable *lat,long* was introduced as a fixed variable. This improved model predictions significantly, as it explained 87% of the model deviance. While assessing dageraad abundance it became clear that a high number of sites that produced above-average dageraad CPUEs were sampled in the summer sampling trip of 2007, resulting in abnormally high dageraad CPUE. This spatial bias produced significant differences in normalized CPUE predictions for 2007 between models, whereby the model containing *lat,long* as a fixed variable was notably lower (1.85) than that without (2.30). The opposite effect was seen in 2012, where the model containing the fixed spatial variable produced notably higher normalized CPUE predictions

(1.27) than that without (0.91), suggesting more sand substrate sites were sampled in 2012 than normal. It is likely that the ‘biased’ site selections for these sampling trips were coincidental, despite a randomized sampling protocol. The differences in predicted CPUE estimates between the two models for 2007 and 2012, show that this ‘bias’ is accounted for through the incorporation of site-specific variability (*lat,long*).

Autocorrelation within model residuals is recognized as a major statistical obstacle when assessing changes in abundance (Zuur et al. 2009, Dray et al. 2012). Spatial autocorrelation was found to have significantly more influence on fish abundance in the TNP MPA than temporal autocorrelation (Chapter 3), and consequently the latter was disregarded as only a single correlation structure can be embedded in model residuals (Zuur et al. 2009). The consequence of ignoring spatial autocorrelation is an overestimation in confidence, shown by artificially narrow confidence intervals in the GAM predictions. This is a result of a decrease in the number of degrees of freedom in the sample to less than that estimated from the number of observations. In the case of dageraad, the narrow confidence intervals resulted in all annual abundance estimates being significantly different from that of the intercept. In contrast, the GAMM that accounted for spatial autocorrelation only found abundance estimates for 2009 and 2010 to be significantly different. An overestimation of confidence increases the likelihood of a Type I error (incorrect rejection of the null hypothesis), obscuring the true relationship between response and explanatory variables (Dray et al. 2012, Hamylton 2013). In the context of LTM, where biodiversity data are expensive to collect and cost-efficiency is paramount (Vos et al. 2000, Molloy et al. 2010, Bernard 2013), the incorporation of spatial variables to account for dependency and autocorrelation is imperative, particularly where spatial stratification is sacrificed for temporal repetition.

4.4.3 TEMPORAL TRENDS IN SIZE COMPOSITION

As with diversity and abundance, length-frequency distributions were relatively stable and no significant differences were found for roman and steentjie, while fransmadam only exhibited a single year (2013) that was significantly different from the null model. Populations within MPAs are expected to have more stable size distributions than those outside, due to the fluctuation caused by recruitment variability being smoothed out by the comparatively larger proportion of older fish in an unexploited environment (Froese et al. 2008, Babcock et al. 2010). Roman annual length-frequency distributions showed no deviation from the null model whatsoever, and when combined with abundance results, it is clear that the roman population in the TNP MPA is in a hyper-stable state. The interpretation of fransmadam and steentjie length-frequency distribution is less definitive due to the selective nature of the hooks towards larger fish (max observed length: 323 and 310 mm respectively), which has been documented in various other angling studies (Punt et al. 1996, Götz et al. 2007). High variability occurred within the smaller bins of the length-frequency distributions (<200 mm) for both species, after which consistency between years increased. This is likely another sampling artefact, whereby the number of small fish caught (<200 mm) was predominantly determined by chance as opposed to relative abundance. Consequently these size classes were under-sampled and exhibit the high variability indicative of an insufficient sub-sample. As a result, tests on annual differences in length-frequencies are likely to be on the conservative side (inflated probability of a Type I error) for small species due to artificially high variability in their lower size classes. In such cases, interpretation must be done with caution.

Dageraad displayed a high level of annual variability in length-frequency distribution, with the years 2007, 2008, 2011 and 2013 all found to deviate significantly from the null distribution. The observed pattern indicates variation in recruitment strength, whereby cohorts of relatively large fish in 2007 and 2008 could be seen to increase in size, but decrease in abundance, in 2009. These large fish then decreased drastically in abundance in 2010 and a cohort of small fish appeared as the first sign of the recruitment pulse. This pulse approximately doubled in abundance in 2011 and its growth could be tracked by distinct cohorts to 2013. An exact explanation for the disappearance of the larger fish is unknown, but such a definitive pattern indicates an emigration from the sampling area as opposed to mortality. It is widely acknowledged that dageraad populations are under severe pressure from exploitation, and populations outside of MPAs are considered to have decreased drastically in recent years. Research on the current status of the species is regarded as high priority (Mann 2013), and in 2014 the species was classified as Critically Endangered according to the IUCN red listing scheme (Winker et al. 2014a). Providing decision makers with evidence that the TNP MPA, through the emigration of large dageraad, promotes the longevity of the commercial linefishery outside of the MPA offers yet another reason as to why MPAs are such a fundamental tool in ecosytem-based management strategies.

Such recruitment patterns are not unusual in LTM datasets, and Barrett et al. (2007) found evidence of similar patterns in *Latridopsis forsteri* in a 10-year study of MPAs in Tasmania. Cyclical recruitment patterns inevitably influence annual abundance estimates (Barrett et al. 2007, Babcock et al. 2010) and the lowest dageraad CPUE values were observed in 2009 and 2010, which corresponded to the years that were dominated by smaller fish. Biological events such as this are difficult to account for in temporal assessments and often lead to false conclusions when assessed over a short period, as found by Barrett et al. (2007) in their reassessment of *L. forsteri* in the Maria Island National Park MPA a decade after the initial assessment (Edgar and Barrett 1999, Barrett et al. 2007). Had this study covered a period of four years or less (2007–2010) the outlook for dageraad would have indeed been different, as a perceived decrease in both abundance and average size would have suggested the population was declining rapidly. The importance of sustainable LTM programmes when assessing fisheries therefore cannot be overstated, because only once a dataset reaches a timespan greater than the time a biological event takes to reach completion can its full potential be realized. It is predicted that the annual CPUE of dageraad in the TNP MPA will increase for the next 2-3 years before this cyclical recruitment event reoccurs.

Assessing mean sizes of species differs from abundance in that the data are in the form of a length-frequency distribution whereby two aspects may differ: location of the mean and the shape of the distribution (Langlois et al. 2012a). Previously, two tests for significant variation in length-frequency distributions were predominantly employed: the student's *T*-test or ANOVA and the Kolmogorov–Smirnov test. The former are parametric tests based on differences between means, while the latter is a non-parametric test that compares the largest point differences between cumulative length-frequency distributions (Langlois et al. 2012a). In contrast to these, the KDE method applied in this study has the ability to test both differences in mean location and distribution shape. The advantage of KDEs is that the optimal kernel size is selected through calculations based on data distribution as opposed to investigators arbitrarily choosing histogram bins (Sheather and Jones 1991, Langlois et al. 2012a). Significance is obtained through a permutation test, which is a simple, robust and 'distribution free' procedure (Anderson 2001). The advantage of using KDEs is evident in this study, as the method was able to detect obvious differences in annual length in dageraad, unlike the ANOVA (Appendix 4.3) or the Kolmogorov–Smirnov test. Beyond detecting these differences, the graphical representation of annual KDEs against the null distribution allowed a clear visualization of the dageraad recruitment process and the tracking of cohorts through time. The method was also able to detect high variability in the smaller size classes of fransmadam and steentjie caused by the size selectivity of angling. It is therefore advised that KDEs be applied in conjunction with traditional methods when assessing annual variability in size distributions.

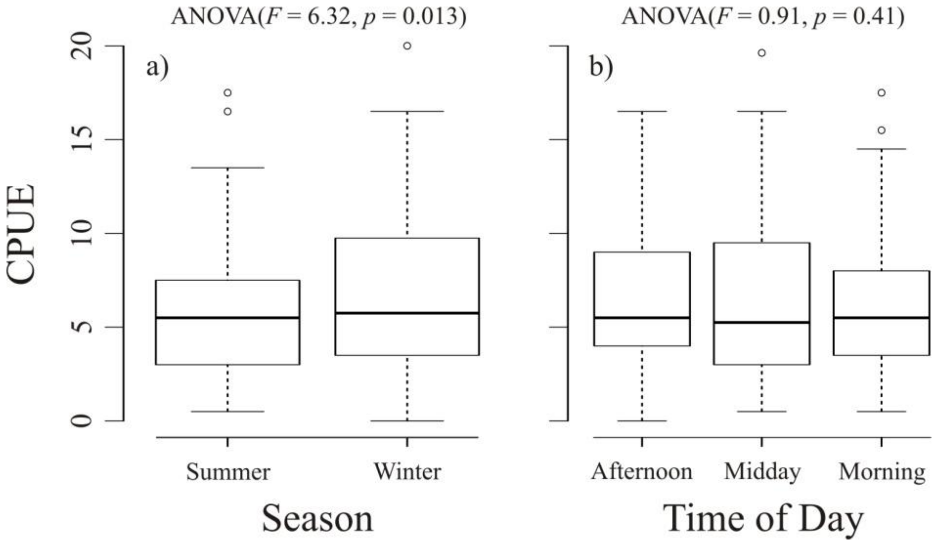
4.5 CONCLUSIONS

After 50 years of protection from exploitation, temporal population trends within the TNP MPA show a fairly high level of long-term stability, as can be anticipated of a subtidal assemblage that is dominated by highly resident reef fishes. This general statement is, however, limited to those species for which individual assessments were possible, and little inference could be made with regard to community composition as a result of sampling selectivity. The study highlighted the inadequacy of angling as an ecosystem monitoring method on a variety of fronts, an opinion that has been previously expressed by others (Bennett and Attwood 1991, Bennett et al. 2009, Götz et al. 2007). Angling's high selectivity, for both species and size, impaired the ability to detect potential trends and consequently decreased inference confidence. If single species management plans become obsolete and are replaced by ecosytem-based management strategies (Pikitch et al. 2004, Fletcher et al. 2010), the future of angling as a monitoring technique is questionable. Although useful in specific circumstances (e.g., mark-recapture or where physical samples need to be retained), angling introduces far too much variability to accurately assess whole communities confidently. The study also highlighted the effects of extreme environmental conditions on abundance estimates, and the inability of models to accurately account for these events. In such cases, it is advisable to determine boundary limits to environmental parameters prior to analyses. Thorough examination of dageraad abundance and size distribution showed long-term stability despite significant annual fluctuations. This conclusion was only possible as a result of the rigorous sampling design, a large number of spatial and temporal replicates and choice of appropriate statistical methods. The importance of incorporating spatial dependency and autocorrelation in temporal analyses was also reiterated. Avoiding this statistical pitfall is especially pertinent to LTM, where the spatial component is often overlooked in an attempt to establish temporal trends. Additionally, the use of KDEs combined with permutation tests was found to be a more accurate method of assessing variability in length-frequency distributions than traditional methods. The continual improvement of statistical methods is essential to providing scientists and managers with the most accurate data possible. In this context, LTM datasets provide more than just an opportunity to assess current ecological states; they provide scientists with the opportunity to develop methods specifically to deal with natural variability, which exists in all LTM datasets. This also highlights the importance of short-term experiments and observations within LTM programmes. Current misconceptions define LTM as an entity separate from general ecological research, the latter being specific and question driven. The relevance of LTM programmes would undoubtedly increase if researchers would formulate ecological studies within a LTM context, thereby creating a win-win situation. Finally, the temporal trends established in this study will provide future scientists and managers with essential baseline data against which comparisons can be made.

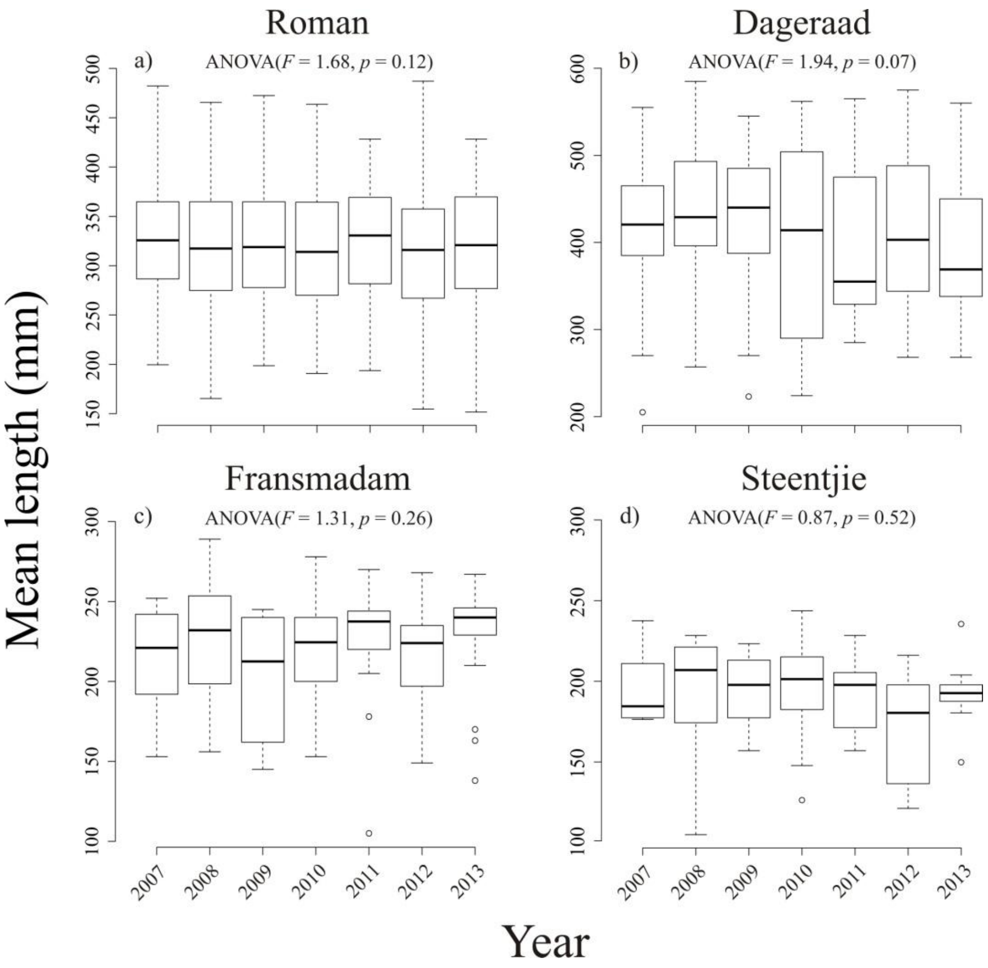
4.6 APPENDICES

Appendix 4.1: List of principal components (PCs) from the principle component analysis (PCA) to assess the influence of species on annual ichthyofaunal variability.

	PC1	**PC2**	**PC3**	**PC4**	**Importance**
% of total variance	10.1	6.5	6.2	5.7	-
Cumulative % of variance	10.1	16.7	22.9	28.6	-
Species scores					
Chrysoblephus laticeps	0.507	0.108	-0.059	0.077	**0.278**
Mustelus mustelus	-0.372	-0.010	0.182	0.267	**0.243**
Acanthistius sebastoides	0.155	-0.448	0.089	-0.072	**0.238**
Chrysoblephus cristiceps	0.319	-0.277	-0.175	0.167	**0.237**
Pterogymnus laniarius	-0.022	0.014	-0.453	0.155	**0.230**
Pomatomus saltatrix	-0.042	0.016	-0.065	-0.471	**0.228**
Boopsoidea inornata	0.316	0.286	0.135	-0.145	**0.221**
Spondyliosoma emarginatum	0.216	0.385	0.104	0.047	**0.208**
Chrysoblephus gibbiceps	0.132	-0.420	0.020	0.035	**0.196**
Galeichthys ater	0.077	-0.352	0.181	-0.176	**0.194**
Pomadasys olivaceum	-0.098	0.040	-0.149	-0.395	**0.190**
Argyrozona argyrozona	-0.035	-0.087	-0.403	0.084	**0.179**
Galeorhinus galeus	-0.226	-0.024	0.193	0.293	**0.174**
Cheimerius nufar	-0.030	0.078	-0.370	-0.024	**0.145**
Diplodus capensis	0.118	0.061	0.249	-0.253	**0.144**
Haploblepharus edwardsii	-0.044	-0.124	0.268	-0.211	**0.134**
Pagellus bellottii natalensis	-0.115	0.039	-0.259	-0.223	**0.131**
Petrus rupestris	0.221	-0.214	-0.145	0.100	**0.126**
Pachymetopon aeneum	0.215	0.194	0.043	0.044	**0.088**
Atractoscion aequidens	0.022	-0.177	-0.130	-0.188	**0.084**
Chelidonichthys kumu	-0.207	-0.047	0.059	0.177	**0.080**
Galeichthys feliceps	-0.152	-0.080	-0.007	-0.190	**0.066**
Sphyrna spp.	-0.152	0.019	-0.108	-0.160	**0.061**
Carcharhinus brachyurus	-0.104	0.070	-0.073	-0.172	**0.051**
Sarpa salpa	0.001	0.119	-0.145	0.081	**0.042**
Poroderma africanum	0.139	-0.028	0.107	0.064	**0.036**



Appendix 4.2: Variability in mean catch-per-unit-effort (CPUE) between (a) *season* and (b) *time of day*, with corresponding levels of significance.



Appendix 4.3: Variability in mean annual lengths of the four most abundant species (a) roman, (b) dageraad, (c) fransmadam and (d) steentjie, with associated levels of significance.

Appendix 4.4: Deviance tables explaining the importance of variables in the general additive models (GAMs) used to describe temporal trends in species catch-per-unit-effort (CPUE) data.

All species

	Resid.df	Deviane	df	∆ Deviance	p-value	% variation explained
Null	242.0	1621.1				
+ Year	236.0	1522.3	6.0	-98.8	-	30.56%
+ Season	235.0	1486.6	1.0	-35.7	0.002	11.04%
+ Temperature	234.0	1412.3	1.0	-74.3	< 0.001	22.98%
+ Lat-Long	230.2	1297.8	3.7	-114.5	< 0.001	35.42%
					Total	**19.94%**

Roman

	Resid.df	Deviane	df	∆ Deviance	p-value	% variation explained
Null	242.0	1752.3				
+ Year	236.0	1667.6	6.0	-84.7	-	27.40%
+ Season	235.0	1584.6	1.0	-83.0	0.298	26.85%
+ Temperature	234.0	1516.9	1.0	-67.7	0.584	21.90%
+ Lat-Long	230.2	1443.2	3.9	-73.7	< 0.001	23.84%
					Total	**17.64%**

Dageraad

	Resid.df	Deviane	df	∆ Deviance	p-value	% variation explained
Null	242.0	893.64				
+ Year	236.0	804.26	6.0	-89.4	-	28.92%
+ Season	235.0	792.15	1.0	-12.1	0.298	3.92%
+ Temperature	233.9	791.4	1.0	-0.8	0.584	0.24%
+ Lat-Long	225.4	523.2	8.6	-268.2	< 0.001	86.77%
					Total	**41.45%**

Fransmadam

	Resid.df	Deviane	df	∆ Deviance	p-value	% variation explained
Null	242.0	409.77				
+ Year	236.0	401.21	6.0	-8.6	-	2.77%
+ Season	235.0	398.6	1.0	-2.6	0.739	0.84%
+ Temperature	232.1	363.7	2.9	-34.9	0.003	11.29%
+ Lat-Long	229.6	348.65	2.5	-15.1	0.055	4.87%
					Total	**14.92%**

Steentjie

	Resid.df	Deviane	df	∆ Deviance	p-value	% variation explained
Null	242.0	303.18				
+ Year	236.0	285.36	6.0	-17.8	-	5.77%
+ Season	235.0	282.82	1.0	-2.5	0.842	0.82%
+ Temperature	230.3	254.68	4.6	-28.1	0.026	9.10%
+ Lat-Long	228.4	248.52	1.9	-6.2	0.121	1.99%
					Total	**18.03%**

Smooth-hound

	Resid.df	Deviane	df	∆ Deviance	p-value	% variation explained
Null	242.0	397.42				
+ Year	236.0	376.59	6.0	-20.8	-	6.74%
+ Season	235.0	373.81	1.0	-2.8	0.435	0.90%
+ Temperature	229.8	345.99	5.2	-27.8	0.007	9.00%
+ Lat-Long	226.7	327.64	3.1	-18.4	0.022	5.94%
					Total	**17.56%**

CHAPTER FIVE

COMPARATIVE ASSESSMENT OF ANGLING AND STEREO BAITED REMOTE UNDERWATER VIDEOS (STEREO-BRUVS) AS TECHNIQUES FOR MONITORING THE SUBTIDAL ICHTHYOFAUNA OF THE TSITSIKAMMA NATIONAL PARK MARINE PROTECTED AREA

5.1 INTRODUCTION

5.1.1 IMPORTANCE OF METHODS RESEARCH

Methods research is fundamental to ecology (Elphick 2008) as it identifies the most efficient techniques by which the current ecological knowledge base can be expanded. It enables researchers to select the most appropriate method(s) and provides a comprehensive understanding of the biases of each method, which in turn aids the interpretation of observed patterns (Yoccoz et al. 2001). Method research does this by addressing two fundamental problems: (i) improvement of data-gathering to reduce biases or increase precision and (ii) the development of statistical methods that can account for biases or uncertainty in the collected data (Elphick 2008). Throughout this study there has been an emphasis on the latter problem, whereby new statistical methods have been employed in an attempt to overcome the observed biases associated with angling. This course of methods research could best be termed ‘reactive’, and despite being progressive, the fundamental limitations of the data still remain.

The improvements in computing power since the 1990s (Megrey and Moksness 1996) meant a large proportion of fisheries research focused on developing statistical means of dealing with imperfect datasets (Maunder and Punt 2013). Recently, more attention has been paid to the fundamental problem, which relates to limitations of sampling techniques. In this respect, fishery-dependent techniques generally concentrate on commercially lucrative species groups (Worm and Branch 2012, Ricard et al. 2012) and areas of high fish density (Maunder and Punt 2004), and are, therefore, inappropriate for sampling vulnerable species and ecosystems such as reef complexes, particularly within MPAs. The reasons for this are numerous, but most notable are the non-reporting of bycatch species, non-random sampling designs, the species-specific selectivity and inherently destructive nature of fishery-dependent techniques. There is also a growing sentiment that catch data recorded by the industry may be inaccurate or untrustworthy (Cotter and Pilling 2007). Alternatively, fishery-independent techniques such as angling, fish trapping and underwater visual census (UVC) are more appropriate for ecological sampling, but still possess specific biases (Cappo et al. 2004, Colton and Swearer 2010, Langlois et al. 2010, 2012a, 2015, Pelletier et al. 2011, 2012, Harvey et al. 2012, Lowry et al. 2012, Bernard 2013). Fish trapping has a high mortality rate (Bernard 2013), and its employment over an extended period will impact the population under assessment in a compounding manner, leading to a cumulative bias. Although it is non-destructive, UVC is restricted to depths of less than 30 metres and disregards populations found in deeper habitats (Götz 2006, Bennett et al. 2009, Bernard 2013). As such, angling was considered the most appropriate traditional sampling method; consequently fish-trapping and UVC were excluded from this study. This chapter focuses on the ‘proactive’ aspect of methods research through the introduction of a relatively new sampling method known as Stereo Baited Remote Underwater Video system (stereo-BRUVs) to the Tsitsikamma National Park (TNP) marine protected area (MPA) long-term monitoring (LTM) programme in an attempt to overcome the fundamental sampling biases observed within the angling data.

5.1.2 HISTORY OF REMOTE UNDERWATER VIDEO TECHNIQUES

Video techniques, in the form of Remote Underwater Video systems (RUVs), have been employed in marine ecology since the 1960s when they were first used to investigate fish behaviour (Mallet and Pelletier 2014). Since then, RUVs have undergone numerous developments, one of the most important being the shift from linked systems (live-feed to the surface where the video is recorded) to autonomous systems that can be left on the seabed independent of the surface attachment (Bernard 2013, Mallet and Pelletier 2014). This advance dramatically increased sampling efficiency as numerous RUVs can be deployed simultaneously. The introduction of bait (BRUVs) to attract fish, and increase sampling efficiency, was another significant improvement of video techniques. The presence of bait has been shown to increase count data precision, and BRUVs were found to be superior to RUVs and fish traps at surveying the entire TNP ichthyofauna (Bernard and Götz 2012, Bernard 2013). The latest considerable development in BRUVs was the introduction of stereo-video (stereo-BRUVs), which enable researchers to accurately measure fish length using specifically designed computer software that requires stereo-video input (footage captured simultaneously from independent cameras with an overlapping field of view). Size structure information is important in understanding the ecology of fish populations (Pauly et al. 1998) because a number of biological parameters such as growth rate, maturity and mortality rates are all related to body length (Pauly 1980, Froese and Binohlan 2000, 2003). When employed in conjunction with age data (length-age relationship), this information provides the basis for fishery assessments (Hilborn and Walters 1992) and ecological studies on the effects of fishing (Froese et al. 2008, Götz et al. 2008b). The stereo-video technique was first employed by Harvey and Shortis (1996), and in recent years stereo-BRUVs have been shown to be a cost effective sampling tool (Watson et al. 2010, Langlois et al. 2010, Bernard 2013). Applications of the method include describing spatial (Moore et al. 2011) and temporal (McLean et al. 2011) changes in fish assemblages as well as the effects of protection through MPAs (Watson et al. 2007, 2009, Langlois et al. 2012b). Baited remote underwater stereo-video systems are currently gaining global acceptance as the most appropriate non-destructive method of monitoring ichthyofauna and have been employed in Alaska (Williams et al. 2010), Australia (Watson et al. 2005, 2010, Langlois et al. 2010, 2012a, Dorman et al. 2012, Fitzpatrick et al. 2012, Harvey et al. 2012, Holmes et al. 2013), Fiji (Goetze et al. 2011), New Zealand (Zintzen et al. 2012), United Kingdom (Unsworth et al. 2014) and South Africa (Bernard et al. 2014).

