

**AN ASSESSMENT OF THE EFFECTIVENESS OF THE ST LUCIA MARINE
RESERVE (KWAZULU-NATAL, SOUTH AFRICA) IN THE PROTECTION OF
SURF-ZONE ANGLING FISH SPECIES**

by

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As the candidate's supervisors we have ~~have not~~ approved this thesis for submission



Signed:

Name: Paul Cowley

Date: 8 August 2016



Signed:

Name: Sean Fennessy

Date: 10 August 2016

PREFACE

The research contained in this thesis was completed by the candidate while based at the Oceanographic Research Institute (ORI), a department of the South African Association for Marine Biological Research (SAAMBR) based in Durban. ORI is affiliated to the School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, Durban, South Africa. The research was financially supported by SAAMBR, Marine and Coastal Management of the then national Department of Environmental Affairs and Tourism, the iSimangaliso Wetland Park Authority and the KwaZulu-Natal Department of Economic Development, Tourism and Environmental Affairs.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

A handwritten signature in black ink, appearing to read 'Paul Cowley', with a long horizontal stroke extending to the right.

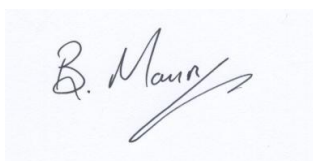
Signed: Paul Cowley (Primary supervisor)

Date: 8 August 2016

DECLARATION 1: PLAGIARISM

I, Bruce Quintin Mann, declare that:

- (i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;
- (ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;
- (iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;
- (iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a) their words have been re-written but the general information attributed to them has been referenced;
 - b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;
- (v) where I have used material for which publications followed, I have indicated in detail my role in the work;
- (vi) this dissertation is primarily a collection of material, prepared by myself and published as journal articles. In some cases, additional material has been included;
- (vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

A handwritten signature in black ink on a light blue background. The signature reads "B. Mann" with a stylized flourish at the end.

Signed: Bruce Q. Mann

Date: 17 August 2016

DECLARATION 2: PUBLICATIONS

The publications (chapters 3-6) are included here from the published versions. The abstracts from each paper have been removed and are included in the overall conclusion in Chapter 7. Similarly, the references from each paper have been removed and compiled into an overall reference list at the end of the thesis. My role in each paper is indicated. The * indicates corresponding author.

Chapter 3

Mann BQ*, Winker H, Maggs JQ, Porter S. 2016. Monitoring the recovery of a previously exploited surf-zone fish community in the St Lucia Marine Reserve, South Africa, using a no-take sanctuary area as a benchmark. *African Journal of Marine Science* 38(3): 423-441.

The research reported on in this paper is based on the data I collected from 50 field trips conducted in the St Lucia Marine Reserve over a 10-year period (November 2001 to July 2011). I designed the study, collected and analysed the data and wrote the paper. Dr Henning Winker provided assistance with effort standardisation and analysis of catch-per-unit-effort data, Mr Jade Maggs assisted with extraction and analysis of the data and Dr Sean Porter assisted with analysis of catch composition data and the use of PERMANOVA. Mr Maggs also participated in a number of field trips over the 10-year period.

Chapter 4

Mann BQ*, Cowley PD, Fennessy ST. 2015. Movement patterns of surf-zone fish species in a subtropical marine protected area on the east coast of South Africa. *African Journal of Marine Science* 37(1): 99-114.

This paper provides an analysis of fish movement data collected using conventional tag-recapture methods using dart tags in the St Lucia Marine Reserve between 2001 and 2013. I designed the study, collected and analysed the data and wrote the paper. Dr Paul Cowley and Dr Sean Fennessy (my supervisors) provided advice on the content and structure of the paper. Both Dr Cowley and Dr Fennessy participated in a number of field trips over the 12-year period.

Chapter 5

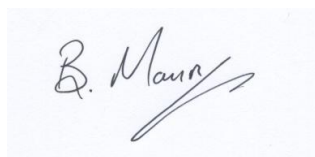
Mann BQ*, Lee B, Cowley PD. 2016. Growth rate of speckled snapper *Lutjanus rivulatus* (Teleostei: Lutjanidae) based on tag-recapture data from the iSimangaliso Wetland Park, South Africa. *African Journal of Marine Science* 38(1): 111-118.

This paper focuses on an analysis of growth data for *Lutjanus rivulatus* from a tag-recapture study data conducted in the St Lucia Marine Reserve between 2001 and 2013. I designed the study, collected and analysed the data and wrote the paper. Mr Brendon Lee assisted with modelling the growth data and Dr Paul Cowley provided advice on the content and structure of the paper. Both Mr Lee and Dr Cowley participated in a number of field trips over the 12-year period.

Chapter 6

Mann BQ*, Cowley PD, Kyle R. 2016. Estimating the optimum size for inshore no-take areas based on movement patterns of surf-zone fishes and recommendations for rezoning of a World Heritage Site in South Africa. *Ocean and Coastal Management* 125: 8-19.

This paper provides a best estimate for the minimum size and spacing required for adequate protection of resident surf-zone angling fish species within the iSimangaliso Wetland Park using areas zoned for no-take. I designed the study, collected and analysed the data and wrote the paper. Dr Paul Cowley participated in a number of field trips and assisted with advice on the content and structure of the paper. Dr Scotty Kyle provided advice on the current and proposed zonation within the park and its feasibility for implementation.

A handwritten signature in black ink on a light blue background. The signature reads "B. Mann" with a stylized flourish at the end.

Signed: Mr Bruce Q. Mann

Date: 17 August 2016

ACKNOWLEDGEMENTS

At the outset I would like to express my gratitude to the conservationists and forward thinking people that led to the proclamation of the St Lucia Marine Reserve back in 1979. It has been and continues to be a real privilege to work in such a beautiful place and to experience and learn about the exceptional biodiversity within this magnificent Marine Protected Area (MPA). There are many people who have contributed in many different ways to the success of this project but I would like to single out just a few of them. Dr Colin Attwood (University of Cape Town - UCT) was instrumental in helping me design the sampling protocols used and to secure the initial funding required for this project when he was still working for Marine and Coastal Management (MCM) of the then Department of Environmental Affairs and Tourism. Being able to fish with Colin and his team in the De Hoop MPA gave me many of the ideas on how to structure and run this project. Similarly, Dr Paul Cowley (South African Institute for Aquatic Biodiversity - SAIAB) and Dr Warren Potts (Rhodes University) and their team in the Tsitsikamma MPA contributed to my ideas around the structuring of this project and Paul has been both a good friend and a reliable supervisor for the write-up phase of this thesis. Mike Tyldesley (Ezemvelo KwaZulu-Natal Wildlife – EKZNW) and Russell Hand were solid supporters of this project from the word go, even contributing to the original project design over a few cold ones at the “Mahogany Reef” in Durban! Mike has been my other “team leader” throughout the 12 year duration of this project; his unwavering dedication and support has been truly admirable and is greatly appreciated. Then to the amazing team of anglers that I have fished with on this project over the years, I am truly indebted to all of you for your contributions and ongoing enthusiasm. By way of acknowledgement I have included all your names and the number field trips that you have fished on in the list below. Dr Sean Fennessy (Oceanographic Research Institute - ORI) is thanked for his support and guidance as my other academic supervisor and Dr Angus Macdonald (University of KwaZulu-Natal - UKZN) is thanked for his assistance as my administrative supervisor within UKZN. Marinel Janse van Rensburg and Mariana Tomalin (ORI) are thanked for their assistance in producing the maps used in this thesis.

The ongoing support from my colleagues at the ORI, the research department of the South African Association for Marine Biological Research (SAAMBR), is gratefully acknowledged. Without the long-term commitment shown by this remarkable organization, this project would never have been able to continue for the duration that it has. Thanks to Dr Larry Oellermann, current SAAMBR CEO, for encouraging me to do this PhD and for allowing me to take a six-month sabbatical to get the bulk of the work written up. Funding and logistical support for this project has been obtained from a number of different organizations including SAAMBR, MCM, National Research Foundation (NRF), EKZNW, the iSimangaliso Wetland Park Authority and the KZN Department of Economic

Development, Tourism and Environmental Affairs. I am extremely grateful to all these organizations and the many people that I have dealt with within them for their support.

I would thank my parents Annette and the late Quintin Mann for their love and guidance and giving me the opportunity to develop my career in marine biology and to pursue my passion for fish and fishing. To other members of my family and all my friends, thank you all for your support and understanding - I told you I was a tortoise and that this was going to be a long haul but I would get there eventually! Last but not least I would like to thank my wife Judy for her ongoing support, encouragement and love and for painstakingly editing many of the chapters in this thesis. Judy without your support I would never have achieved this milestone!

List of participants that have fished in the St Lucia Marine Reserve surf-zone fish monitoring and tagging project and the number of field trips they had completed up until December 2013.

Name	Angler code	Trips fished
Anderson, Brian	BA	12
Asherwood, Jeff	JA	10
Attwood, Colin	CA	1
Ballard, John	JL	1
Bellis, Mike	MB	7
Beukes, Gerhard	GB	1
Bok, Andre	AN	3
Botha, Alan	AB	2
Bowles, Neil	NB	1
Cannon, Chris	CC	2
Chater, Simon	SC	10
Costello, John	JC	1
Cowley, Paul	PC	5
Cox, Kevin	KC	9
Crabb, John	JB	1
Crowe, Devon	DC	1
de Clercq, Cassie	CQ	4
de Gaspary, Glenn	GD	1
de Villiers, Div	DD	1
Dunlop, Stuart	SD	7
Farquhar, Mike	MF	3
Fennessy, Sean	SF	5
Ferguson, Terry	TF	1
Funston, Paul	PF	1
Garratt, Pat	PA	7
Gavin, Rob	RG	1
Goncalves, Miguel	MG	1
Goodwin, Gavin	GG	8
Goss, Pat	PG	1
Hand, Russell	RH	27
Hayes, Desmond	DH	1
Heath, Nigel	NH	1
Hecht, Tom	TH	4

Heydenryck, Glanville	GH	1
Humphries, Keith	KE	3
Humphries, Kevin	KH	6
Humphries, Steven	SH	2
Hutchings, Larry	LH	1
Judd, Chris	CJ	1
Karon, Mike	MK	11
Kitching, Tom	TK	2
Kun, Jules	JK	7
Kyle, Justin	JU	1
Kyle, Robert	RK	14
Lamberth, Steven	SL	1
Lee, Brendon	BL	1
Lewis, Hylton	HL	1
Liversage, Terrance	TL	1
Maggs, Jade	JM	3
Mann, Arthur	AM	13
Mann, Bruce	BQ	59
Mann, Ken	KM	1
Mann, Roger	RM	9
Mapstone, Edwin	EM	1
Massyn, Peter	PM	2
McFerren, Doug	DO	8
Murgatroid, David	DM	5
Murray, Ian	IM	1
Naidoo, Deon	DN	1
Palk, John	JO	17
Parker, Denham	DE	1
Phillips, Roy	RP	2
Potts, Warren	WP	2
Powell, Arthur	AP	1
Pradervand, Pierre	PP	1
Pretorius, Alwyn	AL	1
Pretorius, Dean	ON	1
Punt, Ian	IP	1
Pybus, Julian	JP	9
Ramkissoon, Nicholas	NR	2
Rapson, Bryan	BI	1
Rapson, Wesley	WR	2
Rebeck, Barry	BR	3
Renald, Hilton	HR	8
Richardson, Dean	DR	1
Roseveare, Trevor	TR	1
Shaw, Cambell	CS	2
Simmonds, Bobby	BS	2
Smith, Alex	AS	6
Smith, Craig	CR	1
Smith, Daniel	DA	1
Smith, Lawrence	LS	1
Sookoo, Ori	OS	1
St. Clair-Mulley, Grant	GS	3
Stamatis, Demetri	DS	1
Stander, Freek	FS	2
Talbot, Peter	PT	1

Tedder, Barry	BT	7
Thomassen, Craig	CT	1
Tyldesley, Mike	MT	53
van Aswegen, Vincent	VV	1
van der Merwe, Pieter	PV	15
van Huyssteen, Daniel	DP	5
Venter, Jan	JV	1
Verster, Chris	CV	1
von Schoor, Lionel	LV	1
Vorster, Willie	WV	2
Walter, Jörg	JW	1
Wareham, Barry	BW	4
Wilkinson, Chris	CW	2
Wood, Aidan	AW	6

ABSTRACT

Relatively little was known about the effectiveness of St Lucia Marine Reserve within the iSimangaliso Wetland Park in protecting the surf-zone fish community. In order to address this question, a monitoring project incorporating catch-and-release research fishing using a trained team of volunteer anglers was implemented from November 2001 to November 2013 (12 years). A stratified sampling design was developed whereby an equal amount of standardised fishing effort was applied both in the no-take sanctuary area between Leven Point and Red Cliffs and in the adjacent previously exploited area between Cape Vidal and Leven Point. Trends in catch-per-unit-effort (CPUE) and mean fish size over the first 10 years provided evidence of recovery of four of the most common angling fish populations in the previously exploited area following the implementation of the beach vehicle ban and consequent cessation of shore angling in January 2002. Use of conventional tag and recapture methods revealed that the majority of surf-zone angling fish species displayed station-keeping behaviour and occupied relatively small home ranges, seldom exceeding more than one kilometre of suitable habitat along the coast. However, four of the five most recaptured species also showed evidence of ranging behaviour as some individuals abandoned their home range and travelled distances of up to 125 km. The dominance of station-keeping behaviour suggests that the St Lucia Marine Reserve sanctuary zone provides an important refuge for these species, with some export to adjacent areas. Growth rate of speckled snapper (*Lutjanus rivulatus*), was assessed using tag-recapture data and revealed that this is a very slow growing species. Slow growth, coupled with high site fidelity, suggests that this species is vulnerable to exploitation and that a precautionary approach towards its future management is appropriate. Based on home range size and a literature review of the area required to protect a viable population of resident surf-zone fish species, minimum effective size of no-take areas (NTAs) was estimated. To ensure adequate connectivity between protected fish populations, optimal spacing of NTAs was estimated based on movement patterns of fish species displaying ranging type behaviour, as well as best available information on the distribution of eggs and larvae. This revealed that NTAs of 3-6 km (linear distance) of suitable surf-zone reef habitat, spaced every 15-20 km apart, could provide sufficient protection and connectivity for surf-zone fish populations. The implications of these results are considered with respect to the availability of suitable surf-zone reef habitat, existing patterns of human use and the current zonation of the inshore zone within the iSimangaliso Wetland Park and recommendations for improvements are made.

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CHAPTER 1: GENERAL INTRODUCTION

Traditional methods of managing linefish¹ stocks in South Africa such as minimum size limits and daily bag limits have proved inadequate to sustain stocks of certain species and are difficult to enforce effectively (Attwood and Bennett 1995a; Brouwer et al. 1997; Sauer et al. 1997; Dunlop and Mann 2012a; 2013a). Consequently, the use of no-take marine protected areas (MPAs) as an additional management option to ensure sustainable use of some linefish species, particularly slow-growing and more resident species, has received considerable research attention (Buxton and Smale 1989; Bennett and Attwood 1991; 1993; Attwood and Bennett 1995b; Cowley et al. 2002; Götz et al. 2008; Kerwath et al. 2013; Maggs et al. 2013a, 2013b). In addition to overall biodiversity protection, MPAs in which no fishing is allowed enable resident fish populations to recover to natural levels of carrying capacity and to seed adjacent exploited areas either through emigration of juvenile and/or adult fish (i.e. spillover) or by dispersal of eggs and larvae (i.e. seeding) (Russ and Alcala 1996; McClanahan and Mangi 2000; Roberts et al. 2001; Russ et al. 2003; Gell and Roberts 2003; Halpern 2003; Harrison et al. 2012; Kerwath et al. 2013; Maggs et al. 2013b). The large sizes that adult reef fish attain in suitably protected areas also enhance reproductive output (i.e. more eggs produced and better survival of offspring) and ensure maintenance of genetic integrity of exploited stocks (Berkeley et al. 2004; Palumbi 2004; Field et al. 2008). While there is some debate in the literature as to whether MPAs can increase yield of fished stocks due to the resultant loss of fishing area (for protection) and the concentration of fishing effort in the remaining area (Hilborn et al. 2004; Botsford et al. 2009; Kearney et al. 2012), there is increasing evidence that under the right circumstances they can (Harrison et al. 2012; Kerwath et al. 2013) but each MPA requires a case-by-case evaluation with appropriate monitoring (Hilborn et al. 2004; Sale et al. 2005).

The St Lucia Marine Reserve was proclaimed in 1979 (Mann et al. 1998) and extends from one kilometre south of Cape Vidal (28° 07' S; 32° 33' E) to White Sands (27° 27' S; 32° 41' E) 11 km north of Sodwana Bay, and extends three nautical miles (5.6 km) out to sea (see Figure 1.1 below and Figure 2.1 in Chapter 2). This MPA now forms part of the iSimangaliso Wetland Park, a World Heritage Site established in 1999. The central part of the MPA between Leven Point and Red Sands, a distance of ~25 km, was proclaimed as a no-take sanctuary area and has been effectively policed by Ezemvelo KwaZulu-Natal Wildlife (EKZNW, previously Natal Parks Board) since its proclamation in 1979. However, it is increasingly evident in South Africa and elsewhere, that without convincing

¹ The term “linefish” refers to fish caught by means of hook and line but excludes industrial longlining (Mann 2013)

evidence of their conservation value, no-take MPAs run the risk of being re-opened to exploitation (Russ and Alcala 1996; McClanahan and Mangi 2000; Venter and Mann 2012). It is thus surprising that relatively little work has been done to evaluate the management effectiveness of this MPA.

Within the offshore environment, Garratt (1993) investigated the effectiveness of this MPA in the protection of an adult spawning population of the endemic slinger (*Chrysoblephus puniceus*) and the Oceanographic Research Institute (ORI) undertook an annual underwater visual census (UVC) inside and outside the sanctuary area between 1987 and 1992 using a number of indicator fish species (Chater et al. 1995). More recently, Floros (2010) undertook an UVC study to investigate the effectiveness of different levels of protection (i.e. zonation) on coral reef fish communities in both the St Lucia and the adjacent Maputaland Marine Reserves. The only study that has focussed on surf-zone linefish species involved two brief, informal catch-and-release fishing experiments conducted on 25-27 October 1985 and again on 17-19 November 1988, which revealed substantial differences in catch and size composition of fishes caught inside and adjacent to the sanctuary area (Junor 1989).

It was therefore deemed important to evaluate the effectiveness of the St Lucia Marine Reserve Sanctuary in terms of its ability to provide a refuge for resident surf-zone angling fish species, to maintain some spawner biomass of these species and to sustain or increase yield in the adjacent exploited areas through spillover. This could be done by means of a carefully designed and standardised research fishing project to measure catch composition, catch-per-unit-effort (CPUE) and fish population size structure both inside and adjacent to the no-take sanctuary area (i.e. by using the sanctuary area as a benchmark). Furthermore, by simultaneously using conventional dart tagging (Dunlop et al. 2013), information could be gleaned on the movement patterns and growth rate of important surf-zone angling fish species. This information could then be used to estimate the optimal size that no-take MPAs need to be in order to effectively protect viable populations of surf-zone fishes (Attwood and Bennett 1995b; Attwood 2002) within the Delagoa Bioregion (Sink et al. 2012).

The concept of evaluating MPA effectiveness in the protection of shore angling fish communities is not new in South Africa and the establishment of this project benefitted greatly from two other similar projects, one in the De Hoop MPA started in 1984 (Bennett and Attwood 1991; Bennett and Attwood 1993; Attwood and Bennett 1994; Attwood and Bennett 1995b; Attwood 2002; 2003) and the other in the Tsitsikamma MPA started in 1993 (Cowley et al. 2002; Attwood and Cowley 2005; Götz et al. 2008). While the techniques used were similar, this project differed in the sense that the fish communities being sampled were representative of the Delagoa Bioregion and more typical of an Indo-Pacific ichthyofauna whereas the species sampled in the De Hoop and Tsitsikamma MPAs were typical of the Agulhas Bioregion with a higher level of endemism (Solano-Fernández et al. 2012). These long-term monitoring projects have generated extremely useful data including information on

catch trends, changes in species composition, spatial and temporal changes in fish population size structure, estimation of fishing mortality rates, growth rate estimates, etc. This highlights the need for, and outcomes from, this type of monitoring project.

The overarching goal of this project was to address the question of whether the St Lucia Marine Reserve Sanctuary was providing a refuge for surf-zone angling fish species and whether the adjacent exploited areas were benefitting from spillover. The project started in November 2001 but in January 2002 legislation was promulgated under the National Environmental Management Act (Act No. 107 of 1998) to limit the use of off-road vehicles in the coastal zone (Government Gazette No. 22960). This resulted in shore anglers, who were now restricted to walking, being unable to fish more than ~5 km (i.e. beyond reasonable walking distance) north and south of the beach access point at Cape Vidal. Consequently, the primary goal of this study was modified to assess the potential recovery of a fish community in a previously exploited area using the no-take sanctuary area as a benchmark. Specific objectives of this study were: 1) To compare the species composition, CPUE and size composition of surf-zone fishes within the St Lucia Marine Reserve Sanctuary with that of an adjacent, previously exploited area south of Leven Point by means of research angling from the shore and to monitor the response of the fish community over time; 2) To determine movement patterns of important shore-angling species on a fine spatial scale (< 100 m) by means of dart tagging and to describe patterns of residency and dispersal by tagged fish and to investigate the potential occurrence of spillover from the no-take sanctuary; 3) To use tag-recapture data to investigate the growth rate of speckled snapper *Lutjanus rivulatus*; 4) To use fish movement patterns (residency and dispersal patterns) to investigate the minimum size and spacing of no-take MPAs required to protect viable populations of surf-zone angling species within the Delagoa Bioregion.

This thesis is presented as a set of papers that have been published in peer-reviewed scientific journals. As a consequence there is some overlap and repetition, especially in terms of methods, in the various chapters. Chapter 1 (this chapter) presents a brief overview of the rationale for the study. Chapter 2 covers the study site and a general description of the methods used. The following four chapters respectively address each of the above objectives. Chapter 3 provides a comparison of catches between the St Lucia Marine Reserve sanctuary area and the adjacent previously exploited area south of Leven Point over a period of 10 years (2002-2010) (Mann et al. 2016a). Chapter 4 investigates the movement behaviour of the dominant fish species caught based on a tag-recapture study with a focus on five of the most commonly recaptured species (Mann et al. 2015). Chapter 5 focuses on estimating growth rate of the most commonly recaptured species in this study namely speckled snapper (*Lutjanus rivulatus*) using tag-recapture data (Mann et al. 2016b). Chapter 6 examines effective size and spacing of no-take MPAs within the iSimangaliso Wetland Park, specifically with regard to surf-zone angling fish species (Mann et al. 2016c). Finally, Chapter 7

provides a general conclusion to the study and some recommendations for improved monitoring and management of the iSimangaliso Wetland Park and other MPAs in South Africa.



Figure 1.1a: An aerial photograph of the St Lucia Marine Reserve Sanctuary looking southwards towards Leven Point (Photo: B. Mann).



Figure 1.1b: Research fishing in the St Lucia Marine Reserve north of Cape Vidal on a calm, clear day (Photo: P. Cowley).

CHAPTER 2: STUDY SITE AND DATA COLLECTION

2.1 Study site

The St Lucia Marine Reserve was proclaimed in 1979 and extends from one kilometre south of Cape Vidal ($28^{\circ} 07' S$; $32^{\circ} 33' E$) to White Sands ($27^{\circ} 27' S$; $32^{\circ} 41' E$) 11 km north of Sodwana Bay, and extends three nautical miles (5.6 km) out to sea (Figure 2.1). This marine protected area (MPA) now forms part of the iSimangaliso Wetland Park, a World Heritage Site established in 1999 in northern KwaZulu-Natal (KZN), South Africa. The central part of the MPA between Leven Point and Red Cliffs, a distance of ~25 km, was proclaimed as a no-take sanctuary area.

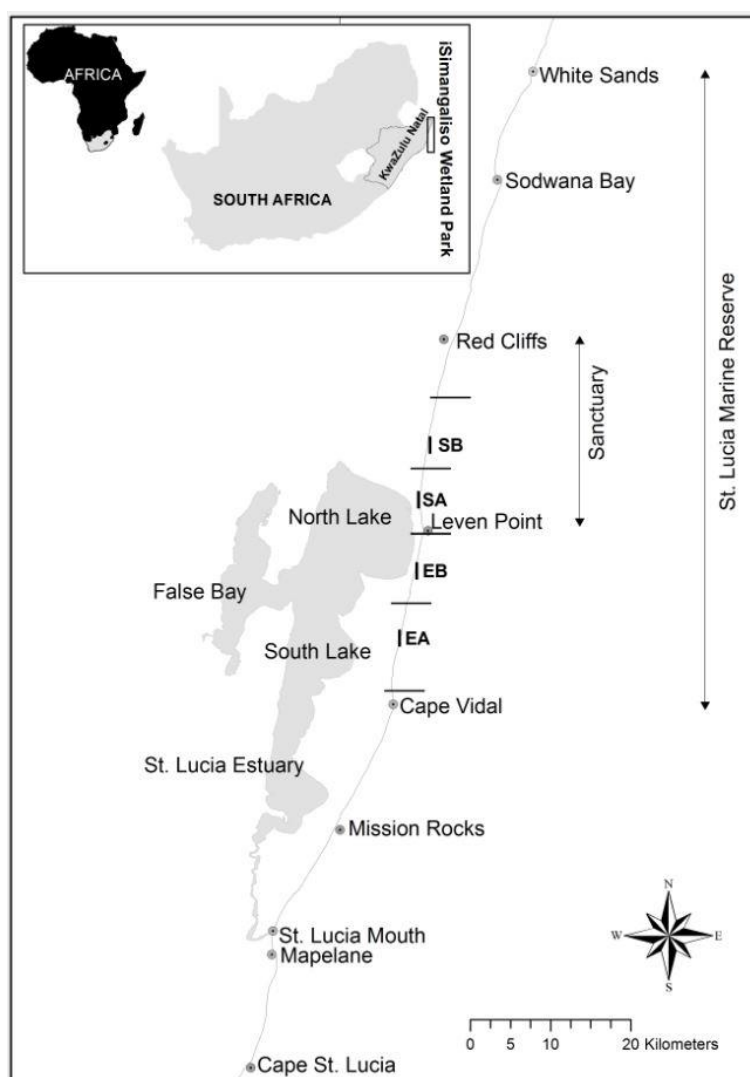


Figure 2.1: Map of the St Lucia Marine Reserve and Sanctuary showing the sampling areas used in this study (denoted by short, bold vertical lines, EA and EB are in the previously exploited area, while SA and SB are within the no-take sanctuary area). Note that the new sampling areas (as of November 2011, with their boundaries indicated by horizontal lines) simply represent northward and southward extensions of the original EA, EB, SA and SB sampling areas.

2.2 Data collection

Data collection for this long-term monitoring project relied on the assistance of volunteer anglers. Anglers belonging to the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORICFTP) (Dunlop et al. 2013) who resided in KZN and who had tagged 100 or more fish were contacted and asked whether they would be interested in being involved in the St Lucia Marine Reserve surf-zone fish monitoring and tagging project. A total of 32 anglers were selected in this manner and given an introductory presentation on the aims of the project and the methods to be used. These anglers were then trained how to record the relevant data and how to handle and tag fish correctly. The 32 selected anglers were used on a rotational basis for each field trip. The rationale behind using the same pool of anglers was to keep fishing effort as consistent as possible. However, in order to reach a wider spectrum of anglers to enable more people to learn and benefit from the experience of fishing in an MPA, one or two guest anglers were invited along on each field trip.

From November 2001 to November 2006, six field trips were carried out per year (Jan, Mar, May, Jul, Sep & Nov) with accommodation based at Cape Vidal which provided the most convenient base. This frequency was reduced to four trips per year (February, May, August, November) from February 2007 to November 2013 due to financial constraints. During each field trip, research fishing was conducted by eight anglers in four selected two-kilometre areas (EA, EB, SA and SB). Each of these areas was divided into 100 m sections using a Geographic Positioning System (GPS) that were distinguishable by numbered marker poles. Two of the 2 km areas (SA and SB) were inside the no-take sanctuary area (between Leven Point and Red Cliffs) and two (EA and EB) were in the previously exploited area (between Leven Point and Cape Vidal) (Figure 2.1). On each day, one team of four anglers fished in one of the previously exploited areas (EA or EB) and the other team of four anglers fished in one of the sanctuary areas (SA or SB). This was rotated each day so that at the end of the four-day field trip each area had been fished by each one of the two teams providing a robust approach for comparing catches between the sanctuary and the previously exploited area south of Leven Point. Daily fishing localities (pole number) within each sampling area were selected based on which areas were the most likely to produce fish given the prevailing conditions. However, a maximum of two hours of continuous fishing effort was spent at a site to ensure that fishing effort was not all concentrated at the same locality and was more evenly dispersed throughout the sampling area. Similarly, if a fishing locality was selected and it proved to be unproductive, a minimum of 15 minutes had to be spent fishing at that locality before moving.

Two four-wheel drive (4x4) vehicles were used to transport the two groups of anglers along the beach from Cape Vidal to their respective fishing areas each day. Fishing was conducted on the four days around spring tide (or as near to this as logistically possible) and all beach driving was restricted to

the low shore three hours before and after low tide (which is around 09h40 on spring low days). Hence, the daily fishing expeditions, including driving to the fishing areas, were around 12 hours in duration. All four sample areas were similar in terms of surf-zone habitat (i.e. all contained both sandy and rocky shores with some patchy sub-tidal reef habitat).

While the sampling strategy was kept as consistent as possible, a few important changes were made over the 12-year duration of the project (November 2001 to November 2013). The first of these was a southward shift of the SA sampling area by 1.2 km after the first three years (January 2005) to include more suitable rocky habitat (i.e. the northern 1.2 km of this zone consisted primarily of sand and was thus not directly comparable to the other three selected zones). A second change that took place was that initially (2002-2003) fishing was largely confined to daylight hours. However, it soon became apparent that this was not practical as departure from the sampling areas at the end of each day had to take place within three hours of low tide, which meant that as the tide got progressively later each day during the fieldtrip, the research team wasted considerable time after dark waiting for the tide to subside. Consequently, the sampling strategy was modified to allow anglers to fish after dark using headlights. A third major change was made to the sampling strategy after 10 years in November 2011. Each of the four 2 km sampling areas was enlarged to cover approximately 10 km of coastline (Figure 2.1). Instead of using numbered poles, a GPS unit was used to determine the exact fishing locality within each ~10 km area and the original system of positions every 100 m was simply extended north and south using a Geographical Information System (GIS). The purpose of this change was two-fold, namely; 1) to reduce the inevitable habitat bias associated with the use of the smaller, 2 km areas and 2) to reduce the bias in determining fish movement patterns based on recaptured tagged fish only caught within the initial four 2 km sampling areas (i.e. there was no fishing in between the originally selected sampling areas).

Standardised rock-and-surf fishing gear (i.e. 3-4.5 m graphite surf rods, multiple or fixed spool reels with braid or monofilament line ranging between 9-23 kg breaking strain) was used and anglers were only allowed to use one rod at a time. A maximum of two hooks per trace was allowed and hook sizes could range between 1/0 and 7/0. However, if anglers decided to target big fish such as giant kingfish (*Caranx ignobilis*), blacktip sharks (*Carcharhinus limbatus*) or giant sandsharks (*Rhynchobatus djiddensis*) using specialized techniques (e.g. sliding large baits using non-return clips, use of wire traces, or hooks >7/0, etc.), such fishing effort was recorded separately. Use of barbless hooks was strictly enforced (barb on the hook crimped using long-nose pliers) as this inflicted less damage and made release of the fish considerably quicker and easier (Casselman 2005). If the fish was gut-hooked (hook lodged in the oesophagus) no attempt was made to remove the hook and the trace was simply cut as near to the eye of the hook as possible (Casselman 2005). A note was made by the angler if the fish was released with the hook still ingested. Use of circle hooks was encouraged (Cooke and Suski

2004) but not enforced due to the higher price of these hooks and the preferences of some anglers. Hook size and type of hook used (i.e. J-hook or circle hook) was recorded for every fish caught from July 2008 onwards. A range of bait types was used including sardines (*Sardinops sagax*), chokka squid (*Loligo reynaudi*), Indian Ocean squid (*Uroteuthis duvaucelii*) and pink prawn (*Haliporoides triarthrus*). When available, additional baits such as chub mackerel (*Scomber japonicus*), redeye sardine (*Etrumeus* spp.), East Coast rock lobster (*Panulirus homarus*) and octopus (*Octopus vulgaris*) were also used. Bait type used for every fish caught was recorded for the first six years of the project (i.e. November 2001 to May 2008).

All fish caught were covered with a wet cloth and quickly measured by the angler on a wet plastic stretcher with a sheathed stainless steel ruler down the centre (Figure 2.2) before being returned unharmed to the water. Emphasis was placed on keeping the fish out of water for as short a time as possible and all surfaces were kept moist to reduce injury and stress (Casselmann 2005). A bucket of seawater was kept close by to immerse the fish prior to and following measuring and tagging. Selected species greater than 300 mm fork length (FL) were tagged using plastic dart tags (Hallprint) supplied by the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP) (Dunlop et al. 2013). D-tags (85 mm in length by 1.6 mm in diameter) were used on smaller fish (300-600 mm) while A-tags (114 mm long by 1.6 mm diameter) were used on larger fish and sharks (> 600 mm). The only exception to this rule was for speckled snapper (*Lutjanus rivulatus*) that were tagged from 280 mm FL due to their suitability for tagging at a relatively small size. All catch, effort and tagging data were recorded by each angler on a slate on a daily basis. Effort data recorded included date, angler name, sampling area (i.e. EA, EB, SA or SB), time fished at each 100 m locality (pole number), targeting (i.e. small or big fish) and tackle lost (i.e. number of hooks, swivels and sinkers lost while fishing). Catch data recorded included tag number (if the fish was tagged or recaptured), species, length in millimetres (fork length [FL], total length [TL] or pre-caudal length [PCL] depending on the species), locality (pole number = GPS position), time the fish was caught and any relevant comments. Comments recorded included bait type, hook type and size, whether the fish had swallowed the hook, whether the fish was a recapture or whether the fish had a tagging scar (i.e. had previously been tagged but the tag had been shed). Note was also made of the condition of the fish on release (i.e. if it was bleeding badly, if it was weak or if it died). During each fishing day sea temperature was recorded at high tide using a thermometer, maximum wind strength and direction was recorded using a handheld anemometer, while swell height and cloud cover were estimated. Sea temperature data were augmented by data retrieved from an underwater temperature recorder (UTR) moored off Leven Point in 16 m of water (Jennifer Olbers, Ezemvelo KwaZulu-Natal Wildlife, pers. comm.).

At the end of each day's fishing, each angler read out his catch and effort data to the project leader (BQ Mann) who recorded all the data onto specially prepared data sheets. These data were subsequently captured onto an MS-Access database in the office for later analysis. Following each field trip a brief report was prepared and circulated to funding and management agencies, as well as to all anglers that had previously participated in the project. At the end of each calendar year an annual report was compiled on the overall results of the project. Analyses for these reports and for much of this thesis (except where indicated otherwise) were undertaken using MS Access queries and MS Excel. All tag and recapture data were also captured onto the ORI-CFTP database (Dunlop et al. 2013) to assist with obtaining recapture data of fish that were recaptured by members of the public (i.e. fish tagged in the MPA by the research team but recaptured by members of the public elsewhere along the coast).