5.1.3 UNDERSTANDING SAMPLING BIAS

An underlying assumption of ecological sampling is that the detection probability of an individual is equal amongst all species as well as proportional to abundance (MacNeil et al. 2008a, 2008b). In reality, the ability to detect an individual varies between species and between sampling methods. This inherent variability is referred to as ‘sampling bias’, and exists in all situations where a subsample of a population is taken to represent that entire population. Sampling biases can be sufficiently strong to produce erroneous conclusions and/or inconsistencies across survey methods (Willis et al. 2000). Therefore, understanding and making subsequent statistical allowances for method-specific biases, is the responsibility of the ecologists implementing the research. However, quantifying the extent of bias is difficult because sample populations can rarely be compared against ‘true’ populations in ecology, as entire populations are seldom sampled. Instead ecologists are forced to compare one method against another in an attempt to understand their disadvantages, and each is assessed in a ‘trade-off’ manner. This task is made substantially more difficult when respective indices of relative abundance are incompatible (e.g., CPUE and MaxN). As such, the outcome of these comparisons are often predictable, and many ecologists have suggested a combination of sampling techniques that complement each other as the most appropriate sampling strategy (Watson et al. 2005, Colton and Swearer 2010). The constraint of these types of recommendations is that multi-method sampling strategies are often too expensive and/or simply impractical and have rarely been implemented successfully, beyond methods based research, in fisheries ecology. This is particularly true for LTM programs (Bernard 2013).

5.1.4 BIASES ASSOCIATED WITH ANGLING, BRUVS AND STEREO-BRUVS

Previous comparisons between BRUVs and angling reveal a similar level of precision of count data (Willis et al. 2000), but BRUVs have been shown to be more suitable to investigate reef fish assemblages due to the selectivity of angling (Harvey et al. 2007). Bennett et al. (2009) confirmed the selective nature of angling in the TNP MPA and its inadequacy in monitoring entire fish assemblages. Numerous studies have highlighted the biases derived from angling as a result of hook size selectivity and species-specific competition for a baited hook (Millar and Fryer 1999). Despite this, Langlois et al. (2012a) found no differences in length estimates derived from stereo-BRUVs and angling.

The complexities in determining the exact area sampled when using bait, or the distance over which fish may be attracted to the bait, has the potential to introduce biases in BRUVs. These biases have been modelled extensively using MaxN and arrival time, in conjunction with knowledge of current velocities, fish swimming speeds and models of bait plume behaviour, to estimate absolute density (Cappo et al. 2004, Watson et al. 2005, Heagney et al. 2007). On the other hand, the biases have been completely ignored on the presumption that their overall effects do not justify the complexity involved in accurately predicting the area of influence (Harvey et al. 2012, Bernard and Götz 2012, de Vos et al. 2014). MaxN has therefore been regarded as a ‘conservative estimator of the relative abundance of a species’ (Harvey et al. 2012). Similarly, the calculation of optimal deployment times for BRUVs has resulted in a wide range of estimates in past studies, including 15 minute (Watson et al. 2005), 30 minute (Willis et al. 2000, Malcolm et al. 2007) and 60 minute deployment times (Watson et al. 2007, 2009, Harvey et al. 2007, Colton and Swearer 2010, Bernard 2013). Within South Africa, there has been a consensus that longer deployments of 60 minutes should be set as a method standard to aid comparability (Bernard and Götz 2012, de Vos et al. 2014) as this deployment time will provide more comprehensive ichthyofaunal surveys (Watson et al. 2007, Bernard 2013). The influence of bait type on fish assemblages has also been thoroughly assessed (Dormann et al. 2007).

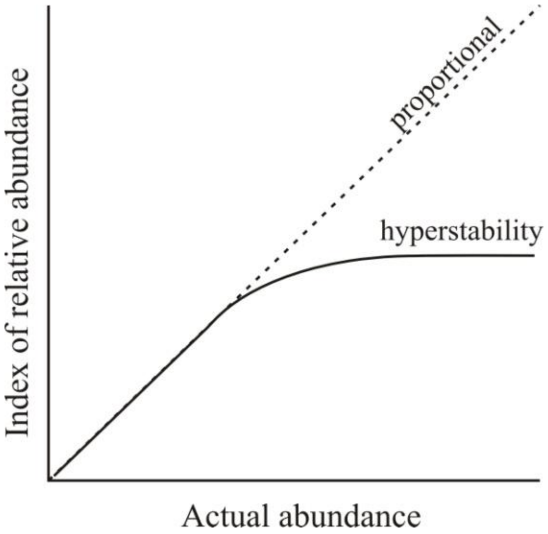


Figure 5.1: Theoretical diagram illustrating the non-linear relationship between the index of abundance (CPUE or MaxN) and actual abundance as a result of hyperstability.

Both BRUVs and angling estimates may be influenced by a phenomenon known as hyperstability, which usually occurs at high fish densities (pers. obs.). In this context, hyperstability describes the non-linear relationship between the index of relative abundance (CPUE or MaxN) and the ‘true’ abundance (Figure 5.1). Specifically, CPUE can become insensitive to further increases in abundance when handling time (time taken to retrieve fish, re-bait and cast line) is long relative to soak time (time taken for a fish to bite with the bait present in the target habitat); fish simply cannot be caught any faster. With regard to BRUVs, it is possible that high densities of fish could fill the field of view, also causing insensitivity to further increases in abundance (Willis et al. 2000, Cappo et al. 2004). Similarly, aggressive behaviour of large predators, such as roman, around the bait canister may limit the number of conspecifics or other species within the field of view, producing conservative MaxN estimates.

5.1.5 STUDY AIM

The aim of this study was a comprehensive comparison between data collected using angling and stereo-BRUVs based on each method's ability to accurately survey the ichthyofauna of the TNP MPA. To achieve this, comparisons were made on four different levels: (i) observed species diversity, (ii) relative abundance estimates, (iii) species-specific size distributions and (iv) the power of each sampling method to detect changes in species abundance. To realize these aims, multivariate analyses were performed to provide insight into method driven variability in fish assemblages, mainly through the use of graphics, ordination and PERMANOVA. Generalized Linear Models (GLMs) were coded to predict standardized indices of relative abundance for angling (CPUE) and stereo-BRUVs (MaxN). The kernel density estimate (KDE) technique was applied to assess species-specific size distribution variability between methods (Langlois et al. 2012a) in an attempt to overcome the limitations of mean length comparisons. Hook selectivity was evident in angling data and consequently accounted for in the comparison of KDEs. Finally, power analyses were conducted to assess the variability within the data and the number of samples required to detect a 10% growth in the populations over a five-year period for each method.

5.1.6 STUDY OBJECTIVES

The objectives of this study include:

- Identify differences in observed ichthyofauna (presence/absence and relative abundance) between sampling methods
- Identify species whose presence and/or abundance are most influenced by a sampling method
- Compare species-specific estimates of relative abundance across categorical variables with abundance gradients (e.g., *substrate: reef-sand*)
- Assess possible sampling-induced biases in species-specific length-frequency distributions
- Estimate the power of angling and stereo-BRUVs to detect changes in abundance of species in the TNP MPA by calculating the number of samples needed to detect a significant increase in species abundance for each sampling method

5.2 METHODS AND MATERIALS

5.2.1 DATA COLLECTION

The research was conducted on Rheeders reef complex within the TNP MPA (Section 2.1) and sample site selection was based on a stratified random scheme described in Sections 2.2.5. Two sampling methods were employed: angling, which is described in Section 2.2.2, and baited remote underwater stereo-video systems (stereo-BRUVs) described in Section 2.2.3. Sampling was conducted with four stereo-BRUVs, which were deployed simultaneously in the study area, but a minimum of 300 m apart, based on the same stratified sampling design that was employed for the angling survey. A total of 48 stereo-BRUVs samples were collected over three consecutive biannual trips.

5.2.1.1 ENVIRONMENTAL VARIABLES

Water *temperature* (average bottom temperature recorded during angling at a site) was recorded using a submersible temperature logger (HOBO Temperature Logger - Onset Computer Cooperation) that was attached to the anchor line a meter above the anchor chain when angling, and attached to the stereo-BRUVs frame when collecting video footage. Site *depth* was recorded off the boat’s echo sounder and s*ubstrate* and *profile* were inferred from a bathymetric map (Figure 2.4), and confirmed on the video footage for stereo-BRUVs sites. If the *substrate* and/or *profile* at a sampling site derived from the bathymetric map didn’t match with the information provided by the video footage for that site, preference was given to the information gathered from the video footage.

5.2.2 DATA ANALYSIS

It must be noted that there were seven years of angling data available, but only 1.5 years (three biannual sampling trips) of stereo-BRUVs data available for analyses. Spatial variables have been shown to overpower temporal variables in their influence on fish distribution in the TNP MPA (Section 3.3.3), and it was therefore decided that limiting the angling dataset to trips when stereo-BRUVs data were collected simultaneously would increase variability to undesirable levels. Therefore, all comparisons made between angling and stereo-BRUVs included all seven years of angling data.

5.2.2.1 VIDEO ANALYSIS

Analysis of stereo-BRUVs footage was conducted in EventMeasure 3.55 software (www.seagis.com.au). The analysis involved recording an index of relative abundance (MaxN), which is defined as the maximum number of individuals of a species observed in a single video frame for the entire one hour of footage. The fork length (FL) of individuals within the MaxN frame was measured digitally using EventMeasure 3.55, as described in Section 2.2.3.

5.2.2.2 MULTIVARIATE COMPARISON OF OBSERVED ICHTHYOFAUNA

Ranked species abundance (dominance) curves were produced for each sampling method to visualize the effects of selectivity on observed fish ichthyofauna. Species were ranked in decreasing order of abundance and expressed as a percentage of the total abundance. The x-axis was log-transformed to enable a better visualization (Clarke and Warwick 1994). A *t*-test was performed on the mean Shannon–Wiener indices (Shannon 2001) to determine if the diversity of the observed communities differed between angling and stereo-BRUVs.

Non-metric multidimensional scaling (nMDS) based on Bray–Curtis square-root transformed data (Field et al. 1982, Clarke and Ainsworth 1993) was carried out on abundance and presence/absence data to visually compare fish assemblages recorded by each method. Ellipses displaying 90% confidence intervals were superimposed in plots, as well as the directional weighted averages (WA) of the species that had the most influence on ichthyofaunal variability in the angling and stereo-BRUVs datasets.

Permutational multivariate analysis of variance (PERMANOVA) was employed to test for differences in the observed ichthyofauna (Anderson 2001). Due to the insufficient number of sites sampled on sand with stereo-BRUVs, PERMANOVA analyses were restricted to sites with reef substrate. As previously described in Section 4.2.2.1 and Equations 4.1-4.4, PERMANOVA is a multi-level routine that measures ordination dissimilarities based on a Euclidean distance matrix. Significance is determined through permutation, whereby data is shuffled n_{boot} times, each creating a 'pseudo' *F-statistic* (F^{π}), which is then compared to the original F-*statistic* (F) and takes the form:

$$p = \frac{No.of\, F^{\pi} \geq F}{n_{boot}} \qquad \text{(Eq. 5.1)}$$

The PERMANOVA routine was run in the R programming environment using the 'adonis' function in the 'vegan' package (Oksanen et al. 2013).

5.2.2.3 COMPARISON OF SPECIES ABUNDANCE

Generalized linear models (GLMs) were applied to compare species-specific abundance estimates between angling (CPUE) and stereo-BRUVs (MaxN). As neither CPUE nor MaxN are 'true' indices of absolute abundance, nor are they directly comparable, GLMs were independently fitted to data from each method. The underlying hypothesis is that distinct abundance gradients exist between the selected categorical variables (*Season*: summer-winter; *Substrate*: reef-sand; *Profile*: high-low; *Depth*: shallow-deep). If the two sampling methods, and their unique indices of relative abundance, are comparable, these gradients should hold true regardless of the index employed. The GLM for CPUE took the form:

$$CPUE = year + temperature + season + substrate + profile + depth + \varepsilon \qquad \text{(Eq. 5.2)}$$

and the GLM for MaxN took the form:

$$MaxN = temperature + season + substrate + profile + depth + \varepsilon \qquad \text{(Eq. 5.3)}$$

Both CPUE and MaxN were expressed as counts and models were run using a Poisson distribution. Each Poisson GLM was assessed for over-dispersion, as judged by the dispersion parameter being >1.1, and where applicable replaced by quasi-Poisson error models. In order to facilitate this comparison, species-specific abundance estimates were predicted using the independent GLMs and the results were normalized to the average predicted abundance estimate within each method. This was done for the five most abundant species (roman, dageraad, steentjie, fransmadam and smooth-hound).

5.2.2.4 COMPARISON OF SIZE COMPOSITION

Kernel density estimates (KDEs) were employed to assess variability in size distributions between sampling methods. This procedure was first described by Langlois et al. (2012a) and previously described in this study (Section 4.2.2.3). A KDE is a non-parametric density estimator that describes the shape of the distribution through two parameters: the kernel (*K*) and a smoothing parameter (*h*). These parameters are used to produce a null model, which is a KDE representation of the combined size distributions from angling and stereo-BRUVs data. Significance differences were tested by comparing the KDEs for each sampling method against the null model using a permutation test. The permutation test employed an iteration process whereby the length-frequency data are resampled 10,000 times without replacement and each resampled dataset randomly assigned to a sampling method. Kernel densities were fitted to each of these resampled datasets and compared to the null model KDE to provide a total of 10,000 comparisons each with a unique 'pseudo' *F*-statistic value, denoted as F^{π}. The *p*-value was calculated using the test statistic describe by Equation 5.1 under the assumption that if the effect of sampling method on size structure was negligible, the observed *F*-statistic value (*F*) would be similar to the average F^{π} value obtained through random shuffling of length-frequency data.

Significant deviations from the null model were indicated through *p*-values; however, the length 'regions' within each size distribution that were responsible for these deviations could only be indicated visually. This was done by producing a plot of the null model (± SE) using the 'sm.density.compare' function, upon which the observed KDEs were overlaid (Langlois et al. 2012a).

Hook selectivity in angling's size distribution data was accounted for by fitting the following logistic ogive model:

$$P(L)_{angling} = \frac{1}{1+e^{-(L-L_{50})/\delta}} \qquad \text{(Eq. 5.4)}$$

where $P(L)_{angling}$ is the proportion of fish selected in the length class L, L_{50} is the length-at-50%-selectivity and δ is the width of the ogive curve. Length-at-50%-selectivity is estimated by minimizing the sum-of-squares. The calculated selectivity of each length class in the angling data, $P(L)_{angling}$, was then applied to stereo-BRUVs data to create comparable length-frequency datasets by calculating:

$$N^*(L)_{SBRUV} = P(L)_{angling} \times N(L)_{SBRUV} \qquad \text{(Eq. 5.5)}$$

where $N(L)_{SBRUV}$ is the original stereo-BRUVs length-frequency data and $N^*(L)_{SBRUV}$ is the modified dataset that accounts for hook selectivity.

5.2.2.5 POWER ANALYSES

The statistical power of angling and stereo-BRUVs to detect changes in abundance for six common species (roman, dageraad, fransmadam, smooth-hound, steentjie and red steenbras) was determined following Monte-Carlo simulation procedures proposed by de Vos et al. (2014). The rate of population change *r* was set at 10% per year, which was assumed to be close to the plausible upper biological limit typical of the long-lived, slow-growing species under assessment (de Vos et al. 2014). Monte-Carlo simulations were run for an increasing population scenario over a timeframe of five years, with a power of 80% and a significance level of $\alpha > 0.05$.

First, GLMs were fitted to MaxN and CPUE data that incorporated *depth* as a categorical variable, as this was the variable upon which sampling stratification was based (Section 2.2.5). The GLM took the form:

$$\ln(\mu_i) = \alpha + \beta_d \times depth_i , \qquad \text{(Eq. 5.6)}$$

where α is the intercept and β_i is the estimated coefficient for *depth*. Both MaxN and CPUE were assumed to follow a Poisson distribution. In cases where over-dispersion was evident the GLM was refitted using the quasi-Poisson distribution and the variance was subsequently corrected using Var = $\mu\phi$ where ϕ is the estimated dispersion parameter (de Vos et al. 2014). The power analyses were based on the Monte Carlo approach whereby a deterministic trend in average abundance (μ_i), measured as MaxN or CPUE, was based on the following equation:

$$(\mu_i)_{z,y+1} = (\mu_i)_{z,y} \times e^r \qquad \text{(Eq. 5.7)}$$

where μ_z is the count value predicted for *depth* z and *year* y, and *r* is the rate of change (+0.1 per year). In each analysis, 500 simulations were performed to determine the power associated with a sample size *n,* where *n* is the number of samples taken per annum. Each simulation generated *n* random abundance values (μ_i) for each of the five years from the designated distribution (Poisson or quasi-Poisson). The simulations were based on a random-stratified design with even allocation of samples taken from each *depth* strata (Bernard 2013, de Vos et al. 2014). Subsequently, a GLM was fitted to the data generated from the simulations in the form:

$$\ln(\mu_i) = \alpha + \beta_d \times depth_i + \beta_r \times year_i , \qquad \text{(Eq. 5.8)}$$

where α is the intercept and β_i is the estimated coefficient for *depth,* and β_r is the estimated trend for *year*. Statistical power at any sample size *n* was calculated as the number of simulations in which β_r was found to be significant ($p<0.05$) as proportion of all the simulations completed (de Vos et al. 2014). Sample sizes were increased systematically in multiples of four, starting from four. A simple asymptotic growth function was fitted to the simulated power curve results in the form:

$$\text{power} = 1 - e^{-bn} \tag{Eq. 5.9}$$

where b is the rate of increase of power. Estimates for the number of samples required to achieve 80% power (n_{p80}) were calculated following the approach suggested by de Vos et al. (2104):

$$n_{p80} = b^{-1} \ln(1 - 0.8) \tag{Eq. 5.10}$$

All power analyses were conducted in R (R Development Core Team 2014) using the ‘MASS’ package (Venables and Ripley 2002).

5.3 RESULTS

5.3.1 COMPARISON OF OBSERVED ICHTHYOFAUNA

A total of 62 fish species were recorded during sampling, with angling recording 41 and stereo-BRUVs 52 species. Half of all recorded species (31) were common to both methods and, of the 31 species that were not in common, 21 were sampled by stereo-BRUVs and only 10 by angling. Species dominance (proportion of overall sample) differed substantially between sampling methods (Figure 5.2): roman dominated angling catches (62%) but was only the third most dominant species observed with stereo-BRUVs (10%). In contrast, steentjie was the most dominant species as indicated by stereo-BRUVs (35%), but was only ranked the fifth most dominant species in angling data contributing a mere 3% to the overall catch. The five most abundant species made up 85% and 68% of the total fish sample from angling and stereo-BRUVs, respectively. Species diversity (Shannon–Weiner index) also differed significantly between the sampling methods with stereo-BRUVs not only sampling a greater proportion of the ichthyofauna than angling, but also doing so more evenly (Figure 5.2). Appendix 5.1 provides a summary of species sampled and their associated frequencies of occurrence and relative abundance statistics.

PERMANOVA results showed significant differences in the observed ichthyofauna between sampling methods for both presence/absence (F = 44.73, p<0.001) and the relative abundance data (F = 33.54, p<0.001). These differences were also evident in the nMDS plot of the presence/absence data (Figure 5.3a) where the primary and secondary components cumulatively explained 78% of the variability. The 90% confidence interval ellipse for the angling data are located almost entirely within that of the stereo-BRUVs data, indicating that angling is only able to sample a fraction of the ichthyofauna that stereo-BRUVs sample.

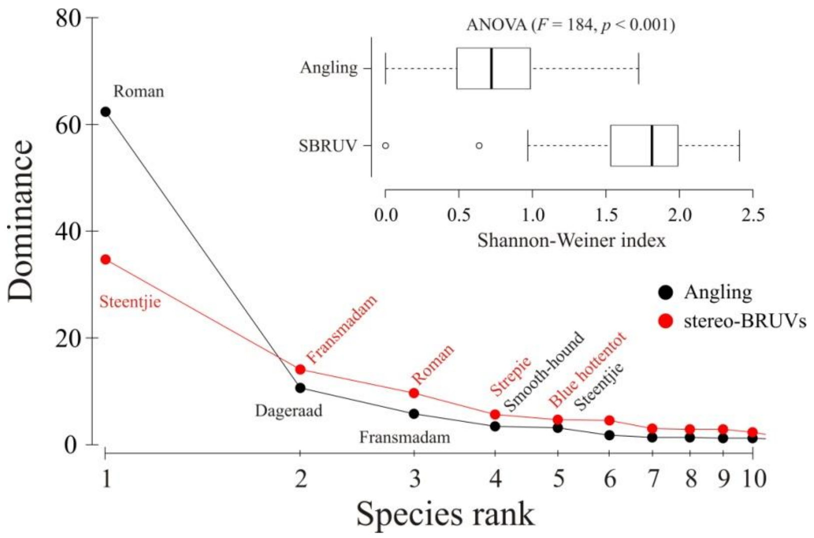


Figure 5.2: Species dominance plot and the mean site diversity (Shannon–Weiner index) of the TNP MPA ichthyofauna observed using angling and stereo-BRUVs.

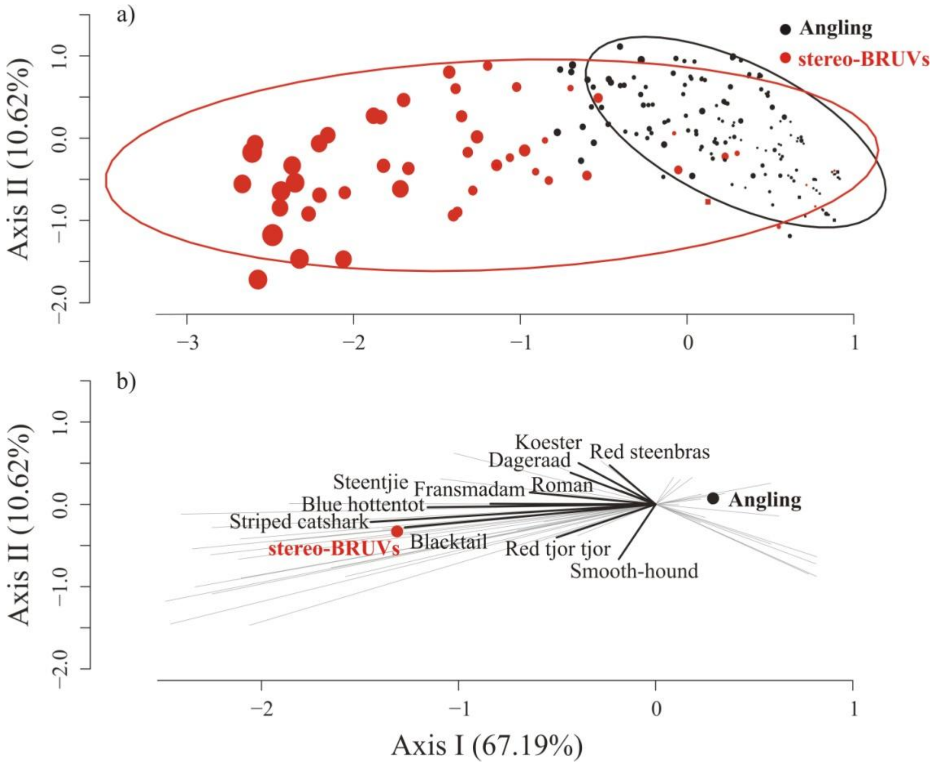


Figure 5.3: Non-metric multidimensional scaling (nMDS) plots for presence/absence data depicting (a) 90% confidence interval ellipses for angling and stereo-BRUVs. The diameter of each circle is scaled to the diversity (total number of species) at each site and, (b) directional weighted averages of the ten species that had the most influence on community assemblage variability (black lines) and the remaining species sampled (grey lines). The circles indicate community centroids for angling and stereo-BRUVs data.

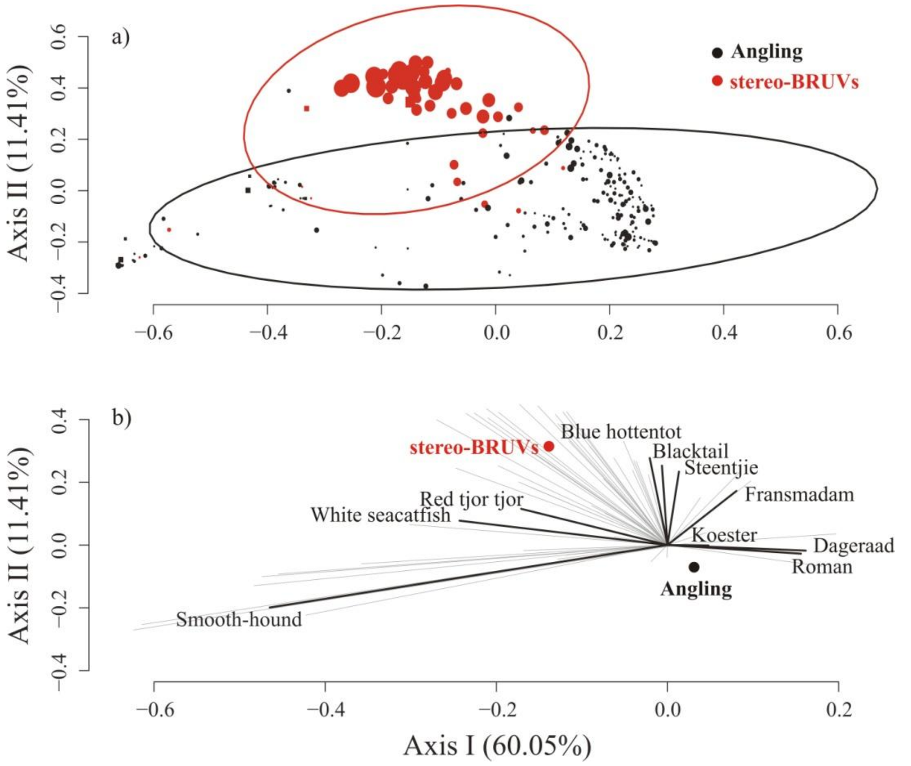


Figure 5.4: Non-metric multidimensional scaling (nMDS) plots for root-transformed abundance data depicting (a) 90% confidence interval ellipses for angling and stereo-BRUVs. The diameter of each circle is scaled to the diversity (total number of species) at each site and, (b) directional weighted averages of the ten species that had the most influence on community assemblage variability (black lines) and the remaining species sampled (grey lines). The circles indicate community centroids for angling and stereo-BRUVs data.

Further contrasts in observed fish assemblages are seen in Figure 5.3b, with angling biased towards large predatory species and stereo-BRUVs having a high occurrence of smaller generalist species.

Assessment of the directional weighted averages (WAs) of the nMDS specify that striped catshark (*Poroderma africanum*), blue hottentot (*Pachymetopon aeneum*), blacktail, (*Diplodus capensis*) and steentjie are commonly present in stereo-BRUVs, but rarely in angling data (Appendix 5.2). In contrast, the high occurrence of large carnivorous species (roman, dageraad, red steenbras and smooth-hound) drives the angling nMDS centroid apart from that of the stereo-BRUVs data.

The primary and secondary components of the nMDS on abundance data cumulatively explain 71% of the variability, suggesting significant differences in observed abundances between sampling methods (Figure 5.4a). The associated 90% confidence interval ellipses indicate that stereo-BRUVs provide more consistent abundance estimates, while variability within angling abundance data is higher. Assessment of directional WA again illustrates the bias of large predators in angling and smaller generalist fish in stereo-BRUVs data (Appendix 5.3). White seacatfish (*Galeichthys feliceps*), blue hottentot, red tjor-tjor (*Pagellus bellottii natalensis*) and blacktail are the major species influencing the position of the stereo-BRUVs data centroid, while roman, dageraad, smooth-hound and koester (*Acanthistius sebastoides*) are the major species influencing the angling data centroid (Figure 5.4b).

5.3.2 COMPARISON OF RELATIVE ABUNDANCE ESTIMATES

Predicted relative abundance estimates of all fish sampled were plotted for influential categorical variables to compare each sampling methods' ability to assess gradients in fish abundance (Figure 5.5).

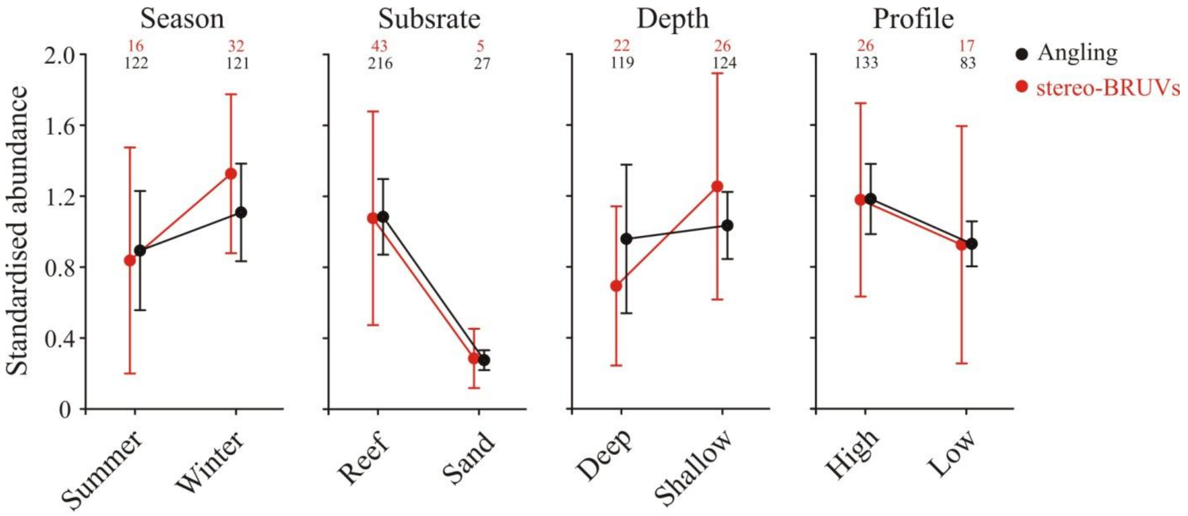


Figure 5.5: Predicted normalized mean and associated standard error (SE) of the total number of fish sampled by angling and stereo-BRUVs. To aid comparison, predictions were made between selected categorical variables that have been shown to influence fish abundance, and the predicted estimates were normalized to the mean abundance estimate of that method. Numbers represent the sample size for each method within each categorical variable.

Visual assessments reveal a high level of consistency in abundance trends for *substrate* and *profile* between methods. The gradient direction remains consistent between sampling methods for *season* and *depth*; however point estimates differ slightly, implying that angling is able to sample more fish in the *deep* areas while stereo-BRUVs are more effective in *shallow* water. Stereo-BRUVs were also able to sample a higher proportion of fish in *winter* than angling.

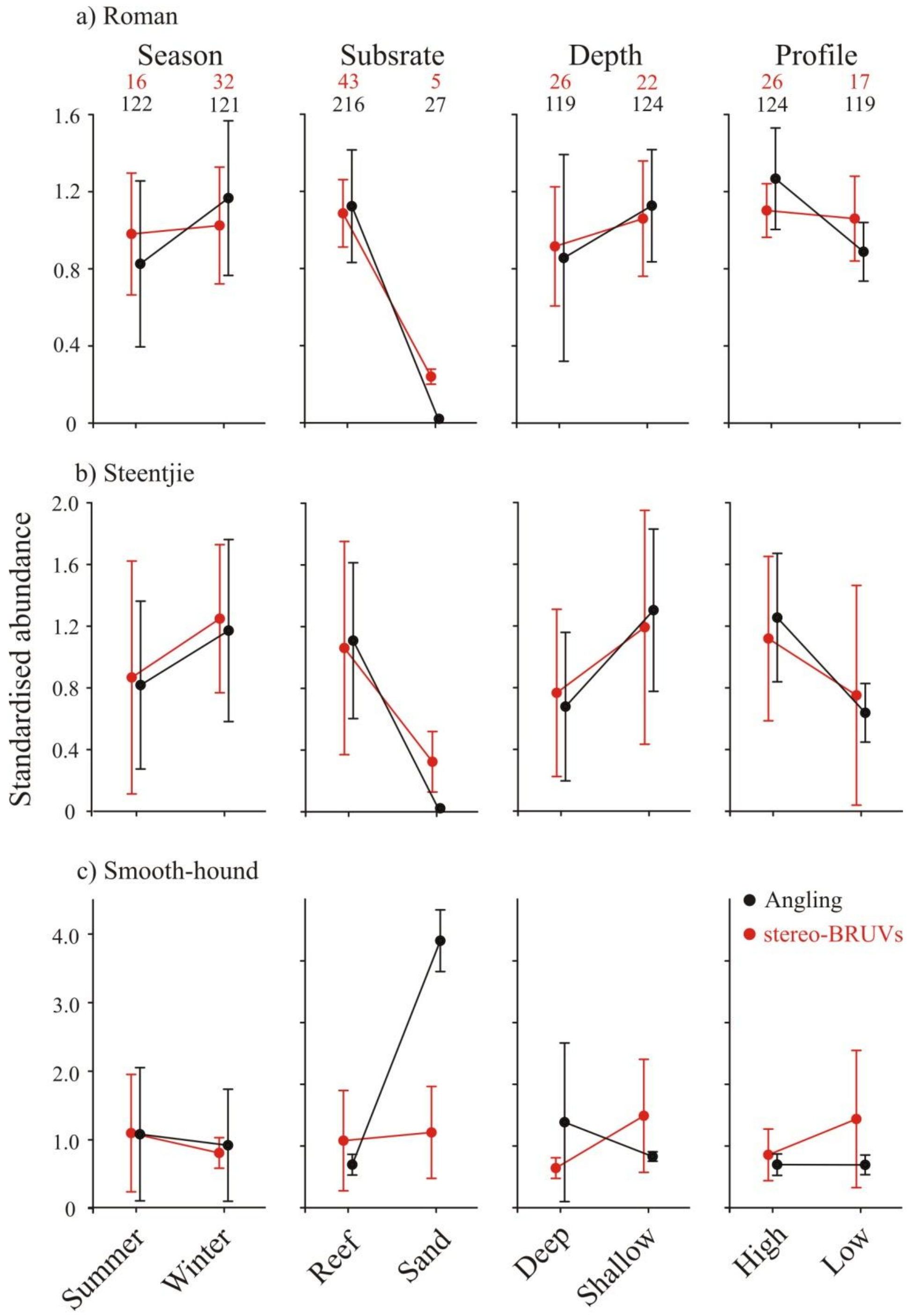


Figure 5.6: Predicted normalized mean and associated standard error (SE) of (a) roman, (b) steentjie and (c) smooth-hound sampled by angling and stereo-BRUVs. To aid comparison, predictions were made between selected categorical variables that have been shown to influence fish abundance, and the predicted estimates were normalized to the mean abundance estimate of that method. Numbers represent the sample size of each method within each categorical variable.

5.3.2.1 ROMAN

Gradient direction was consistent within all categorical variables for roman abundance, suggesting that the two methods yielded equivalent trends. Point estimates differed for *season* and *profile*, which indicate that stereo-BRUVs were less influenced by these variables than angling when assessing roman (Figure 5.6a). The inability of angling to detect roman within the categorical variable *substrate:sand* was also illustrated.

5.3.2.2 STEENTJIE

Relative abundance estimates for steentjie derived from angling and stereo-BRUVs showed a high level of consistency with regard to gradient direction and point estimates (Figure 5.6b). Again the inability of angling to record any fish within the variable *substrate:sand* was observed. The results show that steentjie abundance estimates derived from each method are generally comparable.

5.3.2.3 SMOOTH-HOUND

Smooth-hound abundance estimates were consistent between methods for *season*, however, notable differences were observed in *substrate*, *depth* and *profile* (Figure 5.6c). Abundances were heavily influenced by *substrate* in angling data, with a notably higher proportion of smooth-hounds sampled at *sand* sites. In contrast, stereo-BRUVs estimates of smooth-hound abundance were seemingly unaffected by *substrate* type. Similarly, abundance estimates at different *depths* indicated that angling sampled a higher proportion of smooth-hounds in *deep* areas than stereo-BRUVs. Reef *profile* had an influence on smooth-hound abundance estimates derived from stereo-BRUVs, but was seemingly negligible in angling.

5.3.3 COMPARISON OF SIZE DISTRIBUTIONS

5.3.3.1 ROMAN

A *t*-test revealed that the mean length of roman derived from angling (323 mm) and stereo-BRUVs (285 mm) differed significantly ($t = 5.46$, df = 160, $p<0.001$). This is in agreement with the permutation test on the KDEs, which found that the probability density functions that approximate the angling and stereo-BRUVs size distribution data differed significantly (Figure 5.7a). However, when the selectivity of angling (Appendix 5.5a) was accounted for there was no significant difference between KDEs derived from each method ($p = 0.09$).

5.3.3.2 DAGERAAD

The mean length of dageraad derived from angling (416 mm) and stereo-BRUVs (367 mm) differed significantly ($t = 1.20$, df = 33, $p<0.03$). This was corroborated with the permutation test on the KDEs, which indicated the probability density functions of angling and stereo-BRUVs differed significantly.

However, a visual assessment of the KDEs shows that the only significant deviation from the null distribution occurs in fish <200 mm in length (Figure 5.7b). This was confirmed when no significant difference was observed between KDEs (*p* = 0.14) once the selectivity of angling on dageraad was accounted for (Appendix 5.5b). The results illustrate the ability of stereo-BRUVs to sample the small 'recruitment' cohort of dageraad, while angling fails to identify these individuals due to hook selectivity.

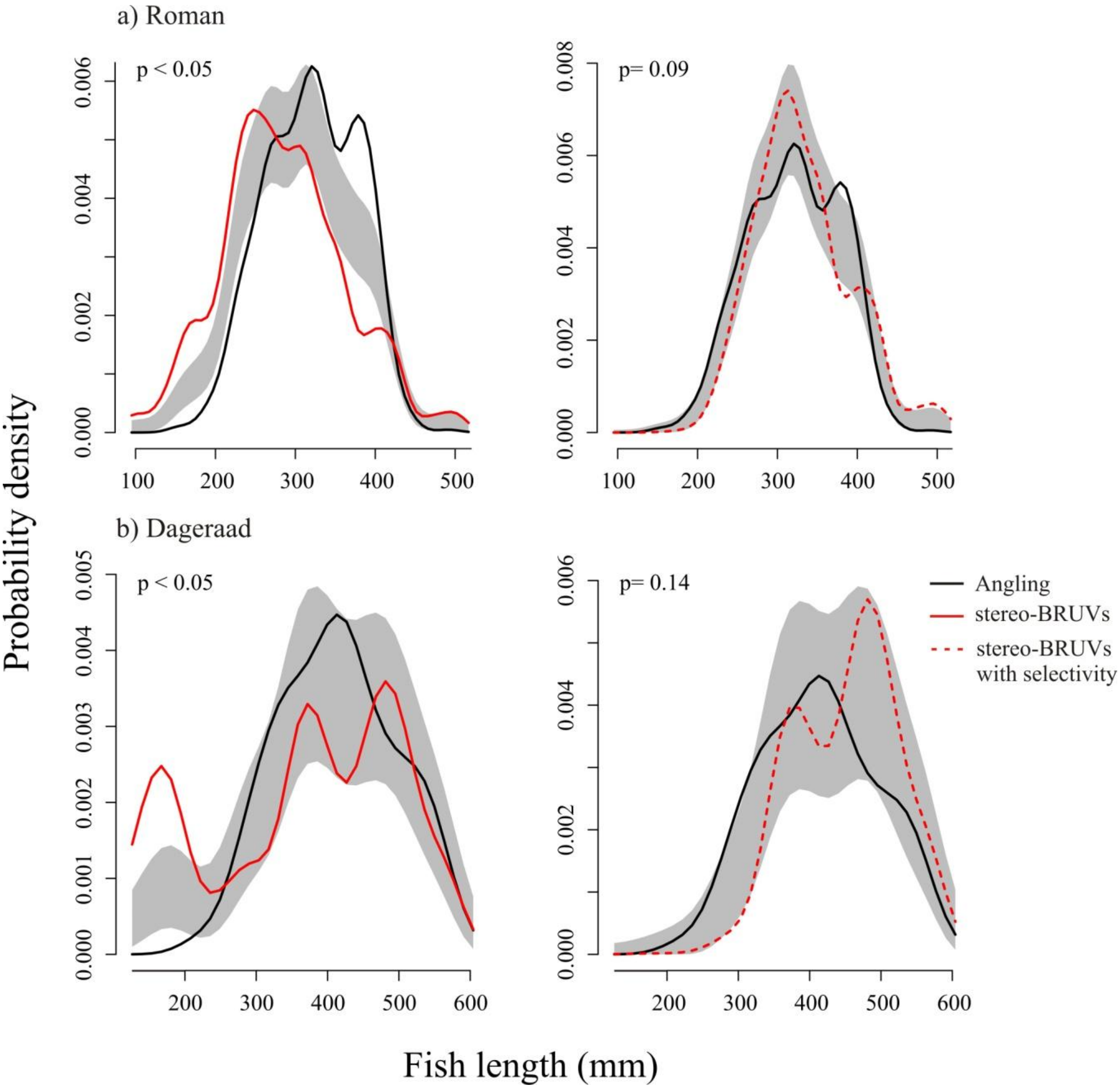


Figure 5.7: Comparisons of length-frequencies and kernel density estimates (KDE) calculated for the two sampling methods (angling and stereo-BRUVs) for the four most abundant species; (a) roman, (b) dageraad, (c) fransmadam, (d) steentjie. Graphs on the left depict direct KDE comparisons and graphs on the right include an adjusted KDE for stereo-BRUVs based on angling's length-at-50%-selectivity (dashed line). The shaded areas represent one standard error either side of the null model, indicating no difference between KDEs for each method. Significance values (*p*) based on permutation tests are also provided.

5.3.3.3 FRANSMADAM

The mean length of fransmadam derived from angling (219 mm) and stereo-BRUVs (188 mm) also differed significantly (*t* = 5.87, df = 226, *p*<0.001). Considerable deviations from the null distribution were illustrated in the KDEs, and permutation tests confirmed these differences. However, once the selectivity of angling was accounted for (Appendix 5.5c) no significant differences (*p* = 0.06) were found between the KDEs calculated for each method (Figure 5.7c). The results confirm that the selective nature of angling neglects a significant proportion of the fransmadam population through its inability to sample small individuals.

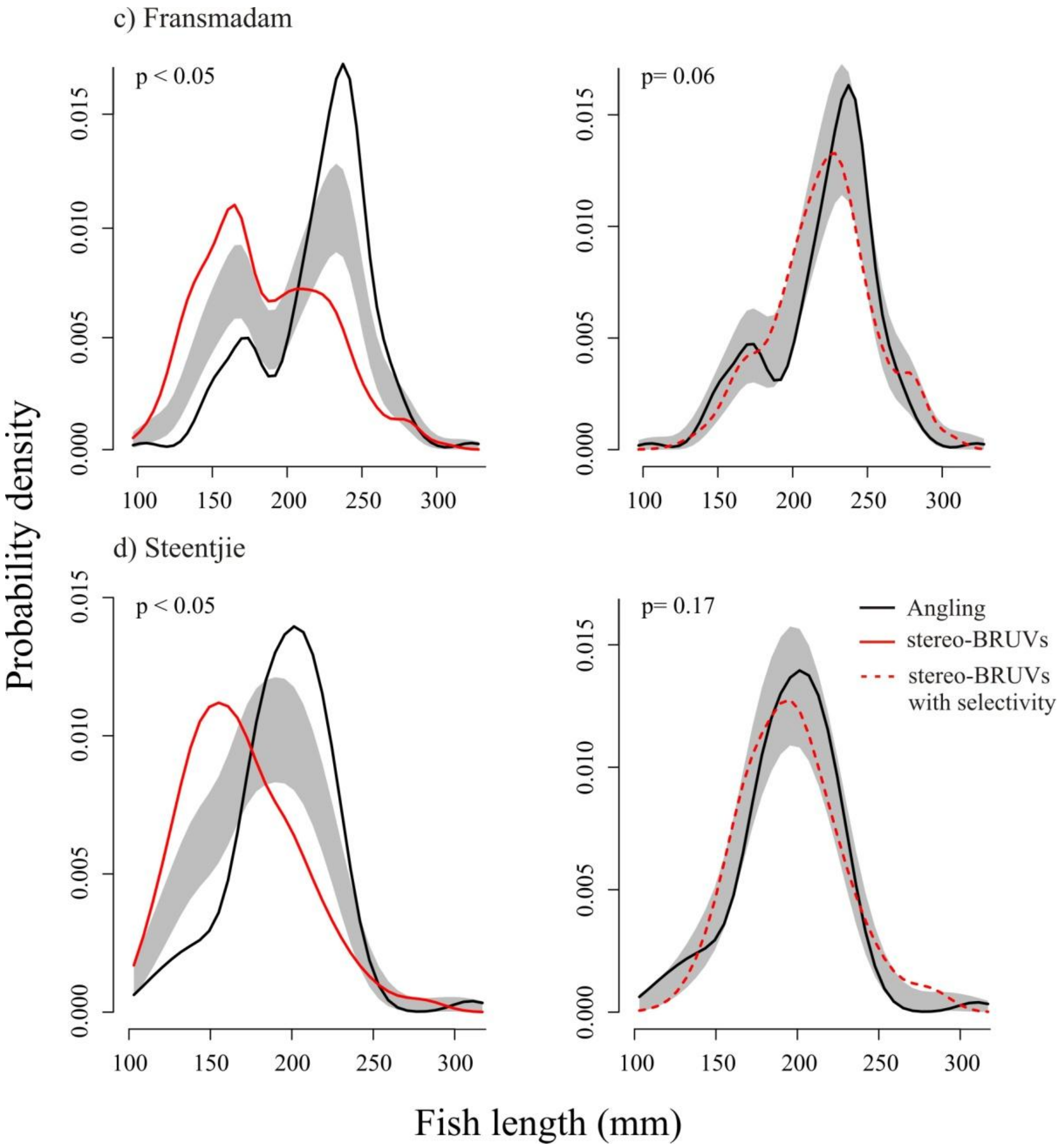


Figure 5.7 (cont.): Comparisons of length-frequencies and kernel density estimates (KDE) observed between the two sampling methods (angling and stereo-BRUVs) for the four most abundant species; (a) roman, (b) dageraad, (c) fransmadam, (d) steentjie. Graphs on the left depict direct KDE comparisons and graphs on the right include an adjusted KDE for stereo-BRUVs based on anglings length-at-50%-selectivity (dashed line). The shaded areas represent one standard error either side of the null model, indicating no difference between KDEs for each method. Significance values (*p*) based on permutation tests are also provided.

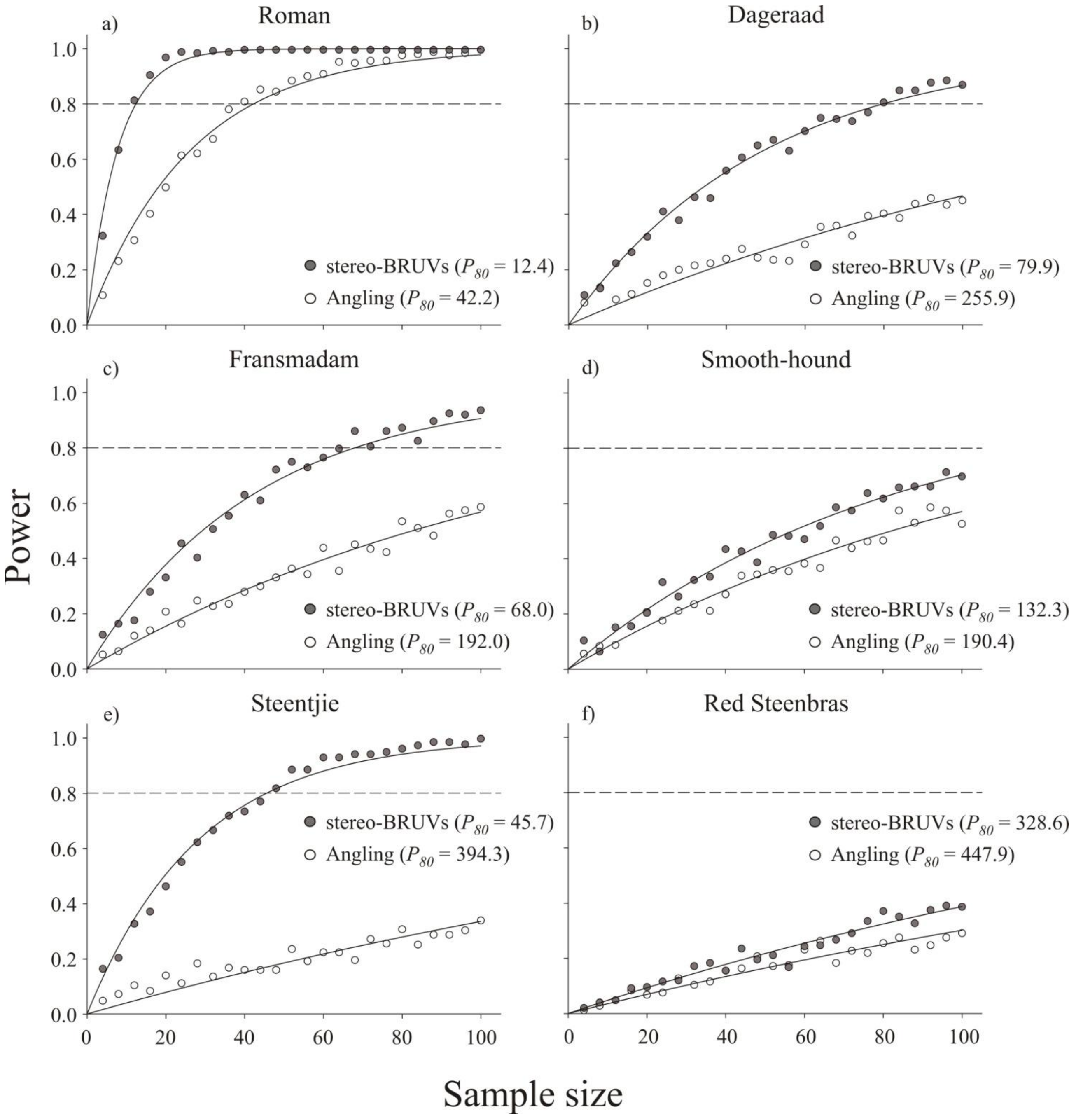


Figure 5.8: The annual sample size required to detect, with a power of 80%, a significant (α = 0.05) increase of 10% year^{-1} in the population size of six of the most abundant species (a) roman, (b) dageraad, (c) fransmadam, (d), smooth-hound (e) steentjie and (f) red steenbras in the Tsitsikamma National Park (TNP) marine protected area (MPA) over a period of five years. Dashed lines indicate a power of 80% and the corresponding number of samples per year to achieve this (P_{80}).

5.3.3.4 STEENTJIE

A comparison of length-frequencies for steentjie revealed results similar to those recorded for fransmadam. The mean length of steentjie derived from angling (195 mm) and stereo-BRUVs (178 mm) differed significantly (t = 3.05, df = 196, p = 0.001). Large deviations of each KDE from the null distribution (Figure 5.7d) suggested that choice of sampling method influenced steentjie's observed length-frequency distribution considerably, which was confirmed by permutation tests on the KDEs. However, no significant differences were found between the KDEs once the selectivity of angling (Appendix 5.5d) was accounted for (p = 0.17). Again the inability of angling to sample small individuals was highlighted within the observed steentjie length-frequency data.

5.3.4 POWER ANALYSES AND THE EFFICACY OF EACH SAMPLING METHOD

The ability of each sampling method to detect a significant increase of 10% of the sampled population per year, over a five-year period, varied notably among species. In all cases, stereo-BRUVs outperformed angling with respect to statistical power and sampling efficiency (Figure 5.8). Roman was the only species in which both stereo-BRUVs and angling met the target power criteria (P_{80}) within a feasible annual number of samples (12 and 42, respectively). With the exception of roman, the annual sample sizes needed to detect the prescribed changes in species population using angling were extremely large. Species with consistently high MaxN values, such as steentjie, fransmadam and dageraad, would require annual sample sizes of 48, 68 and 88, respectively. In contrast, species that had low MaxN scores such as smooth-hound and red steenbras would require relatively large annual sample sizes of 132 and 328, respectively.

5.4 DISCUSSION

The comparative assessment between angling and stereo-BRUVs highlighted a number of differences in the observed ichthyofauna. The dominance of roman during angling was not replicated in the stereo-BRUVs data, indicating that the abundance of this aggressive predator in the TNP MPA is likely exaggerated by angling. Stereo-BRUVs sampled a wider range of species, while also providing a more consistent index of relative abundance than that produced by angling. A comparison of relative abundance estimates indicated that both the sampling methods were, in general, detecting similar environmentally-induced trends. Length-frequency data from the two methods differed significantly amongst the predominant species. However, when the selectivity of angling was taken into account there were no significant differences, confirming that initially observed differences were a result of hook-based size selectivity. Power analyses illustrated that stereo-BRUVs produced data of a higher consistency and outperformed angling in the ability to detect significant species-specific population increases over a period of five years.