Figure 2.2: The project leader (BQ Mann) tags a Natal stumpnose (*Rhabdosargus sarba*) on a plastic landing stretcher (note the stainless steel ruler down the centre of the stretcher, a wet cloth over the head of the fish and the “tagging box” where all relevant data were recorded).

CHAPTER 3: MONITORING THE RECOVERY OF A PREVIOUSLY EXPLOITED SURF-ZONE FISH COMMUNITY IN THE ST LUCIA MARINE RESERVE, SOUTH AFRICA, USING A NO-TAKE SANCTUARY AREA AS A BENCHMARK

Mann BQ, Winker H, Maggs JQ, Porter SN. 2016. *African Journal of Marine Science* 38(3): 423-441.

3.1 Introduction

It is increasingly being recognised that recreational fishing can have a negative impact on fish populations largely because of the cumulative effect of anglers that may number in the thousands (Coleman et al. 2004; Lewin et al. 2006). Intensive angling over a long period of time can result in changes to the exploited fish community and a reduction in abundance and size of target species (Lewin et al. 2006). Examples of such changes have been widely documented, including in the KwaZulu-Natal (KZN), South Africa, recreational shore fishery (Dunlop and Mann 2012a). No-take marine protected areas (MPAs) where no fishing or extractive use is allowed have been recognised as an important addition to conventional fisheries management tools such as size limits, bag limits and closed seasons (Griffiths et al. 1999; Botsford et al. 2009a). In this respect, well enforced no-take MPAs enable resident fish populations to recover to natural carrying capacity and to seed adjacent exploited areas either through emigration of post-larval fish (i.e. density dependent spillover) or by dispersal of eggs and larvae (i.e. seeding) (Gell and Roberts 2003; Halpern et al. 2010a; Aburto-Oropeza et al. 2011; Harrison et al. 2012; Edgar et al. 2014). The large sizes that adult reef fish attain in suitably protected areas can also enhance reproductive output (i.e. greater egg production and improved survival of offspring) and ensures maintenance of genetic integrity of adjacent exploited fish stocks (Berkeley et al. 2004; Palumbi 2004). There is still some debate in the literature as to whether MPAs can increase yield of adjacent fished stocks sufficiently to compensate for the resultant loss of fishing area (for protection) and the concentration of fishing effort in the remaining area (Hilborn et al. 2004; Botsford et al. 2009a; Kearney et al. 2012). However, there is increasing evidence that under the right circumstances they can (Harrison et al. 2012; Kerwath et al. 2013) but this requires a case-by-case evaluation with appropriate monitoring (Hilborn et al. 2004; Sale et al. 2005).

The St Lucia Marine Reserve on the east coast of South Africa was proclaimed in 1979 (Mann et al. 1998) and extends from one kilometre south of Cape Vidal (28° 08'S; 32° 33'E) to White Sands (27° 26'S; 32° 42'E), 11 km north of Sodwana Bay, a distance of ~80 km, and three nautical miles (5.6 km) out to sea (Figure 3.1). This MPA now forms part of the iSimangaliso Wetland Park, South Africa's first World Heritage Site established in 1999. The centre of the MPA between Leven Point (27° 55'S; 32° 35'E) and Red Cliffs (27° 43'S; 32° 37'E), a distance of ~25 km (Figure 3.1), was proclaimed as a no-take sanctuary area and has been effectively policed by Ezemvelo KwaZulu-Natal

Wildlife (previously Natal Parks Board) since the reserve's proclamation in 1979. Considering the relatively low level of recreational shore fishing effort that existed in the sanctuary region prior to proclamation, and that it is adjacent to a terrestrial wilderness area, it is likely that fish populations and the surf-zone habitat in general have recovered to near pristine conditions. Surprisingly, relatively little has been published on the effectiveness of this MPA in the protection of linefish species. Offshore, Garratt (1993) investigated an adult spawning population of slinger (*Chrysoblephus puniceus*) and the Oceanographic Research Institute undertook an annual underwater visual census (UVC) inside and outside the sanctuary area for several years using a variety of indicator fish species (Chater et al. 1995). More recently, Floros et al. (2013) undertook an UVC to investigate the effectiveness of different levels of protection (i.e. zonation) on coral reef fish communities in both the St Lucia and adjacent Maputaland Marine Reserves. Therefore, there was an urgent need to evaluate the effectiveness of the St Lucia Marine Reserve Sanctuary in terms of its function of providing a refuge for surf-zone angling species. This was addressed in November 2001 through the implementation of a monitoring project based on research angling, similar to the studies undertaken elsewhere on the South African coast in the De Hoop (Bennett and Attwood 1991; 1993; Attwood and Bennett 1995b; Attwood 2003), Tsitsikamma (Cowley et al. 2002) and Dwesa-Cwebe MPAs (Venter and Mann 2012).

In January 2002, a ban on beach driving in South Africa was implemented (Government Gazette No. 22960, promulgated in terms of the National Environmental Management Act No. 107 of 1998) (Celliers et al. 2004). While unpopular with more affluent recreational shore anglers that owned off-road vehicles (Dunlop and Mann 2012a), this legislation effectively reduced shore angler access to large areas of the coast, particularly in less developed areas along the KwaZulu-Natal (KZN) north coast, such as within the St Lucia Marine Reserve between Cape Vidal and Leven Point (Mann et al. 2008). Fortuitously the project to monitor the effectiveness of the St Lucia Marine Reserve Sanctuary had just started in November 2001. This provided a means to determine whether there was any recovery in surf-zone angling fish populations in the previously exploited area between Cape Vidal (beyond a reasonable walking distance of ~5 km) and Leven Point, following the implementation of the beach driving ban. Hence the implementation of the ban led to an adjustment of the original aim of the study, but this did not require a change in study design. The primary aim of this study therefore became to use established stock status indicators including trends in species composition, catch-per-unit-effort (CPUE) and population size structure (Mace 1994; Caddy and Mahon 1995; Shin et al. 2005) to compare populations of surf-zone angling fish species within the St Lucia Marine Reserve Sanctuary (an unexploited benchmark) with those in the previously exploited area between Cape Vidal and Leven Point and to monitor if there was any recovery over a 10-year period (i.e. November 2001 to July 2011).

3.2 Material and methods

3.2.1 Data collection

Although a range of different types of community and population indicators can be used in a study of this type (Murawski 2000; Aburto-Oropeza et al. 2011), the three indicators selected (i.e. trends in species composition, CPUE and population size structure) were simple to collect using volunteer anglers and are frequently used in monitoring the South African linefishery (Griffiths et al. 1999). Thirty two volunteer anglers were selected and trained in recording catch-and-effort data. The selected anglers were used on a rotational basis for each field trip (eight anglers per trip). The rationale behind using the same pool of anglers was to keep fishing effort as consistent as possible and after 10 years 56% of the effort was accounted for by only 13 anglers. However, in order to reach a wider spectrum of anglers to enable more people to learn and benefit from the experience of fishing in a MPA, one or two guest anglers were invited on each field trip.

From November 2001 to November 2006, six field trips were conducted per year (Jan, Mar, May, Jul, Sep & Nov). This was reduced to four trips per year (Feb, May, Jul/Aug & Nov) from February 2007 to July 2011 due to financial and logistical constraints. During each four-day field trip, research fishing was conducted by eight trained anglers in four selected 2 km areas (hereafter referred to as sampling blocks in this chapter) demarcated at 100 m intervals using numbered poles, the position of which was determined using a Geographic Positioning System (GPS). Two of these blocks (SA and SB) were inside the no-take sanctuary area (between Leven Point and Red Cliffs) and two were in the previously exploited area (EA and EB) south of Leven Point (Figure 3.1). Further detail on the sampling design is provided in Chapter 4 (Mann et al. 2015).

Standardised rock-and-surf fishing gear (i.e. 3-4.5 m graphite surf rods, multiplier or fixed spool reels with braid or monofilament line ranging between 9-23 kg breaking strain) was used and anglers were restricted to using one rod at a time. A maximum of two hooks per trace was allowed and hook sizes could range between 1/0 and 7/0. However, if anglers decided to target big fish such as giant kingfish (*Caranx ignobilis*), blacktip sharks (*Carcharhinus limbatus*) or giant guitarfish (*Rhynchobatus djiddensis*) using specialized techniques (e.g. large throw baits or sliding baits using non-return clips, wire traces, large hooks > 7/0, big plugs, etc.), such fishing effort was recorded separately. A standard selection of baits was used including sardines (*Sardinops sagax*), chokka squid (*Loligo reynaudi*), Indian Ocean squid (*Uroteuthis duvaucelii*) and pink prawn (*Haliporoides triarthrus*).

All catch-and-effort data were recorded daily by each angler on a slate. Effort data included date, angler name, sampling block (i.e. EA, EB, SA or SB), time (hours) fished at each 100 m marker and target (i.e. small or big fish). In order to ensure that fishing effort was evenly distributed throughout

each 2 km fishing block, a rule was applied whereby a minimum of 15 minutes and a maximum of two hours could be spent at each fishing location (i.e. at each 100 m marker). Catch data included tag number (if the fish was tagged or recaptured), species, length in millimetres (fork, total or pre-caudal length depending on the species), location (100 m marker number), time the fish was caught and any other relevant comments.

3.2.2 Data analysis

Trends in catch composition

Percentage composition of all fish species caught by number was calculated for each sampling block and compared on an annual basis. Data from 2002 to 2011 were used to compare variation in fish community composition between the sanctuary and the previously exploited area, by means of a three factor repeated-measures PERMANOVA based on the Bray-Curtis similarity measure using percentage composition by number and incorporating all 87 species (Anderson 2001). The treatment effect of sanctuary area versus previously exploited area was treated as a fixed factor, with sampling blocks nested within this factor treated as random, and the year considered orthogonal and treated as a fixed factor. The analysis was run using 9999 permutations of residuals under a reduced model with type III sums of squares and Monte-Carlo simulations employed to derive probability values based on the appropriate number of permutations. Post-hoc tests were carried out where applicable. A non-metric multidimensional scaling (nMDS) ordination was used to visualise changes in the fish community through time for each block (Kruskal and Wish 1978). Analyses were performed with the software programme PRIMER 6.1.5 and PERMANOVA+ for PRIMER (Clarke and Gorley 2006; Anderson et al. 2008).

Trends in catch-per-unit-effort (CPUE)

It is generally assumed that CPUE or catch rate is directly related to abundance and takes the form: $CPUE = Nq$, where N is abundance and q is the fraction of the abundance captured by one unit of effort, also known as the catchability coefficient (Maunder and Punt 2004). CPUE is commonly assumed to be linearly proportionate to abundance as long as q remains constant, but in reality this is rarely the case as it may change both spatially and temporally (Beverton and Holt 1957; Campbell 2004; Maunder and Punt 2004). Therefore, it is essential to standardise CPUE data in order to remove most of the annual variation not attributable to changes in fish abundance (Maunder and Punt 2004; Winker et al. 2013). Targeting of big fish as described above was therefore excluded from the analysis. The remaining data (January 2002 - July 2011) were analysed to estimate indices of relative abundance and the dataset contained 1608 catch-per-angler-per-day records for 87 species (data from the first field trip in November 2001 was excluded from the analysis as it was found to be an outlier due to the field methods still being refined).

Standardisation models

Abundance indices for the four most commonly caught species, *Pomadasys furcatus*, *Trachinotus botla*, *Lutjanus rivulatus* and *Diplodus capensis* were standardised using Generalized Additive Mixed Models (GAMMs), which included the covariates year, hours fished (Hours), sampling block (Block), month, an interaction term (year \times block) and angler as a random effect. In an attempt to account for variation in fishing tactics and targeting, an additional factor (FT) was derived from a cluster analysis of the catch composition (He et al. 1997; Winker et al. 2013) (see below). CPUE was modelled as catch in number per species per angler per day. The CPUE records of the four most abundant species (in terms of catch frequency) were fitted by assuming either a Poisson or Quasi-Poisson error model with a log-link function. A Quasi-Poisson was chosen if the dispersion parameter $\phi > 1.1$ (Zuur et al. 2009). All GAMMs were fitted using the ‘mgcv’ and ‘nlme’ libraries in the R statistical environment, as described in Wood (2006).

Clustering of the catch composition data was conducted by applying the non-hierarchical clustering technique ‘CLARA’ (Struyf et al. 1996), also in the R environment, to the catch composition matrix. For this purpose, a data matrix comprising CPUE records for each species was constructed. The data were normalized into relative proportions by weight and square-root-transformed. Subsequently, the identified cluster for each catch composition record was aligned with the original dataset and treated as a categorical variable (FT) in the GAMM (Winker et al. 2013). To select the number of meaningful clusters to be included as predictors in the GAMMs, the approach outlined in Winker et al. (2014) was followed. Accordingly, a Principal Component Analysis (PCA) was applied to the square-root-transformed species composition matrix. The retained principle components (PCs) are those selected as non-trivial based on non-graphical solutions for Catell’s Scree test in association with the Kaiser-Guttman rule (eigen value > 1), called the Optimal Coordinate test, which is available in the R package as ‘nFactors’ (Raïche et al. 2013). The total number of clusters considered was taken as the number of retained PCs plus one (Winker et al. 2014). This approach resulted in the selection of the first three PCs and correspondingly four clusters were selected as optimal for the CLARA clustering technique.

The full GAMM, evaluated for each species i independently, included a thin plate regression for hours and a cyclic cubic smoothing function for month, such that:

$$CPUE_i = e^{\beta_0 + year + s(month) + s(hours) + block + year \times block + FT + \alpha_j} \quad (1)$$

where $s()$ denotes the smoothing functions, FT is the vector of cluster numbers treated as a categorical variable and α_j is the random effect for angler j (Helsler et al. 2004; Weltz et al. 2013). The inclusion

of individual anglers as a random effect provides an efficient way to combine CPUE recorded from various anglers in a single continuous CPUE time-series, despite discontinuity of individual anglers over the sampling period (Helsler et al. 2004). The main reason for treating angler as a random effect was because of concerns that multiple CPUE records produced by the same angler may violate the assumption of independence caused by variation in angling skill, which can result in overestimated precision and significance levels of the predicted CPUE trends if not accounted for (Thorson and Minto 2015). The significance of the random-effects structure was supported for all species by Akaike's Information Criterion (AIC). Sequential F-tests were used to determine the covariates that contributed significantly ($p < 0.05$) to the deviance explained.

Trends in length frequency

Length frequency data were used to investigate the size structure of fish populations over time. Although use of a single size-based indicator can result in certain biases due to variations in year-class strength (Shin et al. 2005), mean length was considered in addition to species composition and relative abundance as another widely used indicator (Froese et al. 2008). Changes in mean length were modelled for the four most commonly caught species, *P. furcatus*, *T. botla*, *L. rivulatus* and *D. capensis*, using the GAMM framework described for the CPUE standardisation, but excluding the effort and targeting covariates hours fished (Hours) and FT, respectively:

$$Length_i = e^{\beta_0 + year + s(month) + block + year \times block + \alpha_i} \quad (2)$$

The standardised species-specific length data were fitted by assuming a Gamma error model with a log-link function. The significance of including angler as a random effect was supported for all species by AIC. As for CPUE, sequential F-tests were used to determine the covariates that contributed significantly ($p < 0.05$) to the deviance explained in the length data. All reference to CPUE and mean length presented in the results refers to standardised data.

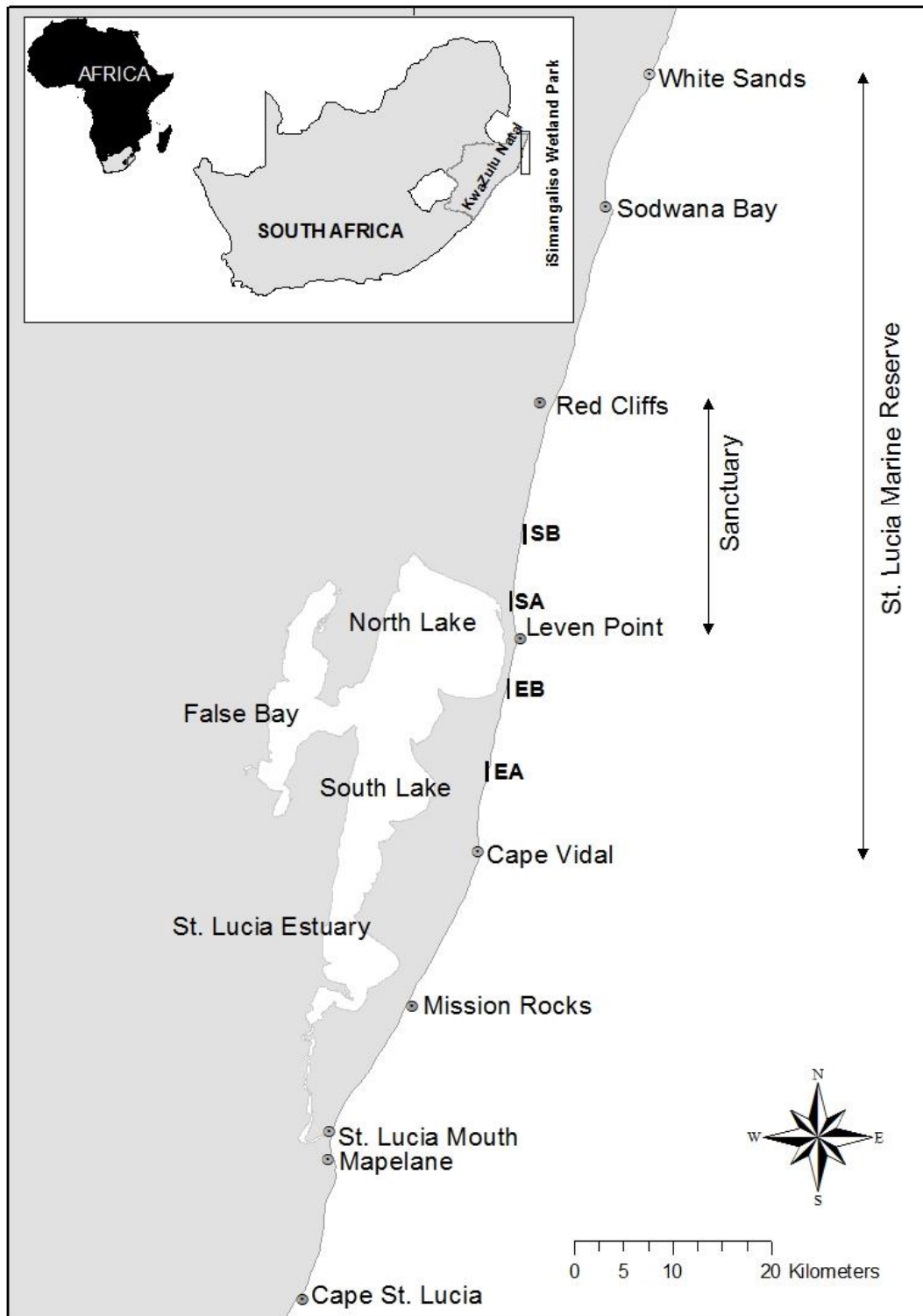


Figure 3.1: Map of the St Lucia Marine Reserve and Sanctuary showing the four 2 km sampling blocks used in this study. EA and EB are in the previously exploited area, SA and SB are in the no-take sanctuary area. Inset shows the iSimangaliso Wetland Park that incorporates the marine reserve.

3.3 Results

A total of 50 field trips (1608 angler days involving a total of 92 anglers) were undertaken between November 2001 and July 2011 during which 12 367 fish were caught comprising 87 species from 37 families (Appendix 3.1).

3.3.1 Trends in catch composition

The species composition was similar in each of the four sampling blocks being dominated by three species namely *Lutjanus rivulatus*, *Trachinotus botla* and *Pomadasys furcatus* (Figure 3.2a-d). EA had the lowest proportion of *L. rivulatus* (7%) and the highest proportion of *T. botla* (27%), whereas SB had a substantially higher proportion of *L. rivulatus* (29%) and a lower proportion of *T. botla* (7%). Overall, considerably more fish were caught in SB than in the other three blocks (Figure 3.2).

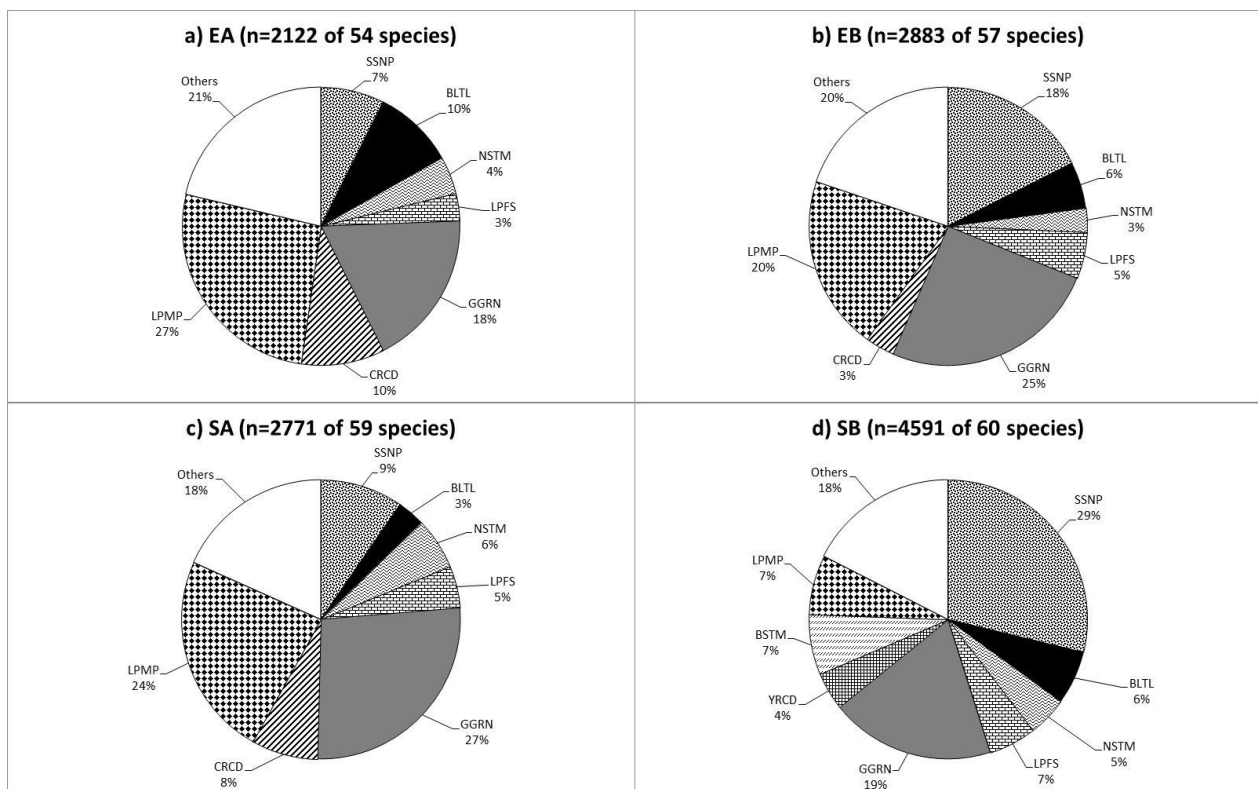


Figure 3.2a-d: Species composition recorded at the four sampling blocks from January 2002 to July 2011 in the St Lucia Marine Reserve. EA and EB were in the previously exploited area, while SA and SB were in the sanctuary area (SSNP=*Lutjanus rivulatus*; GGRN=*Pomadasys furcatus*; LPMP=*Trachinotus botla*; CRCD=*Epinephelus andersoni*; NSTM=*Rhabdosargus sarba*; BLTL=*Diplodus capensis*; LPFS=*Dinoperca petersi*; BSTM=*Rhabdosargus thorpei*; YRCD=*Epinephelus marginatus*).

Analysis of species composition over the 10-year study period revealed subtle differences and changes in each of the four sampling blocks (Figures 3.3 & 3.4). In addition to the above mentioned three dominant species, *Diplodus capensis* and *Epinephelus andersoni* comprised the top five species

in EA (Figure 3.3a). An increase in the percentage contribution of *P. furcatus* was observed from 2008-2011 and a decrease in the percentage composition of *E. andersoni* during 2010-2011 were the only discernible changes in species composition in EA over the 10-year period (Figure 3.3a). In EB, *Dinoperca petersi* replaced *E. andersoni* as one of the top five species (Figure 3.3b). An increasing trend in percentage composition of both *L. rivulatus* and *P. furcatus* was apparent in EB (Figure 3.3b). *E. andersoni* and *Rhabdosargus sarba* combined with the aforementioned three species, dominated catches in SA (Figure 3.3c). Species composition fluctuated widely in SA over the 10-year period. In 2005 catches of *T. botla* increased substantially while the percentage composition of reef-associated fish species such as *P. furcatus* and *L. rivulatus* decreased. This pattern was reversed in 2009 with an increase in reef species and a decrease in *T. botla* (Figure 3.3c). Percentage composition of *R. sarba* in SA was progressively smaller throughout the sampling period. *Rhabdosargus thorpei* and *D. capensis* combined with the top three species, dominated catches in SB (Figure 3.3d). An increase in the percentage composition of *L. rivulatus* from 2008-2011 was the most evident trend in SB over the 10-year period.

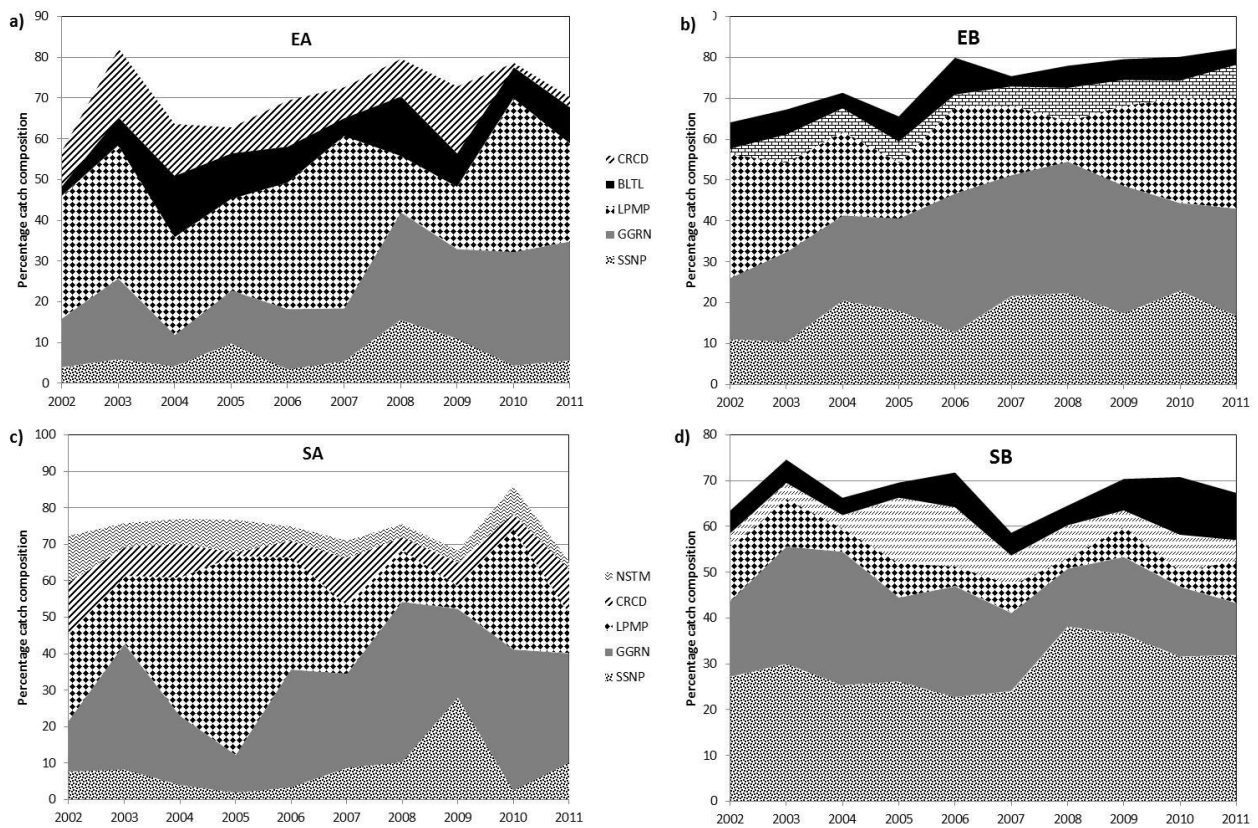


Figure 3.3a-d: Trends in fish species composition at the four sampling blocks in the St Lucia Marine Reserve between 2002 and 2011 (SSNP=*Lutjanus rivulatus*; GGRN=*Pomadasys furcatus*; LPMP=*Trachinotus botla*; CRCD=*Epinephelus andersoni*; NSTM=*Rhabdosargus sarba*; BLTL=*Diplodus capensis*; LPFS=*Dinoperca petersi*; BSTM=*Rhabdosargus thorpei*).

The nMDS ordination indicated that community composition at EA, EB and SA was similar and overlapped during most years (Figure 3.4). SB however, was generally more distinct from the other communities and showed little overlap throughout the study. Analysis of overall trends in Bray-Curtis similarities among the previously exploited (EA & EB) and sanctuary (SA & SB) blocks revealed that three out of the four comparisons showed convergence in community composition, whilst communities within sanctuary block SB showed a trend of divergence. Average \pm SD Bray-Curtis similarities between sanctuary blocks and previously exploited blocks for each year ranged from 48.9 ± 11.3 to $62.7 \pm 7.1\%$.

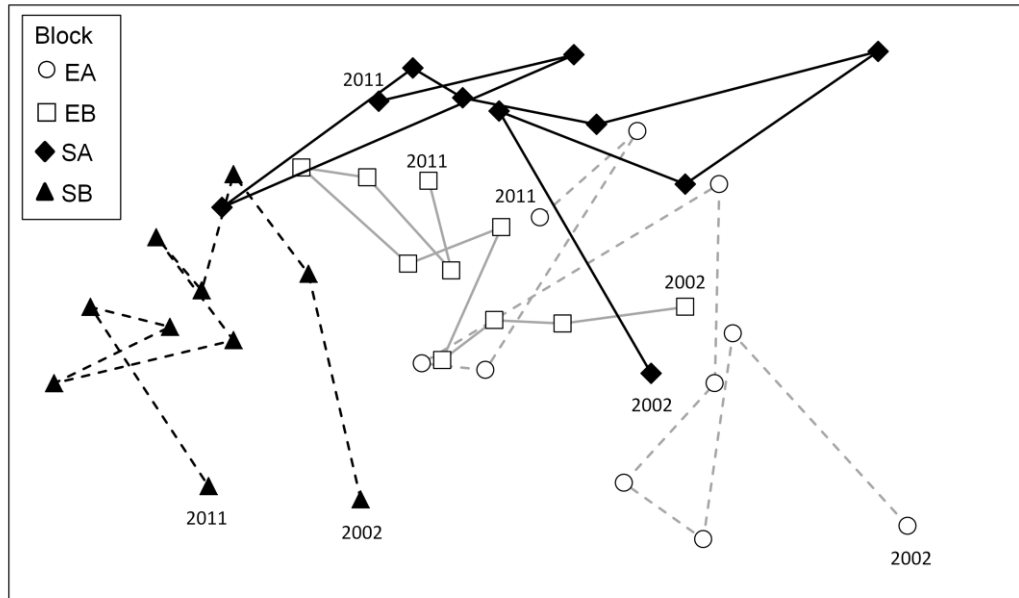


Figure 3.4: An nMDS ordination based on percentage catch composition for the four 2 km sampling blocks in the St Lucia Marine Reserve between 2002 and 2011.

The PERMANOVA found no significant difference in the treatment effect of fish community composition between the sanctuary and previously exploited areas nor in the interaction of this term with year (time) ($P_{(\text{Monte-Carlo})} > 0.1$) (Table 3.1). However, the analysis did reveal significant differences according to year, block nested within treatment and the interaction of blocks nested within treatment with year ($P_{(\text{Monte-Carlo})} < 0.05$). Post-hoc pairwise tests between different years were not significantly different for 62% of the comparisons ($P_{(\text{Monte-Carlo})} < 0.05$).

Table 3.1: Results of PERMANOVA to investigate variation in fish community composition according to the treatment effect of sanctuary area versus previously exploited area, year (time) and sampling block using percentage composition data and the Bray-Curtis similarity distance measure. Significant differences are indicated by an * ($\alpha = 0.05$).

Source of variation	Df	MS	F_{Pseudo}	$P_{(\text{Monte-Carlo})}$
Treatment	1	21266	0.9592	0.4866
Year	9	4321	2.8244	0.0001*
Block(treatment)	2	22172	18.2760	0.0001*
Treatment x year	9	1856	1.2131	0.1505
Block(treatment) x year	18	1530	1.2612	0.0210*
Residual	156	1213		
Total	195			

3.3.2 Trends in catch-per-unit-effort (CPUE)

Standardised abundance trends

Summary statistics for covariates tested in the GAMMs fitted to CPUE data for *P. furcatus*, *T. botla*, *L. rivulatus* and *D. capensis* are shown in Table 3.2. All four species showed significant variation in CPUE over the 10-year period (year) and three of the four species, excluding *P. furcatus*, showed significant seasonal variation in abundance [s(month)]. Annual trends in CPUE were significantly different among the sampling blocks (block × year) and only *D. capensis* did not show a significant effect of targeting effort (FT).

Table 3.2: Summary statistics for covariates tested in the GAMMs fitted to CPUE data for *Pomadasys furcatus*, *Trachinotus botla*, *Lutjanus rivulatus* and *Diplodus capensis* (significant results shown in bold).

Predictor	<i>P. furcatus</i>		<i>T. botla</i>		<i>L. rivulatus</i>		<i>D. capensis</i>	
	F-Test	<i>P</i>	F-Test	<i>p</i>	F-Test	<i>p</i>	F-Test	<i>p</i>
Year	3.282	< 0.001	3.548	< 0.001	3.650	< 0.001	3.361	< 0.001
s(Month)	0.001	0.321	19.26	< 0.001	16.86	< 0.001	8.875	< 0.001
s(Hours)	10.94	< 0.001	21.36	< 0.001	16.08	< 0.001	10.455	< 0.001
Block	1.417	0.236	2.723	< 0.05	8.178	< 0.05	1.826	0.140
Block x year	2.585	< 0.001	2.139	< 0.001	3.159	< 0.001	2.822	< 0.001
FT	40.911	< 0.001	108.348	< 0.001	98.74	< 0.001	0.489	0.689

There was an increase in CPUE for *P. furcatus* from 2002–2008 in the previously exploited areas (EA and EB) after which CPUE fluctuated around the mean of the initially higher sanctuary areas (SA and SB) (Figure 3.5a, b). In contrast to the sanctuary blocks, there were distinct increases in CPUE between 2002 and 2011 in both previously exploited blocks. The difference was strongest in EA with no overlap in 95% CI's (Figure 3.5c). Seasonality revealed no significant variation in CPUE (Table 3.2; Figure 3.5d).

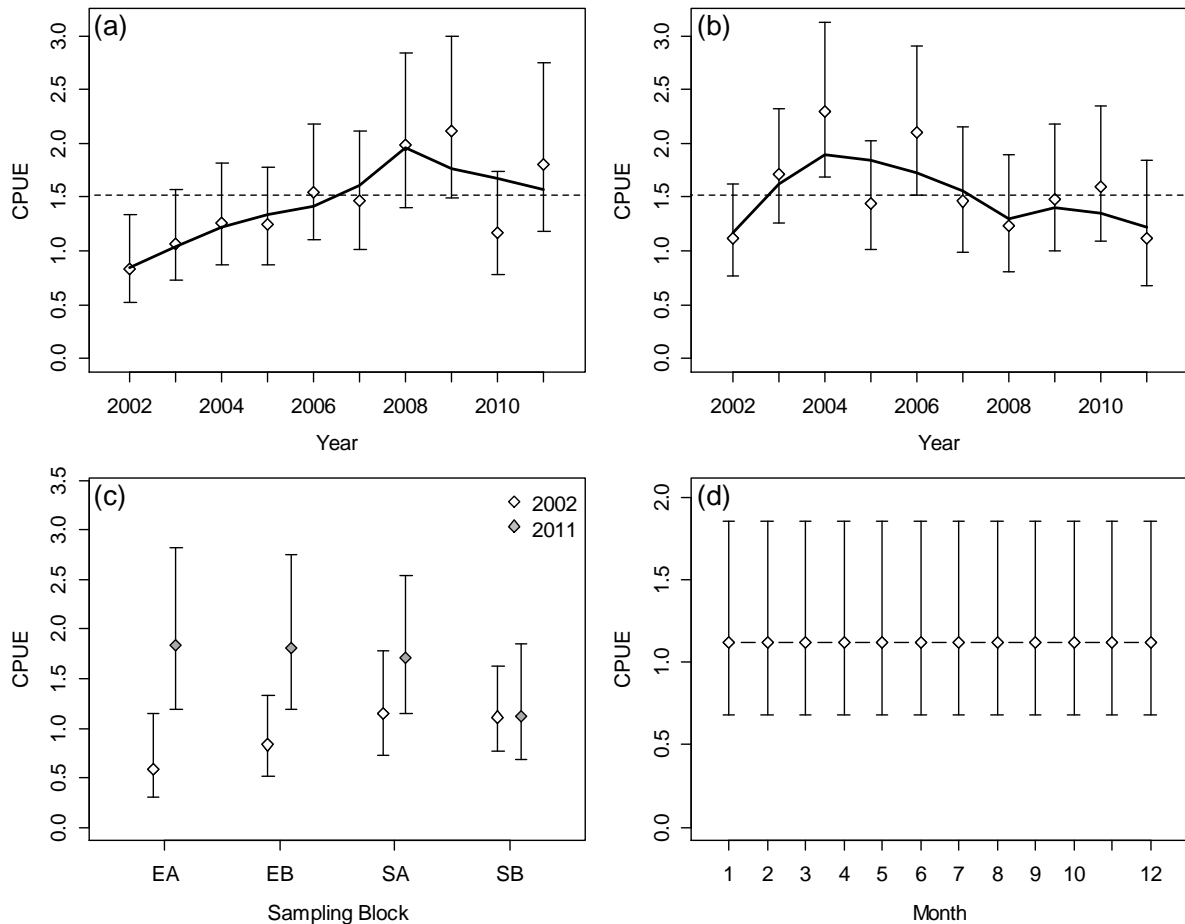


Figure 3.5: Standardised CPUE trends based on the targeting-adjusted GAMM for *Pomadasys furcatus* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised CPUE is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the mean CPUE from the sanctuary area. The 95% CI's are denoted by error bars.

The CPUE for *T. botla* in the previously exploited area remained below the average attained in the sanctuary area until 2009-2011 when it increased, whereas CPUE fluctuated in the sanctuary area with a peak in 2004 (Figure 3.6a, b). Increases in CPUE between 2002 and 2011 were noticeable in both the previously exploited blocks (EA and EB) (Figure 3.6c). Catch rates were highly seasonal with highest CPUE predicted for the warmer summer months from November to May (Figure 3.6d).

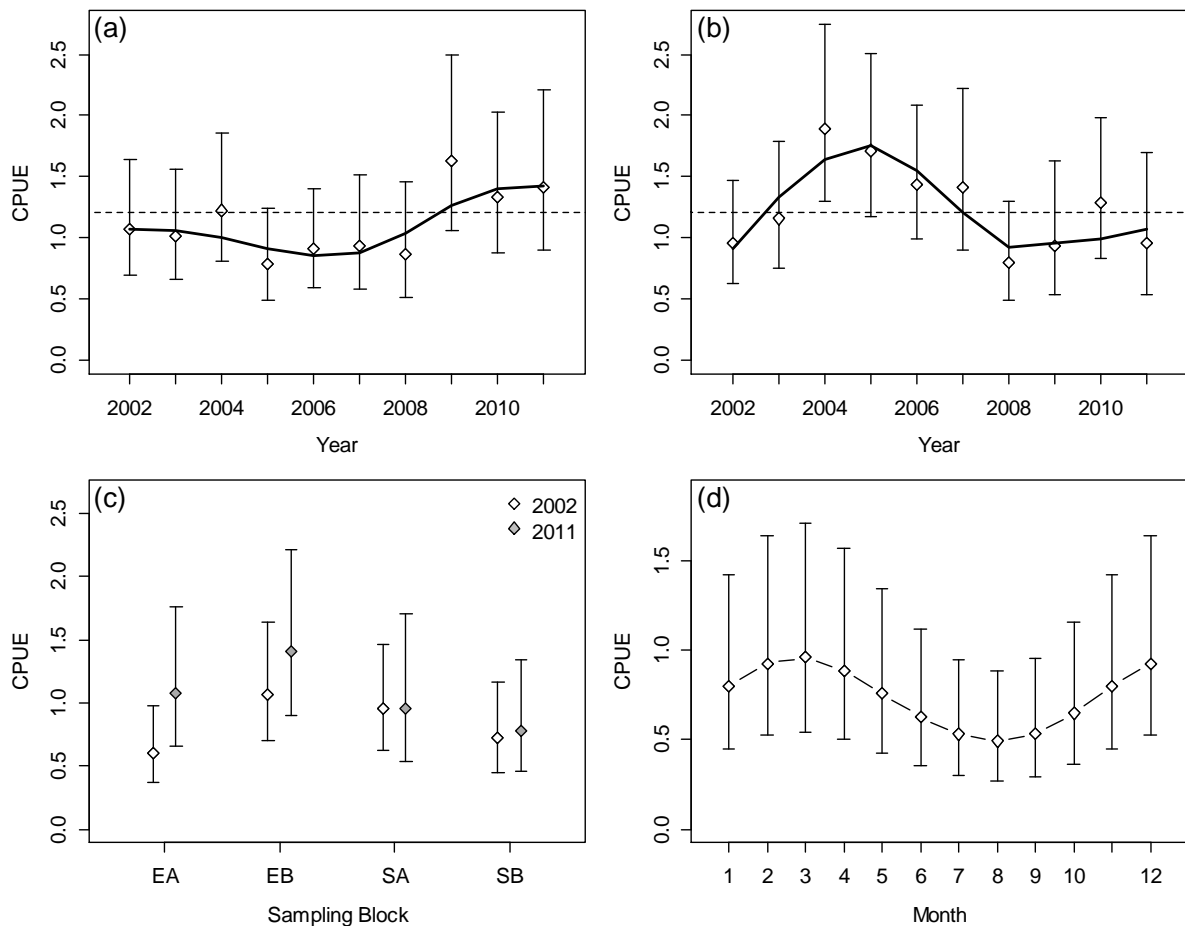


Figure 3.6: Standardised CPUE trends based on the targeting-adjusted GAMM for *Trachinotus botla* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised CPUE is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the mean CPUE from the sanctuary area. The 95% CI's are denoted by error bars.

Lutjanus rivulatus showed a gradually increasing trend in CPUE in both the previously exploited and sanctuary areas but catch rates were consistently higher in the sanctuary areas. This increase was particularly noticeable in both areas from 2008 onwards (Figure 3.7a, b). Catch rates were lowest in the EA block and highest in the SB block with increases between 2002 and 2011 being similar in all four blocks (Figure 3.7c). Catch rates were seasonal with highest CPUE predicted for the summer months from November to May (Figure 3.7d).

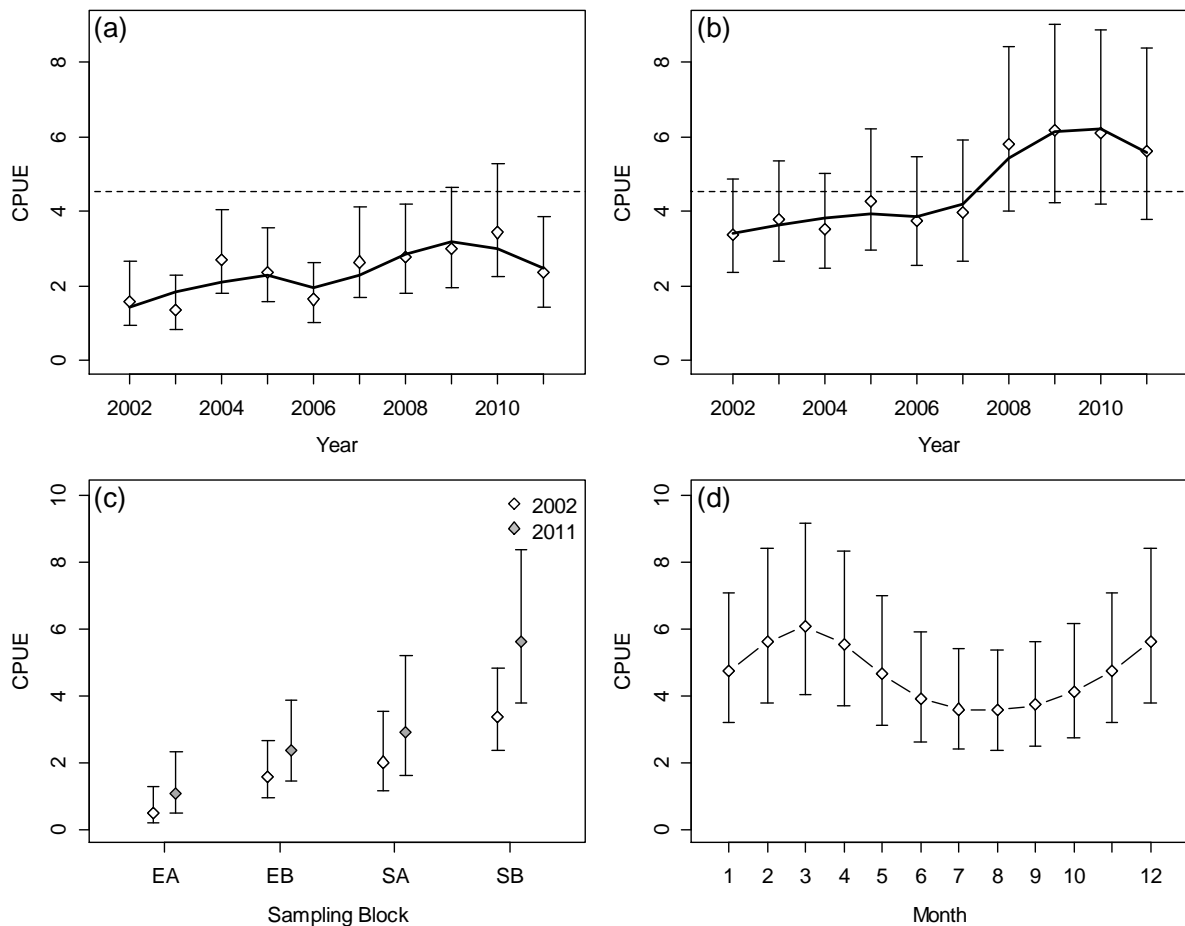


Figure 3.7: Standardised CPUE trends based on the targeting-adjusted GAMM for *Lutjanus rivulatus* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised CPUE is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend and dashed lines in (a) and (b) indicate the mean CPUE from the sanctuary area. The 95% CI's are denoted by error bars.

The CPUE for *D. capensis* increased rapidly from 2002 to 2004 in the previously exploited areas and then remained stable around the mean CPUE recorded in the sanctuary areas (Figure 3.8a). An increase in CPUE in the sanctuary area was also recorded between 2009 and 2011 (Figure 3.8b). These increases were most apparent in the EA and SB blocks between 2002 and 2011 (Figure 3.8c). Some evidence of seasonality was apparent with higher catch rates being predicted for the cooler winter months from April to September (Figure 3.8d).

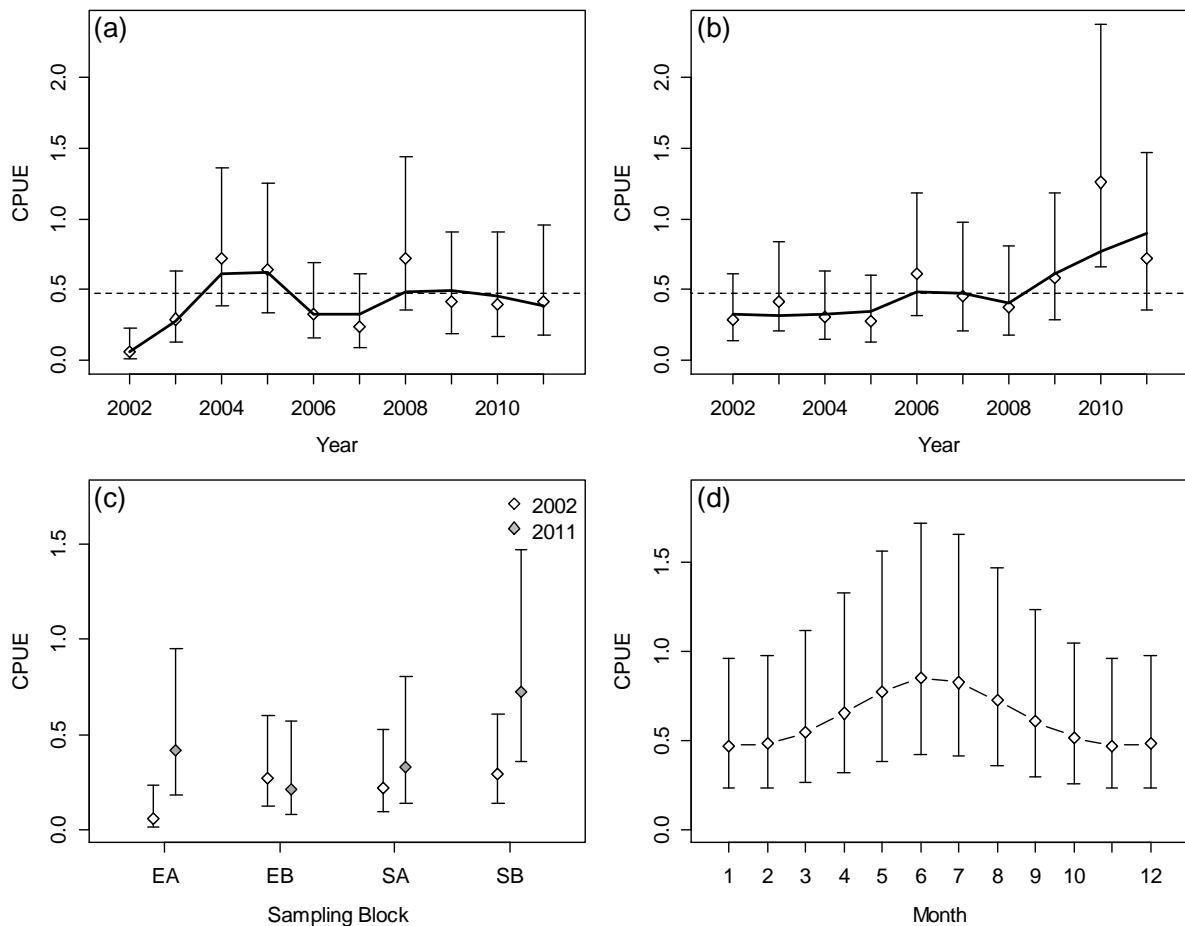


Figure 3.8: Standardised CPUE trends based on the targeting-adjusted GAMM for *Diplodus capensis* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised CPUE is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the mean CPUE from the sanctuary area. The 95% CI's are denoted by error bars.

3.3.3 Trends in mean size

Summary statistics for covariates tested in the GAMMs fitted to length data for *P. furcatus*, *T. botla*, *L. rivulatus* and *D. capensis* are shown in Table 3.3. Three of the four species, excluding *T. botla*, showed significant variation in mean length over the 10-year period (Year) and three of the four species, excluding *P. furcatus*, showed significant seasonal variation in mean length [s(Month)]. All species except *D. capensis* showed significant differences in mean length between sampling blocks (Block). Similarly, annual trends in mean length were significantly different among the sampling blocks (block \times year) with the exception of *D. capensis*.

Table 3.3: Summary statistics for covariates tested in the GAMMs fitted to length data for *Pomadasy furcatus*, *Trachinotus botla*, *Lutjanus rivulatus* and *Diplodus capensis*. Significant differences are shown in bold.

Predictor	<i>P. furcatus</i>		<i>T. botla</i>		<i>L. rivulatus</i>		<i>D. capensis</i>	
	F-Test	<i>P</i>	F-Test	<i>p</i>	F-Test	<i>P</i>	F-Test	<i>P</i>
Year	6.97	< 0.001	1.862	0.053	4.262	< 0.001	2.356	< 0.05
Season(Month)	0.001	0.628	14.50	< 0.001	2.842	< 0.01	2.011	< 0.05
Block	8.776	< 0.001	5.583	< 0.001	8.977	< 0.001	1.315	0.268
Block x year	2.525	< 0.001	2.212	< 0.001	4.191	< 0.001	1.412	0.081

In 2002 and 2003, the mean length of *P. furcatus* was smaller in the previously exploited areas than in the sanctuary areas (< 260 mm FL), but by 2005 the mean length had increased to above the overall mean recorded in the sanctuary areas and remained relatively stable thereafter (Figure 3.9a). There was no significant trend in mean length of *P. furcatus* within the sanctuary areas (Figure 3.9b). The increase in mean length between 2002 and 2011 was most evident in the EA block (Figure 3.9c). There was no change in the predicted mean length of *P. furcatus* seasonally (Figure 3.9d).

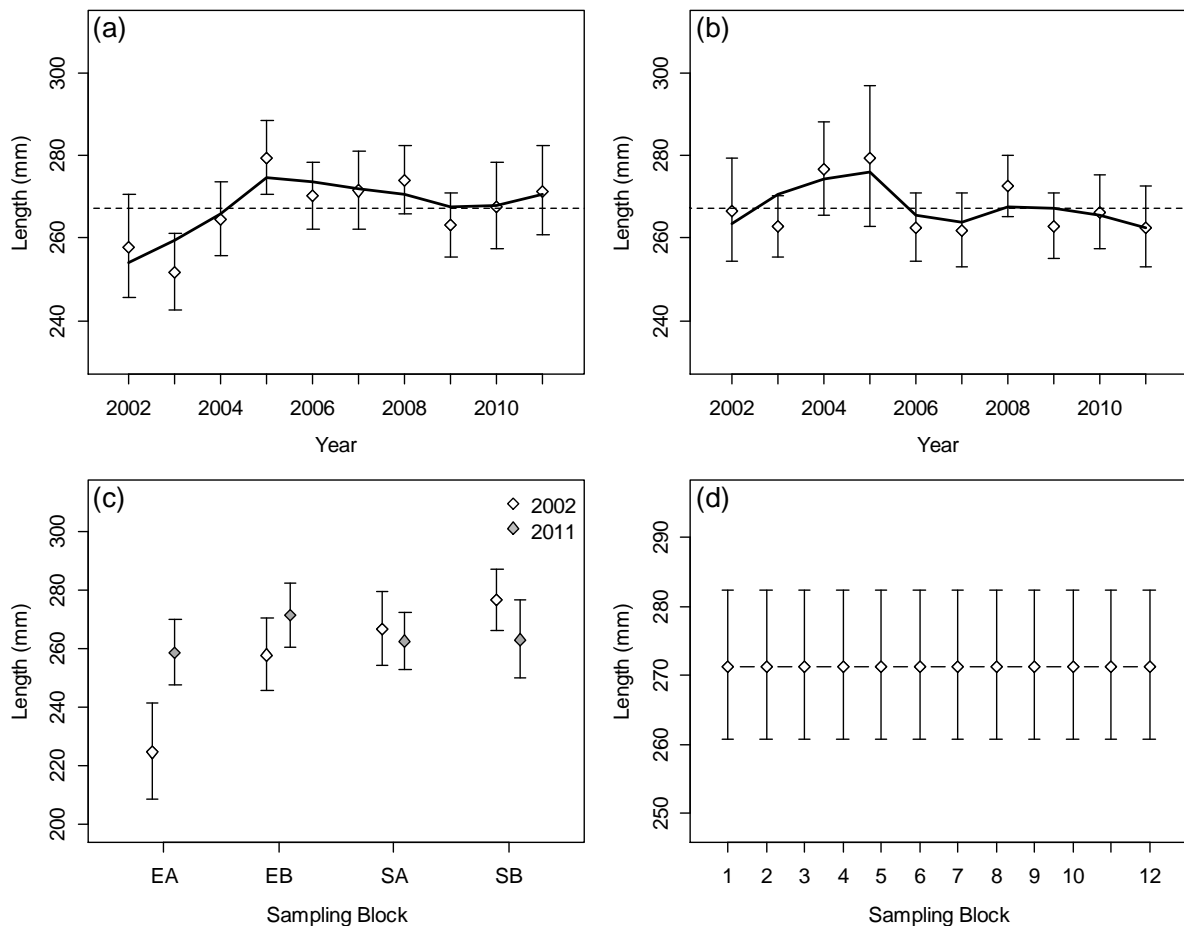


Figure 3.9: Standardised trends in mean length based on the full GAMM for *Pomadasys furcatus* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised mean length is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the overall mean length recorded in the sanctuary area. The 95% CI's are denoted by error bars.

The mean length of *T. botla* was predicted to be consistently smaller in the previously exploited area than in the sanctuary area between 2002 and 2007 (~280 mm FL). Thereafter the size increased and became more similar to the overall mean length of *T. botla* caught in the sanctuary area (~320 mm FL) between 2008 and 2010 but decreased slightly again in 2011 (Figure 3.10a). The mean length of *T. botla* in the sanctuary area fluctuated with no clear trend (Figure 3.10b). Mean length of *T. botla* caught in the SB block was significantly larger than that of fish caught in the other three blocks but there was little difference in mean length in any of the four sampling blocks between 2002 and 2011 (Figure 3.10c). Strong seasonality was evident in the mean length with larger fish caught during the summer months (November to May) (Figure 3.10d).

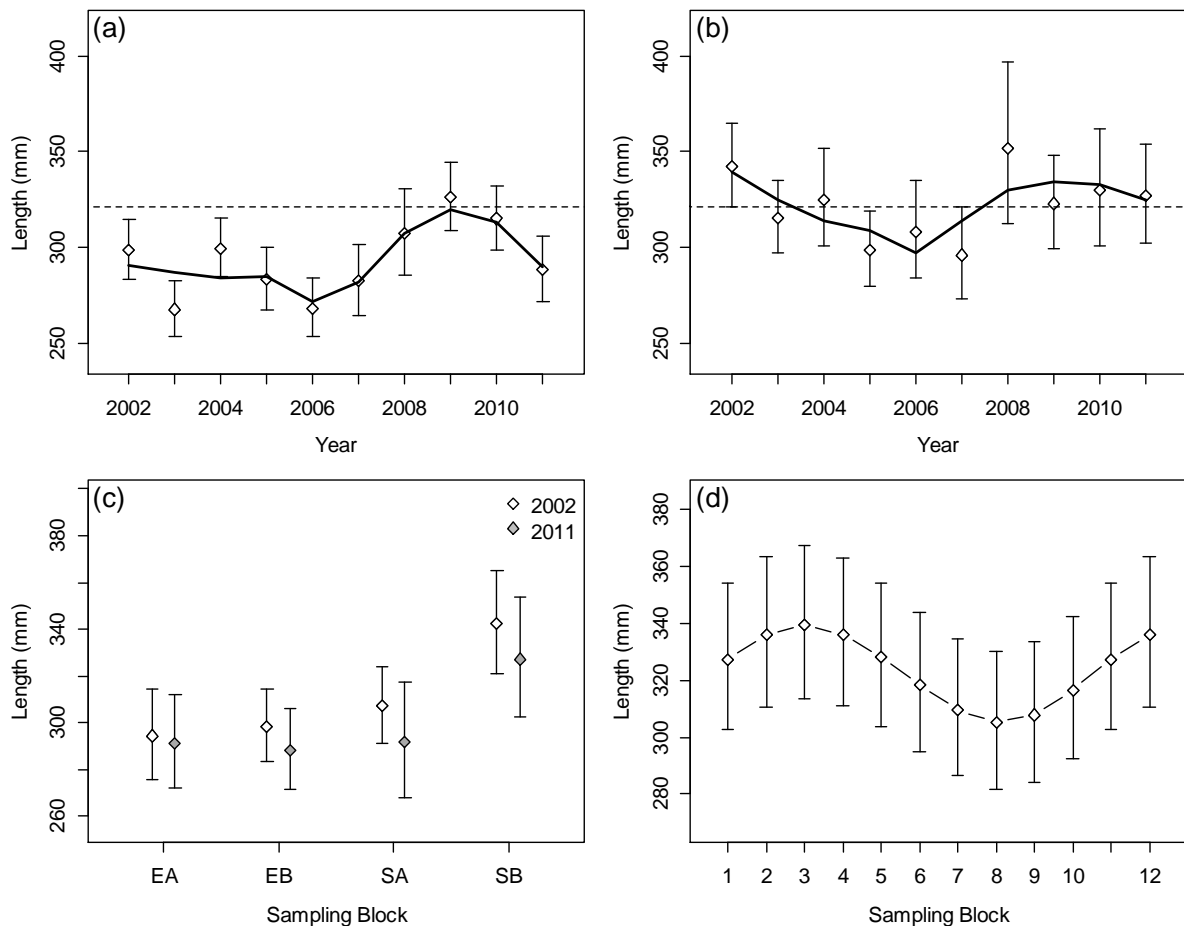


Figure 3.10: Standardised trends in mean length based on the full GAMM for *Trachinotus botla* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised mean length is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the overall mean length recorded in the sanctuary area. The 95% CI's are denoted by error bars.

Lutjanus rivulatus showed a steady increase in mean length between 2002 (278 mm FL) and 2011 (339 mm FL) in the previously exploited area, being substantially smaller in 2002-2004 than the overall mean length recorded in the sanctuary area (Figure 3.11a). The mean length of *L. rivulatus* in the sanctuary area initially declined between 2002 and 2007 whereafter it increased (Figure 3.11b). The increase in mean length between 2002 and 2011 was clearly evident in both the EA and EB sampling blocks (Figure 3.11c). There was evidence of slightly larger fish being caught during spring (August to October) and in mid-summer (January) (Figure 3.11d).

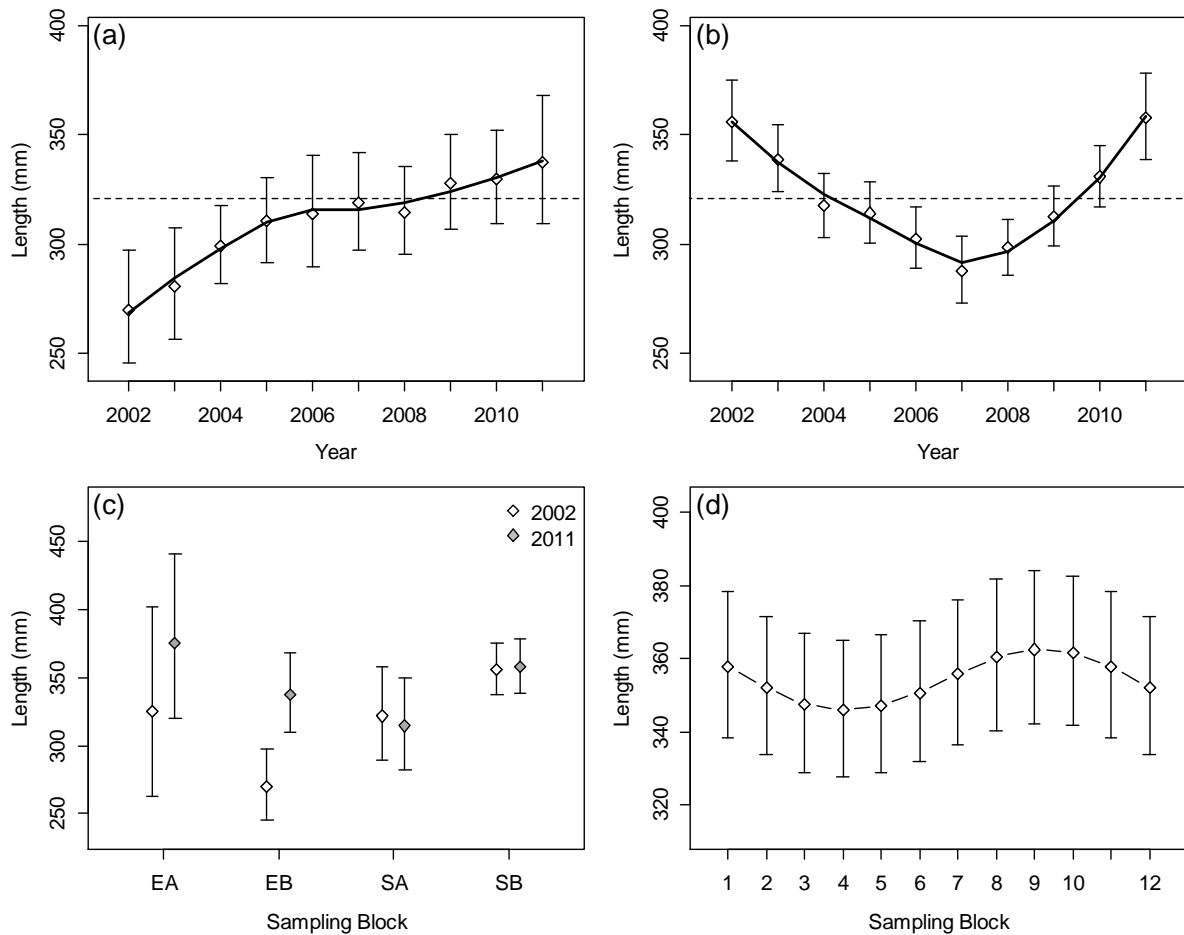


Figure 3.11: Standardised trends in mean length based on the full GAMM for *Lutjanus rivulatus* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised mean length is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the overall mean length recorded in the sanctuary area. The 95% CI's are denoted by error bars.

Diplodus capensis showed a gradual but significant increase in mean length between 2002 and 2011 in the previously exploited area, eventually passing the overall mean size (228 mm FL) recorded in the sanctuary area (Figure 3.12a). There was no clear trend in mean length recorded in the sanctuary area (Figure 3.12b). The significant increases in mean size between 2002 and 2011 were equally noticeable in both the EA and EB blocks (Figure 3.12c). Slightly larger fish were caught during the winter months between May and October (Figure 3.12d).

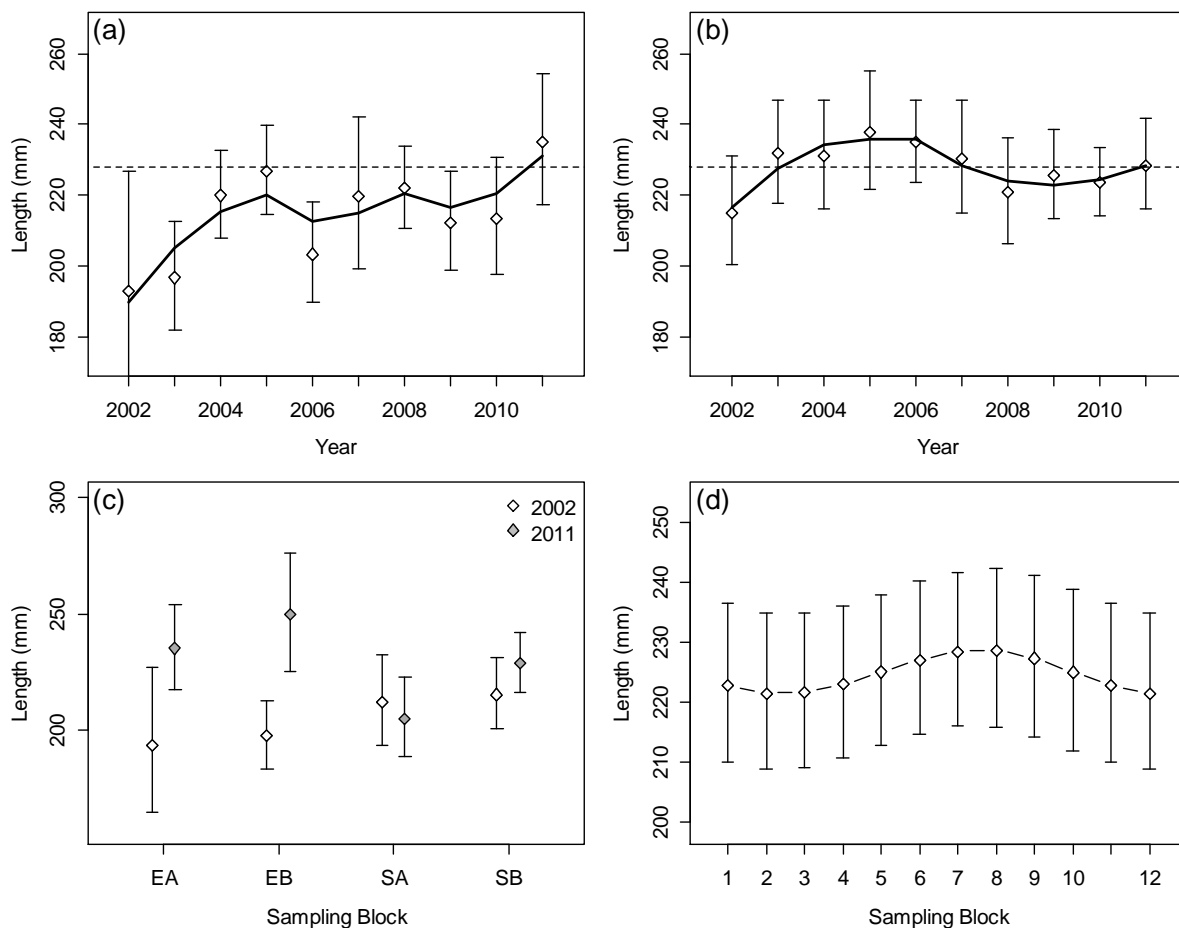


Figure 3.12: Standardised trends in mean length based on the full GAMM for *Diplodus capensis* caught in the St Lucia Marine Reserve from January 2002 to July 2011. Standardised mean length is shown (a) for the previously exploited area (EA and EB), (b) for the sanctuary area (SA and SB), (c) by sampling block (EA, EB, SA and SB) in 2002 and 2011, and (d) by month. Solid lines in (a) and (b) represent loess smoother fits highlighting the underlying trend. Dashed lines in (a) and (b) indicate the overall mean length recorded in the sanctuary area. The 95% CI's are denoted by error bars.

3.4 Discussion

The life history of exploited species has direct implications for resilience to fishing and recovery time (Jennings et al. 1999). Slow growing, late maturing species are likely to take much longer to recover than fast growing, early maturing species. The four most abundant species considered in this study have contrasting life history strategies (Mann 2013) and it was anticipated that fast growing, mobile species such as *T. botla* (Parker et al. 2013) would respond more quickly to the cessation in shore fishing effort than *L. rivulatus* which has been shown to be a highly resident, slow growing species (Mann et al. 2015; Mann et al. 2016b). This would, however, also depend on the initial depletion level. While such difference in response was not clearly evident, the data collected during this study found evidence of recovery for all four of the most common surf-zone fishes in the previously exploited area south of Leven Point following the implementation of the beach driving ban in January

2002. This evidence was strengthened by using the sanctuary area as a benchmark which improved the ability to differentiate between recovery signals and natural population fluctuation. However, despite a concerted effort to standardise the fishing protocol and to ensure that the selected 2 km sampling blocks were as similar as possible, factors such as high natural variability in fish populations, subtle changes in angler behaviour and slight differences in habitat among each of the four sampling blocks, complicated interpretation of the results. No two sites were identical which highlights the importance of adequate replication when comparing sites with different levels of exploitation (Attwood 2003). Furthermore, although the area south of Leven Point was fished by shore anglers using beach vehicles prior to the implementation of the beach vehicle ban, the intensity of fishing declined with distance from the beach access points at Cape Vidal and Sodwana Bay (Figure 3.1; Mann et al. 1997). The contrast in exploitation history between surf-zone fish populations in the no-take sanctuary with those in the previously exploited area was therefore likely to have been less pronounced than might have been the case in more heavily fished areas, and also would have represented something of an exploitation gradient.