5.4.1 COMPARATIVE ASSESSMENT OF OBSERVED ICHTHYOFAUNA

Combined, the sampling methods recorded 62 species of fish, which is in accordance with the numerous studies of the TNP MPA ichthyofauna (Buxton and Smale 1984, Burger 1991, Tilney et al. 1996, Hanekom et al. 1997, Wood et al. 2000, Smith 2006, Bennett 2008, Bernard 2013). Independent assessments of diversity show that each method exhibits unique species selectivity biases, and that angling is more selective than stereo-BRUVs. Data from angling were also characterized by a significantly lower Shannon–Weiner diversity index than data derived from stereo-BRUVs. The fifth most important species according to angling data only accounted for 3% of the overall catch, confirming angling’s inherent selectivity and consequently low species diversity. The extent of this selectivity becomes more apparent when the timeframe that each method was employed for is considered: angling was used over a seven-year period, while stereo-BRUVs were only employed for one and a half years. Consequently, direct comparisons of diversity must be interpreted with care as angling’s ability to survey a community is likely to be exaggerated due to the probability of encountering more species when employed over a longer period of time. This study conclusively demonstrates that stereo-BRUVs are able to sample a significantly greater proportion of the ichthyofauna than angling. In an era where ecosytem-based management (EBM) is the foundation of ecological research (Hall and Mainprize 2004, Pikitch et al. 2004, Branch and Clark 2006), the importance of a comprehensive sampling method is paramount.

The application of ordination techniques revealed further differences in fish assemblages observed with angling and stereo-BRUVs. The 90% confidence interval ellipse for angling presence-absence data fell almost entirely within that of the stereo-BRUVs ellipse, indicating that the community sampled by angling was a subset of that sampled by stereo-BRUVs. The opposite trend was seen in abundance data, where the stereo-BRUVs ellipse was small in comparison to that of angling. This reveals that the abundance estimates from stereo-BRUVs exhibit consistency while the dispersion of samples in the angling data indicates high variability in abundance estimates. In his attempt to optimize LTM sampling protocols, Bernard (2013) suggested that ‘methods that consistently sample species at high abundances would improve diagnostic capability in long-term monitoring’, and consequently concluded that BRUVs were the preferred sampling method for LTM when compared to RUVs, UVC or angling. Results from this study confirm that stereo-BRUVs are able to sample significantly more species, with a higher consistency in relative abundance estimates, than angling and therefore substantiate the findings of Bernard (2013).

5.4.2 COMPARATIVE ASSESSMENT OF RELATIVE ABUNDANCE ESTIMATES

Direct comparisons of relative abundance estimates between angling and stereo-BRUVs were not possible due to the incompatibility of their indices (CPUE and MaxN). As a result, comparisons were limited to assessing the similarities in ‘known’ gradients of abundance caused by influential environmental variables. An example is the distinct decrease in roman abundance from areas where the substrate is predominantly reef to areas of sandy substrate (Götz 2006, Kerwath et al. 2007, Bennett 2008). A relatively high level of congruency was exhibited between GLM results indicating that both methods were consistent in their ability to identify broad abundance trends. There were, however, a few exceptions to these overall similarities. The observed difference in total fish abundance between shallow and deep sites is a direct result of the community sampled by each method. Angling has been shown to select for large predators (e.g., roman and dageraad) whose optimal depth ranges are greater than 20 m while smaller species, which were predominant in stereo-BRUVs data (e.g., steentjie and fransmadam) have optimal depth ranges of less than 20 m (Section 3.3.7). An increase in roman CPUE in winter as a result of more consistent water temperatures (Section 4.3.2) was evident in the angling data, while stereo-BRUVs data was seemingly unaffected by temperature and remained stable. In contrast to stereo-BRUVs, no reef-associated species were identified at sites with sand substrate during angling. This may be due to the comparatively larger amount of bait present when sampling with stereo-BRUVs, which could attract additional fish from patches of nearby reef. The influence of the bait plume was ignored in this study, as in previous studies (Harvey et al. 2012, Bernard and Götz 2012, de Vos et al. 2014) because of the lack of empirical evidence confirming the accuracy in calculating the area of influence. However, the distance of influence of the bait plume has been broadly estimated to range between 90 and 480 m (Ellis and DeMartini 1995, Cappo et al. 2004). Smooth-hound data derived from angling revealed a significant difference between sand and reef sites, with the former producing higher abundance estimates. In contrast, stereo-BRUVs data showed consistency in abundance estimates for smooth-hound between reef and sand sites. This difference may be explained by a hypothesis put forward by Willis et al. (2000) who noted that inter-specific competition for baited hooks would negatively affect angling data, and depress the abundance of the less dominant species. In this case, the presence of roman and dageraad at reef sites decreases smooth-hound CPUE by denying them access to baited hooks. The absence of these sparids in sandy areas results in larger smooth-hound catches. The effects of substrate may also be exaggerated due to the comparatively low number of stereo-BRUVs samples collected on sand sites.

5.4.3 COMPARATIVE ASSESSMENT OF OBSERVED SIZE STRUCTURE

A direct comparison of KDEs for angling and stereo-BRUVs identified significant differences in size distributions for all assessed species (roman, dageraad, steentjie and fransmadam). As the TNP was proclaimed in 1964, it is very plausible that the size structure of the ichthyofauna there possesses a degree of consistency, and that the observed differences in size distributions are likely to be a result of method-specific biases. Angling produced size structures that were consistently larger than stereo-BRUVs for the four assessed sparids. Visual assessment of the KDEs revealed that angling yielded a higher proportion of larger fish than stereo-BRUVs, while the smaller length-frequency bins sampled by stereo-BRUVs were absent in the angling data. These trends indicate hook-based selectivity in angling; a phenomenon that has been previously described in angling surveys on numerous occasions (Millar and Fryer 1999, Götz 2006, Wakefield et al. 2007, Bennett 2008).

The use of KDEs as an alternative method for assessing population size structures was first employed by Langlois et al. (2012a) to quantify possible differences in fish lengths derived from biases in angling and stereo-BRUVs, and the advantages of using KDEs were subsequently highlighted in Section 4.3.4. of this thesis. In contrast to the current study, Langlois et al. (2012a) did not find a significant difference in length distributions and concluded that 'unexpectedly the overall biases and selectivity of fishery-independent linefishing and stereo-BRUVs were similar'. Consequently, they paid no attention to hook selectivity. Their procedure was therefore not appropriate for this study where hook selectivity was obvious, and an additional step to account for this bias was deemed necessary because neglecting it would likely garner criticism. This technique was based on calculating length-at-50%-selectivity by fitting a logistic ogive to angling length-frequency data (Appendix 5.4), and applying this size restriction to the stereo-BRUVs data. In stark contrast to the direct comparisons, all the comparisons that incorporated selectivity had statistically similar size distributions between sampling methods, confirming the selective nature of angling against small fish. The results also demonstrate the ability of the applied statistical technique to account for selectivity biases, thereby facilitating data comparisons. Notably, there was a high level of congruency in proportions of fish over the length-at-50%-selectivity, showing both methods are able to sample very large fish with minimal bias, which has been previously described for angling data (Wirtz and Morato 2001).

Describing an accurate size distribution of a population may be impossible as all methods suffer from biases, particularly towards under sampling small individuals (Rochet and Trenkel 2003, Langlois et al. 2012a). The significance of understanding these biases is reiterated, as it is more important to employ a standardized methodology, with standardized biases, than to attempt to define the most accurate size distribution (Magnuson 1991, Langlois et al. 2012a). Numerous studies have shown that exploitation affects the size of targeted species in a population (Bianchi et al. 2000, Tetreault and Ambrose 2007, DeMartini et al. 2008, Watson et al. 2009) because removing larger individuals results in 'age truncation' (Berkeley et al. 2004). Consequently, size structure has been employed in addition to abundance estimates as a more reliable indicator of stock status (Watson et al. 2009). Importantly, this study demonstrates that stereo-BRUVs can provide robust length-frequency data that could complement age-and-length data collected by angling surveys for single species stock assessments.

The ability of stereo-BRUVs to record incoming cohorts of fish at the smallest size possible is fundamental to monitoring fish stocks as it allows for early detection of recruitment failure, providing a warning system for potential stock collapse. This is particularly true for 'no take' MPAs where a decrease in abundance is theoretically limited to emigration from the area or recruitment failure. For long-lived species, such as sparids, the timeframe needed to witness recruitment failure using angling would far exceed that required for stereo-BRUVs due to hook selectivity delaying mitigation efforts. Future efforts should be focused on comparing the effectiveness of each sampling method using techniques based on length-frequency data, as abundance data alone has been shown to be inadequate in distinguishing differences in fish populations across protection boundaries (Cappo et al. 2003, Watson et al. 2007). It is hypothesized that the results of such a comparison would further confirm stereo-BRUV's suitability over angling as a monitoring technique.

5.4.4 ABILITY TO DETECT POPULATION CHANGE

The results of the power analyses were conclusive, with all six species-specific analyses indicating that stereo-BRUVs required a smaller sample size to detect a 10% change in abundance, over a period of five years, at a power of 80% and an alpha level of 0.5. Roman was the only species for which angling data met the target power criteria (P_{80}) within 100 samples per annum. Bernard (2013) found similar results in power analyses on fish traps, angling, UVC, RUVs and BRUVs in an attempt to optimize the sampling protocol for the TNP MPA. That study concluded that BRUVs were the most (cost-) effective method for surveying subtidal reef fish communities in the warm- temperate regions of South Africa, as it needed the least number of samples to produce statistically robust data. This study corroborates the findings of Bernard (2013) and de Vos et al. (2014) and concludes that the added benefit of length-frequency data makes stereo-BRUVs the most suitable method currently available for monitoring the TNP MPA ichthyofauna.

The index MaxN is considered to provide conservative estimates of abundance for species occurring in high-densities (Willis et al. 2000, Cappo et al. 2003). This was indeed observed in roman that exhibited aggressive behaviour around the bait source. The highest number of roman sampled at a single site during angling was 36 individuals, while the highest MaxN recorded for roman was only 14. In addition, 19% of all angling sites in which roman were caught had a greater total catch of roman than the highest recorded MaxN value of 14. The proportion of zero counts for roman also differed between angling (27%) and stereo-BRUVs (12%). This may be a result of angling's sensitivity to environmental variables, such as water temperatures during upwelling events, which has been shown to influence catch rates as fish feed less. Such variables would have less of an influence on MaxN estimates as roman may still be observed by stereo-BRUVs regardless of whether they are feeding or not.

Territorial behaviour in the presence of bait is hypothesized to underestimate true abundances of high-density predators, providing conservative, and more importantly, consistent MaxN estimates. The high consistency in roman MaxN data is a result of the aforementioned 'hyperstability' that is dependent on the relationship between territorial behaviour and the area of the camera's field-of-view, both of which remain relatively constant. The consequence of artificially increased consistency is an overestimation of statistical power, as seen in the power analysis for roman. Angling has been shown to accurately sample roman abundance (Götz et al. 2007, Bennett et al. 2009, Bernard 2013), and for that reason the calculated number of samples needed to detect a significant change in roman abundance during angling holds a certain degree of confidence. Yet the calculated number of samples needed to detect a population change using stereo-BRUVs is suspiciously lower (42 and 12, respectively). These calculations are based on observed variability within the data, and therefore heavily influenced by the hyperstability bias discussed above. Theoretically, the abundance of roman would have to decrease substantially, so as to overcome the aforementioned relationship between territorial behaviour and area of view, for MaxN data to detect a decrease in a population. As previously mentioned, the ability to detect change in populations using abundance estimates alone is likely inadequate and the inclusion of size structured data is hypothesized to provide a more realistic assessment of predictive power. Chapter six provides a comprehensive comparison of predictive power between angling and stereo-BRUVs employing size structured data in the form of size distributions.

5.5 CONCLUSIONS

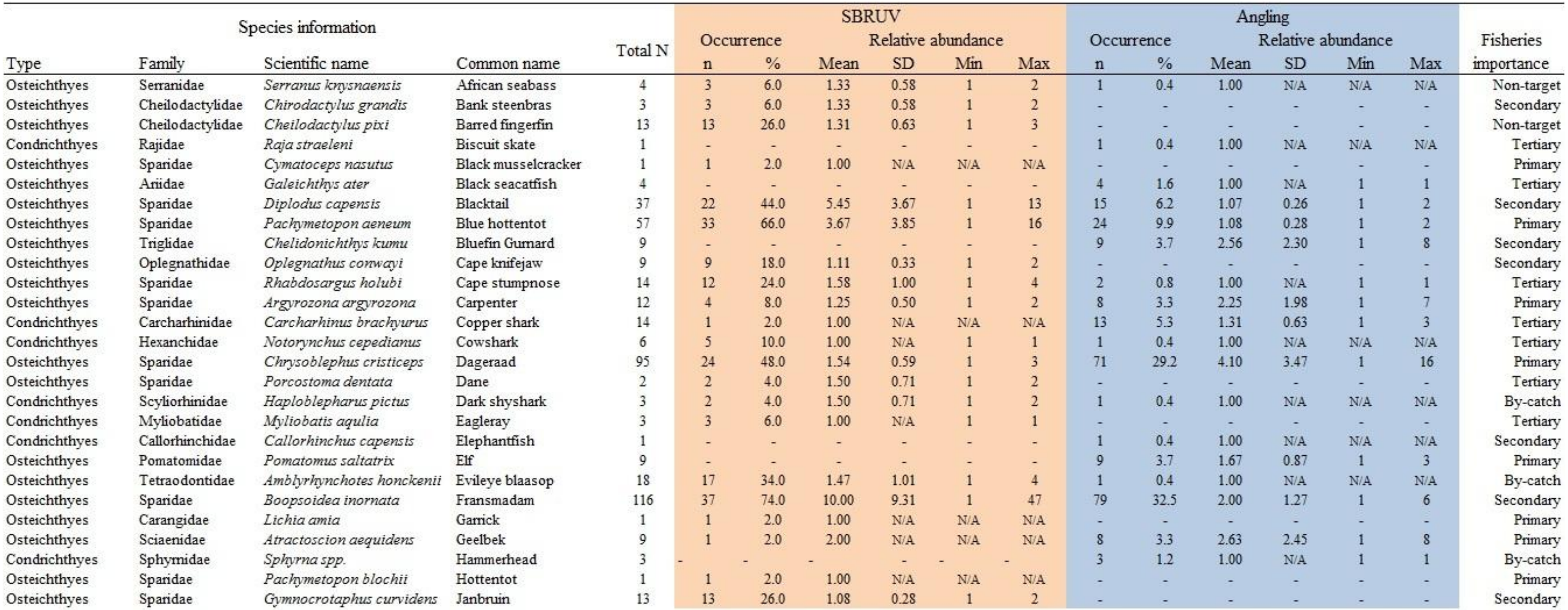
The results of the study indicate that stereo-BRUVs are a superior technique than angling for monitoring subtidal reef ichthyofauna. It must, however, be noted that cost-efficiency was not assessed, and recommendations of this study are based purely on data quality and sample size. The capacity of stereo-BRUVs to survey a significantly larger proportion of the ichthyofauna with minimal length-selectivity biases and a higher power to detect changes in abundance was illustrated. However, the importance of angling as a sampling method cannot be completely disregarded. Previous chapters of this thesis bear testimony to the data derived from angling and its ability to detect trends in specific species. Indeed, angling has been shown to be a highly effective method for surveying the roman population on reefs in the Agulhas ecoregion of South Africa (Götz et al. 2007, Bennett et al. 2009), but this effectiveness is limited to dominant predators. The need to collect physical samples, such as genetic or biomarker material, and mark-recapture experiments will always ensure that angling remains a vital tool in fisheries research. However, as marine scientists are rightfully compelled to broaden their scope of assessments to align with the mandate of ecosytem-based management, holistic and robust sampling techniques such as stereo-BRUVs will be employed more frequently.

There are inherent difficulties when comparing different methodologies, the most notable in this study being the differing indices of relative abundance. Despite standardization within each method, it was decided that these indices were still not directly comparable mainly due to differeing deployment/effort times. As such, only relative trends within data from each method could be visually compared; a limited technique that will be rightfully criticized. Future research must focus on providing a defendable technique to align datasets derived from different sampling methods and ensure indices of relative abundance are comparable. If LTM is to be truly successful, scientists cannot ignore the inevitable development of new technology that could improve sampling techniques and more importantly cost-efficiency. Sampling method standardization should not outweigh the need to employ the optimal sampling technique, but rather the optimal technique should always be employed and procedures for post-hoc standardization of the data developed. In this regard, data from LTM programmes will be of consistent high quality and provide future generations with more accurate historical trends.

Finally, when assessing potential sampling methods for LTM programmes it is essential to consider technological progress, and how possible advances may have an impact in the future. Currently, a major weakness identified in BRUVs is the extensive post-sampling analysis time (Cappo et al. 2003, Colton and Swearer 2010, Bernard and Götz 2012), with an average of 5.68 h required to extract the MaxN index from a BRUV sample collected in the TNP MPA (Bernard and Götz 2012). However, the history of BRUVs is one of technological progress that will undoubtedly continue. Storage capacity, video resolution and, most importantly, system autonomy will improve with time. Although far from complete, progress has been made with regard to system autonomy (Kilpatrick et al. 2011, Pelletier et al. 2012, Chabanet et al. 2012) and unaided species identification and measurement through the use of morphometrics (Shortis et al. 2013, Feyrer et al. 2013). Automated image analysis will be fundamental to minimizing the time needed to analyse stereo-BRUVs samples, and would rid the sampling process of the current ‘analysis bottleneck’, which is commonly experienced. Such technological advances would allow ecological research on fisheries to occur at scales that are currently impractical and unfeasible.

5.6 APPENDICES

Appendix 5.1: List of all fish species recorded during stereo-BRUVs and angling sampling. Occurrence is the number of samples in which the species was recorded (n), as well as the frequency of occurrence (%) in relation to the number of samples collected per method. Descriptive statistics of relative abundance are provided, and were calculated from the samples in which the species were recorded. Species are sorted alphabetically according to common name.



Species information				Total N	SBRUV						Angling						Fisheries importance
					Occurrence		Relative abundance				Occurrence		Relative abundance				
Type	Family	Scientific name	Common name		n	%	Mean	SD	Min	Max	n	%	Mean	SD	Min	Max	
Osteichthyes	Serranidae	*Serranus knysnaensis*	African seabass	4	3	6.0	1.33	0.58	1	2	1	0.4	1.00	N/A	N/A	N/A	Non-target
Osteichthyes	Cheilodactylidae	*Chirodactylus grandis*	Bank steenbras	3	3	6.0	1.33	0.58	1	2	-	-	-	-	-	-	Secondary
Osteichthyes	Cheilodactylidae	*Cheilodactylus pixi*	Barred fingerfin	13	13	26.0	1.31	0.63	1	3	-	-	-	-	-	-	Non-target
Condrichthyes	Rajidae	*Raja straeleni*	Biscuit skate	1	-	-	-	-	-	-	1	0.4	1.00	N/A	N/A	N/A	Tertiary
Osteichthyes	Sparidae	*Cymatoceps nasutus*	Black musselcracker	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Primary
Osteichthyes	Ariidae	*Galeichthys ater*	Black seacatfish	4	-	-	-	-	-	-	4	1.6	1.00	N/A	1	1	Tertiary
Osteichthyes	Sparidae	*Diplodus capensis*	Blacktail	37	22	44.0	5.45	3.67	1	13	15	6.2	1.07	0.26	1	2	Secondary
Osteichthyes	Sparidae	*Pachymetopon aeneum*	Blue hottentot	57	33	66.0	3.67	3.85	1	16	24	9.9	1.08	0.28	1	2	Primary
Osteichthyes	Triglidae	*Chelidonichthys kumu*	Bluefin Gurnard	9	-	-	-	-	-	-	9	3.7	2.56	2.30	1	8	Secondary
Osteichthyes	Oplegnathidae	*Oplegnathus conwayi*	Cape knifejaw	9	9	18.0	1.11	0.33	1	2	-	-	-	-	-	-	Secondary
Osteichthyes	Sparidae	*Rhabdosargus holubi*	Cape stumpnose	14	12	24.0	1.58	1.00	1	4	2	0.8	1.00	N/A	1	1	Tertiary
Osteichthyes	Sparidae	*Argyrozona argyrozona*	Carpenter	12	4	8.0	1.25	0.50	1	2	8	3.3	2.25	1.98	1	7	Primary
Condrichthyes	Carcharhinidae	*Carcharhinus brachyurus*	Copper shark	14	1	2.0	1.00	N/A	N/A	N/A	13	5.3	1.31	0.63	1	3	Tertiary
Condrichthyes	Hexanchidae	*Notorynchus cepedianus*	Cowshark	6	5	10.0	1.00	N/A	1	1	1	0.4	1.00	N/A	N/A	N/A	Tertiary
Osteichthyes	Sparidae	*Chrysoblephus cristiceps*	Dageraad	95	24	48.0	1.54	0.59	1	3	71	29.2	4.10	3.47	1	16	Primary
Osteichthyes	Sparidae	*Porcostoma dentata*	Dane	2	2	4.0	1.50	0.71	1	2	-	-	-	-	-	-	Tertiary
Condrichthyes	Scyliorhinidae	*Haploblepharus pictus*	Dark shyshark	3	2	4.0	1.50	0.71	1	2	1	0.4	1.00	N/A	N/A	N/A	By-catch
Condrichthyes	Myliobatidae	*Myliobatis aqulia*	Eagleray	3	3	6.0	1.00	N/A	1	1	-	-	-	-	-	-	Tertiary
Condrichthyes	Callorhinchidae	*Callorhinchus capensis*	Elephantfish	1	-	-	-	-	-	-	1	0.4	1.00	N/A	N/A	N/A	Secondary
Osteichthyes	Pomatomidae	*Pomatomus saltatrix*	Elf	9	-	-	-	-	-	-	9	3.7	1.67	0.87	1	3	Primary
Osteichthyes	Tetraodontidae	*Amblyrhynchotes honckenii*	Evileye blaasop	18	17	34.0	1.47	1.01	1	4	1	0.4	1.00	N/A	N/A	N/A	By-catch
Osteichthyes	Sparidae	*Boopsoidea inornata*	Fransmadam	116	37	74.0	10.00	9.31	1	47	79	32.5	2.00	1.27	1	6	Secondary
Osteichthyes	Carangidae	*Lichia amia*	Garrick	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Primary
Osteichthyes	Sciaenidae	*Atractoscion aequidens*	Geelbek	9	1	2.0	2.00	N/A	N/A	N/A	8	3.3	2.63	2.45	1	8	Primary
Condrichthyes	Sphyrnidae	*Sphyrna spp.*	Hammerhead	3	-	-	-	-	-	-	3	1.2	1.00	N/A	1	1	By-catch
Osteichthyes	Sparidae	*Pachymetopon blochii*	Hottentot	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Primary
Osteichthyes	Sparidae	*Gymnocrotaphus curvidens*	Janbruin	13	13	26.0	1.08	0.28	1	2	-	-	-	-	-	-	Secondary

Species information					SBRUV						Angling						
				Total N	Occurrence		Relative abundance				Occurrence		Relative abundance				Fisheries importance
Type	Family	Scientific name	Common name		n	%	Mean	SD	Min	Max	n	%	Mean	SD	Min	Max	
Osteichthyes	Parascorpididae	*Parascorpis typus*	Jutjaw	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Non-target
Osteichthyes	Sciaenidae	*Argyrosomus japonicus*	Kob	3	-	-	-	-	-	-	3	1.2	1.00	N/A	1	1	Primary
Osteichthyes	Serranidae	*Acanthistius sebastoides*	Koester	47	13	26.0	1.08	0.28	1	2	34	14.0	1.41	0.61	1	3	Non-target
Condrichthyes	Scyliorhinidae	*Poroderma pantherinum*	Leopard catshark	3	3	6.0	1.00	N/A	1	1	-	-	-	-	-	-	By-catch
Osteichthyes	Carangidae	*Trachurus trachurus*	Maasbanker	6	4	8.0	19.50	36.34	1	74	2	0.8	1.50	0.71	1	2	Tertiary
Osteichthyes	Scombridae	*Scomber japonicus*	Mackerel	2	-	-	-	-	-	-	2	0.8	1.50	0.71	1	2	Tertiary
Osteichthyes	Sparidae	*Pterogymnus laniarius*	Panga	21	12	24.0	1.92	1.00	1	4	9	3.7	1.22	0.44	1	2	Secondary
Osteichthyes	Haemulidae	*Pomadasys olivaceum*	Piggy	14	4	8.0	15.25	17.95	2	41	10	4.1	3.30	3.47	1	11	Tertiary
Condrichthyes	Scyliorhinidae	*Haploblepharus edwardsii*	Puffadder shyshark	30	24	48.0	1.17	0.48	1	3	6	2.5	1.17	0.41	1	2	By-catch
Condrichthyes	Odontaspididae	*Charcharias taurus*	Ragged-Tooth Shark	2	2	4.0	1.00	N/A	1	1	-	-	-	-	-	-	Non-target
Osteichthyes	Sparidae	*Petrus rupestris*	Red steenbras	37	7	14.0	1.29	0.49	1	2	30	12.3	1.13	0.43	1	3	Primary
Osteichthyes	Sparidae	*Chrysoblephus gibbiceps*	Red stumpnose	9	6	12.0	1.00	N/A	1	1	3	1.2	1.33	0.58	1	2	Primary
Osteichthyes	Sparidae	*Pagellus bellottii natalensis*	Red tjor-tjor	43	17	34.0	4.29	7.17	1	24	26	10.7	1.19	0.49	1	3	Tertiary
Osteichthyes	Clupeidae	*Etrumeus whiteheadi*	Redeye roundherring	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Secondary
Osteichthyes	Cheilodactylidae	*Cheilodactylus fasciatus*	Redfingers	14	14	28.0	1.07	0.27	1	2	-	-	-	-	-	-	Non-target
Osteichthyes	Sparidae	*Chrysoblephus laticeps*	Roman	223	45	90.0	5.62	2.31	3	14	178	73.3	9.62	6.24	1	36	Primary
Osteichthyes	Sparidae	*Lithognathus mormyrus*	Sand steenbras	10	8	16.0	1.75	1.75	1	6	2	0.8	1.00	N/A	1	1	Tertiary
Osteichthyes	Sparidae	*Cheimerius nufar*	Santer	16	11	22.0	2.18	1.40	1	5	5	2.1	1.60	1.34	1	4	Primary
Osteichthyes	Sparidae	*Polysteganus undulosus*	Seventy-four	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Non-target
Condrichthyes	Dasyatidae	*Dasyatis brevicaudata*	Shorttail stingray	3	3	6.0	1.00	N/A	1	1	-	-	-	-	-	-	Tertiary
Condrichthyes	Carcharhinidae	*Mustelus mustelus*	Smooth-hound	60	20	40.0	1.45	0.69	1	3	40	16.5	2.30	2.41	1	12	By-catch
Condrichthyes	Carcharhinidae	*Galeorhinus galeus*	Soupfin shark	8	-	-	-	-	-	-	8	3.3	1.25	0.46	1	2	Secondary
Condrichthyes	Rajidae	*Rostroraja alba*	Spearnose skate	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Non-target
Condrichthyes	Carcharhinidae	*Triakis megalopteris*	Spotted gullyshark	2	1	2.0	1.00	N/A	N/A	N/A	1	0.4	1.00	N/A	N/A	N/A	By-catch
Osteichthyes	Sparidae	*Spondyliosoma emarginatum*	Steentjie	94	41	82.0	22.34	15.06	1	50	53	21.8	1.64	1.33	1	8	Secondary
Osteichthyes	Sparidae	*Sarpa salpa*	Strepie	14	10	20.0	14.70	16.13	1	47	4	1.6	1.25	0.50	1	2	Tertiary
Condrichthyes	Scyliorhinidae	*Poroderma africanum*	Striped catshark	45	38	76.0	1.92	1.02	1	5	7	2.9	1.57	1.51	1	5	By-catch
Condrichthyes	Scyliorhinidae	*Halaelurus natalensis*	Tiger catshark	2	1	2.0	2.00	N/A	2	2	1	0.4	1.00	N/A	N/A	N/A	By-catch
Osteichthyes	Cheilodactylidae	*Chirodactylus brachydactylu*	Twotone fingerfin	26	26	52.0	1.27	0.53	1	3	-	-	-	-	-	-	Tertiary
Osteichthyes	Sparidae	*Sparodon durbanensis*	White musselcracker	1	-	-	-	-	-	-	1	0.4	1.00	N/A	N/A	N/A	Primary
Osteichthyes	Ariidae	*Galeichthys feliceps*	White seacatfish	35	19	38.0	1.53	1.02	1	4	16	6.6	2.19	2.01	1	7	Tertiary
Osteichthyes	Sparidae	*Rhabdosargus globiceps*	White stumpnose	6	6	12.0	3.17	5.31	1	14	-	-	-	-	-	-	Primary
Osteichthyes	Serranidae	*Epinephelus marginatus*	Yellowbelly rockcod	2	1	2.0	1.00	N/A	1	1	1	0.4	1.00	N/A	N/A	N/A	Primary
Osteichthyes	Carangidae	*Seriola lalandi*	Yellowtail	1	1	2.0	1.00	N/A	N/A	N/A	-	-	-	-	-	-	Primary
Osteichthyes	Sparidae	*Diplodus hottentotus*	Zebra	12	12	24	1.08	0.29	1	2	-	-	-	-	-	-	Secondary

Appendix 5.2: Weighted averages from non-metric multidimensional scaling (nMDS) on presence/absence data for the ten most important species. The weighted averages are derived from the observed ichthyofauna sampled using angling and stereo-BRUVs.