Overall, species diversity and catch rates were lowest in the EA block closest to Cape Vidal and highest in SB near the centre of the sanctuary area (Mann and Tyldesley 2013). This supports the observation of a gradient in fish population densities and highlights the value of no-take MPAs in protecting a greater biomass of fishery species (Aburto-Oropeza et al. 2011; Maggs et al. 2013a; Edgar et al. 2014). Trends in stock status indicators used in this study suggested a fairly rapid initial recovery (3-4 years) of all four of the main fishery species (*P. furcatus*, *T. botla*, *L. rivulatus* and *D. capensis*), in the previously exploited sampling area (EA & EB), similar to the findings after the closure to angling of the De Hoop Marine Reserve in South Africa's Western Cape province (Bennett and Attwood 1991; 1993). However, the recovery observed in EB was generally more apparent and sustained (Figure 3.3b). The proximity of EB to the sanctuary (4 km) suggests that this area probably received greater benefit from spillover and larval export than EA which is further away (12 km). Such recoveries in fish density and associated fishery benefits close to the boundaries of no-take MPAs have been well documented in the literature (Gell and Roberts 2003; Russ et al. 2003; Halpern et al. 2010a).

3.4.1 Trends in catch composition

The annual variation in catch composition and fish abundance may have been linked to various environmental parameters that potentially masked the evidence of community recovery. These included aspects such as recruitment variability and habitat changes. For example, the increase in percentage contribution of *L. rivulatus* in both the sanctuary blocks from 2007 to 2009 (Figure 3.3c-d) may have been linked to a good recruitment event. This suggestion is supported by the higher catch rates (Figure 3.7b) and lower mean size of fish caught in the sanctuary area during this period (Figure

3.11b). This recruitment event is also likely to have affected the increases in species contribution and catch rate of *L. rivulatus* observed in the previously exploited areas. Another example is the sudden increase in the percentage composition of *T. botla* in 2005 in SA and the simultaneous decline in reef-associated species such as *P. furcatus* and *L. rivulatus* (Figure 3.3c). A sand inundation event took place during 2005 which covered many of the surf-zone reefs in the SA block and which led to a resultant change in species composition. This situation was reversed in 2009 when a scouring event exposed many of the surf-zone reefs resulting in an influx of reef-associated species. The dynamic nature of surf-zone reefs with regard to regular sand inundation is thus an important factor that needs to be considered when comparing surf-zone fish populations.

Analysis of catch composition (Figure 3.4) highlighted the fact that while the four sampling blocks were similar in terms of the fish communities present (Table 3.2), SB was significantly different from the other three blocks. SB contained the most extensive reef structure of the four blocks and it is likely that this availability of reef habitat resulted in some of the differences observed. In addition, the relatively close proximity (~400 m) of SB to Leadsman Shoal (an offshore reef of 7.3km² in size) may have influenced the species composition because fish from this large offshore reef complex may move into the surf-zone and *vice versa*. This highlights the importance of habitat quality and connectivity when selecting no-take MPAs to maximize their effectiveness (Green et al. 2014). Most importantly, there was an indication of convergence in the other three sampling blocks (Figure 3.4) suggesting that the fish community was becoming more similar and stable as would be expected after a period of 10 years with no fishing mortality (Jennings and Kaiser 1998; Lester et al. 2009; Aburto-Oropeza et al. 2011).

3.4.2 Trends in catch-per-unit-effort (CPUE)

A comprehensive approach was used to standardise CPUE data in an attempt to remove most of the variation not attributable to annual changes in fish abundance, building on the methods in Winker et al. (2013; 2014). The potentially confounding sources of variation that were accounted for included month, block, targeting effects and variations in individual angler CPUE. Significant variation in CPUE could be attributed to persistent differences in individual angler skill and behaviour, which was incorporated in the standardisation in the form of a random effects term (Helser et al. 2004; Weltz et al. 2013). Of the fixed effects, the categorical predictor derived from clustering of catch composition explained much of the observed deviance, indicating that substantial variation in the CPUE data was removed by including the targeting effect. However, given that CPUE was aggregated by angler and day, but that anglers typically employed multiple fishing tactics in terms of the choice of hook sizes, bait, and target species, it was not possible to infer distinct, species-specific fishing tactics from the aggregated daily angler catch composition data. Therefore, it is likely that some bias remained due to optimising the choice of fishing tactics during the course of the fishing day. A standard rig frequently

used by anglers on this project consisted of a two-hook trace with the top hook being smaller (1/0 or 2/0) baited with prawn or squid, and the bottom hook being larger (4/0 or 5/0) baited with sardine. This trace effectively targeted species such as *T. botla* and *P. furcatus* on the top hook and species such as *L. rivulatus* and *E. marginatus* on the bottom hook. Depending on the type of surf-zone habitat such a baited trace was cast into (i.e. reef or sand), a large variety of species could be expected to take the bait. Identifying precise species targets is thus extremely difficult using this method of fishing.

Another aspect that was difficult to account for in the CPUE analysis was the improved fishing skill of the team over time. After 10 years of fishing the same 2 km blocks, anglers gained local knowledge and learnt where the most productive areas were and fishing effort became more focused in these areas (despite the application of the two-hour rule per 100 m locality). Anglers also learnt how best to target certain species. For example, *L. rivulatus* and *D. petersi* feed more prolifically in the first few hours of darkness which resulted in improved targeting at this time. An example of this behaviour was the increase in fishing effort expended at dusk and during the first few hours of darkness at localities such as SB2 and SB20. Both these localities consist of extensive reef habitat with large numbers of *L. rivulatus* and the observed increase in CPUE for this species in SB from 2007 onwards (Figure 3.7a, b) was possibly related to this learnt angler behaviour. Although anglers had equal opportunity to learn at all sites, such behaviour changes potentially improved catch rates but were not necessarily related to an increase in fish abundance. The influence of improved fishing skill (often referred to as effort creep) is frequently acknowledged in studies evaluating long-term catch and effort data series but is difficult to factor into such analyses (Griffiths 2000; Attwood 2003), particularly when stocks show a positive trend rather than a negative one as is often the case in exploited fisheries. Monitoring programmes such as this should therefore attempt to standardise the methods used beforehand in order to reduce this type of variability.

Despite these challenges, analysis of trends in standardised CPUE provided useful indicators of relative abundance of the dominant surf-zone angling species (Figures 3.5-3.8), which are considered to be relatively unbiased compared to any alternative fisheries-dependent data sources. Of the four most common species analysed (*P. furcatus*, *T. botla*, *L. rivulatus* and *D. capensis*), all showed increases in abundance in the previously exploited area. Somewhat surprisingly, two of the species (*L. rivulatus* and *D. capensis*), also showed similar increases in abundance in the sanctuary area. This was not anticipated as it was assumed that species protected in the sanctuary for >30 years would have reached levels close to their carrying capacity and should thus have revealed more stable trends in abundance (Lester et al. 2009). The reasons for the observed increases are probably related to factors such as successful recruitment events as has been described above for *L. rivulatus*, as well as improved angling skill. The decrease in *T. botla* CPUE in the sanctuary areas could have been related

to insufficient resolution in the catch composition data to account for a gradual switch in targeting with more effort being focused on catching reef fish species, particularly in SB.

3.4.3 Trends in mean size

Some studies have suggested that monitoring of mean length in fish populations can be a relatively weak indicator of stock status especially when only one such size-based indicator is used. This is because there are a variety of spatial and temporal factors which can affect this such as sampling within nursery areas, periodic recruitment events, gear selectivity, etc. (Griffiths et al. 1999; Attwood 2003; Shin et al. 2005; Froese et al. 2008). However, the monitoring of fish length in this study provided a particularly useful indicator, largely because it was used in combination with the other two methods. Annual tracking of mean length of target species such as *P. furcatus*, *L. rivulatus* and *D. capensis* showed convincing evidence of recovery in the previously exploited area within the first 2-4 years (Figures 3.9, 3.11, 3.12). These increases were expected as resident fish species are generally able to increase in size (and number as shown above) with a cessation in fishing mortality. The trend in mean length of *T. botla* in the previously exploited area was more difficult to interpret although it too eventually showed an increase in mean length between 2008-2010 (Figure 3.10). Time series of *T. botla*, both in terms of abundance and mean length, were highly seasonal with more and bigger fish being caught during the summer months. This seasonality coupled with the wider ranging movement behaviour of this species (Chapter 4, Mann et al. 2015), may have compromised the ability to clearly track changes in its mean size compared to that of more resident species.

Complex inter-specific interactions such as competition between species may affect the time taken for fish communities to return to a “climax” state (Lester et al. 2009) and this state may never be reached if the ecosystem is irreparably damaged (Jennings and Kaiser 1998). While the surf-zone habitat in both the no-take sanctuary and previously exploited area was believed to be in a relatively healthy condition, studies of this nature need to be conducted over a long period, especially in the case of monitoring slow growing, long-lived fish species (Abesamis et al. 2014). An important observation made during the study was the small mean size of some of the fish species caught, especially the serranids, supporting the suggestion that the surf-zone provides an important nursery habitat for these species, with adults moving out into deeper water with increasing size/age (Chapter 4, Mann et al. 2015). Another important point to emphasize with regard to monitoring of fish size structure in no-take MPAs is that it provides information that is extremely useful for the calculation of reliable estimates of natural mortality for comparison with exploited populations as was done during this study for *R. sarba* (James et al. 2004) and *T. botla* (Parker et al. 2013).

3.5 Conclusion

Evidence provided by this study suggests that areas of the South African coastline that were previously only accessible by means of beach vehicles prior to 2002, are likely to have had some recovery of resident surf-zone fish populations. However, such recovery may have greatly benefitted from the close proximity of a no-take MPA or other natural refuge from which an element of adult spillover and/or larval export would have occurred (Halpern et al. 2010a). This highlights the importance of having a network of no-take MPAs to increase resilience of exploited fish populations (Gaines et al. 2010). In contrast to the many environmental benefits associated with the beach driving ban, there are also a few negative aspects. Shore-angling is now more concentrated at beach access points along the coast, resulting in areas of local depletion of some resident fish populations (Mann et al. 2008; Parker et al. 2013). In addition, in some areas of the Eastern Cape this spatial shift in fishing effort has also resulted in greater effort being placed on other more accessible fishing areas such as estuaries (Cowley et al. 2013), which are vulnerable nursery areas for estuarine-dependent marine fish species.

With regard to future monitoring of MPAs, several important points learnt during this study need to be highlighted: 1) The use of no-take MPAs as a benchmark is highly desirable in long-term monitoring programmes to enable distinction to be made between natural variability and human-induced changes. 2) Monitoring programmes of this nature must be carefully designed, rigidly implemented and be run for a long time period (>10 years). 3) Sampling areas must have similar habitat to reduce any confounding effects of the environment and increase confidence in the detection of fishing related inter-annual changes. 4) Sampling must cover the seasons systematically because of strong seasonal variation in abundance of some fish species. 5) It is important to monitor different attributes of fish populations and communities to strengthen results (e.g. species composition, relative abundance and population size structure). 6) The consequences of any changes to the sampling design in such programmes must be carefully evaluated before being implemented. 7) The use of volunteers in such programmes requires careful management and training but has important spin-offs in terms of costs and angler awareness.

Appendix 3.1: Number of fish species caught, tagged and recaptured in the St Lucia Marine Reserve from November 2001 to July 2011 (species arranged according to the classification of Smith and Heemstra [1991] except in the case of species names subsequently revised).

Family	Species	Common name	Number caught	Number tagged	Number recaptured
Carcharhinidae	<i>Carcharhinus brevipinna</i>	Spinner shark	1	1	0
Carcharhinidae	<i>Carcharhinus limbatus</i>	Blacktip shark	13	13	0
Carcharhinidae	<i>Rhizoprionodon acutus</i>	Milkshark	3	3	0

Sphyrnidae	<i>Sphyrna zygaena</i>	Smooth hammerhead	1	1	0
Odontaspidae	<i>Carcharias taurus</i>	Spotted ragged-tooth	2	2	0
Rhinobatidae	<i>Rhinobatos annulatus</i>	Lesser guitarfish	10	8	0
Rhinobatidae	<i>Rhinobatos leucospilus</i>	Greyspot guitarfish	3	3	0
Rhinobatidae	<i>Rhynchobatus djiddensis</i>	Giant guitarfish	52	47	5
Dasyatidae	<i>Himantura fai</i>	Roundnose stingray	7	7	0
Dasyatidae	<i>Himantura gerrardi</i>	Sharpnose stingray	43	42	0
Dasyatidae	<i>Himantura leopard</i>	Honeycomb stingray	24	24	0
Elopidae	<i>Elops machnata</i>	Ladyfish	1	1	0
Albulidae	<i>Albula oligolepis</i>	Bonefish	214	154	0
Muraenidae	<i>Echidna nebulosi</i>	Floral moray	1	0	0
Muraenidae	<i>Gymnothorax undulates</i>	Leopard moray	118	0	0
Muraenidae	<i>Uropterygius tigrinus</i>	Tiger reef-eel	3	0	0
Plotosidae	<i>Plotosus nkunga</i>	Eel-catfish	29	1	0
Belonidae	<i>Strongylura leiura</i>	Yellowfin needlefish	2	0	0
Belonidae	<i>Tylosurus crocodilus</i>	Crocodile needlefish	1	0	0
Hemiramphidae	<i>Hyporhamphus affinis</i>	Tropical halfbeak	1	0	0
Serranidae	<i>Epinephelus andersoni</i>	Catface rockcod	577	268	49
Serranidae	<i>Epinephelus macrospilos</i>	Bigspot rockcod	27	9	0
Serranidae	<i>Epinephelus marginatus</i>	Yellowbelly rockcod	335	231	50
Serranidae	<i>Epinephelus malabaricus</i>	Malabar rockcod	7	5	0
Serranidae	<i>Epinephelus tukula</i>	Potato bass	205	191	8
Teraponidae	<i>Terapon jarbua</i>	Thornfish	2	0	0
Pomatomidae	<i>Pomatomus saltatrix</i>	Elf	118	34	0
Haemulidae	<i>Plectorhinchus chubbi</i>	Dusky rubberlip	2	2	0
Haemulidae	<i>Plectorhinchus flavomaculatus</i>	Lemonfish	132	118	8
Haemulidae	<i>Plectorhinchus gibbosus</i>	Harry hotlips	9	9	0
Haemulidae	<i>Plectorhinchus playfairi</i>	Whitebarred rubberlip	42	35	1
Haemulidae	<i>Plectorhinchus schotaf</i>	Minstrel rubberlip	18	14	0
Haemulidae	<i>Plectorhinchus sordidus</i>	Redlip rubberlip	2	2	0
Haemulidae	<i>Pomadasys commersonii</i>	Spotted grunter	2	1	0
Haemulidae	<i>Pomadasys furcatus</i>	Grey grunter	2733	646	48
Haemulidae	<i>Pomadasys kaakan</i>	Javelin grunter	1	1	0
Haemulidae	<i>Pomadasys multimaculatum</i>	Cock grunter	4	4	0
Haemulidae	<i>Pomadasys olivaceus</i>	Pinky	2	0	0
Dinopercidae	<i>Dinoperca petersi</i>	Cave bass	611	384	78
Lutjanidae	<i>Lutjanus argentimaculatus</i>	River snapper	15	13	2
Lutjanidae	<i>Lutjanus fulviflamma</i>	Dory snapper	1	0	0
Lutjanidae	<i>Lutjanus gibbus</i>	Humpback snapper	1	1	0
Lutjanidae	<i>Lutjanus rivulatus</i>	Speckled snapper	2250	972	419
Lutjanidae	<i>Lutjanus russellii</i>	Russell's snapper	171	18	0
Sparidae	<i>Diplodus hottentotus</i>	Zebra	24	14	1
Sparidae	<i>Diplodus capensis</i>	Blacktail	731	4	0
Sparidae	<i>Lithognathus mormyrus</i>	Sand steenbras	8	0	0
Sparidae	<i>Rhabdosargus sarba</i>	Natal stumpnose	549	438	12
Sparidae	<i>Rhabdosargus thorpei</i>	Bigeye stumpnose	383	36	0

Dichistidae	<i>Dichistius multifasciatus</i>	Banded galjoen	12	4	0
Kyphosidae	<i>Kyphosus bigibbus</i>	Grey chub	1	1	0
Kyphosidae	<i>Neoscorpis lithophilus</i>	Stone bream	165	92	0
Ephippidae	<i>Tripterodon orbis</i>	Spadefish	3	3	0
Gerreidae	<i>Gerres acinaces</i>	Smallscale pursemouth	2	0	0
Gerreidae	<i>Gerres methueni</i>	Evenfin pursemouth	1	1	0
Drepanidae	<i>Drepane longimanus</i>	Concertina-fish	3	3	0
Mullidae	<i>Parupeneus indicus</i>	Indian goatfish	17	4	0
Sciaenidae	<i>Argyrosomus japonicus</i>	Dusky kob	27	25	2
Sciaenidae	<i>Umbrina robinsoni</i>	Baardman	18	18	0
Carangidae	<i>Carangoides armatus</i>	Longfin kingfish	5	4	0
Carangidae	<i>Carangoides ferdau</i>	Blue kingfish	15	12	0
Carangidae	<i>Carangoides fulvoguttatus</i>	Yellowspotted kingfish	9	8	0
Carangidae	<i>Caranx heberi</i>	Blacktip kingfish	166	118	5
Carangidae	<i>Caranx ignobilis</i>	Giant kingfish	61	59	0
Carangidae	<i>Caranx melampygus</i>	Bluefin kingfish	30	20	2
Carangidae	<i>Caranx papuensis</i>	Brassy kingfish	28	24	0
Carangidae	<i>Caranx sexfasciatus</i>	Bigeye kingfish	10	4	0
Carangidae	<i>Gnathanodon speciosus</i>	Golden kingfish	2	2	0
Carangidae	<i>Scomberoides commersonianus</i>	Talang queenfish	2	2	0
Carangidae	<i>Scomberoides lysan</i>	Doublespotted queenfish	3	0	0
Carangidae	<i>Scomberoides tol</i>	Needlescaled queenfish	2	1	0
Carangidae	<i>Trachinotus africanus</i>	Southern pompano	25	24	0
Carangidae	<i>Trachinotus baillonii</i>	Smallspotted pompano	2	1	1
Carangidae	<i>Trachinotus botla</i>	Largespotted pompano	2119	1030	10
Rachycentridae	<i>Rachycentron canadum</i>	Prodigal son	3	3	0
Echeneidae	<i>Echeneis naucrates</i>	Shark remora	9	1	0
Cirrhitidae	<i>Cirrhitus pinnulatus</i>	Marbled hawkfish	11	1	0
Pomacentridae	<i>Abudefduf sordidus</i>	Spot damsel	100	0	0
Labridae	<i>Thalassoma purpureum</i>	Surge wrasse	2	1	0
Polynemidae	<i>Polydactylus plebeius</i>	Striped threadfin	13	3	0
Blenniidae	<i>Istiblennius edentulus</i>	Rippled rockskipper	1	0	0
Blenniidae	<i>Scartella emarginata</i>	Maned blenny	2	0	0
Acanthuridae	<i>Acanthurus leucosternon</i>	Powder-blue surgeon	1	0	0
Scombridae	<i>Scomberomorus commerson</i>	King mackerel	3	3	0
Tetraodontidae	<i>Amblyrhynchotes honckenii</i>	Evileye puffer	1	0	0
Tetraodontidae	<i>Lagocephalus inermis</i>	Smooth puffer	1	0	0
Diodontidae	<i>Diodon hystrix</i>	Porcupinefish	1	0	0
37 Families	87 Species		12367	5229	701

CHAPTER 4: MOVEMENT PATTERNS OF SURF-ZONE FISH SPECIES IN A SUBTROPICAL MARINE PROTECTED AREA ON THE EAST COAST OF SOUTH AFRICA

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4.1 Introduction

The world's oceans are experiencing biological change at an unprecedented rate through the depletion of fish populations and the degradation of marine habitats (Pauly et al. 2002; Myers and Worm 2003; Hutchings and Reynolds 2004). Recent analyses of fishery catches indicate that 70% of all the world's harvested fish populations are overexploited (FAO 2012; Pitcher and Cheung 2013). As a consequence, traditional methods of fisheries management have been criticised heavily and there has been a call for more effective management and conservation of marine fish populations (Mora et al. 2009). Among the alternative approaches advocated is the development of more holistic management strategies, such as an ecosystem-based approach to management, and the establishment of no-take marine protected areas (MPAs) (Halpern et al. 2010b).

Over the past 25 years, MPAs have increasingly been promoted to complement conventional fisheries management of surf-zone angling fish species in South Africa (Bennett and Attwood 1991, 1993; Attwood and Bennett 1994; Attwood et al. 1997b; Brouwer et al. 1997; Cowley et al. 2002; Mann et al. 2003; Attwood and Cowley 2005; Götz et al. 2008; Dunlop and Mann 2012a; Venter and Mann 2012). This is because, on their own, the fisheries management approaches of using daily bag limits, minimum size limits and closed seasons have been unable to arrest a decline in abundance of many important linefish species (Griffiths 2000; Mann 2013). Fully protected no-take MPAs displace fishing effort from an area, thereby providing resident marine species with a refuge from fishing (Sobel and Dahlgren 2004). In South Africa, as in many other parts of the world, overexploited fish species have often been found to be more abundant and of a larger mean size in areas where they are protected from fishing (Buxton and Smale 1989; Bennett and Attwood 1991, 1993; Buxton 1993a; Garratt 1993; Cowley et al. 2002; Halpern and Warner 2002; Götz et al. 2009; Maggs et al. 2013a). Population recovery within the boundaries of a no-take protected area can provide insurance against management failure in fished areas (Bohnsack 1990, 1996) and, from a fisheries perspective, can lead to replenishment of nearby fished areas through density-dependent spillover of post-settlement fishes and seeding of eggs and larvae (Bohnsack 1996; Russ 2002; Sale et al. 2005; Harrison et al. 2012).

South Africa's growing MPA network is providing an important conservation tool for biodiversity protection and a valuable complementary measure for the management of fish stocks (Sink et al. 2012). However, MPAs can displace fishers from their fishing grounds, which can result in discontent

within fishing communities (Sowman et al. 2011; Venter and Mann 2012). Worldwide, opposition from local fishing communities is one of the principal impediments to MPA establishment and their long-term success (Gell and Roberts 2003). However, support may be gained from an affected fishing community by providing robust evidence of enhanced fish abundance adjacent to a no-take area. Increases in catch per unit effort (CPUE) and fish density close to MPA boundaries have provided circumstantial evidence that no-take areas can enhance adjacent fished areas (McClanahan and Kaunda-Arara 1996; Russ and Alcala 1996; McClanahan and Mangi 2000; Roberts et al. 2001; Maypa et al. 2002; Russ et al. 2003; Abesamis and Russ 2005; Maggs et al. 2013a; Mann and Tyldesley 2013). However, demonstrating empirically that a no-take area is exporting fishes to adjacent fished areas requires knowledge about fish movement patterns (Attwood and Bennett 1994; Attwood and Cowley 2005; Grüss et al. 2011; Maggs et al. 2013b) and dispersal of fish eggs and larvae (Harrison et al. 2012), which is often lacking in the understanding of fish ecology (Sale et al. 2005).

Levels of residency within a no-take zone and dispersal of subadult and adult fish into adjacent exploited areas can be assessed using tag-recapture methods, which provide valuable information on fish movement behaviour. In South Africa, a long history of tag-recapture research (Dunlop et al. 2013) has shown that most heavily exploited linefish species are typically resident (Attwood and Bennett 1994; Cowley et al. 2002; Griffiths and Wilke 2002; Brouwer et al. 2003; Attwood and Cowley 2005; Kerwath et al. 2007a, 2013; Götz et al. 2008; Maggs et al. 2013b). However, many of these studies also reported some dispersal from MPAs into adjacent fished areas.

Using the results of an on-going tag-recapture project, this study evaluated conservation and fisheries management effectiveness of the St Lucia Marine Reserve, an MPA within the iSimangaliso Wetland Park, a World Heritage Site on the northern KwaZulu-Natal coast of South Africa. The aim of the study was to investigate the movement behaviour of common surf-zone fish species found in the MPA. Key questions included: i) does the no-take sanctuary area within the St Lucia Marine Reserve maintain resident populations of surf-zone fish species; and ii) is there potential for spillover of these fishes to adjacent fished areas? In order to answer these questions, a wide variety of surf-zone fish species, which are locally representative of targeted shore-angling species, were tagged with conventional plastic dart tags (Dunlop et al. 2013). Based on the number of recaptures, the general movement behaviour of these species was described and the five most-commonly recaptured species were investigated in greater detail.

4.2 Material and methods

4.2.1 Study area

The St Lucia Marine Reserve forms part of the iSimangaliso Wetland Park and stretches from 1 km south of Cape Vidal (28°08' S, 32°33' E) to White Sands (27°26' S, 32°42' E) 11 km north of Sodwana Bay, a distance of ~80 km, and extends three nautical miles (5.6 km) out to sea (Mann et al. 1998). The no-take St Lucia Marine Reserve sanctuary area is situated centrally between Leven Point (27°55' S, 32°35' E) and Red Cliffs (27°43' S, 32°37' E), a distance of ~25 km (Figure 4.1). The shoreline is predominantly sandy and is backed by high vegetated dunes, but the surf zone itself consists of both sand and scattered low-relief reefs comprised of sedimentary beach rock (Ramsay 1996). The MPA was established in 1979 and compliance has been well-enforced by the conservation authority Ezemvelo KwaZulu-Natal Wildlife (Ezemvelo), primarily because it is adjacent to a terrestrial protected area and there are only two public access points (i.e. Cape Vidal and Sodwana Bay), both of which are within the iSimangaliso Wetland Park. The MPA is zoned so that no fishing is allowed by the public in the no-take sanctuary area, but shore fishing is allowed south of Leven Point and north of Red Cliffs. However, the proclamation of a beach driving ban in December 2001 (RSA 2001) has effectively precluded shore anglers from fishing further than walking distance (~5 km) north of Cape Vidal and south of Sodwana Bay, thus effectively increasing the size of the no-take area with regard to shore-angling. Recreational boat-based angling and spearfishing are still permitted south of Leven Point and north of Red Cliffs, but only pelagic gamefish species may be caught. No commercial linefishing, trawling or longlining is permitted anywhere within the MPA (iSimangaliso Wetland Park Authority 2011).

4.2.2 Data collection

From November 2001 to November 2006 six field trips were carried out per year (January, March, May, July, September and November). From February 2007 to November 2013 this was reduced to four trips per year (February, May, August and November) as a result of financial and logistical constraints. During each field trip, research linefishing was conducted by eight anglers in four selected 2 km areas marked off at 100 m intervals using numbered poles, the positions of which were determined using a Global Positioning System (GPS) device. Two of the 2 km areas (SA and SB) were inside the no-take sanctuary area (between Leven Point and Red Cliffs) and two (EA and EB) were in the previously exploited area south of Leven Point (Figure 4.1).

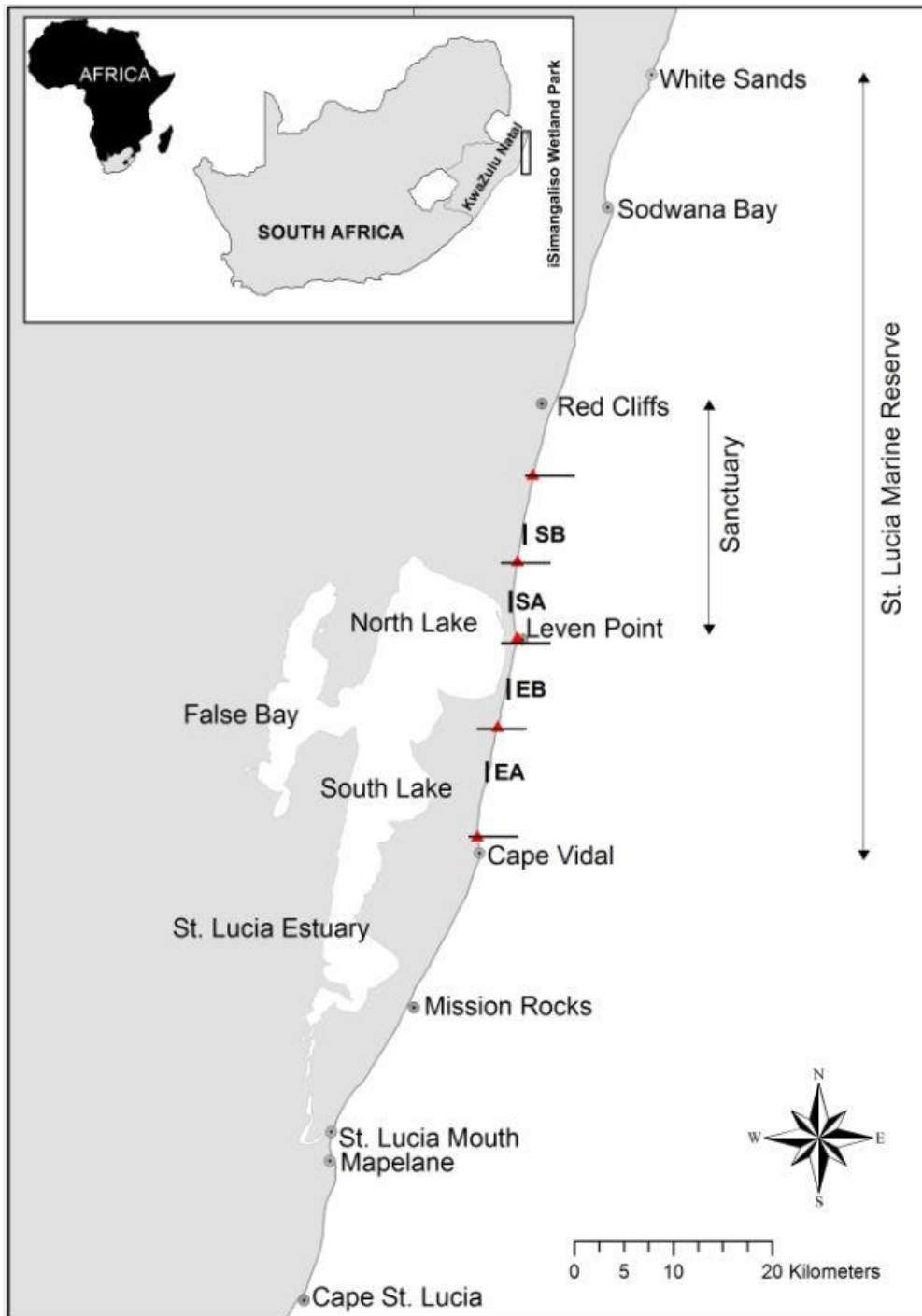


Figure 4.1: Map of the St Lucia Marine Reserve and Sanctuary within the iSimangaliso Wetland Park showing the sampling areas in this study (EA and EB are in the previously exploited area, while SA and SB are within the no-take sanctuary area). Note that the extended sampling areas (as of November 2011) simply consisted of northward and southward extensions (shown by horizontal lines) of the original 2 km sampling areas.

On each day, one team of four anglers fished in one of the previously exploited areas (EA or EB) and the other team of four anglers fished in one of the sanctuary areas (SA or SB). This was rotated each day so that, at the end of four days, each area had been fished by each of the two teams, providing a

statistically robust sampling protocol that enabled comparison of catches between the sanctuary zone and the previously exploited area (Mann and Tyldesley 2013). Two 4×4 vehicles were used to transport the anglers daily between the sampling areas, with the overnight base at Cape Vidal. Fishing was conducted during the day and into the first few hours of darkness, over the semi-diurnal spring tides (or as near to them as logistically possible) and all beach driving was restricted to the low shore three hours before and after low tide. All four sampling areas were selected to be as similar as possible in terms of surf-zone habitat (i.e. all contained both sandy and patchy reef habitat subtidally), but some areas inevitably had more complex reef structure than others.

Although it was understood that the sampling strategy needed to be kept as consistent as possible, an important change was made after the first 10 years of the project, in November 2011. Each of the four 2-km sampling areas was enlarged to cover ~10 km of coastline. Instead of using numbered poles to indicate fishing locality, a GPS device was used to determine the exact fishing localities within each ~10-km sampling area (i.e. the original system of numbered localities every 100 m was simply extended north and south using a GIS). The purpose of this change was two-fold, namely: (i) to reduce inherent sampling bias whereby anglers exerted more effort at certain favoured localities within the 2-km sampling areas based on the complexity of reef habitat present; and (ii) to increase the scope for detecting fish movements over a wider area (i.e. between the original 2-km sampling areas).

Standardised rock-and-surf fishing gear (i.e. 3–4.5 m graphite surf rods, multiplier or fixed-spool reels with braided or monofilament line ranging between 9 and 23 kg breaking strain) was used and anglers were allowed to use only one rod at a time. A maximum of two hooks per trace was allowed and hook sizes ranged between 1/0 and 7/0 (unless targeting big fish [see Chapter 2] in which case larger hooks could be used). Use of barbless hooks was strictly enforced (the barb on the hook being crimped using long-nose pliers) as this inflicted less damage on the fish and made their release considerably quicker and easier (Casselmann 2005). If a fish was ‘gut-hooked’ (i.e. with the hook lodged in the oesophagus) no attempt was made to remove the hook and the snood was simply cut as near to the eye of the hook as possible (Schaeffer and Hoffman 2002; Butcher et al. 2010). Use of circle hooks was encouraged (Cooke and Suski 2004) but not enforced due to the higher price of these hooks and the gear preferences of some anglers.

All fish caught were covered with a wet cloth and quickly measured on a wet plastic stretcher with a sheathed stainless steel ruler along the centre, before being returned to the water. Emphasis was placed on keeping the fish out of the water for as short a time as possible and all surfaces were kept moist to reduce injury and stress (Casselmann 2005). Selected species >300 mm fork length (FL) - or total length (TL) in the case of serranids and sciaenids - were tagged using plastic dart tags

(Hallprint[®]) supplied by the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP) (Dunlop et al. 2013). D-tags (85 mm in length and 1.6 mm in diameter) were used on smaller fish (300–600 mm) whereas A-tags (114 mm long and 1.6 mm diameter) were used on larger fish and sharks (>600 mm). The only exception to this rule was for *Lutjanus rivulatus*, which were tagged from lengths of >280 mm FL, on account of their suitability for tagging at a relatively small size.

Each time a fish was tagged or recaptured, the tag number, species, length (mm FL, TL or PCL), date, time and locality (determined using the numbered poles or, subsequently, the GPS position) was recorded. A note was made if the hook had been cut off and left in the fish or if there was a tagging scar present on the fish, indicating that it had been previously tagged but the tag had been shed. Aside from fish recaptured by the research team, members of the angling public also reported recaptures from adjacent exploited areas north-east and south-west of the study site. Fish recaptured by members of the angling public were reported through the ORI-CFTP, which uses locality codes along the coast with a resolution of approximately one kilometre (Dunlop et al. 2013).