Species	**Weighted averages**		
	1	**2**	**3**
Roman	-0.177	0.163	-0.052
Smooth-hound	-0.187	-0.667	0.274
Red steenbras	-0.233	0.475	0.328
Dageraad	-0.391	0.501	0.314
Koester	-0.432	0.385	0.458
Red tjor tjor	-0.503	-0.403	-0.174
Fransmadam	-0.639	0.145	-0.285
Steentjie	-0.838	0.006	-0.194
Blue hottentot	-1.157	-0.036	0.095
Blacktail	-1.272	-0.280	-0.059
Striped catshark	-1.446	-0.215	0.224

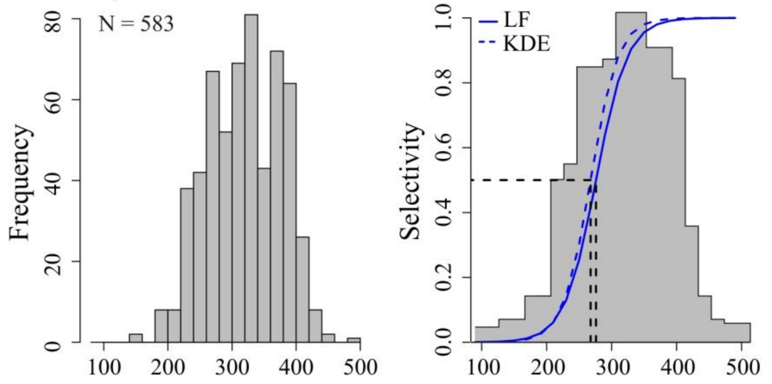
Appendix 5.3: Weighted averages from non-metric multidimensional scaling (nMDS) on abundance data for the ten most important species. The weighted averages are derived from the observed ichthyofauna sampled using angling and stereo-BRUVs.

Species	**Weighted averages**		
	1	**2**	**3**
Dageraad	0.162	-0.018	-0.059
Roman	0.156	-0.028	0.018
Fransmadam	0.081	0.172	0.057
Koester	0.048	-0.001	-0.094
Blue hottentot	0.013	0.234	0.060
Blacktail	-0.006	0.253	0.070
Steentjie	-0.021	0.277	0.074
Red tjor tjor	-0.171	0.115	-0.119
White seacatfish	-0.243	0.078	-0.306
Smooth-hound	-0.465	-0.199	0.191

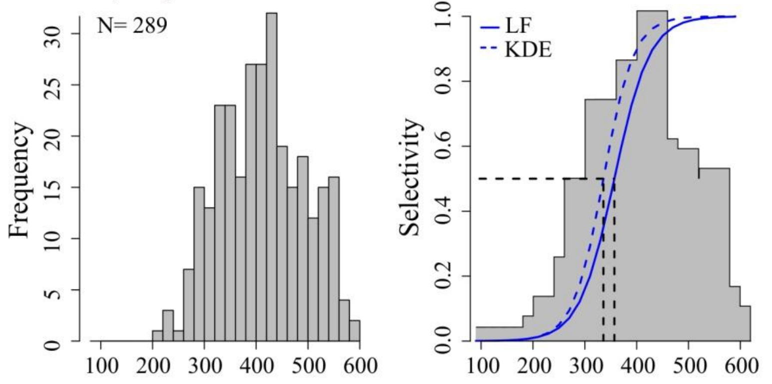
Appendix 5.4: Method-specific length-at-50%-selectivity estimates (SL_{50}) and their associated ogive width (δ) values for the four most abundant species in the TNP MPA. Calculation of these estimates is based on length-frequency data.

Species	**Angling**		**stereo-BRUVs**	
	SL_{50}	δ	SL_{50}	δ
Roman	296.3	30.5	207.8	23.3
Dageraad	357.0	33.8	149.8	12.0
Fransmadam	199.1	18.5	142.1	11.8
Steentjie	165.8	11.9	129.4	7.6

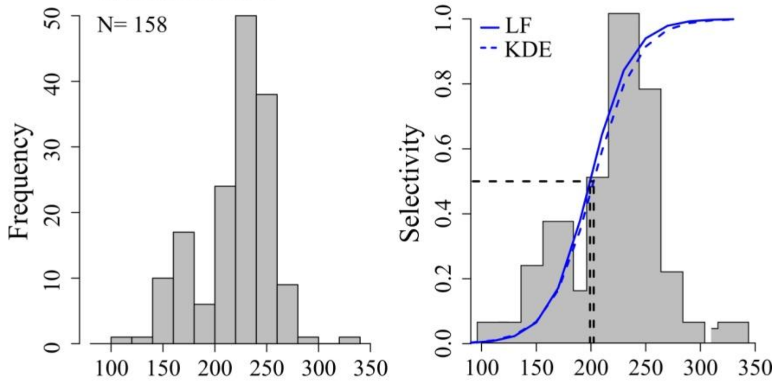
a) Roman



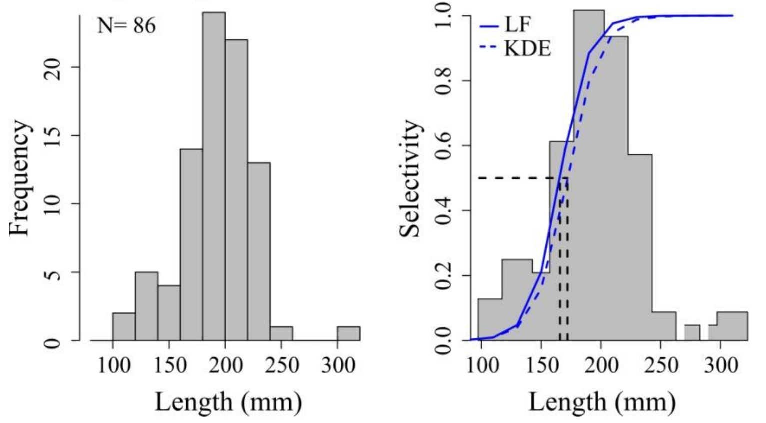
b) Dageraad



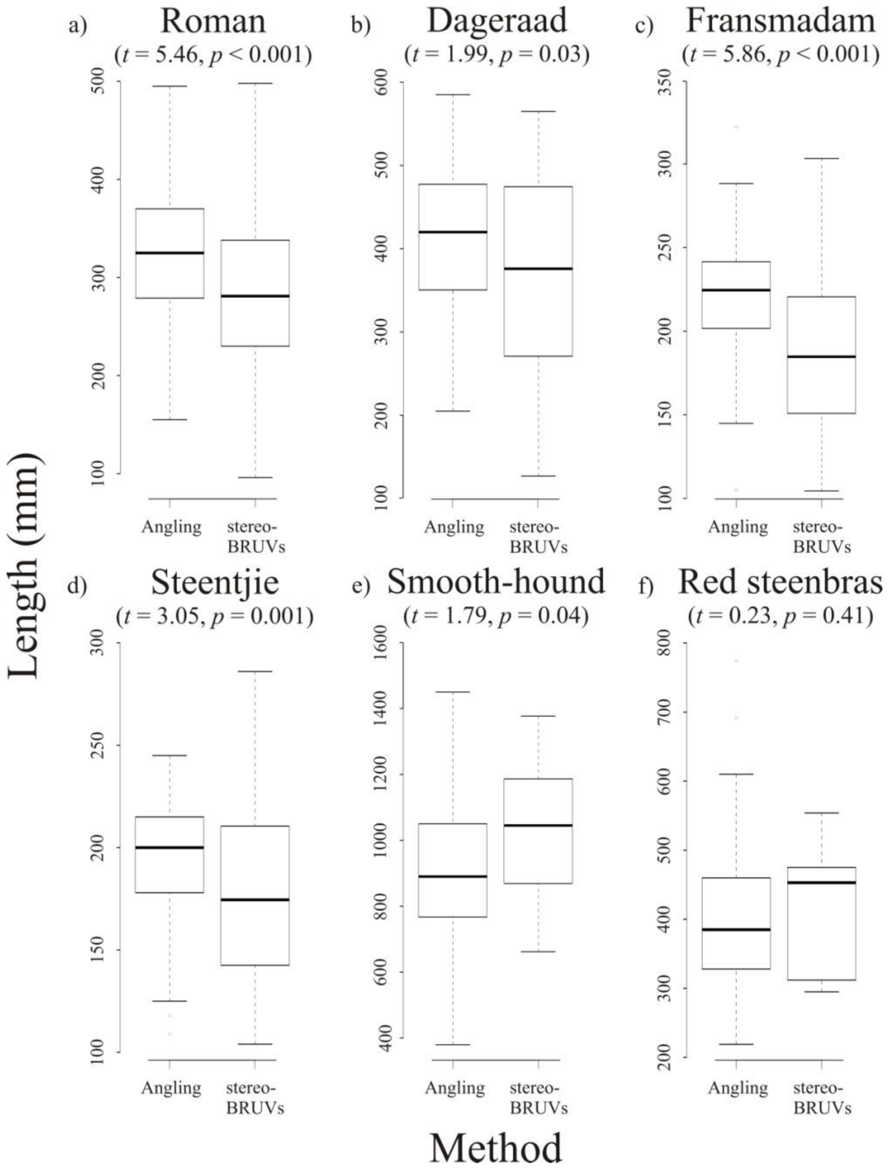
c) Fransmadam



d) Steentjie



Appendix 5.5: Length-frequency histograms and selectivity curves, with their associated length-at-50%-selectivity estimates, (dashed lines) for the four most abundant species in the TNP MPA; (a) roman, (b) dageraad, (c) fransmadam and (d) steentjie. All analyses are based on angling data. The figure depicts a comparison between length-at-50%-selectivity estimates calculated from length-frequency data and kernel density estimates (KDEs).



Appendix 5.6: Variability in mean lengths derived from angling and stereo-BRUVs data for six species; (a) roman, (b) dageraad, (c) fransmadam, (d) steentjie, (e) smooth-hound and (f) red steenbras. *T*-tests and associated levels of significance are included.

CHAPTER SIX

DEVELOPING A SIMULATION TESTING FRAMEWORK FOR EVALUATING LONG-TERM MONITORING SAMPLING METHODS

6.1 INTRODUCTION

6.1.1 A PARADIGM SHIFT FROM METHOD COMPARISON TO METHOD EVALUATION

In order to effectively monitor trends in fish populations, and design management strategies that respond to observed changes, effective and standardized methods for measuring fish abundance must be readily available. Information pertaining to method performance and suitability gained from traditional method comparisons is inherently limited, as ecologists are forced to compare one method against another in a 'trade-off' manner. The benefits of method comparisons are obvious, as stated in the previous chapter, as they provide insight into method-specific biases, which can then be accounted for. However, a distinction must be drawn between method comparison and method evaluation. Fundamentally, the word 'comparison' is defined as 'an estimate of similarities or differences' and describes an appraisal of one or more characteristics against each other. In contrast, a method evaluation aims to present a tangible appraisal of sampling-induced error specific to a method, providing a review of accuracy, precision and overall method performance. In marine ecology, method comparisons have commonly become synonymous with method evaluations, despite their obvious differences. The underlying philosophy is that the method that provides a greater spectrum of consistent information is unquestionably the superior method, as more data presumably lead to greater accuracy and precision. Numerous examples of such assumptions exist (Colton and Swearer 2010, Watson et al. 2010, Pelletier et al. 2011, Lowry et al. 2012, Harvey et al. 2012, Bernard and Götz 2012). Although some of these studies may be correct to assume that the most appropriate sampling method can be determined through comparative means alone, they are seemingly incomplete. A definitive evaluation of data accuracy is impossible if the true population is unknown. Often tentative recommendations indicate the ambiguity of evaluating a sampling method when the true population is unknown, leading to indecisive outcomes such as impractical multi-technique sampling strategies (Watson et al. 2005, Colton and Swearer 2010).

Identification of biases may be gained through traditional method comparisons, but uncertainty regarding the consequence of this bias will persist while the true population remains unknown. To overcome this uncertainty completely the population being sampled must be known; a situation that is highly improbable in subtidal marine ecology, but fortunately can be produced for the sake of method evaluation through simulation testing.

6.1.2 SIMULATION TESTING

Simulation testing involves generating data by means of an 'operating model' (Figure 6.1) and evaluating candidate estimation procedures and/or methods in terms of their ability to recover operating model properties (Thorson et al. 2012). The specific intricacies of operating models differ vastly depending on the type of data required, but in most cases these models aim to replicate natural ecosystems under prescribed conditions. The power of the procedure is that the prescribed conditions, whether environmental or managerial, can be easily modified to produce an endless number of possible permutations, known as 'scenarios'. The entire process is well suited for evaluating sampling methods as the true pattern in abundance is known (Lynch et al. 2012).

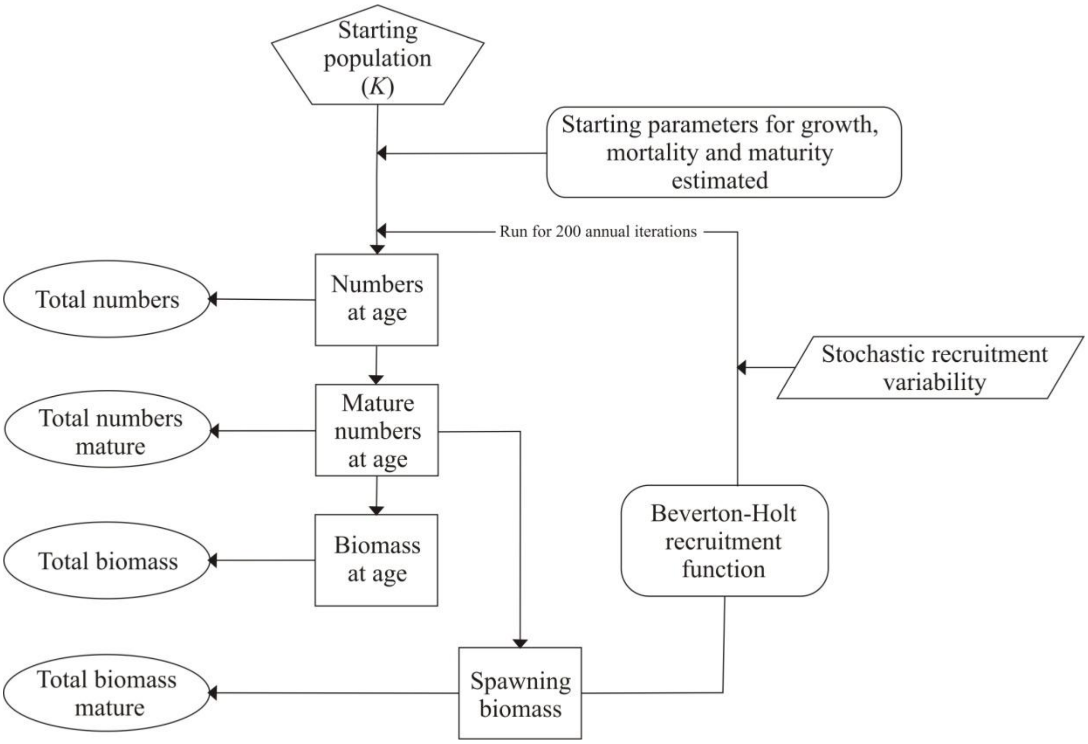


Figure 6.1: Conceptual diagram of the operating model used to generate the simulated 'true' population. An arrow from *a* to *b* indicates that *b* is derived from *a*.

Simulation testing was first developed to aid decision making within management procedures, where a set of rules that utilize pre-specified data to provide recommendations for management actions were evaluated (Butterworth et al. 1997). Since then the scope at which simulation testing is being implemented in fisheries science is growing due to scientists recognizing the importance of knowing the parameters of the population in question. To date, simulation testing has been commonly used to evaluate the ability of assessment models to accurately and precisely estimate stock conditions under a range of scenarios (Punt et al. 2002, Booth and Quinn 2006, Kell et al. 2007, Thorson et al. 2012), to evaluate ecological implications of different management strategies (Smith et al. 1999, Brown and Walker 2004, Punt 2006, Butterworth 2007, Rademeyer et al. 2007, Punt et al. 2013), to identify model misspecification (Peterman 2004, Piner et al. 2011, Deroba et al. 2014), and to quantify the effect of observation and process errors (Linton and Bence 2008, Wetzel and Punt 2011, Deroba and Schueller 2013, Winker et al. 2014b).

6.1.3 STUDY AIM

The aim of this chapter was twofold: firstly, to provide a comprehensive evaluation of the ability of angling and stereo-BRUVs to accurately describe a long-term trend within a simulated population of roman, (*Chrysoblephus laticeps*); secondly, to produce a framework for evaluating sampling methods using simulation testing. To achieve these aims, a stochastic age-structured model was developed and used as an operating model to simulate 'true' population trajectories. This 'true' population initially fluctuated around carrying capacity, resembling a situation that may be found in the Tsitsikamma National Park (TNP) marine protected area (MPA) after 50 years of protection. After an initial period of 10 years, a population decline was induced in order to test the capacity of each sampling method to correctly describe the decreasing population. Once the declining roman population had been generated it was then sampled by simulating relative abundance indices and size frequencies derived from each sampling method, which were fitted to an age-structured estimation model. Evaluating method accuracy was done by comparing the estimated abundance and spawner-biomass indices against the 'true' population trend.

6.1.4 STUDY OBJECTIVES

The objectives of this study include:

- Calculate the deviation of each method's observed data from the 'true' simulated population data
- Identify the most suitable method for long-term monitoring (LTM) of roman in TNP MPA
- Compare relative abundance estimates (CPUE and MaxN) and spawner-biomass as monitoring indices
- Assess the importance of length structured data in LTM programmes
- Provide a framework for comprehensively evaluating LTM sampling methods using simulation testing

6.2 METHODS AND MATERIALS

6.2.1 SIMULATED POPULATION DYNAMICS

Simulation testing is a powerful tool to evaluate the performance of sampling and/or statistical methods (Thorson et al. 2012, Lynch et al. 2012, Winker et al. 2014b). The advantage of this approach is that the simulated abundances are known, so that each sampling method can be tested in terms of how well it tracks 'true' abundance trends. Initially, a population of roman was created using a stochastic Age-Structure Production Model (ASPM) simulated over a 50 year 'burn in' period to replicate the theoretical 'pristine' conditions observed in TNP MPA after 50 years of protection. The final year population from this 'burn in' period was taken as the starting population for the 'true' abundance trend

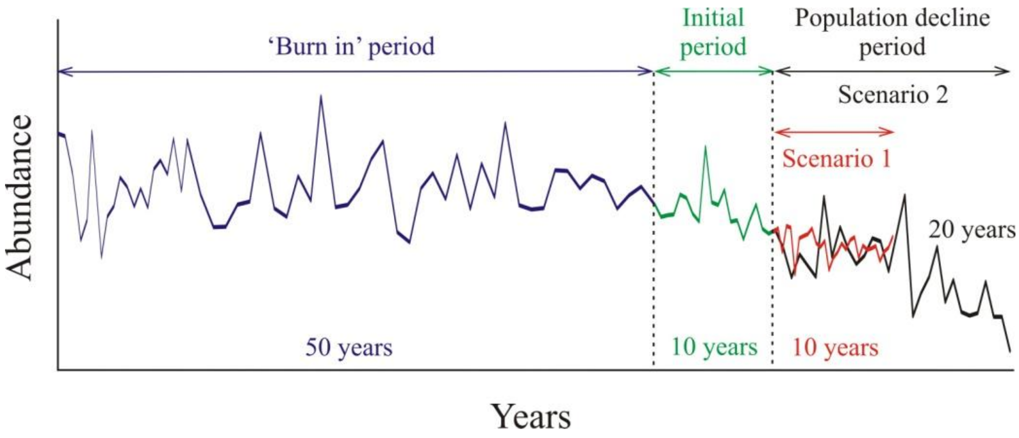


Figure 6.2: Schematic illustrating the various periods and scenarios used in producing the simulated roman population. All method assessments are based on data derived from the 'population decline period' only.

of roman, while the rest of the data from the 'burn in' period was discarded. This starting year of 'true' abundance was then further simulated over a period of 20 years (scenario 1) and 30 years (scenario 2) using the same ASPM. In each scenario, an initial 10 year period was simulated before the population decline was induced (Figure 6.2), resulting in a 10 year population decline for scenario 1, and a 20 year population decline for scenario 2. All method assessments ignore the 'initial' period and are solely based on data derived from the period after the population decline was induced. As such, scenario 1 and scenario 2 are from here on referred to as the '10-year scenario' and '20-year scenario', respectively.

The induced population decline is fundamental to evaluating sampling methods, as the primary objective of LTM programmes is to detect changes over time. Therefore method suitability ought to be evaluated using data that possess a temporal abundance gradient; a declining population in this case. The initial period of stability serves the purpose of providing a reference point against which the extent of the observed population decline, as well as the timeframe needed to realize this decline, can be compared between methods.

6.2.1.1 ASSUMPTIONS

The ASPM was reliant on three fundamental assumptions. These were: (i) prior to the implementation of any simulated condition, the roman population fluctuated around carrying capacity, K; (ii) mortality was limited to natural mortality only, which is assumed to be constant, and no mortality as a result of exploitation was included; (iii) immigration and/or emigration of roman from the study area was deemed negligible (Kerwath et al. 2007) and therefore not considered. Incorporation of these simple assumptions, which are pragmatic, creates a situation in which an observed population decline could, theoretically, only be the result of sequential annual recruitment failures. This lends itself to a robust population model free of the numerous parameter estimations necessary in traditional population modelling.

6.2.1.2 NUMBERS-AT-AGE

The ASPM model was developed to describe stochastic population dynamics that are governed by the following dynamic population equations:

$$N_{y,t} = \begin{cases} N_{y,1} = R_y & \text{if } t = 1 \\ N_{y-1,t-1}\exp(-M) & \text{if } 1 < t < t_{\max} \\ N_{y-1,t-1}\exp(-M)/(1-\exp(-M)) & \text{if } t = t_{\max} \end{cases} \qquad \text{(Eq. 6.1)}$$

where N_t is the number of individuals at age *t*, in year *y*, $t_{\min}$ is the smallest considered age class, $t_{\max}$ is the plus group, and M_t is the rate of natural mortality of a fish at age *t*.

6.2.1.3 SPAWNER-BIOMASS

Annual spawner-biomass was expressed as a function of mature males and females, as has been suggested for protogynous fish (Brooks et al. 2008). Annual spawner-biomass was calculated as:

$$SB_y = \sum_{t_{\min}}^{t_{\max}} N_{y,t} w_t \psi_t \ , \qquad \text{(Eq. 6.2)}$$

where SB_y is the spawner-biomass in year *y*, w_t is the weight-at-age *t* and ψ_t is the proportion of mature fish at age *t*.

6.2.1.4 RECRUITMENT

Recruitment was implemented as a function of the Beverton–Holt stock-recruitment relationship (Beverton and Holt 1957), which was re-parameterized by the parameter of ‘steepness’:

$$R_y = \frac{SB_{y-1}}{\alpha + \beta SB_{y-1}} \exp\left(\varepsilon_y - \frac{\sigma_R^2}{2}\right) \text{ where } \varepsilon_y \sim N\left(0, \sigma_R^2\right). \qquad \text{(Eq. 6.3)}$$

The recruitment error for year *y* is described by ε_y, which is assumed to be lognormally distributed, and σ_R is the standard deviation of the log-residuals, which was preset to a typical value of 0.5 in this case. The ‘steepness’ parameter *h* is defined as the proportion of pristine recruitment when spawner-biomass is reduced to 20% of pristine levels, such that:

$$\alpha = \frac{SB_0(1-h)}{4R_0 h} \quad \text{and} \quad \beta = \frac{(5h-1)}{4R_0 h} \qquad \text{(Eq. 6.4)}$$

For the purpose of this study, it was assumed that recruitment failure was the result of an environmental disturbance as opposed to spawner-biomass depletion. Therefore, the steepness parameter was set to *h* = 0.99, such that recruitment strength was independent of spawner-biomass.