4.2.3 Data analysis

Dingle (1996) provided a simple classification of animal movement, which was used as broad categories for assessing the movement patterns of fishes in the current study (Table 4.1). Station-keeping generally refers to movements within a home range and is usually linked to foraging. This type of movement is characteristically meandering and repetitive on short time scales and small spatial scales, with the animal frequently changing course as it finds and moves between items (Dingle and Drake 2007). In this study, because of the size of the sampling areas, a fish was considered to be station-keeping if it was recaptured within 2 km of its release site. Ranging implies an exploratory component that takes an individual permanently beyond its home range to settle eventually into a new one. This movement behaviour often ceases once a suitable new home range is found (Dingle and Drake 2007). In this study, fish that had moved >2 km and did not return to their original tagging location were considered to have displayed ranging behaviour. Migration, on the other hand, is generally characterised by persistent directed movements between habitat regions and is normally a round-trip movement that often occurs seasonally (Dingle and Drake 2007).

Table 4.1: Classification of animal movement behaviour proposed by Dingle (1996).

Movement type	Characteristics
Station-keeping:	
Kinesis	Movements that serve to keep an animal stationary
Foraging	Movements within a home-range
Commuting	Diel movements between day and night locations
Territoriality	Territorial defence and aggression, non-overlapping home-ranges
Ranging:	Exploratory movements over wide areas in search of resources
Migration:	Persistent, directed, non-exploratory, predictable, physiological adaption

Station-keeping is a good indicator of the potential for fish retention within a protected area, and was used to quantify the degree of residency (phylopatry). Ranging or migratory behaviour indicates the potential for export of subadult or adult fish to adjacent fisheries.

Station-keeping

A method for quantifying station-keeping behaviour was adapted from Griffiths and Wilke (2002), who used all recorded movements to calculate ‘travel range lengths’ for five sparid fishes. In the current study, station-keeping behaviour was quantified for each species by taking the 95th percentile of intra-study site movement distances only (Maggs et al. 2013b), and excluded all long-distance (>2 km) movements (Attwood and Cowley 2005). The resulting value is referred to as ‘single linear distance’ (SLD) in the current study. Assuming that a fish is randomly drawn from within the boundaries of its home range at first capture (tag-release) and then redrawn from that same home range at a later stage (recapture), the Euclidean distance between the two points (SLD) can be considered to represent some unknown proportion of the length of the home range. Repeating this several times, with different individuals of the same species, provides a good reflection of the degree of residency for that species. To prevent pseudoreplication, the calculation of SLD used only the distance between the original tagging site and the first recapture location. The assumption of all movements <2 km being indicative of station-keeping behaviour was tested (two-tailed *t*-test for unequal variances) by comparing SLD movements of *L. rivulatus* before and following the extension of the 2 km sampling areas in November 2011.

Multiple recaptures, having three or more capture points, provide stronger evidence of the type of area utilisation by an individual fish. In this case, an alternative method for quantifying station-keeping behaviour was applied by taking the ‘greatest linear distance’ (GLD) between all the recapture

locations from the original tagging location (provided that all recaptures were within 2 km of the original tagging location). The resulting estimate was used to compare with the SLD calculated above. Note that in some cases the GLD could be less than the SLD as only multiple recaptures were used to calculate the GLD.

Ranging

The potential of the no-take sanctuary to export fish was evaluated using records of long-distance movements for each species (i.e. tagged fish leaving the sanctuary zone). Whereas most of the recaptures of ranging fish were recorded by the research team within the previously exploited areas (EA and EB) south of the no-take sanctuary area, some recaptures were also reported by members of the angling public through the ORI-CFTP to the north of the sampling areas. Although relatively few long-distance movements were reported, there was potential for non-reporting by members of the public (Dunlop et al. 2013).

Data were tested for normality using a Kolmogorov-Smirnov test. A Chi-square test was used to test the hypothesis that the number of fish that moved north did not differ from the number that moved south. As data were not normally distributed, a non-parametric Mann-Whitney test was used to determine if the distance moved north or south was significantly different. Statistical tests were conducted using MS Excel 2010.

4.3 Results

From November 2001 to November 2013 a total of 59 field trips were conducted, during which 6 613 fish from 71 species were tagged and released. Of these, a total of 1 004 (15.2%) fish from 17 species were recaptured (Table 4.2).

Table 4.2: Species composition of fish tagged and recaptured in the St Lucia Marine Reserve from November 2001 to November 2013 (species arranged according to classification of Smith and Heemstra 1991).

Family	Species	Common name	No. caught	No. tagged	No. recap	% recap
Carcharhinidae	<i>Carcharhinus brevipinna</i>	Spinner shark	1	1	0	0
Carcharhinidae	<i>Carcharhinus limbatus</i>	Blacktip shark	13	13	0	0
Carcharhinidae	<i>Rhizoprionodon acutus</i>	Milk shark	3	3	0	0
Sphyrnidae	<i>Sphyrna zygaena</i>	Smooth hammerhead shark	1	1	0	0
Odontaspidae	<i>Carcharias taurus</i>	Spotted ragged-tooth shark	2	2	0	0
Rhinobatidae	<i>Rhinobatos annulatus</i>	Lesser guitarfish	10	8	0	0
Rhinobatidae	<i>Rhinobatos leucospilus</i>	Greyspot guitarfish	4	4	0	0
Rhinobatidae	<i>Rhynchobatus djiddensis</i>	Giant guitarfish	60	55	5	9.09
Dasyatidae	<i>Himantura gerrardi</i>	Sharpnose stingray	45	44	0	0
Dasyatidae	<i>Himantura leoparda</i>	Honeycomb stingray	28	28	0	0

Dasyatidae	<i>Himantura fai</i>	Roundnose stingray	9	9	0	0
Dasyatidae	<i>Taeniura lymna</i>	Bluespotted ribbontail ray	2	1	0	0
Elopidae	<i>Elops machnata</i>	Ladyfish	1	1	0	0
Albulidae	<i>Albula oligolepis</i>	Bonefish	223	159	0	0
Plotosidae	<i>Plotosus nkunga</i>	Eel-catfish	37	2	0	0
Serranidae	<i>Epinephelus andersoni</i>	Catface rockcod	684	325	57	17.54
Serranidae	<i>Epinephelus macrospilos</i>	Bigspot rockcod	31	11	0	0
Serranidae	<i>Epinephelus marginatus</i>	Yellowbelly rockcod	436	295	73	24.75
Serranidae	<i>Epinephelus malabaricus</i>	Malabar rockcod	8	6	0	0
Serranidae	<i>Epinephelus tukula</i>	Potato bass	255	236	11	4.66
Pomatomidae	<i>Pomatomus saltatrix</i>	Elf	122	35	0	0
Haemulidae	<i>Plectorhinchus chubbi</i>	Dusky rubberlip	4	4	0	0
Haemulidae	<i>Plectorhinchus flavomaculatus</i>	Lemonfish	174	158	10	6.33
Haemulidae	<i>Plectorhinchus gibbosus</i>	Harry hotlips	12	12	0	0
Haemulidae	<i>Plectorhinchus playfairi</i>	Whitebarred rubberlip	53	46	1	2.17
Haemulidae	<i>Plectorhinchus schotaf</i>	Minstrel rubberlip	27	23	0	0
Haemulidae	<i>Plectorhinchus sordidus</i>	Redlip rubberlip	2	2	0	0
Haemulidae	<i>Pomadasys commersonii</i>	Spotted grunter	2	1	0	0
Haemulidae	<i>Pomadasys furcatus</i>	Grey grunter	3224	817	57	6.98
Haemulidae	<i>Pomadasys kaakan</i>	Javelin grunter	1	1	0	0
Haemulidae	<i>Pomadasys multimaculatum</i>	Cock grunter	4	4	0	0
Dinopercidae	<i>Dinoperca petersi</i>	Cave bass	762	479	96	20.04
Lutjanidae	<i>Lutjanus argentimaculatus</i>	River snapper	22	20	2	10
Lutjanidae	<i>Lutjanus gibbus</i>	Humpback snapper	1	1	0	0
Lutjanidae	<i>Lutjanus rivulatus</i>	Speckled snapper	3118	1308	652	49.85
Lutjanidae	<i>Lutjanus russellii</i>	Russell's snapper	241	27	0	0
Sparidae	<i>Diplodus hottentotus</i>	Zebra	28	16	1	6.25
Sparidae	<i>Diplodus capensis</i>	Blacktail	861	4	0	0
Sparidae	<i>Rhabdosargus sarba</i>	Natal stumpnose	664	529	16	3.02
Sparidae	<i>Rhabdosargus thorpei</i>	Bigeye stumpnose	495	43	0	0
Dichistiidae	<i>Dichistius multifasciatus</i>	Banded galjoen	12	4	0	0
Kyphosidae	<i>Kyphosus bigibbus</i>	Grey chub	1	1	0	0
Kyphosidae	<i>Neoscorpis lithophilus</i>	Stone bream	188	106	0	0
Ephippidae	<i>Tripteron orbis</i>	Spadefish	5	5	0	0
Gerreidae	<i>Gerres methueni</i>	Evenfin pursemouth	1	1	0	0
Drepanidae	<i>Drepane longimanus</i>	Concertina-fish	3	3	0	0
Mullidae	<i>Parupeneus indicus</i>	Indian goatfish	23	7	0	0
Sciaenidae	<i>Argyrosomus japonicus</i>	Dusky kob	31	29	2	6.90
Sciaenidae	<i>Umbrina robinsoni</i>	Tasslefish	22	22	0	0
Carangidae	<i>Carangoides armatus</i>	Longfin kingfish	5	4	0	0
Carangidae	<i>Carangoides ferdau</i>	Blue kingfish	17	14	0	0
Carangidae	<i>Carangoides fulvoguttatus</i>	Yellowspotted kingfish	9	8	0	0
Carangidae	<i>Caranx ignobilis</i>	Giant kingfish	90	88	0	0
Carangidae	<i>Caranx melampygus</i>	Bluefin kingfish	44	30	3	10
Carangidae	<i>Caranx papuensis</i>	Brassy kingfish	30	26	0	0
Carangidae	<i>Caranx heberi</i>	Blacktip kingfish	201	141	5	3.55
Carangidae	<i>Caranx sexfasciatus</i>	Bigeye kingfish	24	15	0	0
Carangidae	<i>Gnathanodon speciosus</i>	Golden kingfish	2	2	0	0
Carangidae	<i>Lichia amia</i>	Garrick	1	1	0	0

Carangidae	<i>Scomberoides commersonnianus</i>	Largemouth queenfish	3	3	0	0
Carangidae	<i>Scomberoides tol</i>	Needlescaled queenfish	2	1	0	0
Carangidae	<i>Trachinotus africanus</i>	Southern pompano	27	26	0	0
Carangidae	<i>Trachinotus bailloni</i>	Smallspotted pompano	2	1	1	100
Carangidae	<i>Trachinotus botla</i>	Largespotted pompano	2555	1327	12	0.90
Rachycentridae	<i>Rachycentron canadum</i>	Prodigal son	3	3	0	0
Echeneidae	<i>Echeneis naucrates</i>	Shark remora	9	1	0	0
Cirrhitidae	<i>Cirrhitis pinnulatus</i>	Marbled hawkfish	21	1	0	0
Labridae	<i>Thalassoma purpuraceum</i>	Surge wrasse	5	2	0	0
Polynemidae	<i>Polydactylus plebeius</i>	Striped threadfin	18	3	0	0
Sphyraenidae	<i>Sphyraena putnamiae</i>	Sawtooth barracuda	1	1	0	0
Scombridae	<i>Scomberomorus commerson</i>	King mackerel	3	3	0	0
29 Families	71 Species		15028	6613	1004	15.18

A summary of the movement behaviour of the 17 recaptured species is shown in Table 4.3. Based on the average distance moved, the percentage of individuals of a species that moved >2 km, and any additional supporting evidence from the literature, 14 species could broadly be described as resident station-keepers while the remaining three species displayed movements more typical of nomadic ranging behaviour; however, none could be considered migratory in terms of the definitions used in this study (Table 4.3). Clearly, with the low number of recaptures attained for 12 of the 17 species, these descriptions of movement behaviour should at best be considered preliminary.

The five most-commonly recaptured species were *Pomadasys furcatus*, *Epinephelus andersoni*, *E. marginatus*, *Dinoperca petersi* and *Lutjanus rivulatus*. Overall, 3 224 individuals of these five species were tagged in the four sampling areas and 632 were recaptured at least once (Table 4.4). The species-specific recapture rate, including individuals recaptured more than once, ranged from 7.0% for *P. furcatus* to 49.8% for *L. rivulatus*. Of the 3 224 fishes tagged, 1 958 (60.7%) were tagged at the two no-take areas (SA and SB) and 1 266 (39.3%) at the two previously exploited areas (EA and EB).

Table 4.3: Movement behaviour of 17 fish species recaptured in the St Lucia Marine Reserve between November 2001 and December 2013 (variation is expressed as one standard deviation). Movement type followed by a question mark indicates some uncertainty.

Species	No. of recaps	% recap	Ave distance moved (m)	Max distance moved (m)	% that moved >2 km	Movement type	Supporting literature
<i>Rhynchobatus djiddensis</i>	5	9.09	2 520 ± 2 567	5 200	40%	Nomadic?	Dunlop and Mann (2013b)
<i>Epinephelus andersoni</i>	57	17.54	726 ± 4 536	34 300	1.8%	Resident	Maggs et al. (2013b)
<i>Epinephelus marginatus</i>	73	24.75	262 ± 1 049	6 800	4.1%	Resident	Maggs et al. (2013b)
<i>Epinephelus tukula</i>	11	4.66	182 ± 322	1 100	0%	Resident	Floros and Fennessy (2013)
<i>Plectorhinchus flavomaculatus</i>	10	6.33	90 ± 129	400	0%	Resident	Kaunda-Arara and Rose (2004)
<i>Plectorhinchus playfairi</i>	1	2.17	100	100	0%	Resident?	None
<i>Pomadasys furcatus</i>	57	6.98	137 ± 240	1 100	0%	Resident	This study
<i>Dinoperca petersi</i>	96	20.04	2 259 ± 12 144	90 000	5.2%	Resident	This study
<i>Lutjanus argentimaculatus</i>	2	10	0	0	0%	Resident	Russell and McDougall (2005)
<i>Lutjanus rivulatus</i>	652	49.85	1 141 ± 7 480	125 000	5.8%	Resident	This study
<i>Diplodus hottentotus</i>	1	6.25	0	0	0%	Resident	Cowley et al. (2002)
<i>Rhabdosargus sarba</i>	16	3.02	15 450 ± 57 259	230 000	18.8%	Resident	Mann and Dunlop (2013a)
<i>Argyrosomus japonicus</i>	2	6.90	20 500 ± 9 192	27 000	100%	Resident/ migratory	Griffiths (1996)
<i>Caranx melampygus</i>	3	10	433 ± 513	1 000	0%	Resident	Holland et al. (1996)
<i>Caranx heberi</i>	5	3.55	7 620 ± 10 808	26 000	60%	Nomadic?	None
<i>Trachinotus baillonii</i>	1	100	200	200	0%	Resident?	None
<i>Trachinotus botla</i>	12	0.90	19 317 ± 42 656	114 000	25%	Resident	Parker et al. (2013)

Table 4.4: Tag and recapture details of the five most commonly recaptured species tagged in the St Lucia Marine Reserve from November 2001 to November 2013.

Species	<i>Pomadasys furcatus</i>	<i>Epinephelus andersoni</i>	<i>Epinephelus marginatus</i>	<i>Dinoperca petersi</i>	<i>Lutjanus rivulatus</i>	Total
No. tagged	817	325	295	479	1308	3224
No. recaptured (% recaptured)	57 (7.0%)	57 (17.5%)	73 (24.8%)	96 (20.0%)	652 (49.9%)	935 (28.0%)
No. of single recaptures	51	49	49	71	412	632
No. of multiple recaptures	6	8	24	25	240	303
No. tagged and recaptured in EA*	131 (12)	141(22)	51(4)	67(5)	95(29)	485(72)
No. tagged and recaptured in EB*	246 (20)	76(9)	57(2)	122(36)	280(147)	781(214)
No. tagged and recaptured in SA*	179 (14)	76(17)	36(4)	91(13)	182(97)	564(145)
No. tagged and recaptured in SB*	261 (11)	32(9)	151(63)	199(39)	751(373)	1 394(495)
No. recaptured outside sampling areas**	0	0	0	3	6	9

* Number recaptured (in parenthesis) includes multiple recaptures

** Reported by members of the angling public outside the four sampling areas

4.3.1 Movement patterns

The average distance moved for the five main study species ranged from 137 m for *P. furcatus* to 2 259 m for *D. petersi*, whereas maximum distance moved ranged from 1.1 km for *P. furcatus* to 125 km for *L. rivulatus* (Table 4.5). Average time at liberty varied from 58 days for *E. andersoni* to 375 days for *L. rivulatus*, and maximum time at liberty ranged from 287 days for *E. andersoni* to 3 163 days (8.7 years) for *L. rivulatus* (Table 4.5). While most recaptures were made at the same location where the fish was originally tagged, for those fish that did move away from the tagging locality, none of the five study species showed a persistent trend in the direction of movement (north or south); neither were there significant differences between distances moved in either a northerly or southerly direction for any of the five species (Table 4.5, Figure 4.2).

Table 4.5: General movement patterns of the five study species tagged and recaptured in the St Lucia Marine Reserve from November 2001 to November 2013 (variation shown is standard deviation).

Species	<i>Pomadasys furcatus</i>	<i>Epinephelus andersoni</i>	<i>Epinephelus marginatus</i>	<i>Dinoperca petersi</i>	<i>Lutjanus rivulatus</i>
Average distance moved (m)	137 ± 240	726 ± 4 536	262 ± 1 049	2 259 ± 12 144	1 141 ± 7 480
Maximum distance moved (m)	1100	34 300	6 800	90 000	125 000
Average time at liberty (days)	233 ± 217	58 ± 71	226 ± 245	350 ± 300	375 ± 394
Maximum time at liberty (days)	1 099	287	819	1 367	3 163
Number moved north	14 (25%)	13 (23%)	12 (16%)	23 (24%)	167 (26%)
Number not moved	27 (47%)	32 (56%)	55 (75%)	55 (57%)	334 (51%)
Number moved south	16 (28%)	12 (21%)	6 (8%)	18 (19%)	151 (23%)
Significance of persistence in direction moved (Chi-test)	P = 0.715	P = 0.841	P = 0.157	P = 0.435	P = 0.37
Significance of difference between distances moved in a specific direction (Mann-Whitney test)	P = 0.203	P = 0.51	P = 0.522	P = 0.234	P = 0.477

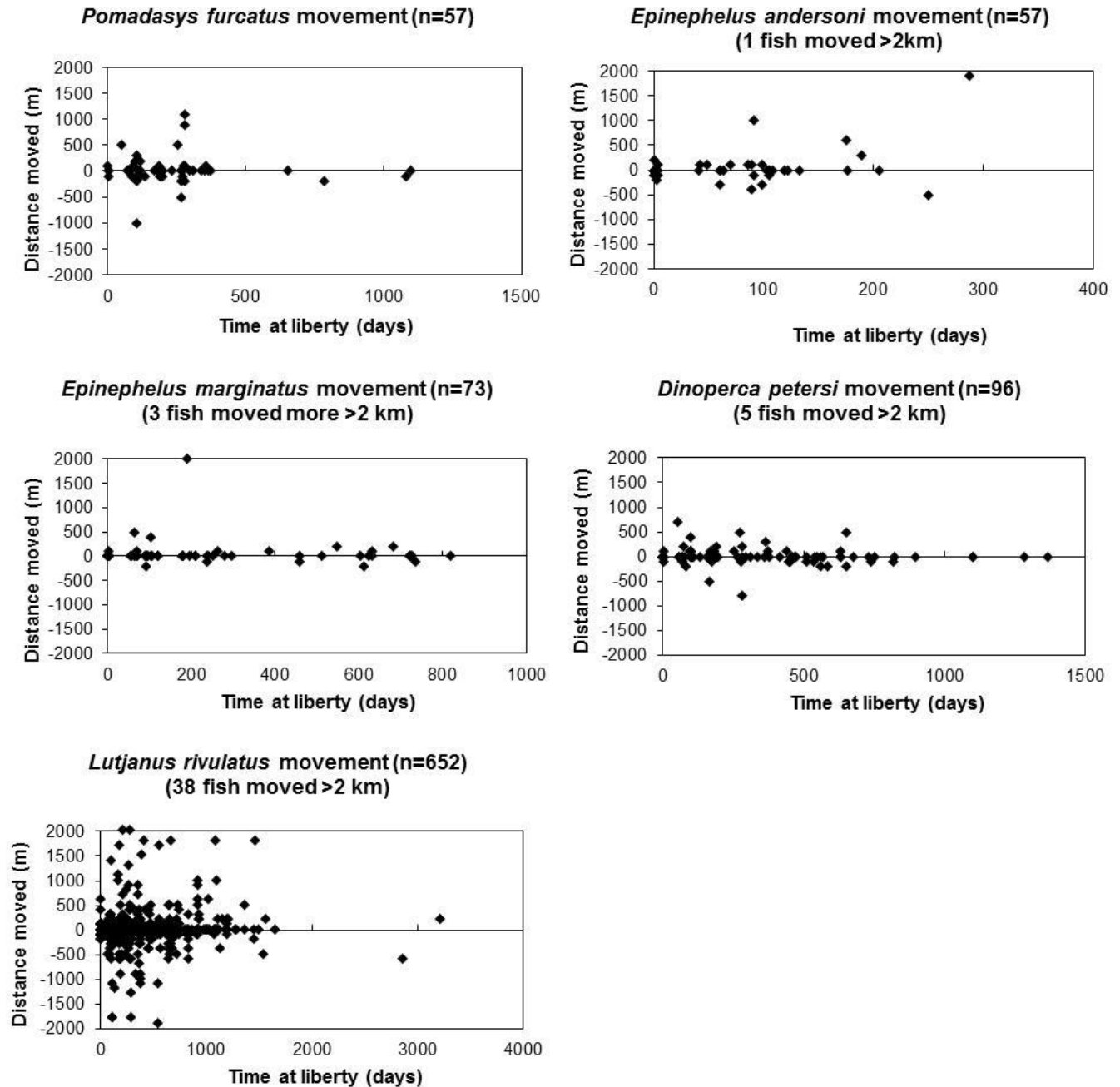


Figure 4.2: General movement patterns of the five main study species tagged and recaptured in the St Lucia Marine Reserve from November 2001 to November 2013 (positive values indicate fish that moved in a northerly direction while negative values indicate those that moved in a southerly direction).

Most individuals of the five main study species (*P. furcatus* 87.7%, *E. andersoni* 84.2%, *E. marginatus* 91.8%, *D. petersi* 87.5% and *L. rivulatus* 78.8%) were recaptured within 200 m of their original release site (Figure 4.3). A test conducted on the distances moved by *L. rivulatus* in the original 2 km sampling areas ($n = 271$) compared to those in the extended ~10 km sampling areas from November 2011 onwards ($n = 141$) showed no significant difference ($p = 0.5$, $df = 196$). The assumption that fish movements within 2 km were reflective of station-keeping behaviour was

therefore considered to be valid. There was little association between fish length and distance moved (Figure 4.4). Similarly, there was no correlation between time at liberty and distance moved (Figure 4.5). Some individuals remained resident for extended periods, while others moved relatively long distances shortly after being released.

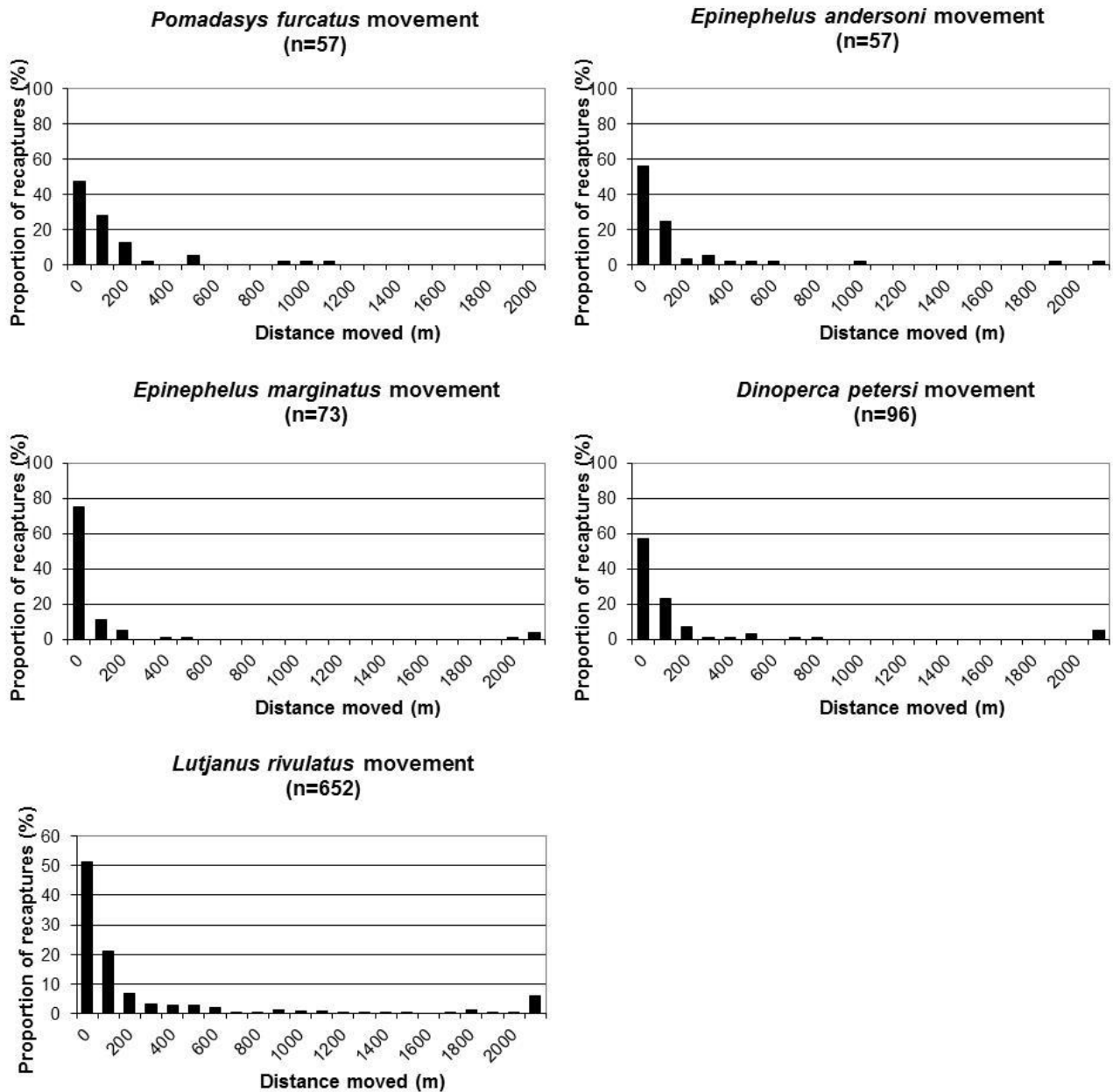


Figure 4.3: Displacement shown by the five main study species in the St Lucia Marine Reserve from November 2001 to November 2013 (bar on the extreme right of each graph represents the percentage of fish that had moved a distance greater than two kilometres).

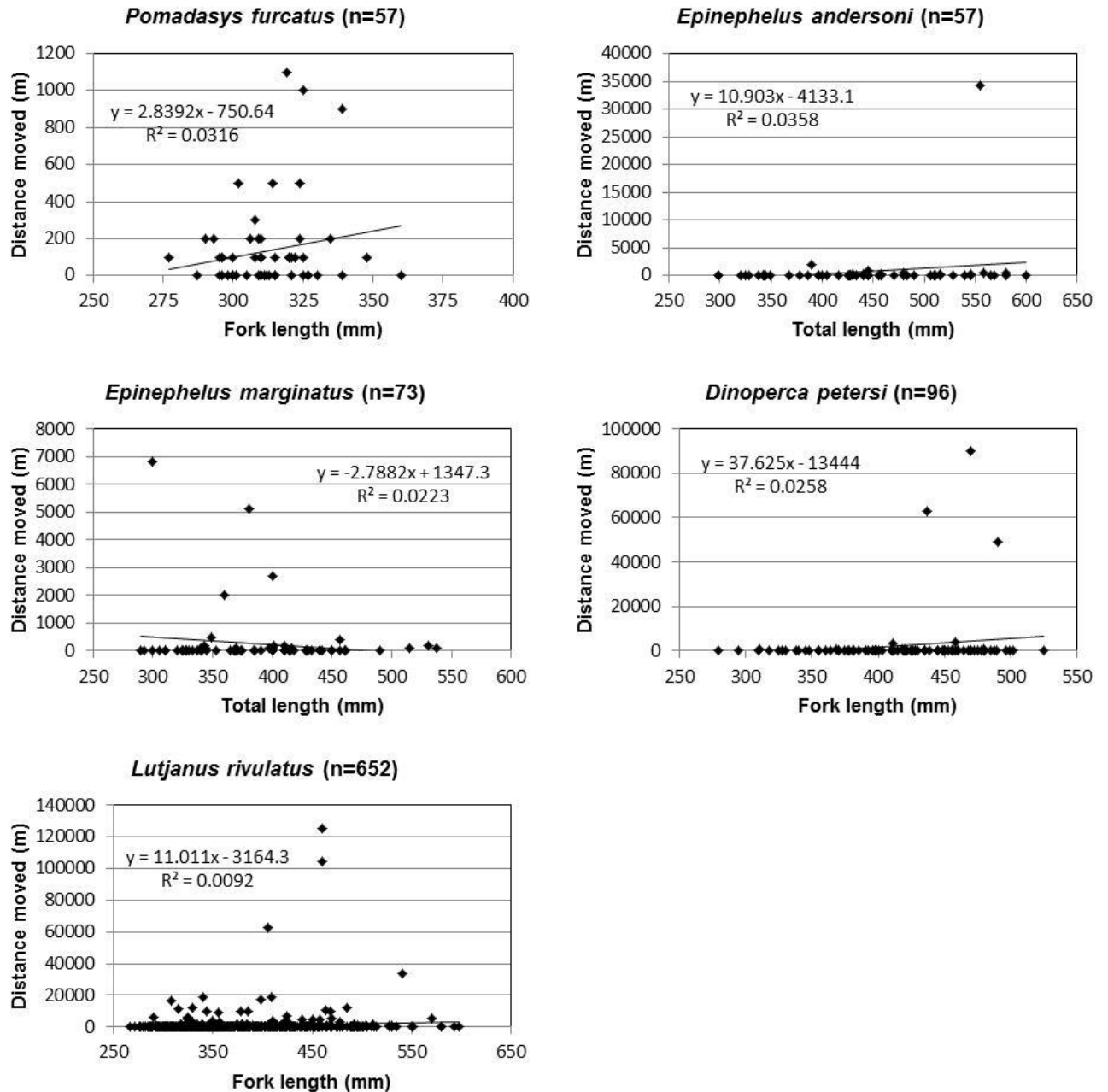


Figure 4.4: Comparison between the length of fish recaptured and the distance moved (m) for each of the five study species tagged and recaptured in the St Lucia Marine Reserve from November 2001 to November 2013.

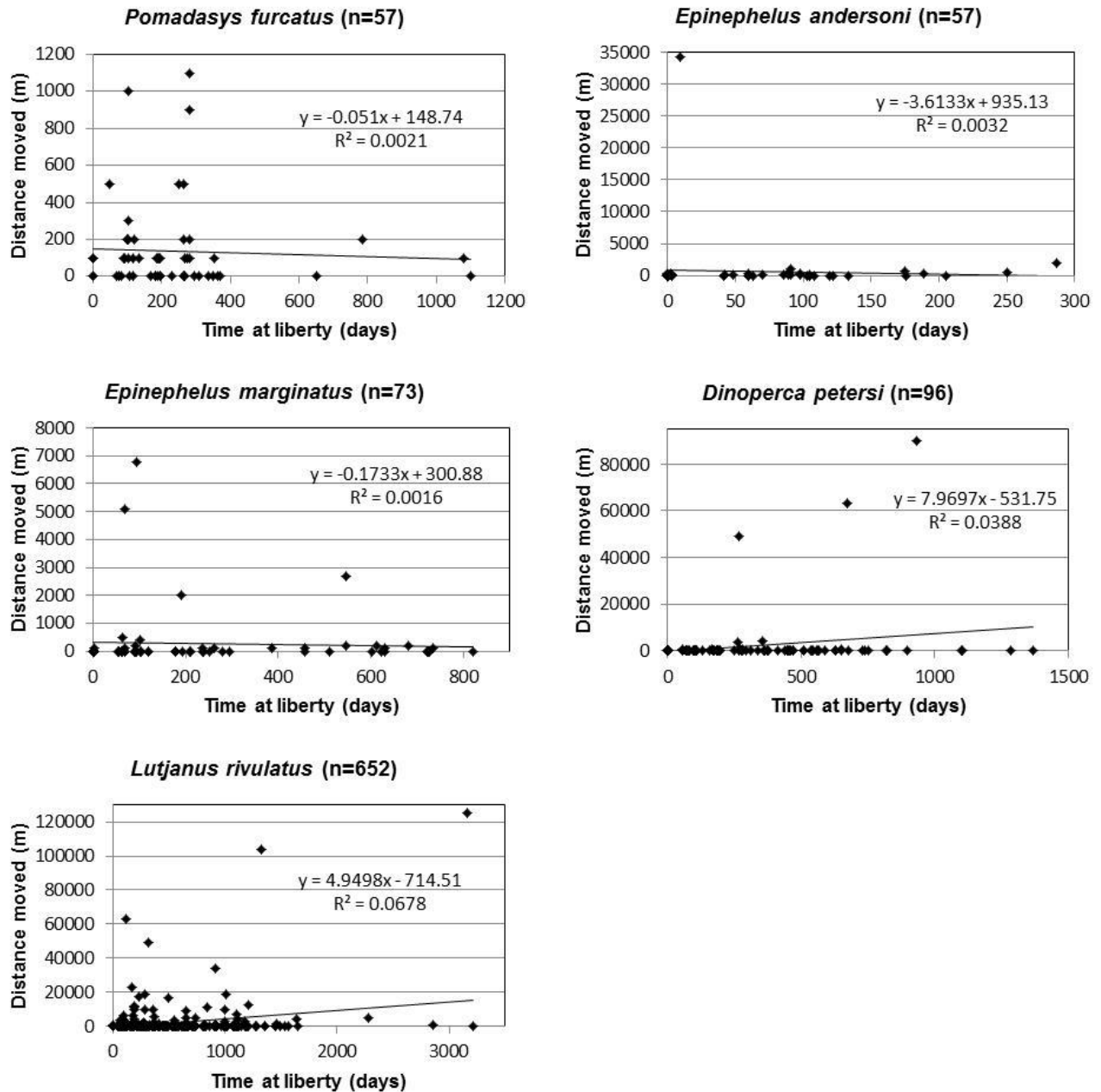


Figure 4.5: Comparison between the time at liberty (days) and the distance moved (m) for each of the five study species tagged and recaptured in the St Lucia Marine Reserve from November 2001 to November 2013.

Most recaptures of the five main study species were taken within the same sampling area where they were originally tagged (i.e. they generally did not move >2 km). Of the remaining fish that did move >2 km, average distances ranged between 4 867 m for *E. marginatus* and 41 920 m for *D. petersi*. *Pomadasys furcatus* did not show any movements >2 km (Table 4.6). The two abovementioned movement patterns were indicative of station-keeping and ranging behaviour, respectively, and the latter was recorded in four of the five main study species.