6.2.1.5 MATURITY

The proportion of mature fish at age t was assumed to follow a logistic ogive and expressed as a function of length-at-age, such that:

$$\psi_t = \frac{1}{1+e^{-(t-tm_{50})/\delta}} \qquad \text{(Eq. 6.5)}$$

where ψ_t is the proportion of mature fish at age t, tm_{50} is the age-at-50%-maturity and δ is taken as 5% of the tm_{50} estimate. Maturity parameters required by the ASPM were obtained by fitting age data to the logistic model described above.

6.2.1.6 GROWTH

Growth in length was modelled, independent of sex, using von Bertalanffy's growth function (VBGF) of the form:

$$L_t = L_\infty(1-e^{-k(t-t_0)}) \qquad \text{(Eq. 6.6)}$$

where L_∞ is the predicted asymptotic fork length (mm), k is the Brody growth coefficient (Brody 1945) and t_0 is the theoretical age at zero length. The weight of an individual at age t was calculated using the length-weight relationship:

$$W_t = aL_t^b \qquad \text{(Eq. 6.7)}$$

where a and b are the length-weight relationship coefficients estimated from a linear regression.

6.2.1.7 SELECTIVITY

For each method, the proportion of fish selected for at length L was calculated using a two-parameter logistic model of the form:

$$S_L = \frac{1}{1+e^{-(L_i-L_{s50})/\delta}} \qquad \text{(Eq. 6.8)}$$

where S_L is the proportion of fish selected for in the length class L, L_{s50} is the length at which 50% of the fish are retained and δ is the parameter that determines the width of the logistic ogive.

The selectivity-at-age was then expressed as function of length-at-age, L_t, such that:

$$S_t = \frac{1}{1+e^{-(L_i-L_{s50})/\delta}} \qquad \text{(Eq. 6.9)}$$

Selectivity parameters required by the ASPM were obtained by fitting length data to the logistic model described above.

6.2.1.8 MORTALITY

Natural mortality (*M*) was not calculated, but rather taken as 0.19 year^{-1}, as calculated by Götz (2006) in the nearby Goukamma MPA. This mortality estimate was applied consistently throughout age and/or length classes. Fishing mortality (*F*) was considered to be zero, thus $M = Z$, where Z is total mortality.

6.2.1.9 BIOLOGICAL PARAMETERS

The biological parameters for roman are listed in Table 6.1. A number of the parameters required by the ASPM were sourced from a biological study of roman within the Goukamma MPA (Götz 2006), which lies roughly 150 kilometres west of the TNP MPA. Although Götz et al. (2008b) suggest that roman may have a slightly larger mean length in TNP (313 mm) than Goukamma (302 mm) the biological estimates derived from the Goukamma study were considered reasonable and provided the most reliable source of information available to this study. However, estimates of maturity parameters were calculated using data from this study.

Table 6.1: Biological and life-history parameters of roman (*Chrysoblephus laticeps*) used in the age-structured production model.

Parameter	Symbol	Value		Source
Natural mortality	M	0.19	year^{-1}	(Götz 2005)
Asymptotic length	L_∞	515	mm FL	(Götz 2005)
Brody growth coefficient	k	0.09	year^{-1}	(Götz 2005)
Theoretical age at zero length	t_0	-1.77	years	(Götz 2005)
Length-weight relationship coefficient	a	0.00006	G	(Götz 2005)
Length-weight relationship coefficient	b	3.0743	g mm^{-1}	(Götz 2005)
Length-at-50%-maturity	Lm_{50}	184	mm FL	This study
Age-at-50%-maturity	tm_{50}	4.27	year^{-1} FL	This study
Width of maturity ogive	δ_ψ	1.22	year^{-1} FL	This study
Age plus group	$t_{\max}$	20	years	(Götz 2005)

6.2.2 SIMULATED SCENARIO

The ASPM was employed to simulate successive recruitment failures over two separate timeframe scenarios of 20 and 30 years. The scenarios entailed an initial 10-year period of a stable ‘initial’ population followed by a 70% decrease in recruitment success (recruitment = 0.3 of the expected recruitment), implemented from year 11 of the simulation onwards. The aim was to replicate consistent recruitment failure (over a 10- and 20-year period) within a previously unexploited population, consequently leading to a decline in overall abundance. A total of 200 simulation datasets were generated for each method (angling and stereo-BRUVs), within the two different timeframe scenarios. All simulations were conducted within the statistical environment R (R Development Core Team 2014).

6.2.3 SAMPLING THE SIMULATED POPULATION

Once the simulated 'true' roman population had been generated, the next step was to sample from this population to create the observed datasets for angling and stereo-BRUVs. This was done using two steps: (i) determining the number of individuals observed at each sampling site over all simulated years and (ii) assigning a length to each observed individual.

6.2.3.1 DETERMINING THE NUMBER OF OBSERVED INDIVIDUALS

Each simulation dataset consisted of 32 sampling sites per method per year, as this is the current sampling strategy in the LTM programme (Section 2.2.5). The number of observed individuals $I_{y,i}$ for method *i* in year *y*, was calculated as:

$$I_{y,i} = q_i EN_{y,i} \qquad \text{(Eq. 6.10)}$$

where q_i is the mean number of individuals sampled by method *i*, calculated from data collected in the TNP MPA. The mean index of abundance (CPUE or MaxN) was then generated by randomly drawing from a quasi-Poisson distribution as a function of $\mu = I_{y,i}$ and the observed dispersion parameter ϕ_i such that each observation follows $y_{y,i} \sim qpois(\mu_i \phi_i)$. The dispersion parameter ϕ_i originated from a Generalized Linear Model (GLM) fitted to abundance data for each method (Table 6.2). Expected numbers (*EN*) refers to the number of individuals in the 'true' population that are available for sampling, and is calculated as:

$$EN_{y,i} = \sum_t N_{y,t} S_{t,i} \exp(M/2) \qquad \text{(Eq. 6.11)}$$

where N_t is the total number of individuals in the 'true' population in year *t*, $S_{t,i}$ is the selectivity of method *i* and *M* is the natural mortality.

6.2.3.2 DETERMINING THE LENGTH OF OBSERVED INDIVIDUALS

Once the number of individuals observed per sampling site was generated, a length had to be assigned to each individual. Again, this was a two-step process whereby an age had to be assigned to an individual before a length could be derived. The age of an individual was assigned using a multinomial approach whereby the known age-frequency distribution of each method was used to determine the probability of a simulated observed individual falling within a given age. This was calculated as a proportion of the total population, such that $p_1 + p_2 + p_3 + ... = 1$ where p_1 is the probability of an individual being assigned to age 1. Based on these probabilities, a simulated observed individual was randomly assigned an age using the 'rmultinomial' package in R. This package generates random samples from multinomial distributions, where both *n* and *p* may vary among distributions.

Once the age of an individual was known, lengths could be generated for these individuals using a two-step process. First, the mean-length-at-age was calculated from the VBGF. This, however, created an ecologically inaccurate dataset, which was limited to lengths corresponding to the mean-length-at-age with zero variability. To overcome this, the final length of an individual was generated by randomly drawing from a normal distribution as a function of the mean-length-at-age $\mu_t = L_t$ and its associated observed $\mathrm{CV_L}$ of 0.1, such that each observation follows $L_t \sim norm(\mu_t, CV_L)$. This enabled the creation of a simulated observed length-frequency dataset comparable to the actual TNP MPA length-frequency data.

6.2.3.3 MODEL PARAMETERS USED TO OBTAIN THE OBSERVED DATASETS

The method-specific parameters employed to determine the number and length of simulated observed individuals are listed in Table 6.2.

Table 6.2: Sampling method parameters for roman (*Chrysoblephus laticeps*) used in the age-structured estimation model.

Parameter	Symbol	Angling		stereo-BRUVs	
Natural mortality	M	0.19		0.19	
Equilibrium spawning biomass	K	1000		1000	
Steepness parameter	h	0.99		0.99	
Catchability coefficient	q	7.06		4.98	
Dispersion parameter	ϕ	5.22		1.43	
Length-at-50%-selectivity	S_L	242	mm FL	182	mm FL
Width of selectivity ogive	δ_S	15	mm FL	22.5	mm FL
Coefficient of variation for L_t	$\mathrm{CV_L}$	0.1		0.1	

6.2.4 ESTIMATION FRAMEWORK

The estimation model was of the same form as the ASPM used as operation model but was coded and fitted using AD-Model Builder (Fournier et al. 2012), called from R. The estimable parameters were q_i, M, $CV_{L,}$, and the observation variance σ^2 (Table 6.2). The choice of K is theoretically arbitrary for this study (here set to K = 1000), because the trends of relative indices (CPUE and MaxN) were normalized by their means to aid comparisons. Similarly, the steepness parameter was not estimated, but fixed to h = 0.99, thereby assuming that recruitment failure was a result of environmental processes rather than spawner-biomass depletion.

The negative of the log-likelihood (-ln*L*) included three contributions: (i) fitting the relative abundance index (CPUE or MaxN) and (ii) fitting the corresponding length data and (iii) minimizing the recruitment residuals.

6.2.4.1 ABUNDANCE INDICES

The contribution of the relative abundance index $I_{y,i}$ for year *y* and method *i* to the negative of the log-likelihood function is based on the assumption that the index is lognormally distributed about its expected value, so that:

$$-\ln L^{I} = \frac{1}{2\hat{\sigma}^{2}} \sum_{y=1}^{Y} (\ln(I_{y,i}) - \ln(\hat{q}_{i}\ EN_{y,i})) \qquad \text{(Eq. 6.12)}$$

where $EN_{y,i}$ is the exploitable numbers of fish available to the sampling method, $\hat{q}_i$ is the estimable catchability coefficient for method *i* and $\hat{\sigma}^2$ is the estimable observation variance.

6.2.4.2 LENGTH DATA

The contribution of the length composition information from method *i* to the negative log-likelihood function is based on the assumption that the catch proportions at length are multinomially distributed, such that:

$$-\ln L^{Len} = -\sum_{y}\sum_{l} N_{y}^{Len,i} \lambda_{l,y,i} \ln(\hat{\lambda}_{l.y,i}) \qquad \text{(Eq. 6.13)}$$

where $\lambda_{l,y,i}$ and $\hat{\lambda}_{l.y,i}$ denote the observed and predicted proportions of fish in length class *l* for year *y* and method *i* and $N_{y,i}^{Len}$ is the effective number of length samples.

To convert the predicted numbers-at-age to predicted numbers-at-length, $\hat{\lambda}_{l.y,i}$, an age-length conversion matrix (ALK) was constructed in the form of the Gaussian density function:

$$\mathrm{ALK}_{t,l} = \frac{1}{\sqrt{2\pi(CV_L L_t)}} \frac{\exp(l - L_t)}{2(CV_L L_t)} \qquad \text{(Eq. 6.14)}$$

where L_t is the predicted length-at-age given the growth function, *l* is the length class and CV_L is the coefficient of variation for L_t. The matrix was rescaled to sum to one over all ages, so that the predicted length compositions for each method in year *y* can be calculated as:

$$\hat{\lambda}_{l,y,i} = \frac{S_{l,y,i} \sum_{t=1}^{t_{\max}} \mathrm{ALK}_{t,l} N_{t,y}}{\sum \left(S_{l,y,i} \sum_{t=1}^{t_{\max}} \mathrm{ALK}_{t,l} N_{t,y} \right)} \qquad \text{(Eq. 6.15)}$$

where $S_{l,i}$ selectivity at length class *l* for method *i*.

6.2.4.3 STOCK-RECRUITMENT RESIDUALS

Deviations about the stock–recruitment relationship were assumed to be lognormally distributed. The contribution of the recruitment residuals ε_y to the negative log-likelihood function is given by:

$$-\ln L^{SR} = \sum_y \frac{{\varepsilon_y}^2}{2\sigma_R^2} \qquad \text{(Eq. 6.16)}$$

where σ_R is set to 0.5 for all stocks under assessment.

6.2.4.4 DATA GENERATION

For each simulation iteration (n_{sims} = 200), abundance and spawner-biomass data were generated and stored in matrices according to simulation year (column) and simulation iteration (row). This resulted in four matrices for abundance: (i) CPUE fitted, (ii) CPUE observed, (iii) MaxN fitted, and (iv) MaxN observed, and three matrices for spawner-biomass data: (i) 'true', (ii) angling estimated and (iii) stereo-BRUVs estimated. Evaluation of each method for accuracy and precision was based on these matrices.

6.2.5 METHOD PERFORMANCE EVALUATION

6.2.5.1 EVALUATING DEVIATIONS FROM THE 'TRUE' POPULATION TREND

To determine the ability of each sampling method to accurately detect population changes, the estimated spawner-biomass ($\hat{r}$) trends were compared to the 'true' spawner-biomass trend for roman (r). As such, total deviation of observed spawner-biomass from the 'true' trend was quantitatively evaluated to determine the accuracy of the estimated trends. To evaluate this, estimated and 'true' spawner-biomass were normalized to their mean, and simple linear regressions were fitted in the form:

$$\overline{SB}_y = a + \hat{r}y + \varepsilon \qquad y = 1,2,.......,N_{yrs} \qquad \text{(Eq. 6.17)}$$

and,

$$SB_y = a + ry + \varepsilon \qquad y = 1,2,.......,N_{yrs} \qquad \text{(Eq. 6.18)}$$

where $\overline{SB}_y$ is the estimated spawner-biomass, SB_y the 'true' spawner-biomass for roman in year y, a is the intercept term and N_{yrs} is the number of simulated years.

Differences in the two linear trends were calculated using a root-mean-squared error (RMSE) (Thorson et al. 2012, Winker et al. 2014b). This method measures the deviation of the estimated trend from the 'true' trend in every simulation run, providing an error distribution in the form:

$$RMSE(r)=\sqrt{\frac{1}{n_k}\sum_{k=1}^{n_k}(r_k-\hat{r}_k)^2} \qquad Error=r_k-\hat{r}_k \qquad \text{(Eq. 6.19)}$$

where RMSE(r) is the error distribution that determines accuracy of the estimated spawner-biomass trend $\hat{r}_k$ compared to the true trend r_k for simulation run k, where n_k indicates the number of simulations. This procedure was conducted for each method, and the one which produced, on average, the lowest cumulative estimation error was considered the most accurate sampling method.

The goodness-of-fit of annual observed (a_y) and fitted ($\hat{a}_y$) CPUE and MaxN indices, as well as the accuracy of annual estimated spawner-biomass ($s\hat{b}_y$) to true spawner-biomass (sb_y) were also evaluated. The indices were rescaled through normalization by the mean and compared using the root-mean-squared error method (Thorson et al. 2012, Winker et al. 2014b) of the form:

$$RMSE(y)=\sqrt{\frac{1}{n_k n_y}\sum_{k=1}^{n_k}\sum_{y=1}^{n_y}(\hat{I}_{y,k}-I_{y,k})^2} \qquad \text{(Eq. 6.20)}$$

where RMSE(y) is the error distribution that determines accuracy of the annual observed estimates in relation to the fitted estimates. Here, $I_{y,k}$ is the normalized abundance (CPUE or MaxN) or spawner-biomass, n_k indicates the number of simulation runs and n_y is the number of years in the simulation. The fitted normalized abundance index $\hat{I}_{y,k}$ is calculated such that:

$$\hat{I}_{y,k}=\frac{a_{y,k}}{\frac{1}{n_y}\sum_{y=1}^{n_y}a_{y,k}} \qquad \text{(Eq.6.21)}$$

or, in the case of spawner-biomass:

$$\hat{I}_{y,k}=\frac{sb_{y,k}}{\frac{1}{n_y}\sum_{y=1}^{n_y}sb_{y,k}} \qquad \text{(Eq. 6.22)}$$

where k is the simulation run and y is the simulation year. As before, comparisons of the goodness of fit for annual estimates of observed abundance (a_y) and spawner-biomass (sb_y) were achieved by calculating the difference in RMSE(y) between the normalized CPUE and MaxN. The method that produced, on average, the lowest cumulative estimation error was considered the most accurate method for abundance and spawner-biomass estimation.

6.3 RESULTS

6.3.1 OBSERVED DATA GENERATION

As an example, a single simulation run from the model is illustrated in Figures 6.3 and 6.4, for observed and fitted abundance indices (CPUE and MaxN) and estimated and 'true' spawner-biomass over the 10- and 20-year scenarios, respectively.

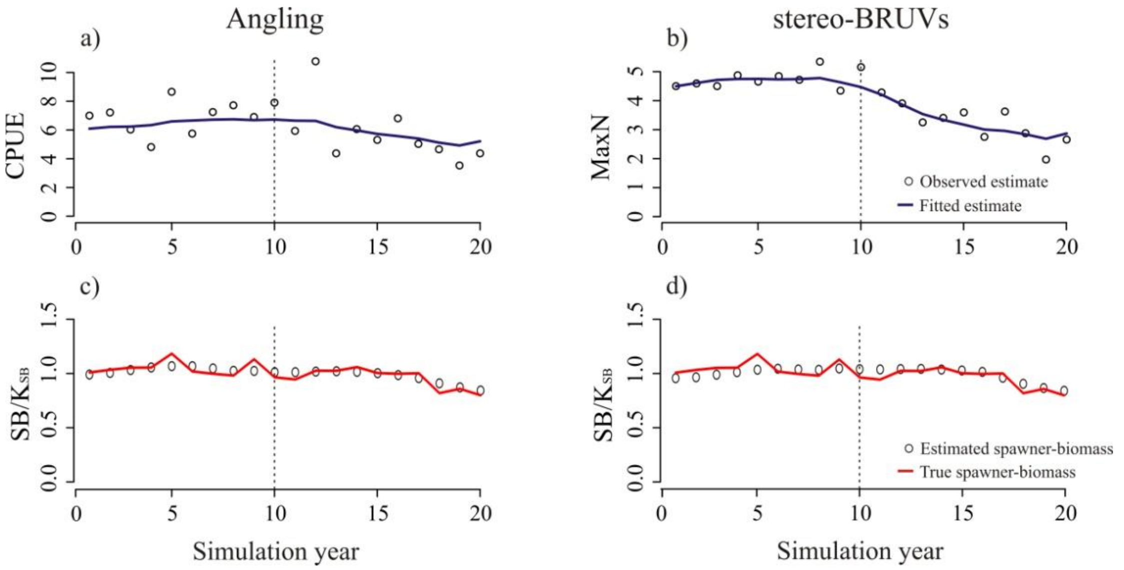


Figure 6.3: An example of observed and fitted indices of roman relative abundance, estimated and 'true' spawner-biomass for angling (a,c) and stereo-BRUVs (b,d) using the 10-year simulation scenario. Spawner-biomass was normalized to the spawner-biomass at carrying capacity (K_{SB}). The dashed line represents the year at which the simulated recruitment failure was introduced to the model.

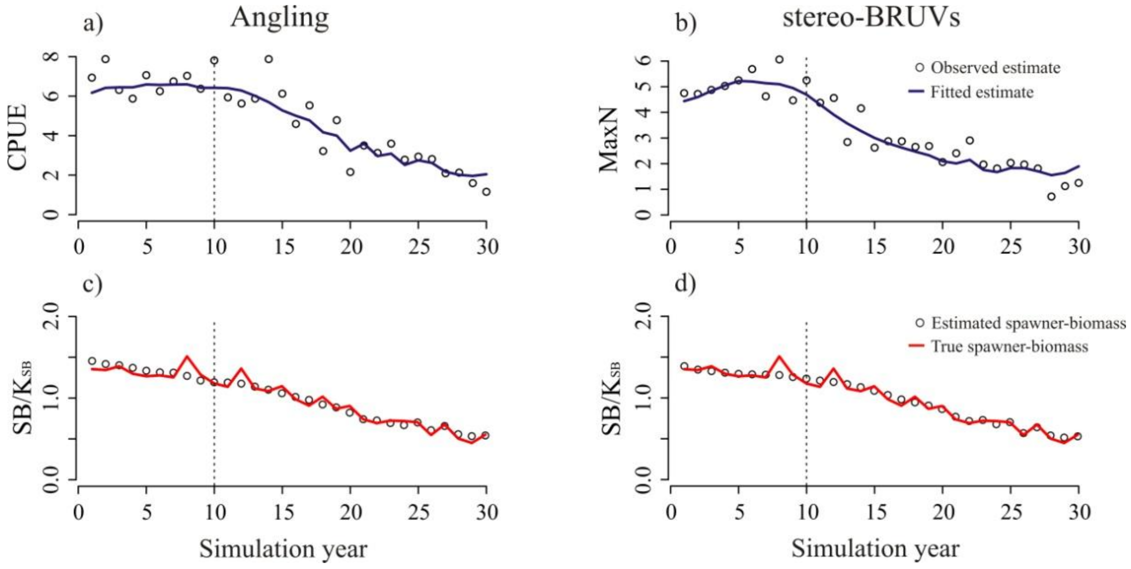


Figure 6.4: An example of observed and fitted indices of roman relative abundance, estimated and 'true' spawner-biomass for angling (a,c) and stereo-BRUVs (b,d) using the 20-year simulation scenario. Spawner-biomass was normalized to the spawner-biomass at carrying capacity (K_{SB}). The dashed line represents the year at which the simulated recruitment failure was introduced to the model.

The 10-year scenario example illustrates that the induced population decline was more pronounced in MaxN data than in CPUE, due to a 'lag' effect of increased selectivity in angling. As expected, abundance and spawner-biomass estimates derived from the 20-year scenario example (Figure 6.4) illustrated a more prominent population decline. Specifically, the increased ability of angling to detect this decline was evident, as observed CPUE data from the 10-year scenario possessed notably high variability. In all cases, normalized spawner-biomass (SB/K_{SB}) estimates were inherently less variable than abundance indices. These examples show that 20 years is a sufficient period of time for the simulated roman population decline to be identified by each method given the scenario of 70% decline in recruitment success (recruitment = 0.3 of expected value). An example of spawner-biomass and abundance inter-annual variability within the observed population is presented in appendices 6.1 and 6.2, respectively.

6.3.2 EVALUATION OF METHODS USING POPULATION TRENDS

6.3.2.1 ABUNDANCE ESTIMATES

Predicted declines based on the fitted and observed abundance estimates (CPUE and MaxN) are illustrated in Figure 6.5. A distinct selectivity 'lag' is apparent in CPUE data as the induced decline is only observed from year 14 onwards, but is evident as early as year 11 in MaxN data.

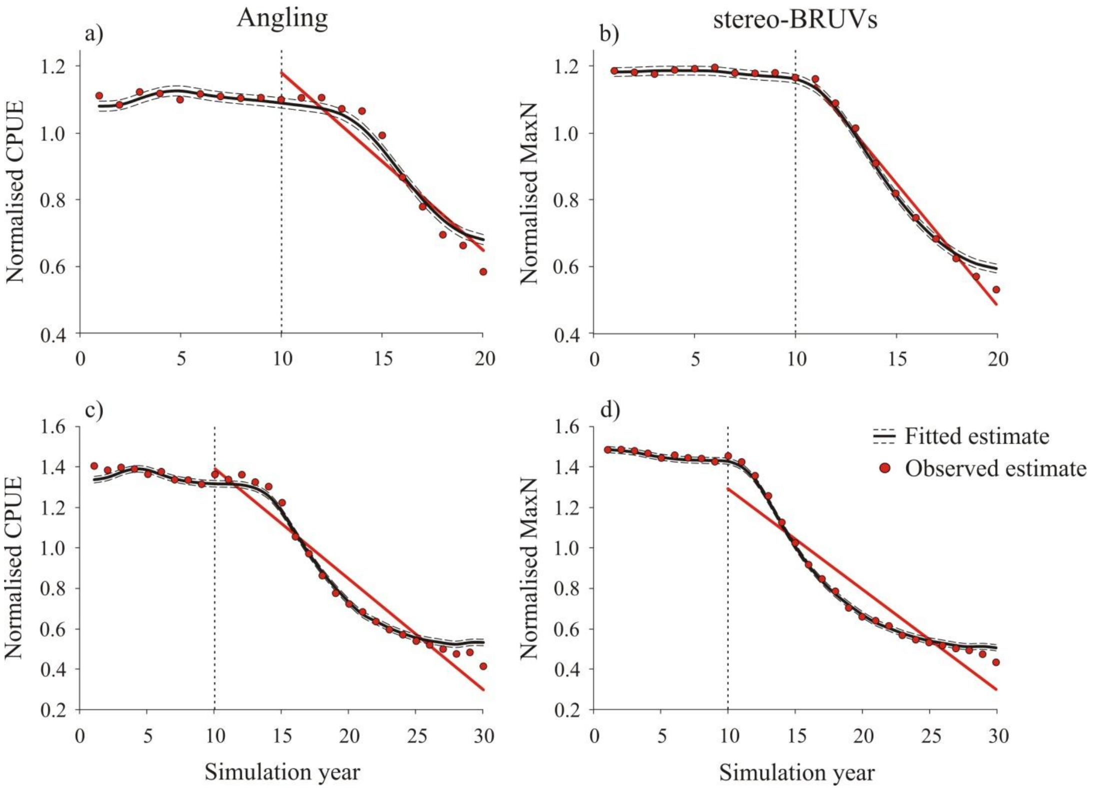


Figure 6.5: An evaluation of simulated observed and fitted relative abundance estimates of roman for angling (a,c) and stereo-BRUVs (b,d) over a 10- and 20-year period. The dashed line represents the year at which the simulated recruitment failure was introduced to the model, while the solid lines are linear regressions describing the simulated population decline.

In all cases, observed abundance estimates for the final two years of the simulation are particularly inaccurate. In contrast to the 10-year scenario, both methods produce remarkably similar regression trends and observed point estimates over the 20-year period. Regressions for both methods seem to underestimate the rate of the population decline over 20 years, which is likely a result of the linear model's inability to describe the initial 'steepness' of declining trend followed by a levelling period.

6.3.2.2 SPAWNER-BIOMASS ESTIMATES

The ability of each sampling method to detect the 'true' population decline using spawner-biomass is illustrated in Figure 6.6. Both angling and stereo-BRUVs' linear regressions underestimate the rate of population decline over the 10-year scenarios, however, this underestimation is greater within the angling data. As is the case with the abundance data, spawner-biomass estimates derived from angling and stereo-BRUVs were remarkably similar over a 20-year scenario. Spawner-biomass estimates derived from both methods are able to describe the 'true' population decline for the 20-year scenarios more accurately than abundance estimates. Point estimate deviations from the 'true' population, for both methods and scenarios, are most noticeable immediately after the induced recruitment failure.

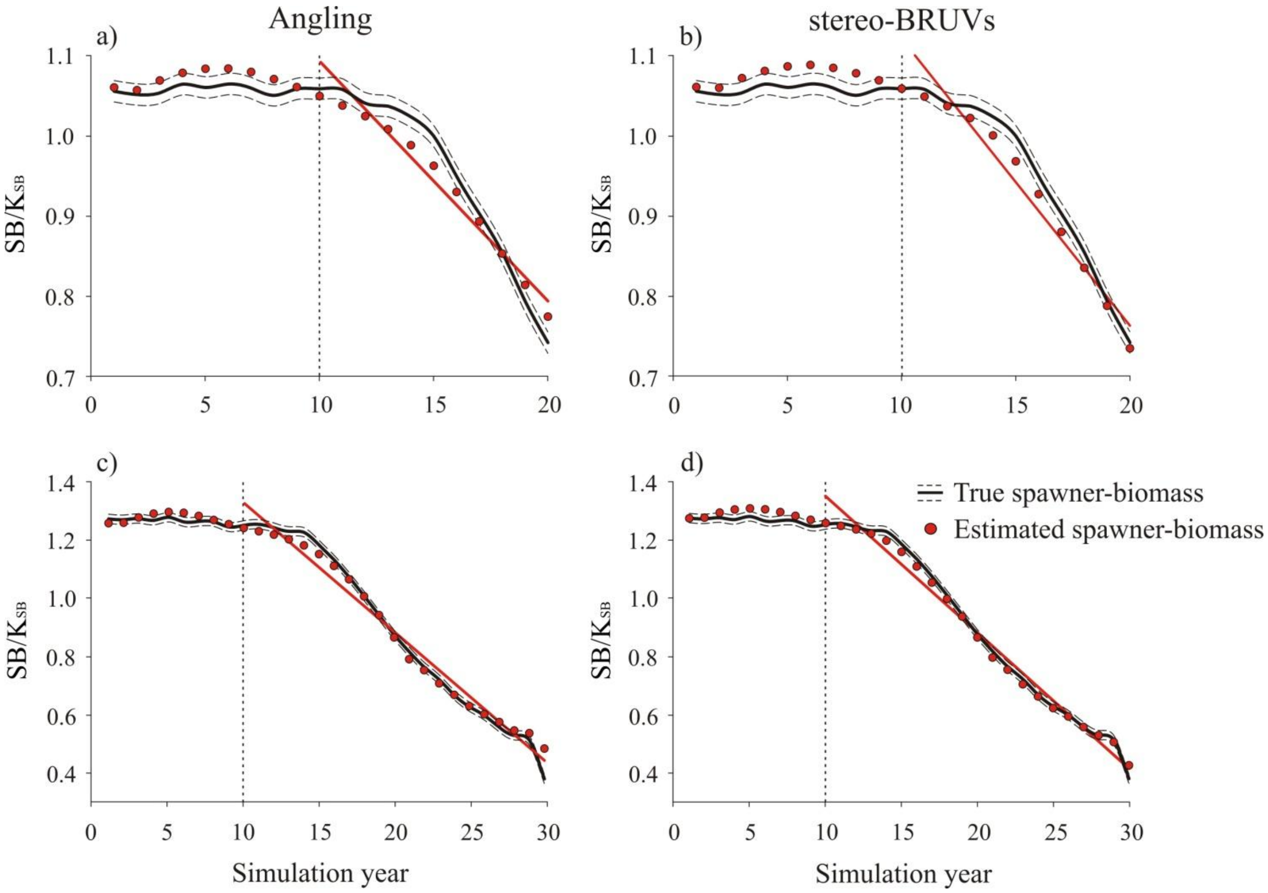


Figure 6.6: A comparison of simulated 'true' and estimated spawner-biomass estimates of roman for angling (a,c) and stereo-BRUVs (b,d) over a 10- and 20-year period. Spawner-biomass is normalized to the spawner-biomass at carrying capacity (K_{SB}). The dashed line represents the year at which the simulated recruitment failure was introduced to the model, while the solid lines are linear regressions describing the simulated population decline.

6.3.3 METHOD ACCURACY AND PRECISION

6.3.3.1 POPULATION GRADIENT AND METHOD ACCURACY

The performance of each method to accurately describe the simulated population decline was evaluated using the RMSE of the deviation of estimated spawner-biomass gradients from the ‘true’ spawner-biomass gradient. An obvious difference between sampling methods is seen in the 10-year scenarios (Figure 6.7a), where the mean error, and error distribution, from angling data is greater than that from stereo-BRUVs. The inflated positive mean error produced by angling indicates a systematic bias resulting in a consistent underestimation of the ‘true’ population decline, corroborating the trends in Figures 6.5a and 6.6a. In contrast, the mean error for stereo-BRUVs is all but exact (-8.2e^{-5}), signifying that the method provides unbiased inference regarding trends over 10 years. The error distribution decreases for both methods over the 20-year period (Figure 6.7b), but the overall result is consistent as stereo-BRUVs remain the more accurate method. In contrast to the 10-year scenario, both methods produce positive errors over 20 years and thus marginally underestimate the simulated ‘true’ decline over an extended period.

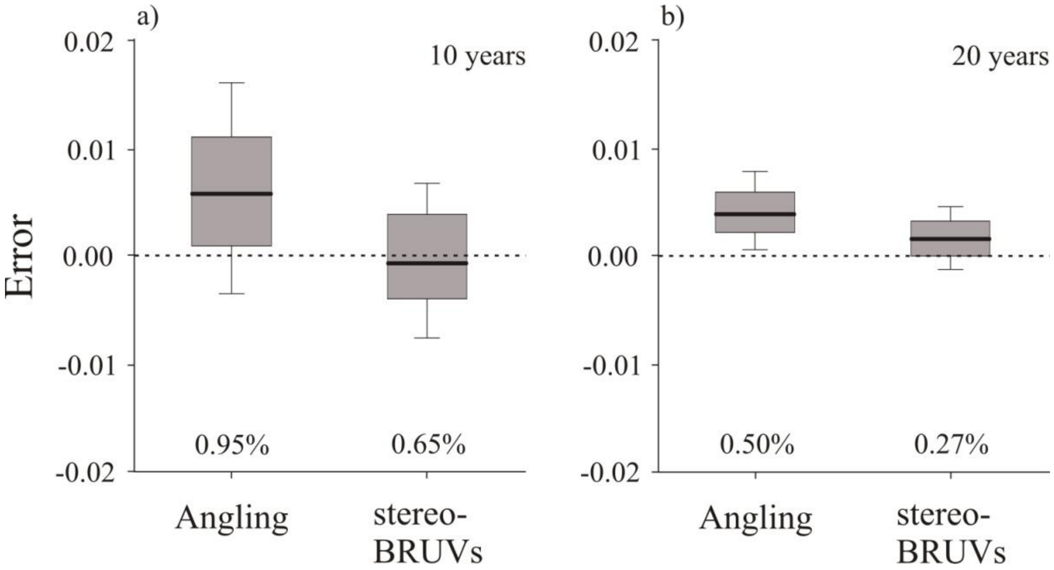


Figure 6.7: An evaluation of method accuracy and bias, for the slope of the simulated population decline over (a) 10- and (b) 20-year period. Values indicate the mean-root-squared error value expressed as a percentage. Only years after the simulated recruitment failure was induced are included.

6.3.3.2 ANNUAL ABUNDANCE AND SPAWNER-BIOMASS ESTIMATES

In addition to evaluating the population gradient, the accuracy of annual abundance (CPUE and MaxN) and spawner-biomass point estimates was assessed using RMSE values (Table 6.3). The results substantiate previous findings that stereo-BRUVs provide the most accurate annual estimates of spawner-biomass as the method consistently produces lower RMSE values than angling when compared

Table 6.3: Root-mean-squared-error values, expressed as percentages, for angling (CPUE) and stereo-BRUVs (MaxN) over a 10- and 20-year simulation scenario. The indices that are included are abundance estimates and spawner-biomass estimates.

	10 years		20 years	
	Angling	stereo-BRUVs	Angling	stereo-BRUVs
Abundance	13.96	8.72	15.64	9.74
Spawner-biomass	7.28	6.56	7.37	6.24

to the 'true' spawner-biomass. The inflated RMSE values for abundance estimates derived from angling indicate that observation error within CPUE data is greater than within MaxN data. In addition, RMSE values for CPUE and MaxN increase with time, while spawner-biomass RMSE values remain relatively consistent in both the 10- and 20-year scenarios. These findings imply that the inclusion of length structured data to the model enhances the accuracy of observed data by decreasing the variability around annual estimates. Appendix 6.2 depicts the high level of variability within annual abundance estimates (CPUE and MaxN) derived from multiple simulation runs, while variability within annual spawner-biomass estimates is notably less (Appendix 6.1).

6.4 DISCUSSION

In Chapter 5 it was hypothesized that a method evaluation that incorporated population size structure would validate stereo-BRUVs as the preferable monitoring technique. The results of this study strongly support this, as a simulation-based evaluation concluded stereo-BRUVs data are more accurate than data derived from angling for LTM of roman in the TNP MPA study area. Disadvantages associated with angling data include high variability and the presence of a 'lag' period associated with hook based size selectivity. As a result, angling produces comparatively inaccurate estimates of population decline over 10 and 20 years. Both methods underestimate the rate of population decline over 20 years, suggesting a systematic bias may exist. Despite the high variability in abundance data (CPUE and MaxN), spawner-biomass could be accurately estimated, which can be attributed to the inclusion of size data (Ono et al. 2014). The study emphasizes the importance of simulation testing as an evaluation tool in ecological research, as it can calculate the accuracy and precision of sampling methods in a controlled environment where the 'true' dynamics of the hypothetical population are known (Anderson et al. 2014).

6.4.1 METHOD EVALUATION

Root-mean-squared error values were employed to evaluate the performance of each sampling method; a statistical procedure that has been previously applied with success (Thorson et al. 2012, Winker et al. 2014b). These values calculate the total error associated with all deviations of observed values from the expected values, with the assumption that the lower the total error the higher the data accuracy. This procedure was applied in two different manners. The first was to measure the deviation of annual fitted point estimates of abundance to observed point estimates, providing a ‘goodness of fit’ test for the estimation framework model. The second application was to assess the ability of each method to accurately describe population trends by comparing data derived from each method to the ‘true’ trends. This was achieved by measuring the deviation of the estimated spawner-biomass gradient from the ‘true’ spawner-biomass gradient to (i) identify whether any of the methods over- or underestimated trends in spawner-biomass, and (ii) identify whether differences in error for annual abundance estimates translated into differences when identifying abundance trends (Thorson et al. 2012).

The RMSE values for annual abundance estimates indicate that stereo-BRUVs data were consistently more accurate than angling data. The variability in CPUE data was derived from the high dispersion factor (ϕ) with a value of 5.22, signifying that the data was considerably overdispersed. Overdispersion is described as the presence of unexpectedly high variability in count data, to such an extent that the variance is greater than the mean (Zuur et al. 2009). The high variability within CPUE data (Appendix 6.2) inevitably leads to less precise annual abundance estimates, which is an unfavourable characteristic of angling data that has been previously noted in ecological studies (Bennett and Attwood 1991, Götz et al. 2007, Bennett et al. 2009).

Abundance data derived from both methods exhibited a ‘lag’ period between the year in which the recruitment failure was induced and the first sign of population decline. The lag was characterized by stable abundance estimates despite a known decline in recruitment numbers. Data derived from stereo-BRUVs had a lag of only a year, as opposed to the four-year lag seen in angling data (Figure 6.5). This is a direct result of the size selectivity observed when using 4/0 hooks, shown by S_{L50} values of 242 and 182 mm FL, for angling and stereo-BRUVs, respectively. The difference in selectivity estimates extends the timeframe needed to witness recruitment failure in angling data, which is particularly pronounced in slow growing species such as roman.

Stereo-BRUVs outperformed angling in the ability to accurately describe the ‘true’ spawner-biomass gradient over the 10- and 20-year scenario (Figure 6.7). Comparing estimated and ‘true’ spawner-biomass gradients is considered a suitable performance evaluation index because it assesses each method’s ability to accurately describe a population decline. The gradient described by stereo-BRUVs data in the 10-year scenario was found to be very accurate (RMSE = -8.2e^{-5}), while angling data strongly underestimated the ‘true’ gradient. Size selectivity also played an important role in spawner-biomass data accuracy as the estimated length-at-50% maturity was calculated as 184 mm FL, which is very similar to the S_{L50} of stereo-BRUVs (182 mm FL) but far less than that of angling (242 mm FL). The ability of stereo-BRUVs to record incoming cohorts of mature fish at the smallest size possible is fundamental to monitoring as it allows for early detection of recruitment failure, the advantage of which is obvious within an adaptive management framework.

Both methods produce positive errors in the 20-year scenario and thus marginally underestimate the simulated ‘true’ decline over an extended period. This indicates that a slight systematic bias is present within the results, which may be due to the linear regression applied to describe the decline being inappropriate. In marine ecosystems population declines are rarely linear, but generally exhibit an exponential decay form (Hilborn and Walters 1992). However, to allow for simple comparisons between methods, a linear model was applied in this circumstance. This model was seemingly appropriate for the 10-year scenario where the induced decline was relatively recent and maintaining population carrying capacity was heavily reliant on consistent recruitment (Hilborn and Walters 1992). As such, population decline during this time was directly proportional to recruitment failure, creating a linear trend. However, over an extended period the decline slowed due to the restrictions governing population dynamics (Hilborn and Walters 1992), and the linear model’s ability to accurately describe the population trend decreased. In such a case, the use of an exponential decay model may be more suitable and future investigation into the effects of model selection on gradient error results is necessary.

6.4.2 COMPARISON OF INDICES: RELATIVE ABUNDANCE OR SPAWNER-BIOMASS?

In addition to evaluating sampling methods, the simulation framework enabled a comparison of population indices: relative abundance and spawner-biomass. The obvious attributes of both have been previously discussed, but to reiterate, relative abundance (CPUE and MaxN) indices are comparatively imprecise due to inherently high variability, while spawner-biomass attains increased consistency and accuracy by incorporating length-structured population data. However, when assessed with respect to LTM programmes of reef fish within MPAs, the greater relevance of spawner-biomass over abundance estimates becomes more apparent.

Firstly, the three pragmatic assumptions of the simulation framework were introduced in an attempt to replicate a hypothetical decline in the roman population within the TNP MPA over an extended period, which was not the product of fishing exploitation. By applying these assumptions a condition exists whereby the consistent population decline is theoretically limited to being a consequence of consecutive recruitment failures, the cause of which remains immaterial for this study. In such a circumstance the ability to monitor recruitment numbers would prove ideal, but this is improbable. It would therefore seem logical to monitor an index that is correlated with recruitment numbers, such as spawner-biomass. The exact relationship between the abundance of spawners and the number of recruits produced is one of contention (Hilborn and Walters 1992, Marshall et al. 1998), but there is a central predisposition that recruitment is positively correlated with spawner-biomass (Myers and Barrowman 1996). In contrast, the absence of population structure information in relative abundance indices (CPUE and MaxN) has ensured that any direct correlation between recruitment numbers and these indices has to be avoided, as it would possess an unacceptable degree of extrapolation. The simulation framework demonstrated the correlation between recruitment failure and a decline in spawner-biomass through consistent estimate accuracy, confirming that spawner-biomass is the more appropriate index for monitoring potential recruitment failures. Therefore spawner-biomass is the most appropriate index for monitoring resident reef fish species within a well established ‘no take’ MPA, because recruitment failure is assumed to be the most likely cause of population decline based on the aforementioned assumptions. Importantly, the comparison of indices highlights the need to collect length-frequency data in LTM programmes.

6.4.3 FURTHER DEVELOPMENT OF THE EVALUATION FRAMEWORK

This study provides a novel application of simulation testing to evaluate LTM sampling method accuracy and performance. Nevertheless, the research remains a work in progress as there are potentially more applications than just those explored in this study. One such application stems from the incompatibility of datasets, which arises with the introduction of a new sampling method. This is a major limitation within LTM because it inhibits progressive sampling strategies, as scientists generally opt for sampling standardization and continuity over optimization.

Parameters such as the catchability coefficient (q) and selectivity (S_L) play an integral role in stock assessment model outcomes (Hilborn and Walters 1992). Both of these parameters are dependent on sampling gear, and the effect of differing values of q and S_L on abundance accuracy as has been highlighted in this study. However, there is potential to standardize data obtained from different methods through the introduction of a correction factor. This could be achieved through manipulation of q within the evaluation framework developed in this study, with additional correction being applied to the length-frequency data to ensure that the size structures are comparable. A method to calculate a correction factor that accounts for differences in trawl gear efficiency and selectivity over time is already available (Lewy et al. 2004), and the manipulation of q within an ASPM framework has also been thoroughly explored to account for time-varying catchability in stock assessment models (Wilberg et al. 2009, Thorson and Berkson 2010, Thorson 2011, Carvalho et al. 2014). By applying similar parameter manipulation within this framework, data derived from different sampling methods could be compared directly, allowing for LTM programmes to be adaptive without sacrificing data continuity.

Although the development of a correction factor did not fall within the scope of this study, it remains a priority for future work due to its application within the TNP MPA LTM programme, which aims to replace angling with stereo-BRUVs. Such a framework development would likely make a significant contribution to the efficacy of LTM programmes as continual optimization would ensure data are of consistently high quality, providing future generations with more accurate and precise historical trends.

6.4.4 INCORPORATING SIMULATION TESTING IN ECOLOGY

Simulation testing has rarely been successfully implemented in marine ecological research, despite it being a common statistical tool in the closely related field of fisheries management (Dakos et al. 2012, Thorson et al. 2014). Within a fisheries management context, Butterworth and Punt (1999) state that there are two main reasons for evaluating alternative candidate management procedures by simulation: (i) their relative performances can be assessed, and (ii) their anticipated performance with respect to specified management objectives can be determined. Here, the focus is on optimizing management strategies, with little focus on sampling methodology as data collection within this industry is generally fishery-dependent (Hilborn and Walters 1992). In contrast, marine ecological research relies heavily on fishery-independent data where sampling methods and design are of paramount importance (Rotherham et al. 2007, Bennett et al. 2009). By shifting the focus from managerial optimization within fisheries to sampling design and/or strategy optimization, simulation testing provides a readily available technique for application within the field of marine ecological research. For example, Dorner et al. (2013) used empirically based simulation modelling of 48 sockeye salmon (*Oncorhynchus nerka*) populations to examine how reliably alternative monitoring designs and methods were able to distinguish between changes in density-dependent versus density-independent components of productivity. In doing so, they were able to isolate and identify the relative contribution of a climate-driven covariate to population fluctuations (Dorner et al. 2013). Similarly, simulation testing has been used to evaluate the performance of the Trawl and Acoustic Presence/Absence Survey design (TAPAS) in reducing the variability in the estimated biomass of patchily distributed species (Spencer et al. 2012).

Recently, simulation testing has been employed to evaluate alternative fish abundance indices when sampling with video monitoring techniques such as stereo-BRUVs (Schobernd et al. 2013). The aforementioned study has obvious implications for the present study, as it suggests that MeanCount (defined as the mean number of fish observed in a predefined series of snap-shots over a viewing interval) may be a more accurate and precise index of abundance than MaxN (Schobernd et al. 2013). However, a number of fundamental flaws exist within this study, particularly the assumption that fish behaviour remains constant between low and high abundance situations, the unconventionally short timeframe (20 minutes) of videos from field experiments and the obvious manipulation of graph axes to over emphasize non-linear trends to meet predefined objectives. As such, the conclusions of the study should be viewed with caution. Nevertheless, the ability of MaxN to accurately describe true abundance under conditions of high fish density (hyperstability) has previously been questioned within this thesis (Chapter 5). There is a clear need for further research into the extent and influence of hyperstability within stereo-BRUVs data, and the evaluation of alternative indices of abundance to minimize its effects.

The vast amounts of funding and time needed to successfully implement a LTM programme within the subtidal marine environment dictates the necessity of an evaluation of sampling design and strategy. Simulation testing offers an efficient and effective means by which this can be done. The flexibility of simulation testing to incorporate an endless number of possible prescribed scenarios makes it a powerful evaluation tool (Lynch et al. 2012). The purpose of this chapter was to illustrate the potential of simulation testing to address a number of methodological research questions and ultimately to optimize LTM programmes.

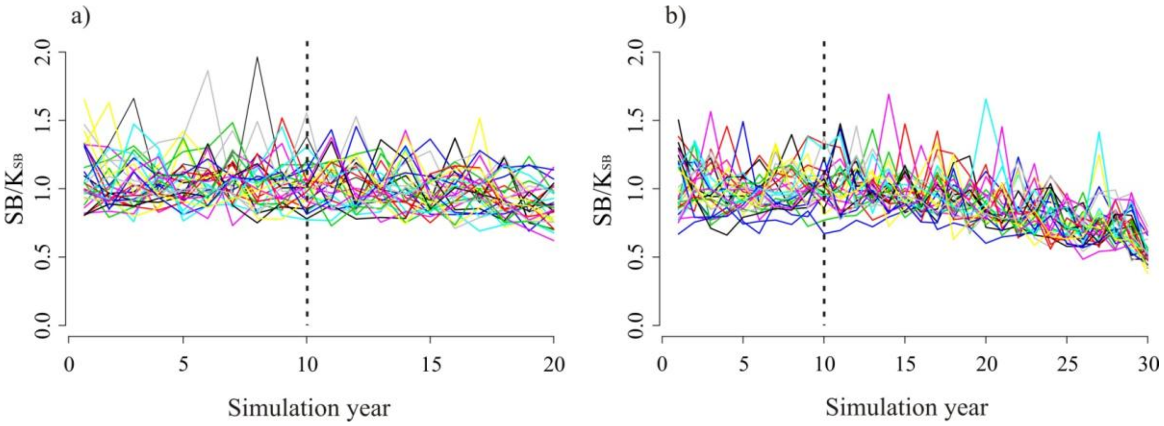
6.5 CONCLUSIONS

The study established that stereo-BRUVs are able to provide more accurate data when describing a simulated population decline of roman over 10- and 20-year periods. As such, the results corroborate the conclusions of Chapter 5, in that stereo-BRUVs are the most appropriate sampling method for LTM of subtidal ichthyofauna in the TNP MPA. Although the evaluation was limited to one species, it has been made explicitly clear throughout this thesis that roman CPUE data were the most reliable and consistent of all the species sampled. As such, the evaluation can be considered a ‘best case scenario’ for angling, which in turn provides insight into the effectiveness of stereo-BRUVs. Disadvantages associated with CPUE data include high variability and the presence of a ‘lag’ period associated with the size selectivity observed when using 4/0 hooks. These attributes are inhibited in MaxN data, allowing for more accurate annual point estimates and description of long-term trends.

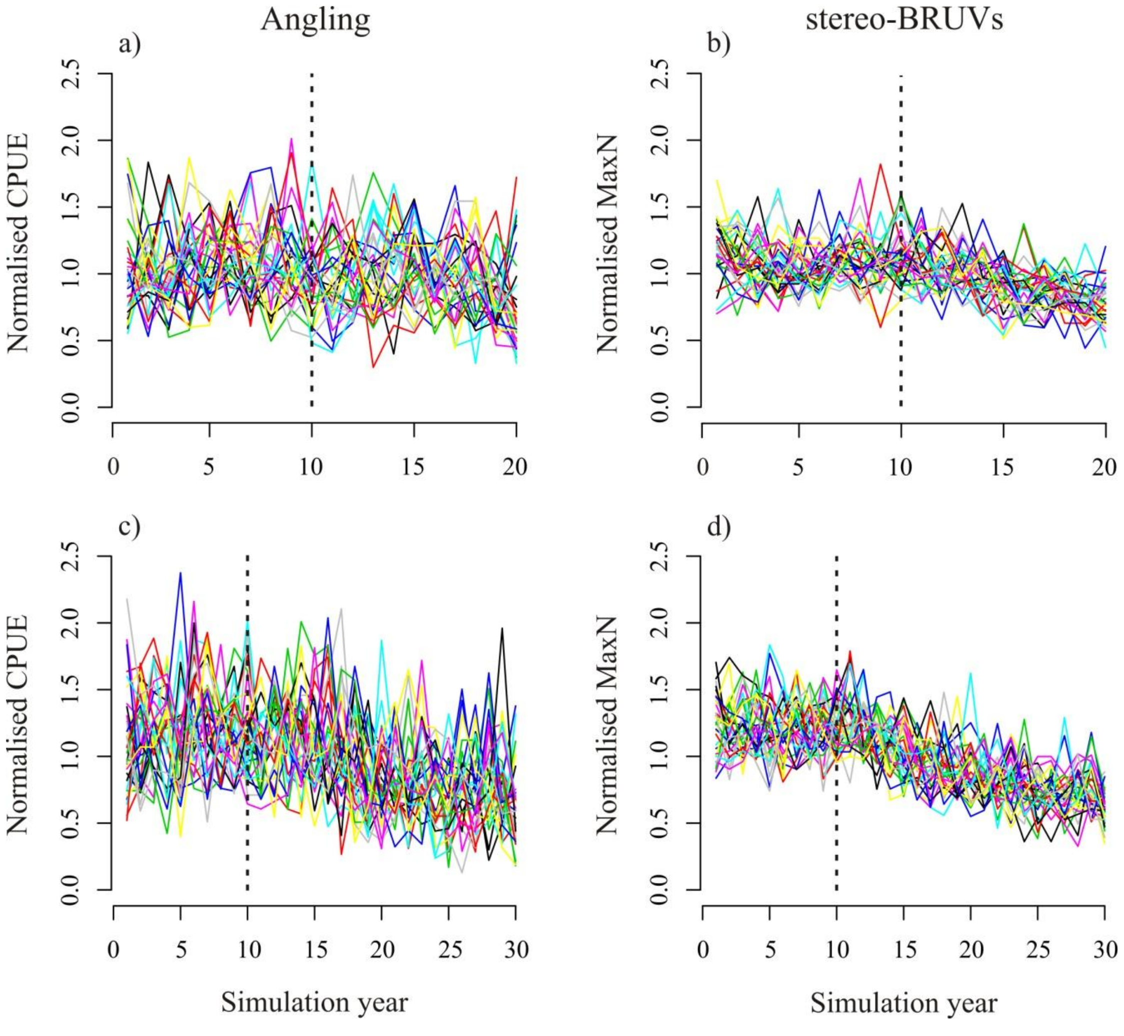
Spawner-biomass trends could be accurately estimated despite high variability in MaxN and CPUE data due to the inclusion of population size structure information, which highlights the importance of collecting length-frequency data. Although ASPMs are widely applied in stock assessments, they remain underutilized in standard fisheries ecology analyses. It is recommended that ASPMs be included as a tool in ecological assessments as they provide more reliable population estimates.