Table 4.6: Average and maximum distances moved by fish showing ranging behaviour (moved >2 km) by four of the five study species (variation shown is standard deviation).

Species	<i>Epinephelus andersoni</i>	<i>Epinephelus marginatus</i>	<i>Dinoperca petersi</i>	<i>Lutjanus rivulatus</i>
No. of ranging fish	n=1	n=3	n=5	n=38
Average distance of ranging movements (m)	34 300	4 867 ± 2 060	41 920 ± 37 791	17 079 ± 26 569
Maximum distance of ranging movements (m)	34 300	6 800	90 000	125 000

Station-keeping

For each species within each of the four sampling areas, recorded movements were generally small, indicating station-keeping behaviour, resulting in SLD and GLD values in the order of a few hundred meters (Table 4.7). SLD and GLD values varied among the study species and the SLD for *P. furcatus* was greater than the GLD value, whereas the GLD for the remaining four species was greater than the SLD. All SLD and GLD estimates were considerably smaller than the size of the no-take zone (i.e. ~25 km).

Table 4.7: Single linear distance (SLD) and greatest linear distance (GLD) determined for recaptures of the five main study species that moved two kilometres or less.

Species	<i>Pomadasys furcatus</i>	<i>Epinephelus andersoni</i>	<i>Epinephelus marginatus</i>	<i>Dinoperca petersi</i>	<i>Lutjanus rivulatus</i>
SLD (m)	700 (n=51)	465 (n=48)	200 (n=46)	365 (n=68)	995 (n=382)
GLD (m)	200 (n=6)	525 (n=8)	740 (n=24)	470 (n=23)	1025 (n=222)

Ranging

Of the 47 individuals that showed ranging behaviour (i.e. moved >2 km), 16 (34%) moved out of the sanctuary area and covered linear distances between 3.5 km and 90 km, whereas six (12.8%) moved from the previously exploited area into the sanctuary area and covered linear distances between 3.5 km and 34.3 km. A further four fish (8.5%) moved from the previously exploited area through the sanctuary area and were recaptured to the north of the sanctuary area, having moved distances of 49–125 km. The remaining 21 fish (44.7%) showed intermediate movements within the sanctuary area or previously exploited area with distances ranging from 2.3 to 12.4 km (Table 4.8). *L. rivulatus* had the greatest proportion of ranging individuals (5.8%) of the five species. Of the fish that showed ranging movements, 53.2% moved in a northerly direction and 46.8% moved in a southerly direction.

Table 4.8: Ranging movements (>2 km) recorded in four of the five study species tagged and recaptured in the St Lucia Marine Reserve from November 2001 to November 2013.

Species	<i>Epinephelus andersoni</i>	<i>Epinephelus marginatus</i>	<i>Dinoperca petersi</i>	<i>Lutjanus rivulatus</i>
No. and range that moved out of the sanctuary	0	0	3 (3.5-90 km)	13 (4.9-63 km)
No. and range that moved into the sanctuary	1 (34.3 km)	1 (5.1 km)	0	4 (3.5-17.3 km)
No. and range that moved through the sanctuary	0	0	1 (49 km)	3 (49-125 km)
No. and range of intermediate movements in the sanctuary	0	2 (2.7-6.8 km)	1 (4.1 km)	15 (2.3-11.8 km)
No. and range of intermediate movements in the previously exploited area	0	0	0	3 (3-12.4 km)
Total	1	3	5	38

4.4 Discussion

4.4.1 General movement behaviour

Although 12 of the 17 species recaptured in this study did not have enough recapture data to make a definitive assessment of their movement behaviour, there was strong circumstantial evidence to suggest that the bulk of the species ($n = 14$) exhibited station-keeping behaviour. This suggests that the St Lucia Marine Reserve sanctuary area provides an effective refuge for many of the important surf-zone fishery species found in this general area. However, there is some evidence of ranging behaviour, indicating that there is some dispersal to adjacent areas which appears to take place during the subadult and adult life history stages. Despite the high average distance moved by *Trachinotus botla* (19.3 km), Parker et al. (2013) classified this species as a surf-zone resident, based on the fact that 78% of recaptures (including those from this study) were caught within 1 km of their original tagging locality. Three individuals in the current study undertook long distance movements ranging from 6.6 to 114 km. Similar results were shown for the congeneric species *T. coppingeri* along the Queensland coast of eastern Australia (McPhee et al. 1999) and *T. carolinus* along the North Carolina coast in the eastern United States (Ross and Lancaster 2002).

Rhabdosargus sarba showed similar movement behaviour, with most (81%) recaptures being taken within 2 km of their original tagging locality. Three fish (19%) undertook longer distance movements ranging from 2.2 to 230 km. These results, coupled with those from the ORI-CFTP, led Mann and Dunlop (2013a) to describe *R. sarba* as a surf-zone resident, with a home range size of approximately 1.1 km (linear distance). Species with a relatively higher proportion of ranging individuals were more difficult to classify. *Rhynchobatus djiddensis* was classified as a nomadic species by Dunlop and Mann (2013b), based on the mean distance of 33 km moved by 194 recaptures extracted from the ORI-CFTP. *Caranx heberi* showed interesting movement behaviour, with three of the five recaptures

moving distances of 3–26 km. Although preliminary, this suggests that this species may be more mobile than some congeneric species such as *C. melampygus* (Holland et al. 1996). *Argyrosomus japonicus* has been the subject of extensive study using both conventional tagging (Griffiths 1996) and acoustic telemetry (Cowley et al. 2008). These authors have confirmed that juvenile *A. japonicus* <1 000 mm TL remain fairly resident in estuarine and surf-zone habitats, whereas adults may undertake seasonal long-distance spawning migrations. The two *A. japonicus* recaptured in this study were both juvenile fish that were recaptured south of the St Lucia Marine Reserve, having moved distances of 14 and 27 km, respectively. Given that this species is uncommon in the St Lucia Marine Reserve and more abundant in the turbid surf-zone off the Mfolozi River and St Lucia Estuary to the south, these recaptures were likely to have represented return movements following the passing of a large cold front and the extension of turbid water from the Mfolozi River northward (pers. obs.), allowing these fish to forage farther north than normal.

The overall lack of migratory fish species such as adult *Pomatomus saltatrix* and *Lichia amia* in catches taken in the St Lucia Marine Reserve highlights the fact that Cape Vidal forms the northern distribution limit for many warm–temperate fish species and acts as a clear biogeographic break (Sink et al. 2012). It is possible that several species of the subtropical fish fauna exhibit migratory behaviour but they are either not well represented in the surf-zone catches (e.g. certain elasmobranch species and pelagic offshore species such as *Scomberomorus commerson*), or to date have yielded insufficient recaptures to reveal distinct migratory behaviour (e.g. *Caranx ignobilis*).

4.4.2 Behaviour of the five main species studied in detail

Two general types of movement behaviour were apparent in four of the five main species that were investigated in detail. Station-keeping was the most commonly recorded movement behaviour, with 95% of recaptured fish falling into this category. Whereas the original project design limited the length of each sampling area to 2 km of shoreline, most recaptures (~86%) were taken within 200 m of their original tagging locality. Thus, even with the subsequent extension of the four sampling sites (EA, EB, SA and SB) to ~10 km of shoreline in November 2011, the distance moved by most recaptures did not change substantially. A test of SLD movements made by *L. rivulatus* before and after the extension of the sampling areas showed that, although the mean distance moved increased from 1 093 m to 1 654 m, there was no significant difference between the two samples ($p > 0.05$). Based on Dingle's (1996) definition of station-keeping (Table 4.1), most of the movements shown by the St Lucia Marine Reserve fishes were of a foraging nature within a relatively small home range size. Ranging behaviour was also apparent, although to a much smaller extent, and accounted for about 5% of the movement behaviour observed in four of the five main study species (no ranging behaviour was observed in *P. furcatus*). Ranging movements varied considerably and ranged from relatively small movements of slightly more than 2 km to substantial movements exceeding 100 km.

Intermediate movements of 2–12 km were more difficult to classify, but fitted well with Dingle's (1996) definition for ranging, described as 'exploratory movements over wide areas in search of resources'. Based on personal observations frequent sand inundation of low profile reefs in the surf-zone may have forced fish to move to a new reef habitat, which could have contributed to some of the intermediate movements observed.

Several tag-recapture studies undertaken along the Eastern and Western Cape coasts of South Africa (Attwood and Bennett 1994; Attwood 2002; Brouwer 2002; Cowley et al. 2002; Griffiths and Wilke 2002; Brouwer et al. 2003; Attwood and Cowley 2005; Kerwath et al. 2007b; Maggs et al. 2013b) and in Australia (Gillanders et al. 2001; Russell and McDougall 2005) have noted similar variation in fish movement behaviour. On a smaller scale, acoustic telemetry studies have also reported similar variation in movement behaviour among individuals within a local population, with a high degree of station-keeping and a smaller component of ranging behaviour (Egli and Babcock 2004; Childs et al. 2008; Kerwath et al. 2008; Hedger et al. 2010).

4.4.3 Reasons for variation in behaviour and relevance to exploitation

Attwood and Cowley (2005) suggested two models to explain similar movement behaviours (i.e. station-keeping and ranging) of *Dichistius capensis*, a warm-temperate surf-zone fish in South Africa. Firstly, these authors proposed polymorphism to explain, that within a species, some individuals remain resident whereas others are nomadic and may move continuously (Attwood and Bennett 1994). Reasons for the differentiation may be either genetic or dependent on social or environmental cues (Swingland 1984; Dingle 1996) and the variation could be used as a hedge against inbreeding in geographically isolated reef fish populations. Their other alternative, the "tourist" model (Craig and Hulley 1994), predicts that individuals of a given species will spend part of their time exhibiting resident behaviour, but will temporarily abandon their home range to feed elsewhere before returning later. Despite the large number of multiple recaptures, this latter behaviour was not observed in *L. rivulatus* (or any of the other four main study species). Many fish were recaptured moving back and forth within their respective home ranges (i.e. moving distances <2 km) but once they had left their home range (i.e. moved distances >2 km), there were no examples of fish returning to their original home range. Although this may have partly been a result of the original, spatially constrained sampling design, the extension of the sampling areas in November 2011 should have effectively overcome this constraint. Based on these observations it is proposed that polymorphism is the more likely model to explain the movement behaviour in *L. rivulatus* and *D. petersi*, but on-going monitoring and/or an acoustic telemetry study would be necessary to test this.

The relevance of these two models to fisheries is that in the case of polymorphism only certain individuals may become available to an adjacent fishery, whereas in the tourist model all individuals

may at some time become available to the fishery (Attwood and Cowley 2005; Maggs et al. 2013b). The possibility of both behaviours being present in a population should also not be discounted; some individuals could be highly resident, with some ranging, whereas others might maintain temporary home ranges. Should the differentiation be due to polymorphism, the effect of differential selection on different movement behaviours could favour one type above another with area-based management (Attwood 2002; Parsons et al. 2010). In addition to removing resident fishes, fishing in an open-access area would also opportunistically remove nomadic (or ranging) individuals that leave a no-take area. This would select for residency in the no-take area, which, although potentially important from a conservation perspective, may have unforeseen ecological consequences for the population as a whole. With the tourist model, in which all individuals move, the population should not suffer from differential selection in the same way (Maggs et al. 2013b).

4.4.4 Station-keeping

Estimates of SLD and GLD calculated in this study varied from 200–700 m for *P. furcatus* to 995–1025 m for *L. rivulatus* (Table 4.7). Such site fidelity can lead to localised depletion of the species in exploited areas, but can be of benefit to the species in protected areas. Compared to the size of the St Lucia Marine Reserve sanctuary zone, which is ~25 km long and 5.6 km wide, these movements are small. In other words, retention of fishes within the no-take sanctuary area is likely to be high. This is supported by the findings of Mann and Tyldesley (2013), who found a greater abundance and mean length of *P. furcatus* and *L. rivulatus* in the St Lucia Marine Reserve sanctuary zone compared to the adjacent previously exploited area south of Leven Point, particularly in the early years of the study soon after shore angling had ceased there (2002–2005). The no-take sanctuary area therefore undoubtedly provides some insurance against fishing pressure in adjacent fished areas by acting as a refuge for resident surf-zone fish species. There is also the potential for these resident fish to spawn within the sanctuary area and provide a source of eggs and larvae that could be dispersed to adjacent fished areas (Brouwer et al. 2003; Harrison et al. 2012), but this aspect was beyond the scope of this study.

4.4.5 Dispersal to fished areas

In this study, 34% of the movements of the five main study species that were classified as ranging were between 3.5 and 90 km, and included three *D. petersi* and 13 *L. rivulatus* individuals that left the sanctuary zone and moved either in a southerly or a northerly direction into the adjacent previously exploited areas. In addition to this, one *D. petersi* and three *L. rivulatus* moved in a northerly direction, passing through the sanctuary zone over distances of 49–125 km (Table 4.8). Movements of these ranging fish were undoubtedly under-sampled, particularly to the north of the sanctuary because, owing to the beach driving ban, very little shore angling takes place between Red Cliffs and ~5 km south of Sodwana (Figure 4.1). In addition, Dunlop (2011) estimated a non-reporting rate of 42% by

members of the angling public, which would further hamper data collection on ranging fishes that had been recaptured. Despite these biases, it can be concluded that the adjacent previously exploited areas were supplied with a limited number of subadult and adult fishes, which had been under temporary protection within the St Lucia Marine Reserve sanctuary zone.

4.4.6 Reasons for dispersal

Many studies have failed to discriminate between spillover and variability in individual movement patterns (Zeller et al. 2003). Spillover, which is the net export of adult fish from a no-take area (Abesamis and Russ 2005), implies that fishes will move from a no-take area, where there is a high concentration of individuals, to areas where fishing has reduced the number and size of fish (Kramer and Chapman 1999). Whereas there may have been some true density-dependent spillover when the areas to the north and south of the St Lucia Marine Reserve sanctuary zone were being fished prior to 2002, Mann and Tyldesley (2013) reported a rapid recovery in the abundance of shore-angling fishes in the adjacent previously exploited areas (as sampled in EA and EB) south of Leven Point following the implementation of the beach vehicle ban and the consequent cessation of shore angling there. This would have quickly reduced the gradient in fish density between the two areas, with the result that much of the dispersal observed in this study is more likely to have been as a consequence of variability in individual movement patterns. This observation is supported by the fact that ranging movements were undertaken by six fish tagged in the previously exploited area that moved into the sanctuary zone.

4.4.7 Unique characteristics of individual species

Pomadasys furcatus

This is a relatively small reef fish species that grows to a maximum size of 50 cm TL (van der Elst 1993), but with few individuals exceeding 40 cm TL (Mann and Dunlop 2013b). It is abundant in the St Lucia Marine Reserve and occurs in large shoals over scattered reef in the surf zone. Because of the minimum tagging size of 300 mm FL stipulated for the project, relatively few (22%) of the *P. furcatus* caught were large enough to tag. Although the recapture rate was the lowest of the five main study species (7%), a large number of fish with tag scars were recaptured (50 fish, or 6.1%), suggesting that tags were relatively quickly shed by this species. If fish with tag scars are included, the recapture rate increases to 13.1%. It is likely that, as a consequence of tagging only the larger fish in the population and the fact that these fish were probably dominant in a given shoal and were likely to feed first at the bait, the proportion of larger adult fish recaptured was artificially elevated. In addition to factors such as hook selectivity, such biases may frequently be overlooked when conducting population assessments using tag-recapture methods.

Epinephelus andersoni

Of the five main study species, the South-East African endemic *E. andersoni* exhibited the shortest time at liberty (58 days \pm 71 SD), and although recapture data suggested a relatively small home-range size (465–525 m), it is believed that this species may display unusual movement behaviour. Mann (2012) found a larger mean size of *E. andersoni* in the previously exploited area (EA and EB) compared to the no-take sanctuary area (SA and SB). Similarly, Maggs et al. (2013a) found a greater abundance of *E. andersoni* in the adjacent exploited area compared to the no-take zone of the Pondoland MPA some 400 km to the south. Whereas this may simply reflect subtle habitat preferences in both studies, anecdotal evidence has shown that adult *E. andersoni* are often among the first species to arrive on newly created artificial reefs or shipwrecks (S. Chater, uShaka Marine World, pers. comm.; S. Bailey, South African Environmental Observation Network, pers. comm.). This has led to speculation that *E. andersoni* may be a nomadic pioneer species capable of rapidly colonising niche space previously occupied by more-resident species such as *L. rivulatus* and *E. marginatus* that have been removed by fishing (Mann 2012; Maggs et al. 2013b). A well-designed acoustic telemetry project would probably be necessary to clarify this. Furthermore, as *E. andersoni* are not common on deeper reefs farther offshore in both the St Lucia and Maputaland MPAs (Floros 2010), the shallow subtidal reefs within the surf-zone provide an important habitat for the conservation of this endemic species. This is particularly relevant because Fennessy and Sadovy (2002) found that most spawning occurs on reefs off northern KwaZulu-Natal and southern Mozambique and they speculated that there may be a northward spawning migration coupled with the possibility of the formation of spawning aggregations.

Epinephelus marginatus

Fennessy (2006) showed that *E. marginatus* are protogynous hermaphrodites with females maturing at 622 mm TL and sex change occurring after reaching a length of 800 mm TL. All the *E. marginatus* individuals tagged in this study, except one fish, were below the size at maturity (size range 300–659 mm TL). This demonstrates that, after moving out of intertidal rockpools where post-larval recruitment occurs (Beckley 2000), *E. marginatus* utilise shallow subtidal reefs in the surf-zone as important nursery habitats where they remain resident for >2 years in relatively small home ranges (200–740 m linear distance). Maggs et al. (2013b) reported similar results in the Pondoland MPA where *E. marginatus* showed extremely high site fidelity and a home range size of 118–154 m in depths of 10–30 m. However, Maggs et al. (2013b) and subsequent monitoring (JQ Maggs, ORI, unpublished data) have recorded a number of ranging movements >100 km undertaken by mature specimens of *E. marginatus*. Maggs et al. (2013b) hypothesised that this may be linked to a north-eastward spawning migration. In the St Lucia Marine Reserve, offshore research fishing has shown that adult *E. marginatus* are relatively common on deeper reefs at depths of 40–120 m (BQM, ORI, unpublished data) and it is likely that juvenile *E. marginatus* move farther offshore onto deeper reefs

with increasing size (Lembo et al. 1999). Given that Fennessy (2006) recorded most reproductive activity for this species in northern KwaZulu-Natal and southern Mozambique, it is likely that the St Lucia and adjacent Maputaland MPAs play an important role in the protection both of juveniles and adults of this species and that a proportion of the adult population spawn within the MPA boundaries, thereby contributing to adjacent fished areas through the south-westerly dispersal of eggs and larvae facilitated by the Agulhas Current (Beckley 1993; Hutchings et al. 2002).

Dinoperca petersi

Surprisingly little is known about the biology of this relatively common species, which is widely distributed in the Western Indian Ocean and which is caught both from the shore and on offshore reefs down to 75 m (Fennessy and Mann 2013). During this study, catches of *D. petersi* were considerably higher after dark, which is consistent with the species' nocturnal behaviour and its tendency to remain in caves and under ledges during the day (van der Elst 1993). Not surprisingly, this species showed extremely high site fidelity, with home range size ranging from 365 to 470 m. Individuals probably remain resident in specific caves or overhangs during the day and move out to forage at night, before returning to the same cave in the morning. The two intermediate ranging movements recorded (3.5 and 4.1 km) were probably instances where the home cave or overhang of an individual had become sanded up, forcing it to relocate to a new reef habitat. The three long-range movements (49, 63 and 90 km) are considered likely to represent examples of the polymorphic behaviour discussed above.

Lutjanus rivulatus

The exceptionally high recapture rate (49.9%) and the large number of multiple recaptures ($n = 222$), with four individual fish being recaptured as many as six times, highlights not only the residency of this species but also its potential susceptibility to overfishing. The species has a tropical Indo-Pacific distribution (Mann and Maggs 2013) and catches south of the boundary of the St Lucia Marine Reserve at Cape Vidal become increasingly rare (JQ Maggs, National Marine Linefish System, ORI, unpublished data). However, it is not known whether this is due to the biogeographic break at Cape Vidal (Sink et al. 2012), with less-suitable habitat to the south, or whether it is a result of overfishing and other anthropogenic influences. There is anecdotal evidence (B Wareham, South African Shore Angling Association, pers. comm.) that suggests that, historically, this species was considerably more abundant in rocky areas along much of the KwaZulu-Natal coast but was depleted rapidly by overfishing.

A large number (1 146 fish or 37%) of the *L. rivulatus* caught in this study were smaller than the stipulated minimum tagging size of 280 mm FL, which highlights the importance of the surf-zone habitat as a nursery area for juveniles of this species. However, many larger fish (790 fish or 25%) that were greater than the reported size at maturity of 370 mm FL (Lau and Li 2000) were also

captured, suggesting that the surf-zone is also an important habitat for adults. Adult *L. rivulatus* have been observed on offshore reefs in the St Lucia and Maputaland Marine Reserves down to a depth of at least 30 m, but they are seldom abundant and are often solitary at this depth (pers. obs.).

An obvious limitation of this study was that only fish movements along the coast within the surf-zone could be monitored and the proportion of fish that moved offshore could not be established. Despite these limitations, it is clear that the St Lucia Marine Reserve Sanctuary provides an extremely important refuge for both juvenile and adult *L. rivulatus*, and although there is a high degree of site fidelity and residency, there is some dispersion into adjacent areas. As this species has a wide Indo-Pacific distribution, these results have important implications for other MPAs within its range.

4.5 Conclusion

The dominance of station-keeping behaviour and maintenance of small home ranges by the five main species investigated in detail indicates that the St Lucia Marine Reserve sanctuary zone affords sufficient protection to potentially allow their populations to reach their carrying capacity within the available habitat. Although some fishes crossed the no-take boundaries into adjacent previously exploited areas, having taken temporary refuge in the no-take sanctuary zone, these movements were not related to fish size or the time at liberty. Similarly, these fish did not swim persistently in a particular direction. Whereas the ranging movements observed were unlikely to have been as a result of density-dependent spillover *per se*, the no-take sanctuary undoubtedly has the ability to contribute to adjacent fisheries via the export of pelagic eggs and larvae spawned within the sanctuary and to a lesser extent through the movement of larger individuals.

CHAPTER 5: GROWTH RATE OF SPECKLED SNAPPER *LUTJANUS RIVULATUS* (TELEOSTEI: LUTJANIDAE) BASED ON TAG-RECAPTURE DATA FROM THE ISIMANGALISO WETLAND PARK, SOUTH AFRICA

Mann BQ, Lee B, Cowley PD. 2016. *African Journal of Marine Science* 38(1): 111-118

5.1 Introduction

Lutjanus rivulatus, commonly known as speckled or blubberlip snapper, is a beautifully coloured and robust reef fish with a tropical Indo-Pacific distribution (Heemstra and Heemstra 2004). It is found on coral and rocky reefs from the surf-zone out to depths of 100 m and is often associated with caves and ledges on high-profile reef (van der Elst 1993). It reaches a maximum size of about 80 cm total length (Randall 1995) and a weight of at least 12.3 kg (SAUFF 2015). It is an important reef predator feeding on a variety of small reef fish, molluscs, crustaceans, polychaetes and other benthic invertebrates (Allen 1985; van der Elst 1993). Despite its wide distribution, relatively little is known about the biology of this species (Mann and Maggs 2013) probably due to low catch contribution in fisheries throughout much of its distribution (Everett et al. 2013). It is likely that high site fidelity (Chapter 4, Mann et al. 2015), coupled with aggressive feeding behaviour (pers. obs.) has resulted in the depletion of local populations. This is particularly true in tropical regions of the western Indian Ocean where high artisanal fishing pressure using a range of gear types would actively target high value species such as *L. rivulatus* and other lutjanid and serranid species (Samoilys et al. 2011).

Given the apparent low abundance and vulnerable nature of *L. rivulatus*, information on growth rate is critical to improving the understanding of the biology of the species, which can then be used to inform better management practises and ensure sound conservation (Gulland 1988). Following an extensive literature search, the only information available on growth rate of *L. rivulatus* was from a study conducted by Munro and Williams (1985) in Papua New Guinea. Given that the study was conducted 30 years ago and that fish growth rates can vary spatially, it was considered important to assess growth rate of a population of *L. rivulatus* in the western Indian Ocean.

The collection of tag-recapture information is expensive and time-consuming (McFarlane and Beamish 1990) and prone to measurement error (Francis 1995), and the growth increment of recovered fish may be biased due to the effect of the tagging procedure or of the tag itself on subsequent growth (Attwood and Swart 2000). However, tag-recapture data can provide an accurate measure of individual fish growth over the period between tagging and recapture events which do not require knowledge of a fish's actual age (Baker et al. 1991). A number of methods have been developed that utilise tag-recapture data to estimate growth model parameters (e.g. McCaughran 1981; Kirkwood 1983; Francis 1988a, 1988b; Baker et al. 1991; Francis 1995). Francis (1988a)

presented a maximum likelihood approach for the analysis of growth increment data derived from tagging experiments. This method describes improved parameters for the von Bertalanffy growth curve that have better statistical properties, and that represent the growth information obtained in tagging data better than do conventional parameters (Cerrato 1990).

This study made use of data collected from a research-based tag-recapture study conducted in the St Lucia Marine Reserve within the iSimangaliso Wetland Park, a World Heritage Site in northern KwaZulu-Natal, South Africa, between November 2001 and November 2014 (see Chapter 4, Mann et al. 2015). While this tag-recapture study was focused primarily on determining fish movement patterns (Chapter 4, Mann et al. 2015), it also provided information on the growth of individual fish recaptured during the study. Furthermore, since the majority of fish were tagged and recaptured by a team of trained research anglers, measurement error that is common in tagging programmes conducted by voluntary members of the angling public (Dunlop et al. 2013) was considered to be minimal. The aim of this study was to estimate the growth rate of *L. rivulatus* through non-destructive sampling in a marine protected area (MPA), using tag-recapture data and the maximum likelihood approach developed by Francis (1988a).

5.2 Material and methods

The general methods adopted in the long-term fish tagging project in the St Lucia Marine Reserve (SLMR) are described in detail by Mann et al. (2015). Shore-based research fishing took place bi-monthly in four designated areas in the SLMR. Fish were caught using barbless hooks, immediately covered with a wet cloth, carefully measured to the nearest mm fork length (FL) on purpose-made PVC stretchers and tagged using external dart tags (D-tags, Hallprint©, Australia) supplied through the Oceanographic Research Institute's Cooperative Fish Tagging Project (Dunlop et al. 2013). Fish were tagged in the dorsal musculature below the posterior dorsal fin spines and the barb of the tag was locked behind a pterygiophore. Care was taken while handling each fish. For example, a bucket of fresh seawater was kept at the tagging station to minimise the period of air exposure while performing the tagging and measuring procedures (Cooke and Sneddon 2007). Generally, only fish greater than 280 mm FL were tagged. The occasions when a fish ingested the hook were noted but no attempt was made to remove the hook and the trace was simply cut as short as possible (Casselman 2005; Cooke and Suski 2005; Wilde and Sawynok 2009). The same process of handling and measuring applied to recaptured fish. With recaptured fish, the tag itself was often covered by a film of biofouling (mainly red algae), which was scraped off with a thumbnail to enable recording of the unique tag number. In instances where the tag had been damaged and the number could not be seen clearly (i.e. rubbed or bitten off), the tag was removed from the fish by making a small incision using a scalpel to dislodge the barb. This enabled the unique number, which was also inscribed near the barb of the tag, to be

read and the fish was then re-tagged using a new tag on the side opposite to that of the original tag. Data on all subsequent recaptures of such fish were linked to the original tag number. Recaptured fish that had shed their tags were often recognised by the presence of tagging scars and were recorded as such.

5.2.1 Data analysis

The tag-recapture data were represented by T_1 , T_2 , L_1 and L_2 where T denotes time (date) and L length (mm, FL). The subscripts 1 and 2 refer to the dates of tagging and recapture, respectively. Increments in length and time are given as ΔL and ΔT , respectively. Growth rates were modelled from the tag-recapture data using the maximum-likelihood approach described by Francis (1988a, 1988b) using the Fish Methods package (Nelson 2014) on the R statistical platform (R Core Team 2015). The usual form of the von Bertalanffy growth function, as used with tag-recapture data, may be written as:

$$\Delta L = (L_\infty - L_1)(1 - e^{-K(t_2 - t_1)}) \quad (1)$$

Francis (1988a) described a re-parameterisation and extension of the Faben's (1965) growth model for tag-recapture data that incorporates seasonal growth:

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 - \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T + (\varphi_2 - \varphi_1)} \right] \quad (2)$$

where

$$\varphi_i = u \frac{\sin[2\pi(T_i - w)]}{2\pi} \quad \text{for } i = 1, 2 \quad (3)$$

The parameters g_α and g_β are the estimated mean annual growth (mm y^{-1}) of fish of initial lengths α mm and β mm, respectively, where $\alpha < \beta$. The reference lengths α (300 mm) and β (600 mm) were chosen such that the majority of values of L_1 , the length at tagging, fell between them. Seasonal growth is parameterised as w (reflecting the portion of the year in relation to 1 January when growth is at its maximum) and u (with $u = 0$ indicating no seasonal growth through to $u = 1$ indicating maximum seasonal growth effect).

The measured growth increment of the i th fish, ΔL_i , has a corresponding expected mean growth increment u_i , where u_i is normally distributed with standard deviation σ_i . In this study, σ_i was assumed to be a function of the expected growth increment u_i :

$$\sigma_i = v\mu_i \quad (4)$$

where v is estimated as a scaling factor of individual growth variability.

The model was fitted by minimizing the negative log-likelihood function λ . For each dataset, made up of $i=1$ to n growth increments:

$$\lambda = \sum_i \ln \left[(1-p)\lambda_i + \frac{p}{R} \right] \quad (5)$$

where

$$\lambda_i = e^{-\frac{1}{2}(\Delta L_i - m)^2 / (\sigma_i^2 + s^2)} \quad (6)$$

$$\left[2\pi(\sigma_i^2 + s^2) \right]^{\frac{1}{2}}$$

When the model is fully parameterised, the likelihood function estimates the population measurement error in ΔL as being normally distributed, with a mean m and standard deviation s . The proportion of outliers was identified by the parameter p , the probability that the growth increment for any individual could exist erroneously in the dataset as any value, within the observed range of growth increments R .

The optimal model parameterisation was determined by following a step-wise fitting procedure. Initially, a simple 3-parameter model was fitted and then parameters were added in the order determined by selecting the parameter that gave the greatest reduction in the Akaike Information Criterion (AIC) value, with unfitted parameters held at zero. When the introduction of an additional parameter did not result in a significantly better model fit, these results were excluded from the analyses.

Growth rates were modelled separately for fish that had been recaptured on single and multiple occasions. Only the initial and final recapture lengths were included in the dataset used to estimate growth rates for multiple recaptures. This was done in order to avoid repeated measurements of individual fish resulting in a lack of independence of the data. The growth rates of single and multiple recaptured *L. rivulatus* were compared using a likelihood ratio test. Similarly, growth rates were modelled separately for fish that had ingested the hook and for those from which the hook was removed. The growth rates associated with deep-hooking and no-hooking treatments were also compared using a likelihood ratio test. The final model using all recapture data was bootstrapped 1 000 times and 95% confidence intervals were calculated for parameter estimates.

5.3 Results

During the 13-year period from November 2001 to November 2014 a total of 1 429 *L. rivulatus* were tagged and 453 (31.7%) individual fish were recaptured one or more times (i.e. a total of 727 recaptures [50.9%], including multiple recaptures). Of the fish recaptured, 291 were recaptured only once, whereas 162 fish were recaptured multiple times (Table 5.1). Of the fish recaptured, 357 had the hook removed whereas 75 had swallowed the hook (note that this was not recorded in 21 of the 453 recaptured fish). In addition, 34 fish (2.4%) were recaptured with tagging scars (i.e. having shed their tags). Time-at-liberty for recaptures ranged from 0 days (i.e. recaptured on the same day) to 3 214 days (8.8 years). Length-at-tagging or recapture ranged from 262 to 597 mm FL (Figure 5.1).

Table 5.1: Number of individual *Lutjanus rivulatus* tagged and recaptured in the St Lucia Marine Reserve between November 2001 and November 2014.

Number of fish tagged	Number of recapture events per fish							Total number of fish recaptured
	1	2	3	4	5	6	7	
1 429	291	97	33	24	3	3	2	453

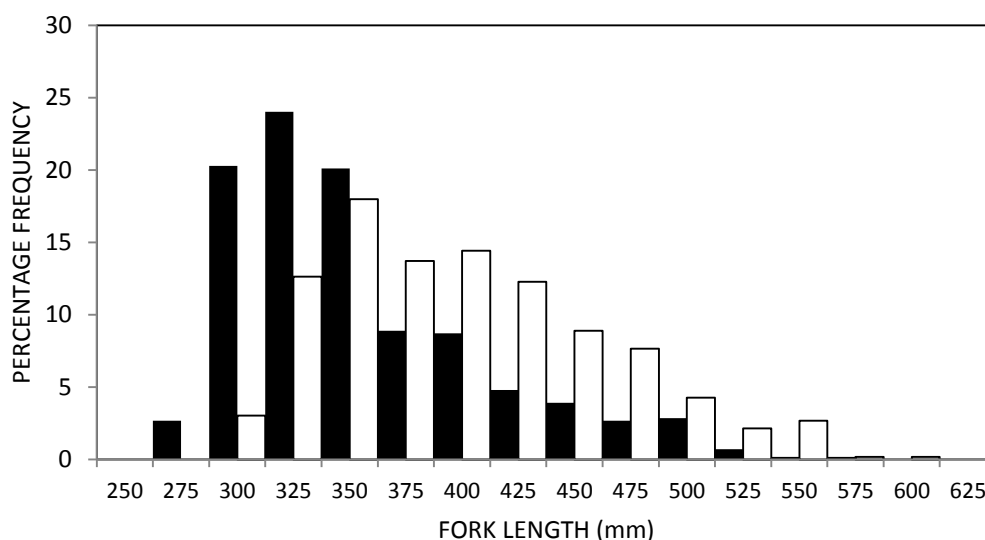


Figure 5.1: Length frequency distribution of 453 *Lutjanus rivulatus* tagged (shaded bars) and recaptured (open bars) in the St Lucia Marine Reserve between 2001 and 2014.

5.3.1 Effects of fishing and tagging on growth

Growth was modelled for each treatment individually (i.e. single recaptures [$n = 291$], multiple recaptures [$n = 162$], hook removed [$n = 357$] and deep-hooked [$n = 75$]). Single- and multiple-recapture datasets were optimally parameterised under the most complex model incorporating

seasonal growth and measurement error estimates. Likelihood ratio tests (Table 5.2) indicated no significant differences in growth between fish that had been recaptured once and those that had been recaptured multiple times ($\chi^2 = 6.27$, $p = 0.099$). Similarly, likelihood ratio tests indicated no significant differences in growth between fish that had ingested the hook and those in which the hook had been removed ($\chi^2 = 2.34$, $p = 0.504$) (Table 5.2). As such, growth was modelled for the combined dataset.

5.3.2 Growth model

To better understand the importance and interpretation of the parameters, a step-wise fitting procedure was followed, starting with the most simple 3-parameter model. The five models for the total dataset ($n = 453$ recaptures) were for all the combinations that improved the fitted model best (Table 5.3). The remaining combinations that improved the fit to a lesser extent or did not improve the fit were excluded.