Finally, the study illustrated that an evaluation framework that utilizes simulation testing has the potential to optimize LTM sampling procedures by addressing a number of methodological questions. These include inference regarding a method’s ability to detect trends as well as data accuracy and precision. Development and potential applications of this framework remain broad, and future analyses should focus on developing a procedure that aligns data collected from different sampling methods, i.e., a framework or standardized procedure that determines and applies correction factors to ensure LTM programmes are able to adapt without losing data continuity. In addition, research into the extent and influence of hyperstability within stereo-BRUVs data is necessary. If we are to promote the use of stereo-BRUVs in LTM programmes, it is of paramount importance that the most statistically appropriate method to enumerate fish from these videos is utilized.

6.6 APPENDICES

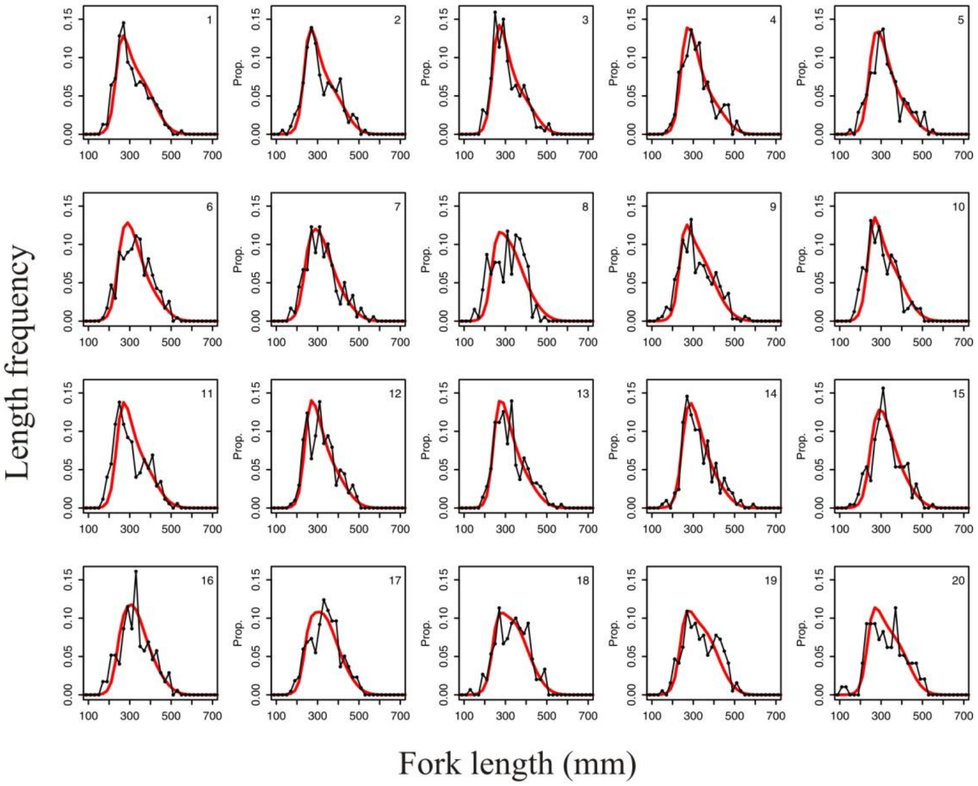


Appendix 6.1: An example of the simulated observed data variability for normalized spawner-biomass over (a) 10 years and (b) 20 years. Each line represents a single simulation run, and only 20 simulation runs (n_{sims} = 20) are presented to aid visualization. The dashed line represents the year at which the induced population decline was introduced to the model.

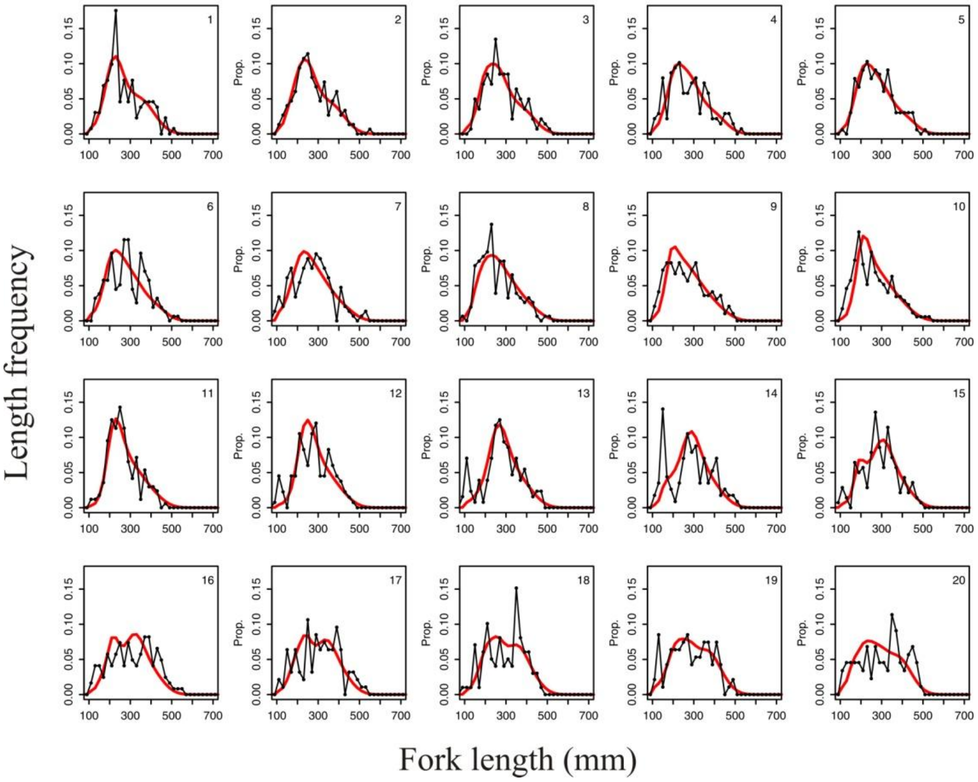


Appendix 6.2: An example of the simulated observed data variability for normalized relative abundance estimates of angling (a,c) and stereo-BRUVs (b,d) over a 10- and 20-year period, respectively. Each line represents a single simulation run, and only 20 simulation runs (n_{sims} = 20) are presented to aid visualization. The dashed line represents the year at which the induced population decline was introduced to the model.

a) Angling



b) stereo-BRUVs



Appendix 6.3: An example of the simulated length-frequency data for (a) angling and (b) stereo-BRUVs data. The black line represents the 'true' simulated data while the red line represents the observed data. Each length-frequency distribution represents one of only 20 simulations to aid visualization.

CHAPTER SEVEN

GENERAL DISCUSSION

There has been a realization that results derived from temporary ecological studies may not be indicative of the overall ecological trend due to an insufficient temporal scale. This has led to more permanent ecological research objectives in the form of long-term monitoring (LTM) programmes. The complications surrounding a lack of historical data (Jackson et al. 2001, Parr et al. 2003) and the 'shifting baseline' problem (Pauly 1995), both of which are all too familiar in fisheries management, reiterate the need for LTM programmes. However, the importance of short-term experiments and observations in providing context for LTM programmes should not be overlooked (Lovett et al. 2007). It is under the adaptive management premise that short-term observations should be utilized in the optimization of the LTM practices. The fundamental challenge with LTM programmes is their longevity. Such programmes are expensive (Bernard 2013) and their continuation is ultimately dependent upon funding. The vast amounts of funding and time needed to successfully implement a LTM programme within the subtidal marine environment dictates the necessity of an evaluation, and adaptation where necessary.

This thesis provides an evaluation of the Tsitsikamma National Park (TNP) marine protected area (MPA) LTM programme, with much emphasis being placed on enhancing sampling methods and statistical processes. This chapter contextualizes the findings of the previous chapters in terms of: (i) an evaluation of the TNP MPA ichthyofaunal diversity and population trends, (ii) the importance of applicable statistical approaches to overcome sampling constraints, (iii) minimizing sampling constraints through method optimization and (iv) recommendations for LTM of reef fishes in South Africa.

7.1 ICHTHYOFAUNAL DIVERSITY AND POPULATION TRENDS

The results of ichthyofaunal diversity and population trends provide an overview of the value of the TNP MPA as a fisheries management tool. In this regard, a more suitable representation of the ichthyofaunal diversity within the MPA only became apparent with the introduction of stereo-BRUVs as a sampling technique (Chapter 5). Angling produced a total of 41 species over 14 sampling events (seven years), while stereo-BRUVs generated 52 species occurrence records in only three sampling events carried out in less than two years. The fairly high ichthyofaunal diversity within the TNP MPA can be attributed to its geographic position as it falls in the centre of the Agulhas Ecoregion, and has a high level of endemism. This central geographic attribute also means that fish populations are less likely to be affected by climatic shifts as a 'buffer' zone exists in either coastal direction. Therefore, its characteristic ichthyofaunal endemism and diversity (Buxton and Smale 1984, Burger 1991, Tilney et al. 1996, Hanekom et al. 1997, Wood et al. 2000, Smith 2006), in conjunction with its geographic location, illustrates the value of the TNP MPA in protecting fisheries and their ecosystems.

The temporal abundance trends of species analysed within the TNP MPA are indicative of a 50-year-old 'no take' sanctuary in that they exhibit a high degree of temporal stability (Chapter 4). In 2014 dageraad was classified as critically endangered according to the IUCN red listing, while a moratorium on catches of red steenbras was implemented in South Africa in 2012 as a last resort to halt the population decline; this decision was subsequently overturned in 2014 despite overwhelming scientific evidence (Winker et al. 2014a). Conversely, these two sparids constitute the second and eighth most abundant species in the TNP MPA according to angling CPUE data, suggesting that current fishery-control management strategies for these species outside MPAs are no longer effective. It is well documented that the effective management of such endemic sparids is dependent on the provision of MPAs in South Africa (Buxton and Smale 1989, Buxton 1990, Bennett and Attwood 1991, Attwood et al. 1997, Brouwer 2002, Cowley et al. 2002, Barrett et al. 2007, Götz et al. 2008a, 2008b, 2009, James et al. 2012, Solano-Fernández et al. 2012, Mann 2013). Yet contention regarding the necessity of the TNP MPA and its efficacy in benefitting resource users, particularly fisheries, is perpetual. In 2007, the Department of Environmental Affairs (DEA), attempted to open the TNP MPA to recreational and subsistence fishing. However media attention created an outcry from the scientific community and the public alike, forcing the idea to be abandoned. The main argument against its opening was based on a report that highlighted the economic value to the TNP and the estimated R31 million net loss in revenue that would occur from opening sections of the MPA (Turpie et al. 2006). In 2010, a second attempt to open the TNP MPA was put forward by the DEA, with the same result. Recent politicking in the TNP area forecasts an eminent third attempt.

The length-frequency distributions of the species investigated were also relatively stable and the mean length of sparids sampled within the TNP MPA was significantly larger than their associated length-at-50% maturity; excluding red steenbras for which TNP MPA has been identified as a nursery area (Buxton and Smale 1989, Brouwer 2002). To benefit fisheries, MPAs are designed to protect spawning stocks while simultaneously improving fishery yields via net emigration of adult fish (spillover) and the export of larvae. The TNP MPA certainly protects endemic sparid spawning stocks, and evidence of adult dageraad spillover was possibly detected in the analysis of annual kernel density estimates; however, more research is necessary to confirm this. Unfortunately, the detection of larval spillover is far more difficult and has yet to be attempted in the TNP MPA.

The results of this study demonstrate the TNP MPA is functioning as expected with regard to protecting a diverse range of fish spawning stocks, including that of vulnerable sparids. These findings vindicate legislation such as the National Protected Area Expansion Strategy (NPAES), which aims to protect 15% of the offshore shelf environment and 25% of the coastal or inshore environment by the year 2030 (DEA 2009). However, the lack of empirical evidence indicating that the TNP MPA's closure has benefited fishers overall, such as that provided by Kerwath et al. (2013a) for Goukamma MPA, is likely to leave the effectiveness of the MPA open for debate.

7.2 THE IMPORTANCE OF APPLICABLE STATISTICAL APPROACHES TO OVERCOME SAMPLING CONSTRAINTS

Sampling bias is likely to exist in all situations where a subsample of a population is taken to be an accurate representation of the entire population. If sufficiently strong, biases can produce erroneous conclusions (Zuur et al. 2009). Ecological research is therefore heavily reliant on understanding and making subsequent statistical allowances for method-specific biases. In this regard, statistical approaches increasingly provide methods of incorporating bias into error structures in an attempt to compensate for the inherent constraints of sampling. However, the ability of statistical methods to account for sampling constraints still has its limitations and their improper application can render invalid results.

A major objective of this thesis was to explore possible statistical procedures to optimize the amount, and quality, of information that can be derived from LTM datasets. Some of these procedures were novel in terms of their field of application, while others expanded on existing procedures to suit the data’s specific requirements. Notably, the process outlining the inclusion of space in temporal analyses was particularly successful (Chapter 4). Spatial analyses in ecology is by no means a novel idea, but this thesis was able to conclusively illustrate the consequences of its exclusion in LTM programmes. The spatial statistics applied are particularly relevant to spatially comparative ecological surveys. Likewise, the use of spatial autocorrelation correlograms to determine the optimal size of sampling units is considered pertinent to a variety of ecological research programmes (Chapter 3). Such methodological adjustments are essential to ensure the optimal use of resources while constantly improving data quality.

Using kernel density estimates (KDEs) to compare the size distributions of sampled fish populations was not a novel application either (Langlois et al. 2012a), but here the process was refined to account for hook selectivity, thereby producing more comparable length-frequency datasets (Chapter 5). Furthermore, the application of KDEs was extended to enable the comparison of more than two length-frequency datasets. This allowed several years of length-frequency data to be quantifiably compared. Previous annual comparisons were reliant on ANOVAs, which identified differences in means and associated variances but could not pinpoint where in the size distribution these differences were centred. By plotting annual KDEs against the null model, represented by a geometric mean of KDEs for all years, the origin of these differences could be identified by KDE values that fell outside of the null model confidence intervals. It was this technique that provided insight into the possible emigration of adult dageraad out of the sampling area; remarkably an ANOVA on annual dageraad lengths found no significant differences (Chapter 5).

Attempts to compare relative abundance estimates from different sampling methods were, however, less successful (Chapter 5). As neither CPUE nor MaxN are indices of absolute abundance, nor are they directly comparable, GLMs were independently fitted to data from each method. These GLMs were based on selected categorical variables with distinct abundance gradients (e.g., *season*: summer-winter), and could only be compared visually; no quantifiable inferences could be made due to method and associated index inconsistency. It was assumed that these gradients would hold true regardless of sampling method. Overall, the results showed a relatively high level of congruency, providing a first indication that both methods were reliable in their ability to identify broad abundance trends. However, this comparison is likely to garner criticism due to a lack of robustness, and future research should therefore focus on providing a more defendable technique to align datasets derived from different sampling methods and ensure that the two indices of relative abundance are comparable.

The potential of utilizing simulation testing to optimize LTM procedures by addressing a number of methodological questions was illustrated in Chapter 6. The objective of developing a simulation-estimation approach for LTM sampling methods was to shift the current methodology assessment theme away from simple comparisons to more rigorous performance evaluations. The advantage of this evaluation approach is that the simulated population trends are known, so that each sampling method can be tested in terms of how well it tracks ‘true’ population trends. The evaluation surpassed any initial expectations in this respect. Key findings include that stereo-BRUVs provide more accurate data than angling and that spawner-biomass trends could be accurately estimated despite high variability in MaxN and CPUE data. The latter finding can be attributed to the inclusion of population size structure (length-frequency data), which provided an important source of information for robustly estimating the population trend. The flexibility of simulation testing to incorporate a large number of possible prescribed scenarios makes it a powerful evaluation tool. There is potential for broadening its applications beyond those explored in this thesis, notably the development of a correction factor to standardize data obtained from different methods. Such development would make a significant contribution to the efficacy of LTM programmes as continual optimization would ensure data is of the highest attainable quality, providing future generations with more accurate and precise historical trends.

While simulation testing is a well-established tool for performance evaluation of fisheries assessment methods (Punt et al. 2002, Booth and Quinn 2006, Kell et al. 2007, Thorson et al. 2012) and management strategies (Smith et al. 1999, Brown and Walker 2004, Punt 2006, Butterworth 2007, Rademeyer et al. 2007, Punt et al. 2013), its application remains vastly underutilized in ecological studies. It is hoped that this study will generate the necessary exposure to ensure it is used more frequently. In this regard, the simulation framework provides a template, which can be developed and expanded on to address pertinent methodological questions.

7.3 MINIMIZING SAMPLING CONSTRAINTS THROUGH METHOD OPTIMIZATION

Another fundamental objective of this thesis was to improve the accuracy of data-gathering methods for LTM of reef fishes. The current ecological prerogative of Ecosystem-Based Fisheries Management (EBFM) and assessing vulnerable species has rendered fishery-dependent techniques largely inappropriate as they are generally limited to target specific, commercially viable, species. This necessitated the evolution of fishery-independent sampling techniques. The implementation of a new sampling method is an extensive process and significant developments were previously made in angling and BRUVs methodology in the TNP MPA (Bennett et al. 2009, Bernard and Götz 2012, Bernard 2013). These were further investigated in this study. A key finding of the method analyses was that the selective nature of angling towards large, more aggressive, predatory species is an undesirable attribute for multispecies ecological assessments; an expected outcome, which has been previously discussed at length (Millar and Fryer 1999, Götz 2006, Wakefield et al. 2007, Bennett 2008). The extent of this selectivity, however, only became apparent with the introduction of stereo-BRUVs. This, in conjunction with recent insight into the unexpectedly high angling mortality rates (Bartholomew and Bohnsack 2005, Cooke and Suski 2005, Arlinghaus et al. 2007, Kerwath et al. 2013b), associated hook size selectivity and angling's inferior ability to detect changes in a population, has led to the discontinuation of angling as a sampling technique in the TNP LTM programme as of January 2014. All subsequent sampling trips will employ stereo-BRUVs as the primary method of data collection.

In addition to their effectiveness in sampling fish communities, stereo-BRUVs display a great potential for technological progress. Their current weakness of intensive post-sampling analysis time is likely to be overcome with the development of automated image analysis programmes in the future, allowing for research on fish communities to occur at scales that are currently impractical and unfeasible. In addition, the ability to archive video footage allows for re-analysis, so new developments can be applied to historic LTM data. This thesis therefore advocates that current and future LTM programmes that aim to assess subtidal reef fishes should focus on employing non-extractive video techniques, such as stereo-BRUVs, as primary method of data collection.

7.4 RECOMMENDATIONS FOR LONG-TERM MONITORING OF REEF FISHES IN SOUTH AFRICA

At present there are no nationally coordinated, standardized fisheries-independent monitoring programmes collecting ecological data of subtidal reef systems in South Africa. Few South African MPAs have LTM programmes in place, while baseline biodiversity assessments are lacking from others. Where monitoring has been conducted it is typically limited in spatial and temporal extent and restricted to shallow depths (<30 m) that are more accessible to traditional monitoring methods, such as underwater visual census (UVC). As such, deeper reefs and their associated species are largely disregarded in national monitoring frameworks despite their ecological and fisheries importance. Furthermore, traditional deep water sampling methods have been found to be inappropriate for assessing rocky reef communities (Bernard and Götz 2012, de Vos et al. 2014), particularly trawls and dredges that are not only inherently biased but also highly destructive. This is counterproductive under the EBFM principle, particularly within MPAs.

The absence of standardized sampling methods between different LTM programmes around South Africa hinders progression, as different techniques vary in their ability to survey fish assemblages. Direct comparisons between programmes utilizing different sampling methods are therefore confounded, preventing macroecological analyses over larger spatial and temporal scales (Murphy and Jenkins 2010). This inherently limits the understanding of how MPA networks improve fisheries and biodiversity conservation in South Africa. For the MPA expansion objectives (NPAES) to be met and accepted, South Africa needs to improve the science base for MPAs by conducting coordinated and standardized monitoring and research at a national scale (Sink et al. 2012).

There is a growing global recognition that high-resolution, non-destructive and in-situ stereo-video techniques (e.g., stereo-BRUVs) can provide an improved understanding of fine-scale ecology on deep and shallow reef habitats and deliver data that support effective and more adaptive EBFM (Watson et al. 2005, 2010, Langlois et al. 2010, Goetze et al. 2011, Bernard et al. 2014, Unsworth et al. 2014). The overall objective of this thesis was to provide insight into sampling and statistical methods for the development of a national BRUVs survey programme to monitor reef fishes in South Africa. Data from this study has contributed to highlighting the opportunities for research on reef fish across the continental shelf of South Africa using stereo-BRUVs (Bernard et al. 2014). In addition, this study aided in contextualizing the advantages and possible pitfalls of using stereo-BRUVs as a method of data collection for a national BRUVs survey programme. This was done through a workshop that incorporated all interested and effected stakeholders, largely from government departments and various research institutes. The key outcome of this workshop was the development of a preliminary standardized BRUVs sampling protocol; particularly the appropriate distribution of spatially explicit research sites amongst participating research agencies, culminating in a nationwide sampling strategy (Attwood et al. 2014). The workshop highlighted specific future research priorities regarding the use of BRUVs, some of which are addressed in this thesis. These include the performance of data derived from stereo-BRUVs compared to that from angling, the relationship between indices of relative abundance (MaxN and CPUE) and the potential implications of 'hyperstability' bias in areas of high fish density.

Briefly, the preliminary sampling protocol is based on deploying mono-BRUVs at regular, but at least annual, intervals by research institutes in their designated sampling areas. This sampling would then be supplemented by periodical deployment of stereo-BRUVs at each sampling area to provide important length-frequency data. The stereo-BRUVs require significantly more capital expenditure than mono-

BRUVs and would be acquired by the research institutes with the financial means and temporarily provided via an open platform to those without stereo-BRUVs when necessary. Hence, the use of mono-BRUVs as primary contributors was a logistical decision to ensure the broader participation by stakeholders, comprehensive spatial and temporal coverage and longevity of the national programme. All collected data, in the form of videos, will be housed by SAEON and disseminated accordingly as it is their mandate to facilitate LTM in South Africa. The standardized protocol allows for individual research institutes to address local, independent ecological questions while simultaneously providing data for the national surveys.

Although still in its infancy, there is a high level of confidence that the national BRUVs survey programme will be realized. Currently, eight conservation and research institutions have committed to participate in the programme (CN, DAFF, DEA, EKZNW, ORI, SAEON, SANP, UCT), sampling a total of 36 reef orientated research areas along the entire coastline of South Africa. In addition, DAFF committed to surveying the offshore areas of the Agulhas Bank from the research ship Ellen Khuzwayo; the first trial survey was conducted in October 2014. The potential value of a systematically applied national BRUVs survey to EBFM in South Africa is enormous and its main objectives include: (i) to provide high resolution species and habitat maps by comprehensive distribution mapping of marine fishes and their associated habitats, (ii) to determine patterns in depth distribution, abundance, biomass and habitat associations for fish populations so as to develop predictive habitat models for reef fishes, (iii) to determine how subtidal reef fish communities respond to protection, and evaluate if the current MPA network will be sufficient under future exploitation and/or climate change scenarios and (iv) to provide species-specific data for stock assessments and conservation status assessments (red listing). Beyond the scientific and management value, hours of video footage will be available for educational purposes to raise awareness regarding the vulnerability of reef fishes and the role of MPAs in protecting reef ecosystems.

7.5 CONCLUSIONS

In an era of unprecedented global biodiversity loss (UNEP 2002, Pereira and Cooper 2006, Hooper et al. 2012), data that can be used to monitor ecosystems and gauge changes in biodiversity through time are essential. As a result, addressing biodiversity information requirements has become one of the fastest growing areas of research in the field of conservation biology (Collen et al. 2013). Climate change and overexploitation of the oceans are global phenomena with global consequences, and therefore need to be confronted on such a scale. Testament to this lies in the commitment to numerous international conservation agreements (CBD, CITES, RAMSAR, ICCAT, UNESCO, UNEP, etc.). The majority of these conservation agreements insist on quantitative accountability through transparent LTM programmes. However, Collen et al. (2013) highlight the growing disconnection between these laudable global commitments to improving the status of biodiversity and the local-scale action required to ultimately ensure their achievement in their aptly titled book, ‘Biodiversity monitoring and conservation: bridging the gaps between global commitment and local action’. In the book they emphasize the practical need to better coordinate LTM programmes, at all scales, to increase the efficiency of gathering knowledge and provide greater management impacts. In an attempt to do so, this thesis provides insight into a method of sampling subtidal reef fish that is widely applicable to various environments up to 250 metres in depth at present (Bernard et al. 2014). Further adaptation of underwater camera housings could provide a method for monitoring beyond the continental shelves (Kilpatrick et al. 2011, Zintzen et al. 2012). Precursory techniques to Stereo-BRUVs (mono-BRUVs, RUVs, DOVs, etc.) have already been successfully applied in numerous countries, and the use of video techniques in fisheries research continues to grow (Bernard et al. 2014, Mallet and Pelletier 2014). A suite of statistical procedures specifically suited for LTM programmes that utilize mono- and/or stereo-BRUVs is also provided to offer scientists an idea of the method’s research potential and possible pitfalls.

It is hoped that the knowledge gained from this thesis will play a role in the advancement of subtidal fishery LTM programmes throughout the world, and thus contribute to the overall understanding of global marine ecosystems. Such information is pivotal to manage the impact of exploitation, coupled with the possible effects of climate change, on nearshore fisheries and biodiversity. At a national level, this thesis aims to contribute significantly to the realization of an annual, national BRUVs survey in South Africa. The objectives of such a multi-institutional undertaking are broad, but the overriding purpose of the programme is to improve the management of South African linefish stocks through providing information for decision making. In a country where the primary conservation legislation mandates the use of conservation management agendas to redress social-economic disparities (DEAT 1998), the effective management of fisheries resources to provide long-term economic benefits is paramount. A successful collaboration between the conservation and research institutions committed to the national BRUVs survey will undoubtedly benefit future marine ecological research in South Africa, and hopefully earn recognition at an international level.

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