Table 5.2: Comparison between growth parameters estimated for single and multiple recaptures and for deep-hooked and unhooked *Lutjanus rivulatus* using a likelihood ratio test. The terms g_{300} and g_{600} refer to fish of reference lengths 300 mm and 600 mm, respectively

Treatment	Sample size (n)	Mean growth rate (mm y^{-1})	χ^2	df	p
Single recapture	291	$g_{300} = 35.08$ $g_{600} = 17.58$	6.27	3	0.099
Multiple recapture	162	$g_{300} = 35.42$ $g_{600} = 16.51$			
Hook ingested	75	$g_{300} = 34.58$ $g_{600} = 17.32$	2.34	3	0.504
Hook removed	357	$g_{300} = 35.16$ $g_{600} = 18.88$			

Table 5.3: Parameters estimated for the growth rate of *Lutjanus rivulatus* in the St Lucia Marine Reserve using five different tag-recapture growth models (after Francis 1988a). Final and best estimates are shown in bold. See methods section for explanation of parameters

Parameter	Symbol (unit)	Model									
		1		2		3		4		5	
		Estimate	Error	Estimate	Error	Estimate	Error	Estimate	Error	Estimate	Error
Mean growth rate	g_{300} (mm y^{-1})	35.620	0.800	34.350	0.920	34.920	0.890	36.430	1.100	35.350	1.100
Mean growth rate	g_{600} (mm y^{-1})	13.100	1.870	15.310	2.330	15.130	2.240	15.720	2.240	18.190	2.320
Seasonal variation	u (year)	*0	0.000	*0	0.000	1.000	0.120	1.000	0.114	1.000	0.108
	w (year)	*0	0.000	*0	0.000	0.108	0.017	0.108	0.016	0.100	0.014
Growth variability	v	*0	0.000	0.203	0.025	0.218	0.023	0.208	0.022	0.239	0.026
Measurement error	s (mm)	14.588	0.485	11.082	0.590	9.177	0.558	9.124	0.553	7.577	0.691
	m (mm)	*0	0.000	*0	0.000	*0	0.000	-1.747	0.750	-1.502	0.680
Outliers	p	*0	0.000	*0	0.000	*0	0.000	*0	0.000	0.009	0.006
Negative log likelihood		1 856.90		1 826.30		1 776.40		1 773.70		1 765.200	
AIC		3 719.80		3 660.60		3 564.90		3 561.30		3 546.400	
Maximum theoretical length	L_{∞} (mm FL)	772.56		841.23		829.45		827.72		918.174	
Growth rate parameter	k ($year^{-1}$)	0.078		0.066		0.068		0.072		0.0588	

*0 parameter held fixed (see explanation in text)

Model 1 is equivalent to the Faben's (1965) method (standard least-squares fit), although the parameters were estimated by minimising the negative log-likelihood. It is necessary to start with this more-complicated fitting method from the outset for comparative purposes (using the AIC), because increasing numbers of parameters are added with the more complex models (Haddon 2011).

Model 1 included only the following essential parameters for the model to run:

- g_{α} – the mean annual growth rate of fish at length α (300 mm was chosen – reflecting the smaller size range of the sample);
- g_{β} – the mean annual growth rate of fish at length β (600 mm was chosen – reflecting the larger size range of the sampled fish);
- s – the root mean square error, which comprises possible measurement error during sampling, individual growth variability and lack of fit of the model.

Model 2 included the growth variability parameter (v). This improved the model fit, as reflected by a reduced negative log-likelihood value and consequently lower AIC value (Table 5.3). The resultant estimate of L_{∞} was slightly greater while the growth rate (K) was reduced.

Model 3 ran all possible combinations for the addition of a 5th parameter, namely seasonal variability. Similar to Model 2, the negative log-likelihood and AIC values were lower (Table 5.3), indicative of an improved fit of the observed data in Model 3. The additional parameters are explained as follows:

- u (year) – where a value of 0 would reflect no seasonal growth variability and 1 reflects strong seasonal variability. The resultant value indicated that there is strong seasonal variation in growth for *L. rivulatus*;
- w (year) – a value reflecting the time (date) as a fraction of the year when growth rate is at a maximum. The value of 0.1 indicated that growth peaked in early February.

Despite attempts to measure fish as accurately as possible, data were prone to a degree of measurement error. The inclusion of two additional parameters, namely measurement error (m) and outlier probability (p), further improved the model. These parameters are explained as follows:

- m – the combined mean measurement error (mm) at tagging and recapture;
- p – the probability that the growth increment for any individual could exist erroneously in the dataset as any value within the observed range of growth increments R .

As with many reef fish species, growth rate declined with increase in length, although there was a high degree of variability in individual growth rates (Figure 5.2). Relatively fast growth (35.35 mm y^{-1}) was recorded in smaller fish compared to larger fish (18.19 mm y^{-1}). There was a strong seasonal influence with fastest growth rate recorded in early February. The mean measurement error in ΔL was low and estimated at -1.502 mm ($\pm 7.577 \text{ SD}$). The probability of outliers detected in the model fit was low (0.009).

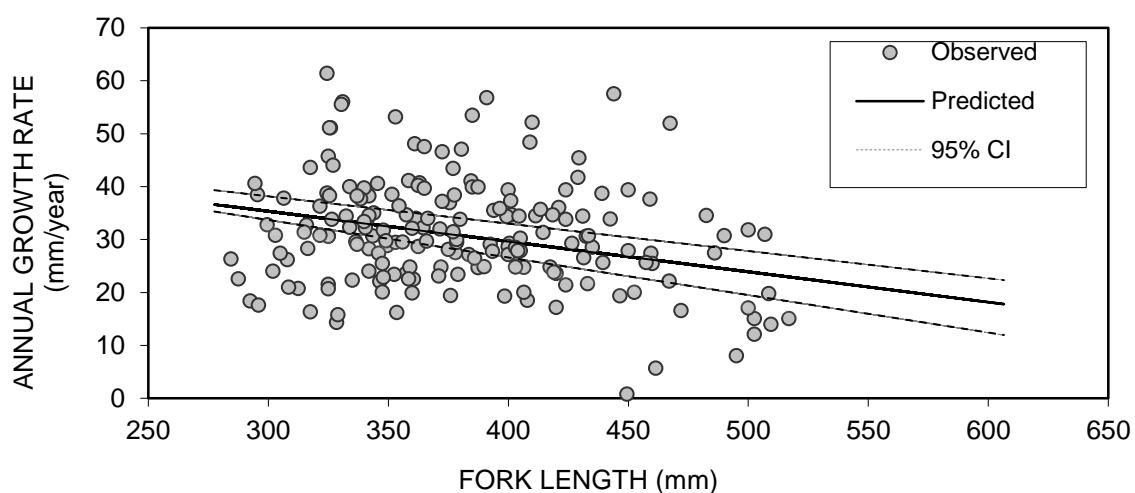


Figure 5.2: Observed and predicted growth rate for all *Lutjanus rivulatus* tagged and recaptured in the St Lucia Marine Reserve between 2001 and 2014 ($n=453$). (Note that observed data points for recaptures < 1 year at liberty were excluded from the figure for clarity).

5.4 Discussion

The high recapture rate observed in this study (32% when considering individual fish and 51% when including multiple recaptures) is seldom achieved in conventional tagging studies (Ortiz et al. 2003; Wild and Sawynok 2009; Dunlop et al. 2013). It exceeds the highest reported recapture rate of 22.9% for *L. sebae* from the Australian National Sportfishing Association's Suntag database (Wild and Sawynok 2009). The exceptionally high recapture rate of *L. rivulatus* can be ascribed to a combination of factors including good fish handling and tagging, suitability of the species for tagging, and the high level of residency and site fidelity displayed by this species (Chapter 4, Mann et al. 2015). The low number of fish observed with tag scars also suggests that this species takes and retains the tag well. Although the effects on growth rate of the tagging procedure and/or the physiological burden of carrying the tag could not be assessed, *L. rivulatus* nevertheless appears to be an ideal species for calculation of growth rate using tag-recapture methods.

5.4.1 Growth model

A complete model of growth for ectothermic fishes must unify both length- and age-based approaches (Francis 1988a; Eveson et al. 2004). Therefore, tag-recapture models, as used in this study, do not provide a complete model of growth due to the absence of age information (Francis 1988a, 1988b, 1995; Gillanders et al. 1999; Attwood and Swart 2000; Welsford and Lyle 2005; Ofstad et al. 2013). When using the VBGF for age-based data, L_{∞} represents the asymptotic mean length-at-age for the population. Hence there may be many individuals with lengths greater (and less) than L_{∞} in the modelled population. However, L_{∞} is inadequate as a growth descriptor when data are not sufficiently extensive to demonstrate asymptotic growth (Lee 2013). By comparison, using tag-recapture data (i.e. length increment data), L_{∞} represents maximum length and is not appropriate as a descriptor even if individual growth of fish is asymptotic. The reason is that when L_{∞} is estimated from tagging data there will be few, if any, individuals with lengths greater than L_{∞} as this would imply negative growth. As such, the L_{∞} parameter derived from tag-recapture data has a fundamentally different meaning to the L_{∞} parameter obtained from length-at-age data (Francis 1988b). Consequently, due to the correlation between L_{∞} and K (as discussed above), the K parameter also has a different meaning/interpretation. Although the L_{∞} value obtained in this study was particularly high ($L_{\infty} = 918$ mm FL) and the K value was very low ($K = 0.06$), the above explanation has reference. The largest fish captured and tagged in this study was 692 mm FL and larger specimens have been caught by members of the public within the iSimangaliso Wetland Park (D Nisbet, KwaZulu-Natal Coast Anglers' Union, pers. comm.).

It is for these reasons that tag-recapture growth modelling primarily solves two parameters, namely g_{α} and g_{β} (i.e. annual growth rate at length α and β). These parameters are also easily obtained from

growth models derived from length-at-age data (including VBGF) and have been shown to be mathematically comparable (Francis 1995). Therefore, the results of growth studies utilising these different types of data are comparable, highlighting the value of growth information that can be extracted from tag-recapture datasets. Wang et al. (1995) and Laslett et al. (2002) described similar maximum likelihood approaches for fitting growth curves to tag-recapture data that have overcome many of the limitations of the traditional Fabens (1965) approach. However, the method described by Francis (1988a) (maximum likelihood estimation of growth and growth variability) remains the most consistently used for describing growth in fish using tag-recapture data (Gillanders et al. 1999; Welsford and Lyle 2005; Haddon 2011).

Acknowledging the above limitations, the present results suggest that *L. rivulatus* is a relatively slow-growing species with an average growth rate of 35.35 mm y⁻¹ for smaller fish ($g_{\alpha} = 300$) and 18.19 mm y⁻¹ for larger fish ($g_{\beta} = 600$). Growth rate at 300 mm FL was significantly faster compared to that of larger fish at 600 mm FL. In order to compare this growth rate to other lutjanid species, the index phi-prime (\emptyset) developed for this purpose by Pauly and Munro (1984), was used. This suggests that the growth rate of *L. rivulatus* in northern KwaZulu-Natal is slower than that estimated for many congeneric species (Table 5.4).

Table 5.4: Published growth parameters for a number of similar congeneric (*Lutjanus*) species based on the median record of phi-prime (\emptyset) obtained from FishBase (Froese and Pauly n.d.) (TL = total length; FL = fork length; SL = standard length)

Species	L_{∞}	k	\emptyset	Region	References
<i>L. analis</i>	86.9 cm TL	0.16	3.08	USA	Burton (2002)
<i>L. argentimaculatus</i>	105 cm TL	0.19	3.32	Malaysia	Ambak et al. (1986)
<i>L. bohar</i>	66 cm FL	0.27	3.07	Kenya	Talbot (1957)
<i>L. campechanus</i>	93.8 cm TL	0.18	3.19	USA	Patterson et al. (2001)
<i>L. erythropterus</i>	60 cm FL	0.41	3.17	Australia	McPherson and Squire (1990)
<i>L. griseus</i>	60 cm FL	0.22	2.9	Cuba	Valle et al. (1997)
<i>L. guttatus</i>	64.2 cm SL	0.19	2.89	Mexico	Cruz-Romero et al. (1996)
<i>L. malabaricus</i>	86 cm SL	0.25	3.27	Australia	McPherson et al. (1985)
<i>L. peru</i>	87 cm TL	0.26	3.29	Mexico	Santamaria and Chavez (1999)
<i>L. rivulatus</i>	91.8 cm FL	0.06	2.69	South Africa	This study
<i>L. sanguineus</i>	89 cm TL	0.24	3.27	Red Sea	Sanders and Morgan (1989)
<i>L. sebae</i>	85.1 cm FL	0.16	3.06	Gulf of Aden	Druzhinin and Filatova (1980)

The growth model also suggested seasonal differences in the growth rate of *L. rivulatus* with fastest growth in early February. This period is associated with the highest annual seawater temperatures recorded in the St Lucia Marine Reserve, averaging around 26 °C (unpublished data). Higher ambient temperatures likely result in an increase in metabolic activity. This is supported by the fact that catch rates for *L. rivulatus* were highest during summer (see Chapter 3, Mann et al. 2016a), suggesting an increase in foraging behaviour that would link directly with increased growth rates.

Life-history parameters such as slow growth, high trophic level and high residency result in fish species being more vulnerable to overexploitation (Smale and Punt 1991; Buxton 1993b). *Lutjanus rivulatus* displays all of these characteristics and a conservative approach is thus required for its management. Although *L. rivulatus* receives some protection from shore-angling within the ~25 km long no-take sanctuary area of the St Lucia Marine Reserve between Leven Point and Red Cliffs (Chapter 4, Mann et al. 2015), it is not currently listed in the suite of fish species regulated by species-specific minimum size and bag limits in South African fisheries legislation (Mann and Maggs 2013). As such, and based on the results of this study, a minimum size limit of 40 cm TL (estimated size-at-maturity is 37 cm FL [Lau and Li 2000]) and a daily bag limit of one fish per person per day is recommended as a precautionary approach for the future management of this species in South African waters.

5.4.2 Effects of fishing and tagging on growth

The use of growth data from tag-recapture studies has often been criticised because of factors such as measurement error and the effects of tagging on growth rate (Attwood and Swart 2000; Brouwer and Griffiths 2004; Griffiths and Attwood 2005; Kerwath et al. 2006). In this study an attempt was made to minimise these factors by using a trained team of anglers who were taught to handle, measure and tag fish correctly. Small D-tags (85 mm x 1.6 mm) were used, applicators were cleaned regularly in alcohol and a minimum tagging size of 280 mm FL was set to prevent tagging stress on smaller fish. Although all fish measurements were taken from the tip of the snout to the fork of the tail, with the fish lying on its side with the mouth closed and touching the head of the steel measuring board (which was encased in a clear plastic sheath down the centre of the stretcher), error occurred if the fish measured was tense rather than relaxed or if the fish was pushed firmly up against the headboard as opposed to just touching it. A degree of measurement error is therefore acknowledged, which was estimated as a mean of only -1.502 mm (SD 7.577 mm).

It has been suggested that discrepancies between tag-recapture growth rates and predictions from other data sources, such as length-at-age data derived from otoliths, are a result of either the capture event itself or the subsequent effect of external tags retarding growth (Attwood and Swart 2000). However, research undertaken on a fast-growing carangid, *Lichia amia*, along the South African coastline revealed similar results when comparing growth rates from tag-recapture and length-at-age data from otoliths (Smith 2008). This was attributed to *L. amia* being a relatively large, robust species where tagging had limited effect in terms of depressing growth. Comparisons of growth rates derived from length-frequency, age-at-length and tagging data on another fast-growing carangid *Seriola lalandi*, in New South Wales, Australia, showed agreement for fish aged 2–4 years, but varied largely for fish with one growth zone (Gillanders et al. 1999). The large differences in growth for younger fish compared to older fish may have been caused by inaccuracies in ageing, the influence of tagging

on growth, within- or between-year differences, and variations in year-class strength (Gillanders et al. 1999). In another example, the growth rates estimated for tagged *Scomberomorus commerson*, although initially slower, portrayed significantly faster growth compared to the growth rates estimated using length-at-age data for larger fish (Lee 2013). This suggests that although external tags may depress growth of younger (smaller) *S. commerson*, this was not the case for fish older than two years (Lee 2013). Unfortunately, it was not possible to determine the length-at-age of *L. rivulatus* in this study, due to the fact that the work was conducted in an MPA where only non-destructive sampling was permitted.

Importantly, there appeared to be no significant effect on growth of *L. rivulatus* through cutting off a barbless hook that had been ingested (Table 5.2). This positive result suggests that deep-hooked fish will often lose the barbless hook after release and that this does not suppress growth substantially. Interestingly, four recaptured individuals had the barbless hook, coated with a hardened white substance, protruding from the anus, having passed right through the alimentary canal. This may represent a mechanism whereby fish can manage sharp objects that are difficult to digest. This result has important implications for catch-and-release fishing, and the use of barbless hooks should therefore be strongly encouraged (Cooke and Suski 2005; Butcher et al. 2010). Similarly, it was shown that the growth rate of fish that had been recaptured more than once was not significantly slower than that of those recaptured only once (Table 5.2). Considering the stress that a fish undergoes during a capture event (Cooke et al. 2006), this is an important result because it suggests that growth rate in an individual of this species will not be suppressed if it is handled well and if the time that it is out of the water is limited to the bare minimum. This finding may well apply more generally.

CHAPTER 6: ESTIMATING THE OPTIMUM SIZE FOR INSHORE NO-TAKE AREAS BASED ON MOVEMENT PATTERNS OF SURF-ZONE FISHES AND RECOMMENDATIONS FOR REZONING OF A WORLD HERITAGE SITE IN SOUTH AFRICA

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6.1 Introduction

Over the past 50 years there has been much discussion globally around the subject of the optimum size of marine protected areas (MPAs) for both biodiversity conservation and fisheries management. In the 1980s this was centred on the “SLOSS” (single large or several small) debate with many authors highlighting the benefits and disadvantages of both options (e.g. Siberloff 1988; Demartini 1993; Attwood et al. 1997a). From a conservation perspective, many previous recommendations for MPA design have conveyed the message “bigger is better” (Sale et al. 2005; McLeod et al. 2009; Wilhelm et al. 2014) as larger MPAs provide protection for a broader range of habitats and species. However, smaller reserves can also be effective for sedentary or range restricted species (Kerwath et al. 2007; Afonso et al. 2011; Green et al. 2015), especially where levels of marine resource utilisation is high (Ban et al. 2011). Current wisdom emphasizes the need for well-designed networks of MPAs (Almany et al. 2009; Botsford et al. 2009b; Lester et al. 2009; Christie et al. 2010; Gaines et al. 2010), which may include a combination of large and small areas to provide protection for everything from seascapes and multiple habitats to individual species or features of important ecological, cultural or even aesthetic value (Kellerher and Kenchington 1992, Attwood et al. 1997a).

There has also been considerable emphasis placed on the value of no-take areas (NTAs) as being fundamental to MPA effectiveness (Kerwath et al. 2013; Buxton et al. 2014; Edgar et al. 2014). This is largely because MPAs where various forms of extractive use are allowed have been shown to be less effective at achieving biodiversity and fisheries objectives than those zoned for no-take (Denny and Babcock 2004; Edgar et al. 2014). Well designed and effectively managed networks of MPAs (including NTAs) are important tools for both fisheries management and biodiversity conservation (Green et al. 2015), with the added benefit of increasing resilience against climate change (McLeod et al. 2009; Green et al. 2014). Based on the deliberations of scientists and MPA practitioners at the recent IUCN World Parks Congress held in Sydney, Australia in November 2014, recommendations were made to increase the global no-take protection target to 30% of marine habitats; a vast increase from the Convention for Biological Diversity’s Aichi Target 11 which was set at 10% in 2010 (MPA News 2014; Thomas et al. 2014).

In South Africa, relatively good progress has been made with the establishment of coastal MPAs since the proclamation of the 336 km² no-take Tsitsikamma National Park in 1964 (Hockey and Buxton 1989; Attwood et al. 1997b). Today, 23 formally proclaimed MPAs have been established in South Africa (excluding the Prince Edward Islands) covering approximately 785 km (21.5%) of the ~3200 km coastline (linear distance), 334 km (9.1%) of which are NTAs (NPAES 2008; Sink et al. 2012). However, in terms of surface area, only 0.4% of South Africa's Exclusive Economic Zone (EEZ) is formally protected (NPAES 2008), leaving much work still to be done.

The St Lucia and Maputaland Marine Reserves (large contiguous MPAs zoned for multiple use) were proclaimed in northern KwaZulu-Natal in 1979 and 1986, respectively, to protect the country's only shallow water coral reef ecosystems (Mann et al. 1998). Boat-based bottom or reef fishing is prohibited throughout both MPAs, while scuba diving, shore angling and boat-based pelagic game-fishing were developed as important tourism attractions (note that no commercial fishing of any type is allowed in either of these MPAs). Both the St Lucia and the Maputaland Marine Reserves were zoned to include large NTAs (locally known as sanctuary areas) where no form of human use was allowed, except that shore-based subsistence linefishing and invertebrate harvesting by local rural communities continued to be allowed in the Maputaland MPA Sanctuary due to their dependence on these resources (Kyle et al. 1997). In December 1999, both these marine reserves were included into the iSimangaliso Wetland Park to become part of South Africa's first World Heritage Site (IMP 2011).

Surprisingly, relatively little work has been undertaken on the surf-zone fish communities found within the St Lucia Marine Reserve and little was known about the effectiveness of the NTA in providing a refuge for these species. This formed the primary motivation for a study initiated in November 2001 aimed at comparing surf-zone fish communities in the NTA with those in an adjacent area exploited by recreational shore anglers between Cape Vidal and Leven Point (Mann and Tyldesley 2013; Mann et al. 2016a). In order to evaluate the effectiveness of this NTA, one of the objectives of the study was to determine the movement patterns and potential spillover of surf-zone angling fish species using conventional tag-recapture methods (see Chapter 4, Mann et al. 2015).

Connectivity of local fish populations through the dispersal of individuals as eggs, larvae, juveniles or adults is a key ecological factor to consider in MPA design (Sale et al. 2005), since it has important implications for persistence of meta-populations and their recovery from disturbance (Botsford et al. 2003; Green et al. 2015). Where movement patterns of fishery species are known, this information can be used to inform decisions taken about the configuration of NTAs to maximize benefits for biodiversity conservation, fisheries management and improving resilience against climate change (Attwood and Bennett 1995b; Kramer and Chapman 1999; Griffiths and Wilke 2002; Botsford et al.

2003; Gaines et al. 2010; Green et al. 2014; 2015). For example, movement studies were used to develop guidelines for sizes of MPAs in a temperate system in California (Gleason et al. 2013; Saarman et al. 2013). More recently Green et al. (2015) provided a detailed review of knowledge on larval dispersal and movement patterns of coral reef fishes and the implications of this for the design of MPA networks. In South Africa, Attwood and Bennett (1995b); Griffiths and Wilke (2002) and Kerwath et al. (2007b) used fish movement patterns determined through conventional tag-recapture and acoustic telemetry studies to estimate effective size of no-take MPAs. The primary aim of this study was to use the movement patterns of important shore-angling fish species in the St Lucia Marine Reserve to determine the minimum size and spacing of surf-zone NTAs throughout the iSimangaliso Wetland Park. In this regard some of the recommendations made by Green et al. (2015) were adopted namely: to design shore-based NTA networks to maximise benefits for local fisheries (i.e. important surf-zone angling fish species); to review the configuration of existing NTAs along the shore to ensure that they are adequate for focal species; and to integrate NTAs with other fisheries management tools where necessary.

6.2 Material and methods

6.2.1 Study Area

The St Lucia Marine Reserve was proclaimed with a NTA extending from Leven Point (27° 55'S; 32° 35'E) to Red Cliffs (27° 43'S; 32° 37'E) a distance of ~24 km and extending three nautical miles (5.6 km) out to sea (Figure 6.1). This area was selected as a no-take zone because of the existence of two large off-shore reef complexes, namely Red Sands Reef (5.5 km²) and Leadsman Shoal (7.3 km²), as well as the importance of the beaches in this area as nesting sites for loggerhead and leatherback turtles. The shoreline and surf-zone in this NTA and adjacent areas comprise large stretches of sandy beaches with scattered outcrops of beach rock and are backed by some of the highest vegetated dunes in the world. The terrestrial area inland of the St Lucia Marine Reserve Sanctuary is a protected Wilderness Area (IMP 2011), which has resulted in limited human access, except along the beach itself. Prior to 2002, a limited number of beach vehicles were allowed to traverse through the sanctuary area during low tide but no stopping was allowed. In January 2002, all beach driving by the public was banned in South Africa (Celliers et al. 2004).

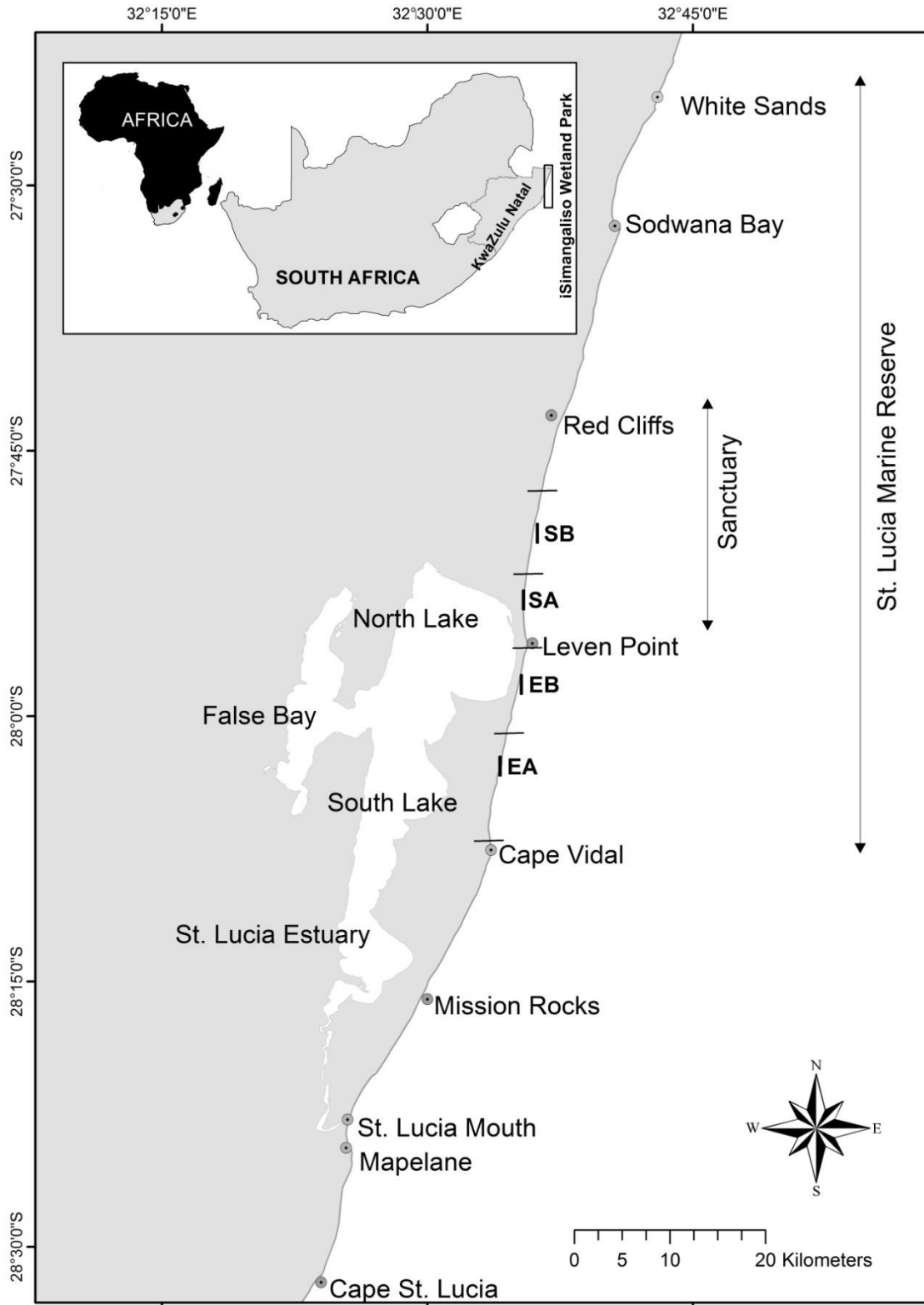


Figure 6.1: Map of the St Lucia Marine Reserve and no-take Sanctuary within the iSimangaliso Wetland Park showing the sampling areas used in this study.

6.2.2 Data collection and interpretation

A long-term tag-recapture study was conducted by the team of trained shore anglers in the St Lucia Marine Reserve between November 2001 and November 2013 using conventional plastic dart tags (Hallprint[®], Australia) supplied through the Oceanographic Research Institute's Cooperative Fish Tagging Project (Dunlop et al. 2013). All research fishing was conducted from the shore and recaptures were caught either by the research team themselves or by members of the angling public in accessible areas outside the NTA. The field methods are described in further detail in Chapter 4 (Mann et al. 2015). In this study we distinguished between station-keeping behaviour within a home range and ranging movements, in which individuals abandon their home range and do not return (Dingle and Drake 2007). Station-keeping behaviour is a good indicator of the potential for fish retention within a protected area, whereas ranging or migratory behaviour indicates the potential for export of sub-adult or adult fish to adjacent fisheries. The home range of a fish is the area in which an individual spends the majority of its time and engages in most of its routine activities including foraging and resting (Kramer and Chapman 1999; Gruss et al. 2011; Green et al. 2015). In this study, home range size was quantified for each species by taking the 95th percentile of intra-study site movement distances only (Chapter 4, Mann et al. 2015), and excluded all long-distance movements (> 2 km) where fish abandoned their home range (Attwood and Cowley 2005; Maggs et al. 2013b). These estimates of home range size, coupled with movements of wider ranging individuals and estimates of passive dispersal of eggs and larvae from the literature, were used to estimate the minimum size of NTAs and their optimal spacing within the iSimangaliso Wetland Park. As the study was limited to surf-zone fish species, only one-dimensional movement (i.e. linear movement along the coast) was considered with distances given in kilometres. Furthermore, as the species tagged are sympatric with overlapping habitats (i.e. all caught within the surf-zone), results obtained for all species with sufficient recapture data were considered.

To estimate the minimum size of NTAs, home range size was doubled in all directions (Green et al. 2015), which effectively meant tripling of home range length along the coast. Ranging movements (i.e. fish that left their home range and did not return) were used to estimate the distance apart that NTAs needed to be in order to ensure connectivity between protected reef fish populations. This was coupled with the best available estimates of larval fish dispersal in the recent literature (Jones et al. 2009; Berumen et al. 2012; Harrison et al. 2012; Almany et al. 2013; Green et al. 2015).

In order to relate the findings of this study conducted in the St Lucia Marine Reserve to the availability of surf-zone reef habitat throughout the iSimangaliso Wetland Park, a habitat mapping exercise was conducted using information collected by Harris et al. (2011) on the occurrence of rocky shores and adjacent surf-zone reef habitat, assigned to 100 m bins, along the entire length of the coastline within the Park. This was verified using aerial photographs, satellite images on Google

Earth[®], as well as an intimate knowledge of the coast by myself. To cater for fish species displaying ontogenetic shifts in habitat use (i.e. moving offshore out of the surf-zone into deeper water habitats with an increase in size/age), the occurrence of deeper reef habitat further offshore was also mapped using data obtained from SeaPLAN (Harris et al. 2011). The locality of surf-zone reef habitat in relation to existing beach access points along the coast was then compared using a Geographical Information System (ArcGIS). The mean distribution of shore-angling effort along the coast was estimated using Ezemvelo KZN Wildlife (Ezemvelo) shore patrol data collected between 2002-2013 (i.e. post beach vehicle ban) from five patrol zones (i.e. Maphelane, St Lucia, Cape Vidal, Sodwana Bay and Bhanga Nek; see Figure 6.3) within the iSimangaliso Wetland Park (Maggs et al. 2014). Current park zonation (IMP 2011) was then overlaid onto this map to identify gaps in the protection of suitable surf-zone reefs and to determine the best options for improved conservation planning.

6.3 Results

6.3.1 Fish home ranges and minimum NTA size

A total of 6 613 fish representing 71 species from 29 families were tagged in this study, of which 1004 fish comprising 17 species from eight families were recaptured (see Chapter 4, Mann et al. 2015). Five resident reef fish species namely *Lutjanus rivulatus*, *Dinoperca petersi*, *Epinephelus marginatus*, *Pomadasys furcatus* and *Epinephelus andersoni* dominated recaptures. A large proportion of the movement behaviour shown by the recaptured species consisted of station-keeping behaviour within relatively small home ranges of 0.1 – 1.9 km (Table 6.1). The remaining individuals undertook ranging type movements of >2 km up to 230 km (except for those species where no ranging behaviour was evident). Migratory-type movement behaviour was not evident amongst any of the species recaptured as no fish showed long-distance movements of a seasonal nature. However, certain species, especially *E. marginatus*, *E. andersoni* and *E. tukula*, displayed ontogenetic habitat shifts, with individuals moving from their nursery surf-zone reefs out to deeper offshore reef habitats with an increase in size/age (Chapter 4, Mann et al. 2015). Some of these larger tagged fish were observed on offshore reefs while scuba diving in the vicinity (pers. obs.). Similarly, no evidence of seasonal movement to spawning aggregation sites was found, although such movements may have been missed due to the spatially and temporarily limited nature of the sampling methods (Chapter 4, Mann et al. 2015). Species associated with sandy habitat in the surf-zone (e.g. *Trachinotus botla*, *Rhabdosargus sarba* and *Rhynchobatus djidenensis*) generally showed larger home range sizes than reef-associated species such as *D. petersi*, *E. marginatus* and *P. furcatus* (Table 6.1). The outcome of this study was influenced by the dominance of *L. rivulatus* with a remarkable 652 recaptures (i.e. 50% recapture rate).

Table 6.1: Home range length and ranging movements determined for 17 fish species recaptured in the St Lucia Marine Reserve between November 2001 and December 2013, with an estimate of minimum no-take area (NTA) length. NTA estimates and supporting literature used by Green et al. (2015) is also shown.

Species	No. tagged	No. of recaps	% Recap	Home range length (km)	Ranging Movements (km)	Minimum NTA length (km) estimate (this study)	NTA estimate by Green et al. (2015)	Supporting literature used by Green et al. (2015)
<i>Rhynchobatus djiddensis</i>	55	5	9.09	1.8 (n=3)	5.2 (n=2)	5.4	N/A	
<i>Epinephelus andersoni</i>	325	57	17.54	0.5 (n=56)	34.3 (n=1)	1.5	N/A	
<i>Epinephelus marginatus</i>	295	73	24.75	0.7 (n=70)	2.7-6.8 (n=3)	2.1	6 km	Afonso et al. (2011) Pillans et al. (2011)
<i>Epinephelus tukula</i>	236	11	4.66	0.7 (n=11)	None	2.1	6 km	Dunlop and Mann (2012b)
<i>Plectorhinchus flavomaculatus</i>	158	10	6.33	0.3 (n=10)	None	0.9	6 km	Kaunda-Arara and Rose (2004) Dunlop and Mann (2012b)
<i>Plectorhinchus playfairi</i>	46	1	2.17	0.1 (n=1)	None	N/A	N/A	
<i>Pomadasys furcatus</i>	817	57	6.98	0.7 (n=57)	None	2.1	6 km	Dunlop and Mann (2012b)
<i>Dinoperca petersi</i>	479	96	20.04	0.5 (n=91)	3.5-90 (n=5)	1.5	N/A	
<i>Lutjanus argentimaculatus</i>	20	2	10	0 (n=2)	None	N/A	6 km	Sawnok (2004) Dunlop and Mann (2012b)
<i>Lutjanus rivulatus</i>	1308	652	49.85	1.0 (n=614)	2.1-125 (n=38)	3.0	6 km	Dunlop and Mann (2012b)
<i>Diplodus hottentotus</i>	16	1	6.25	0 (n=1)	N/A	N/A	N/A	
<i>Rhabdosargus sarba</i>	529	16	3.02	1.9 (n=14)	9.4-230 (n=2)	5.7	N/A	
<i>Argyrosomus japonicus</i>	29	2	6.90	N/A	14-17 (n=2)	N/A	N/A	
<i>Caranx melampygus</i>	30	3	10	0.9 (n=3)	None	2.7	20 km	Holland et al. (1996) Meyer and Honebrink (2005) Tagawa and Tam (2006) Dunlop and Mann (2012b)
<i>Caranx heberi</i>	141	5	3.55	0.6 (n=2)	3-26 (n=3)	1.8	N/A	
<i>Trachinotus bailloni</i>	1	1	100	0.2 (n=1)	None	N/A	N/A	
<i>Trachinotus botla</i>	1327	12	0.90	1.2 (n=9)	6.6-114 (n=3)	3.6	N/A	

Based on the home range lengths determined from the tag-recapture study, estimates for minimum NTA lengths ranged between 0.9 and 5.7 km (Table 6.1). These were generally much smaller than those made by Green et al. (2015) (Table 6.1) as these authors did not clearly differentiate between station-keeping and ranging type movements, as was done in this study. Because most of the surf-zone reef is scattered, low relief reef exposed to frequent sand inundation, these estimates would also be effective for surf-zone fish species preferring a sandier habitat (e.g. *R. sarba* and *T. botla*). An exception to this would be species such as *Caranx melampygus* (and other more mobile fish species) where minimum NTA size would need to be considerably larger (i.e. ~10-20 km in length) (Holland et al. 1996; Meyer and Honebrink 2005).

6.3.2 Distance required between NTAs

In a review of larval dispersal distances of coral reef fish, Green et al. (2015) recommended a maximum distance of 15 km between NTAs to ensure effective connectivity of coral reef fish populations. The average distance moved by 38 *L. rivulatus* displaying ranging behaviour was 17.1 km, and similar to the 15 km spacing between NTAs recommended by Green et al. (2015), to facilitate larval dispersal and effective connectivity of coral reef fish populations. While these ranging individuals may be subject to capture by shore fishers while moving between NTAs, this distance (i.e. 15-20 km) will ensure some connectivity between protected fish populations. Based on these observations, NTAs of 3-6 km in length with suitable surf-zone reef habitat and spaced 15-20 km apart, should provide suitable protection for populations of surf-zone reef fish species and allow for sufficient connectivity between populations. The application of these findings to the iSimangaliso Wetland Park will also ensure that the proposed target of 20-30% of surf-zone reef habitat is effectively protected (MPA News 2014). While the above suggestion may be simplistic and species-specific because of the large range of factors that need to be taken into consideration (e.g. variation in home range size between resident and more mobile species, ontogenetic shifts to deeper reef, migrations to specific spawning areas, surf-zone reef habitat characteristics, etc.), it nevertheless follows best practise guidelines (Green et al. 2015).

6.3.3 Habitat mapping, distribution of shore fishing effort and zonation

A GIS map of the iSimangaliso Wetland Park was created using available data on all rocky shores, surf-zone reefs and offshore reefs along the entire coastline of the park. The map also took into consideration current beach access points, distribution of shore fishing effort and existing park zoning. This exercise revealed the occurrence of surf-zone reef habitat along much of the park's ~185 km coastline, interspersed between sandy bays (Figure 6.2). However, a substantial proportion of this surf-zone reef habitat was limited to a beach-rock ledge, some of which is exposed at spring low tide. The most surf-zone reef habitat was primarily concentrated in the vicinity of points and rocky headlands and was normally found in close association with rocky shores (Figure 6.2).

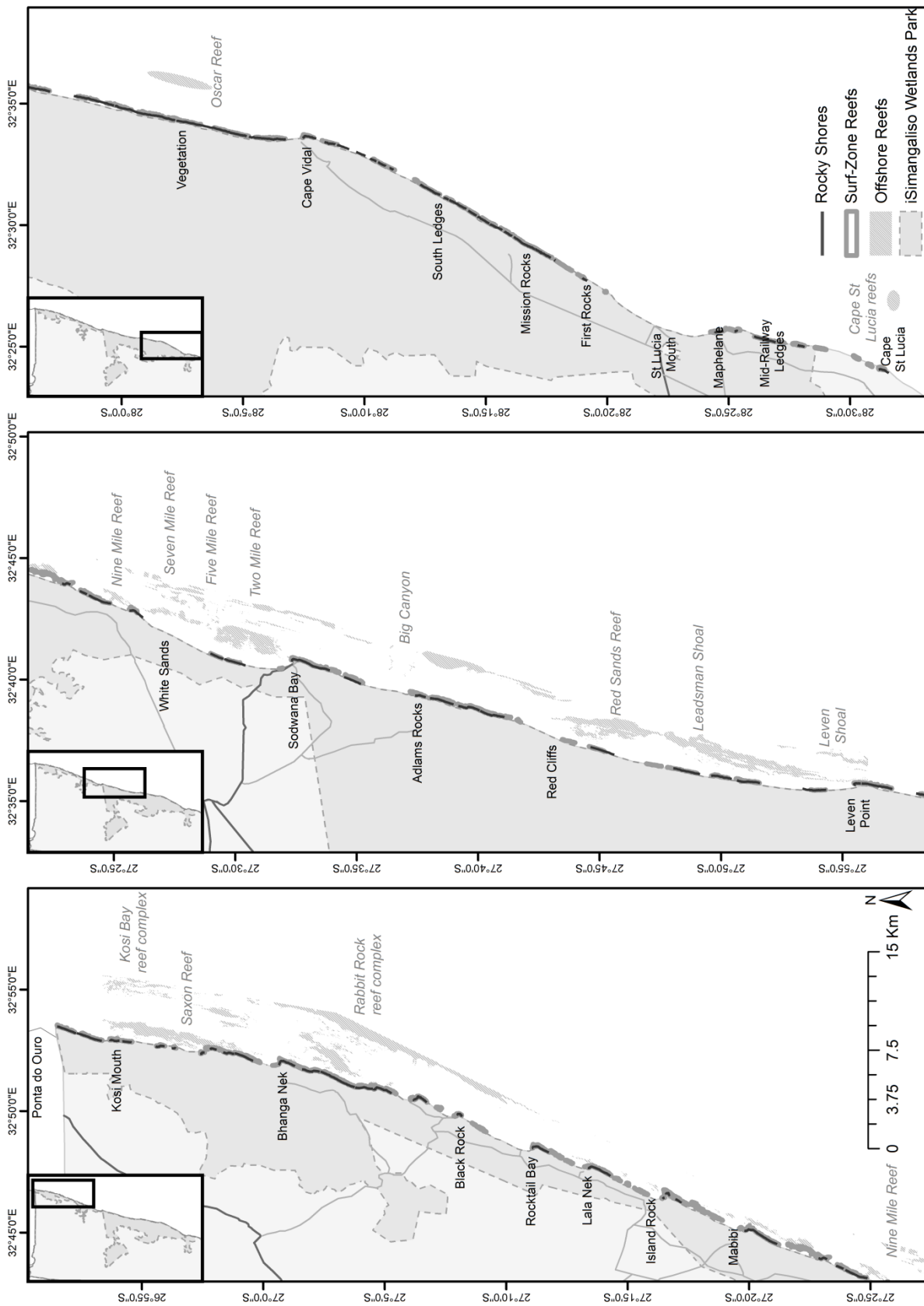


Figure 6.2: A map of the iSimangaliso Wetland Park from Ponta do Ouro to Cape St Lucia showing the locality of rocky shores, surf-zone reefs and offshore reef habitats.

Eleven major public access points were associated with existing roads and park tourism infrastructure and located at (from south to north): Maphelane, St Lucia, Mission Rocks, Cape Vidal, Sodwana Bay, Mabibi, Manzingwenya (Island Rock), Lala Nek, Rocktail Bay, Black Rock and Bhanga Nek (Figure 6.3). Shore angling effort was calculated as a spatial density (anglers.km⁻¹) based on 453 815 shore anglers counted during 40 593 patrols covering 214 551 km, conducted in the iSimangaliso Wetland Park between January 2002 and December 2013 (National Marine Linefish System, unpublished data). Shore angling effort was concentrated in the vicinity (i.e. walking distance of ~5 km) of major access nodes (e.g. Maphelane, St Lucia, Mission Rocks, Cape Vidal, Sodwana Bay and Bhanga Nek). In areas where there was limited road access and the adjacent terrestrial area was protected and not inhabited (e.g. north of Cape Vidal and south of Sodwana), shore fishing effort was very low and non-existent in the NTA between Leven Point and Red Cliffs (Figure 6.3). However, in areas where local communities live adjacent to the coast, such as in the extreme southern and northern areas of the park, shore fishing effort was higher, being primarily of a subsistence nature (Figure 6.3).

The shore and surf-zone (inshore zone) within the iSimangaliso Wetland Park is currently zoned as follows: i) Wilderness zone (no-take area adjacent to a terrestrial wilderness area); ii) No-take sanctuary zone (no-take area); iii) Restricted zone (limited consumptive use allowed but shore-fishing is permitted); iv) Controlled zone (high use area where controlled consumptive use is allowed). The current NTAs (n=6) within the iSimangaliso Wetland Park range in length from 2.2 to 24 km (Figure 6.4), suggesting that ~57 km (31%) of the coastline comprises NTAs and thus achieves the recommended level of no-take protection for shore and surf-zone habitats. In reality however, only the single 24 km NTA between Leven Point and Red Cliffs is effectively managed as a true no-take zone (see Chapters 3 and 4). Consequently, the effective conservation of surf-zone fish species within the iSimangaliso Wetland Park may be compromised. The five other smaller areas zoned as NTAs are either fished by local communities for subsistence purposes (i.e. NTAs north of Sodwana Bay and south of Maphelane) or are not recognised by recreational anglers (i.e. non-compliance) and/or are not enforced by the conservation authorities (e.g. the 10 km NTA north of Mission Rocks) (see Figure 6.4).

Considering the appropriate 15-20 km spacing of NTAs suggested by this study, there are large areas of shoreline that require NTA consideration within the iSimangaliso Wetland Park, such as the area between Red Cliffs and Dog Point (~72 km). Although this area has limited surf-zone reef habitat and is exposed to shore fishing effort, in order to ensure effective connectivity between protected surf-zone fish populations within the iSimangaliso Wetland Park, the implementation of two new NTAs is recommended. The optimal placement of these NTAs would be in the vicinity of Nine-mile Reef north of White Sands and the area near Lala Nek (Figure 6.4).

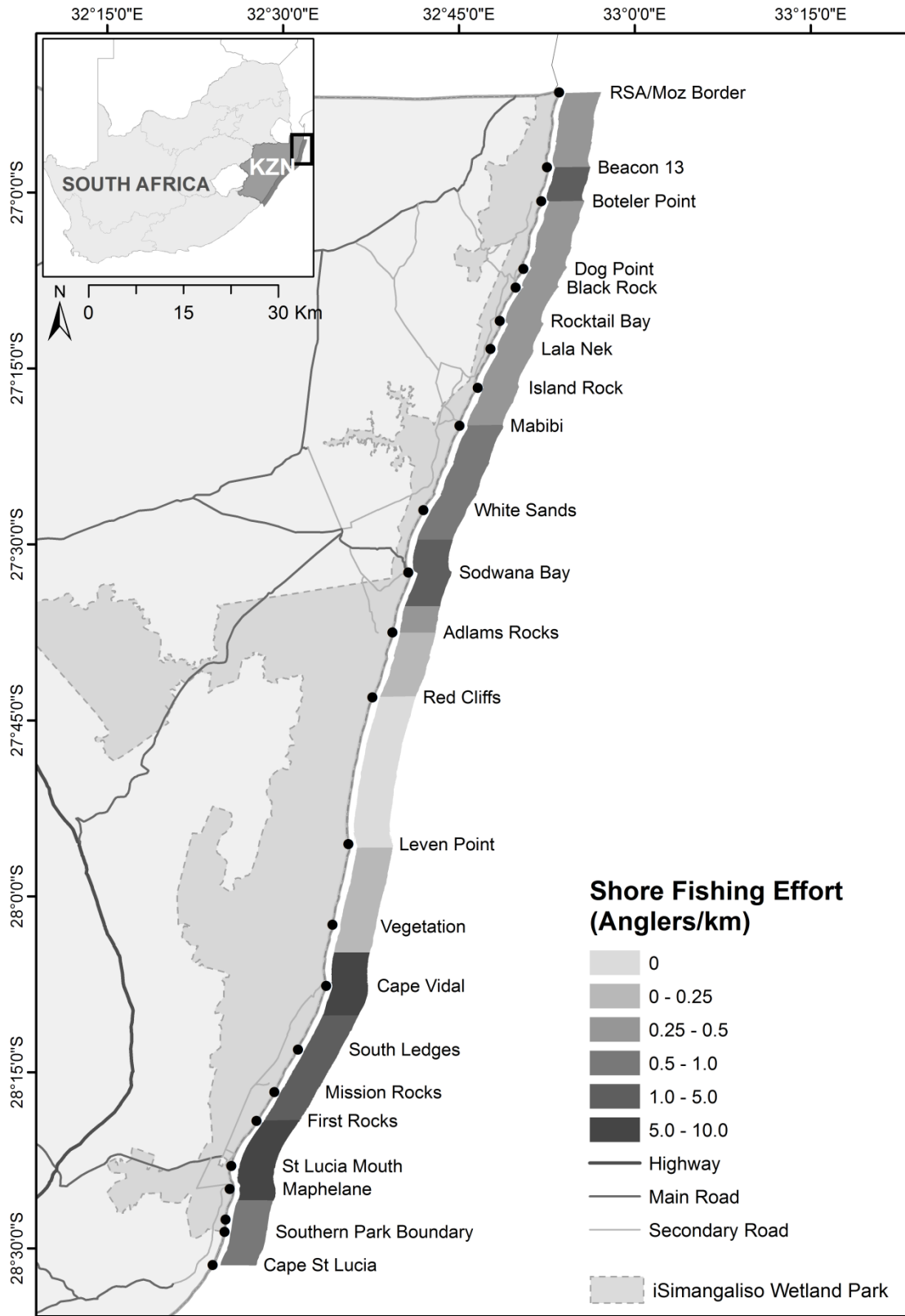


Figure 6.3: Map showing major public access points and the distribution of shore fishing effort along the coast of the iSimangaliso Wetland Park.

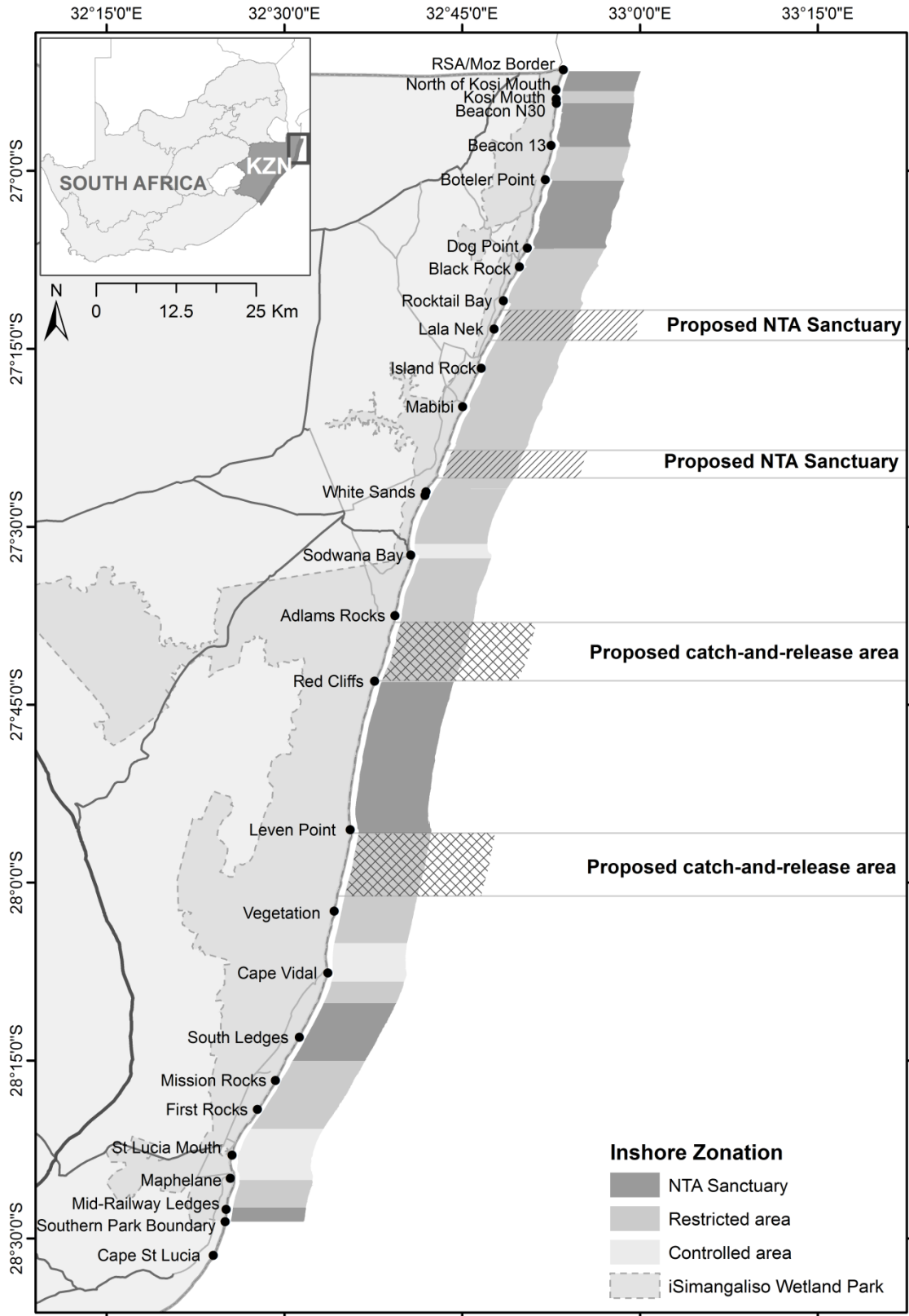


Figure 6.4: Current inshore zonation within the iSimangaliso Wetland Park and the new no-take sanctuary areas and catch-and-release areas proposed by this study.

6.4 Discussion

Green et al. (2015) recommended doubling the home range size (in all directions) to afford sufficient protection for resident coral reef fish species in a no-take area (NTA), while Griffiths and Wilke, (2002) recommended tripling what they called a travel range length (TRL), which included 95% of all displacement from long-term mark-recapture experiments. In essence these concepts are similar, except that Green et al. (2015) used home range size while Griffiths and Wilke (2002) took all movements into consideration, including ranging type movements. Griffiths and Wilke (2002) showed that for typical temperate reef fish, an area equivalent to three TRLs would protect 97.5% of the movement of fish with travel ranges centred within the central TRL. Clearly there are a number of conditions implicit to the approach they used namely: (1) quality and quantity of habitat is more or less the same throughout the area to be protected, (2) juveniles are protected within the NTA, (3) adults inhabiting the core area spawn within the NTA and (4) NTA length is based on the travel ranges of the most mobile representative of the reef ecosystem to be protected (Griffiths and Wilke 2002). A modification of Griffiths and Wilke's (2002) TRL was used in this study in that only station-keeping behaviour (i.e. movements within a home range) was considered, as this made up 94% of the observed movement behaviour (see Chapter 4, Mann et al. 2015). For this reason Point 4 above was not taken into consideration for the estimation of reserve size but rather these ranging movements were used to estimate the distance apart that NTAs needed to be to ensure connectivity.

Another important point for consideration is that Green et al. (2015) primarily used recapture data provided by the ORI-CFTP (Dunlop and Mann 2012 – which included data from this study) to estimate home range size (and thus NTA size) for many of the species under consideration. Locality data on the ORI-CFTP are captured with a much lower spatial resolution (1-5 km) (Dunlop et al. 2013) compared to the 0.1 km resolution used in the current study. Nevertheless, it was clear that relatively small NTAs with a minimum length of 3-6 km of suitable surf-zone reef habitat may provide sufficient protection for a viable population of most surf-zone reef fish species in the iSimangaliso Wetland Park.

While there is increasing evidence of larval retention in localised water circulation patterns (Jones et al. 2009; White et al. 2010; Berumen et al. 2012), considering the average velocity ($>1 \text{ m.s}^{-1}$) and close proximity ($<5 \text{ km}$ offshore) of the Agulhas Current to the coastline in the Maputaland region (Shannon 1989; Beckley 1993; Hutchings et al. 2002), it is considered likely that egg and larval dispersal in this region may be considerably greater than 15 km (Christie et al. 2010). Relatively little work of this nature has been conducted in this area, with the exception of work conducted on the dispersal of barnacle and mussel larvae in the Maputaland Marine Reserve (Reaugh 2006) which showed mean dispersal distances ranging from 30-122 km southwards along the coast. However, in

absence of better information for fish larvae, the Green et al. (2015) recommendation was used as best practise in this study.

Attwood and Bennett (1995b) found that a range of reserve size and spacing combinations satisfied management criteria for the sustainable use of three sympatric surf-zone fish species in the south-western Cape (i.e. *Lithognathus lithognathus*, *Dichistius capensis* and *Diplodus capensis*). While their results were too general to be of specific value (i.e. optimum reserve size of 10-20 km in length with an optimum distance between reserves of 20-40 km), they did suggest that NTAs are a viable option for the management of multispecies shore fisheries. Griffiths and Wilke (2002) found that optimum reserve size for five species of warm-temperate reef fish in the south-western Cape would be about 45 km reserve length, an estimate that was used by Mann et al. (2006) in the establishment of the large offshore NTA in the Pondoland MPA. Kerwath et al. (2007b) predicted that relatively small NTAs of just a few kilometres in extent would be effective in protecting populations of *Chrysoblephus laticeps*, a highly resident reef fish species. Examples of estimating optimum reserve size abound in the literature and a thorough review by Green et al. (2015) suggests that the estimates made in this study (i.e. a NTA of 3-6 km coastline length spaced every 15-20 km) are well within the optimum range. Furthermore, it is likely that this would also be equally important and applicable to a range of intertidal invertebrate species such as *Perna perna*, *Pyura stolonifera*, *Patella* spp. etc. which are harvested by subsistence communities on rocky shores within the Maputaland MPA (Kyle et al. 1997; Tomalin and Kyle 1998; Sink 2001) and in the Sokhulu area south of Maphelane (Harris et al. 2003).

The history of marine zonation within the iSimangaliso Wetland Park stems back to when these MPAs were first proclaimed. The St Lucia Marine Reserve was proclaimed in 1979 (Mann et al. 1998) and the NTA between Leven Point and Red Cliffs was established primarily to protect the offshore reefs in this area (i.e. Red Sands Reef and Leadsman Shoal) (Rudy van der Elst, Oceanographic Research Institute, pers. comm.). This area was equidistant from the two main beach access nodes and boat launch sites at Sodwana Bay and Cape Vidal thus enabling shore anglers (with beach vehicles) and ski-boat anglers to fish 23 km south of Sodwana and 22 km north of Cape Vidal. For many years access for beach vehicles was allowed through the sanctuary at low tide but no stopping or fishing was permitted. Similarly, boats could traverse through the sanctuary but no fishing was allowed and fishing gear had to be stowed. Ski-boat fishing was and still is limited to pelagic game fishing (i.e. no bottom or reef fishing) throughout the remainder of the MPA to ensure protection of resident reef fish (Garratt 1993). Similarly, the adjacent Maputaland MPA was established in 1986 (Mann et al. 1998) and the NTA between Dog Point and Boteler Point was established primarily to protect the important offshore reef complexes in this area (e.g. Rabbit Rock reef complex). While much of the zonation was similar, an important difference between the St Lucia and Maputaland MPAs was that shore fishing and invertebrate harvesting by local communities was

allowed in the Maputaland NTA as it was recognized that fish and marine invertebrates were an important source of protein for the poor rural communities living adjacent to the coast in this area (Kyle et al. 1997). As turtle nesting sites were protected along the entire length of coastline in both these contiguous MPAs, little further attention was initially given to establishing additional NTAs along the shore (Hughes 2012).

A major change to marine zonation occurred after the proclamation of the iSimangaliso Wetland Park (formerly known as the Greater St Lucia Wetland Park) as South Africa's first World Heritage Site in 1999 (IMP 2011). Firstly, the marine area protected within the Park was extended 42 km southwards from 1 km south of Cape Vidal to just north of Cape St Lucia (Mann and van der Elst 2005; IMP 2011). This was done in terms of the World Heritage Convention Act (Act 49 of 1999) and while no new restrictions were placed on user groups initially, stricter controls were gradually phased in by means of internal Park rules.

During the late 1990s a detailed intertidal biodiversity survey of the iSimangaliso Wetland Park was conducted (Sink 2001, Harris et al. 2011), which provided new insights into the location and ecological status of intertidal resources within the park. An important finding of the survey was the existence of a major biogeographic break at Cape Vidal with biota to the north (Delagoa Bioregion) being distinctly more tropical in nature, while that to the south (Natal Bioregion) was sub-tropical and more tolerant of higher turbidity (Sink 2001).

A further change in management was the implementation of the ban on beach driving in 2002 (Government Gazette No. 22960 promulgated under the National Environmental Management Act [Act 107 of 1998]). Based on these governance changes and new insights obtained from spatial planning (Harris et al. 2011), a new zonation plan was proposed and included in the Integrated Management Plan for the iSimangaliso Wetland Park (IMP 2011). These included all the additional NTAs along the coast as shown in Figure 6.4 and were primarily driven by the need to set aside greater areas of rocky shore habitat to protect intertidal rocky shore communities and limit invertebrate harvesting and recreational shore angling. However, most of these shore-based NTAs have not been effective in reducing intertidal invertebrate harvesting and shore fishing, with the exception of the Sokhulu area south of Maphelane (Harris et al. 2003; Harris et al. 2007).

In order to overcome these challenges, the following recommendations are proposed:

1. Existing NTAs in the iSimangaliso Wetland Park need to be clearly demarcated (i.e. signposted) and their position and purpose needs to be effectively communicated to both recreational anglers and subsistence shore fishers and intertidal invertebrate harvesters.

2. While this will inevitably result in initial resistance, demonstration projects should be established to convince resource users of the need for NTAs and ultimately to obtain their support and compliance (e.g. Sokhulu mussel harvesting project [Harris et al. 2007]).
3. If local communities are unwilling to cease harvesting and fishing in existing NTAs, efforts should be made with the affected communities to try and decide on a minimum of 3 km of the best available habitat within existing NTAs where they will agree to stop fishing and harvesting.
4. Gaps in the network of NTAs along the shore should be identified and implemented in consultation with local communities, recreational fishing associations and the general public.
5. Once agreed to by relevant user groups, compliance with NTAs needs to be effectively enforced by the conservation authority (Ezemvelo).
6. Effective monitoring of both recreational shore angling catch and effort (Maggs et al. 2014) and subsistence use of marine living resources (Mann et al. 2014) needs to be continued, as should research monitoring within the NTAs themselves.

With regard to Point 4 above, it is proposed that a 3-6 km stretch of shoreline and adjacent surf-zone reef habitat is protected as an inshore NTA in the vicinity of Nine-Mile Reef. A second 3-6 km inshore NTA area should be established in the vicinity of Lala Nek (Figure 6.4). These two additional NTAs will improve connectivity between existing NTAs both with regard to surf-zone fish species and harvested intertidal invertebrates.

Other gaps include the two large stretches of coastline between Cape Vidal and Leven Point and Red Cliffs and Sodwana Bay which are currently zoned to allow shore fishing (Restricted Zone) but are beyond reasonable walking distance and there is no or limited vehicular access. Unlike the areas to the north of Sodwana Bay, the land adjacent to these areas is unoccupied and much of it falls into a terrestrial Wilderness Area (Figure 6.4). While these areas may currently be functioning as effective NTAs due to limited shore angler access (especially the southern area – see Chapter 3, Mann et al. 2016a), it is suggested that consideration should be given to the establishment of approximately 10 km buffer zones south of Leven Point and north of Red Cliffs as “catch-and-release” areas and that a concession is provided whereby a limited number of anglers, using trained guides, are allowed to access these areas in a strictly controlled manner (Cooke et al. 2006). Although it is understood that there will be a degree of fishing mortality even with good catch-and-release angling practises (Cooke et al. 2006; Danylchuk et al. 2007), with appropriate regulation and angler education, catch-and-release angling could help to enhance the goals of this World Heritage Site. In this respect, a limited number of anglers would be allowed to access this otherwise undisturbed stretch of coastline and experience high quality angling. This would enhance tourism attraction and increase revenue income

to the park but have minimal impact on surf-zone fish populations and this could be considered to be an example of good contemporary conservation practice.

As intertidal rockpools, subtidal gullies and surf-zone reefs form important nursery areas for a number of fish species which move out onto deeper reefs with growth (Beckley 1985; 2000; Smale and Buxton 1989), an important consideration for the establishment of surf-zone NTAs must be connectivity with deeper offshore reefs. Fortunately this linkage is available in all of the inshore NTAs zoned in the iSimangaliso Wetland Park and those proposed in this study (Table 6.2). The fact that no boat-based bottom fishing is allowed throughout the Park will ensure that reef fish that move out on to these deeper reefs will receive protection regardless of whether they fall into zoned offshore NTAs or not.

Some fish species such as *E. marginatus*, *E. tukula*, *E. andersoni* and *L. rivulatus* may undertake seasonal spawning migrations to specific spawning aggregation sites similar to that observed in other serranid and lutjanid species (Sadovy de Mitcheson and Colin 2012), although this type of movement behaviour has not yet been observed in the iSimangaliso Wetland Park. Provision thus needs to be made to allow for this type of movement behaviour and protection of fish spawning aggregations (FSA) should be considered as a high priority (Sadovy and Domeier 2005; Sadovy de Mitcheson and Colin 2012). With the current protection afforded to all bottom/reef fish species throughout the iSimangaliso Wetland Park (because of the prohibition on boat-based bottom fishing), it is believed that protection of existing FSAs for reef fish has already largely been catered for. However, this is not the case with regard to pelagic gamefish species (see Appendix 6.1).

Carangid species such as *Caranx ignobilis*, *C. melampygus*, *C. heberi*, *C. sexfasciatus* and *C. papuensis* are frequently caught by both shore and boat-based anglers (and spearfishers) within the iSimangaliso Wetland Park (National Marine Linefish System, unpublished data). While some of these species have been shown to exhibit strong site fidelity e.g. *C. ignobilis* (Wetherbee et al. 2004; Meyer et al. 2007; Ledee et al. 2015) and *C. melampygus* (Holland et al. 1996; Meyer and Honebrink 2005), they are also known to undertake movements in excess of 10 km (Dunlop and Mann 2012b) and some are known to form spatially and temporally predictable spawning aggregations (e.g. *C. ignobilis*) (R. Daly, Rhodes University, pers. comm.). While these species will likely receive some protection in the larger NTAs such as the St Lucia and Maputaland Marine Reserve sanctuaries, it is proposed that additional species-specific regulations (e.g. reduced daily bag limits, increased minimum size limits and spawning closure management measures) are implemented in the iSimangaliso Wetland Park and in the adjacent Ponta do Ouro Partial Marine Reserve in Mozambique to ensure more effective conservation of these popular gamefish species.

Table 6.2: Linkages between existing or proposed surf-zone NTAs and catch-and-release buffer areas and the occurrence of nearby offshore reefs within the iSimangaliso Wetland Park (from south to north).

Surf-zone NTA	Current inshore zonation	Comments	Adjacent offshore reef	Current offshore zonation	Comments
Mid-railway ledges (2.2 km)	NTA but not enforced	Fished by subsistence shore fishers from Sokhulu	Reef off Cape St Lucia and Jolly Rubino wreck	Restricted (pelagic game-fishing only)	Fished by boats from Maphelane and Richards Bay
Mission Rocks north (10 km)	NTA but not enforced	Fished by recreational shore anglers	Extensive backline reef	Restricted (pelagic game-fishing only)	Fished by boats from St Lucia and Cape Vidal
Leven Point south buffer area (10 km)	Restricted (Proposed catch-and-release area)	Not fished (no access)	Leven Reef	Restricted (pelagic game-fishing only)	Fished by boats from Cape Vidal
St Lucia Marine Reserve Sanctuary (24 km)	NTA (sanctuary)	Not fished and effectively enforced	Leadsman Shoal and Red Sands Reefs	NTA (sanctuary)	Well enforced, limited boundary encroachment
Red Cliffs north buffer area (10 km)	Restricted (Proposed catch-and-release area)	Fished by subsistence shore fishers from KwaMabila	Northern part of Red Sands Reef and scattered backline reef	Restricted (pelagic game-fishing only)	Fished by boats from Sodwana Bay
Nine-mile surf-zone (5 km)	Restricted (Proposed NTA)	Fished by subsistence shore fishers from KwaMabila and recreationalists	Nine-mile Reef	Restricted (pelagic game-fishing only)	Fished by boats from Sodwana Bay
Lala Nek surf-zone (5 km)	Restricted (Proposed NTA)	Fished by subsistence shore fishers from KwaDapha and recreationalists	Scattered deep reefs >40m	Restricted (pelagic game-fishing only)	Limited boat-based fishing
Maputaland Marine Reserve Sanctuary (11 km)	NTA but subsistence harvesting allowed	Fished by subsistence shore fishers from KwaDapha	Rabbit Rock Reef complex	NTA (sanctuary)	No fishing allowed but limited enforcement capacity
Beacon 13 north (7 km)	NTA but subsistence harvesting allowed	Fished by subsistence shore fishers from eNkovukeni	Saxon Reef	NTA (sanctuary)	Boat-based poaching from Ponta do Ouro (Mozambique)
Kosi Mouth north (3.2 km)	NTA but subsistence harvesting allowed	Fished by subsistence shore fishers from eNkovukeni and Ponta do Ouro and recreationalists	Kosi Reef complex	NTA (sanctuary)	Boat-based poaching from Ponta do Ouro (Mozambique)

6.5 Conclusion

An obvious weakness of this study was the lack of recaptures from some of the more mobile species, such as carangids, which may have home ranges considerably greater than two kilometres (Holland et al. 1996; Wetherbee et al. 2004; Meyer and Honebrink 2005; Meyer et al. 2007). For this reason estimates provided in this study should be considered as minimum estimates for NTA size and are generally more applicable to resident reef fish species found in the surf-zone. Based on the home range sizes of these latter species, the minimum effective length of NTAs in the iSimangaliso Wetland Park was estimated to be 3-6 km of coastline consisting of suitable surf-zone reef habitat. Taking into account both ranging movements of adult and sub-adult fish, as well as passive drift of fish eggs and larvae, the distance required between NTAs was estimated to be 15-20 km in order to retain sufficient connectivity. Using these estimates and considering the availability of suitable habitat, existing distribution of shore fishing effort and the current zonation applied in the park, two new NTAs are proposed at Nine-mile Reef and Lala Nek. Furthermore, two ~10 km catch-and-release buffer areas are proposed for the area north of Red Cliffs and south of Leven Point to enhance tourism but limit impact on surf-zone fish communities. If supported by the relevant authorities, implementation of these recommendations should be subject to a thorough stakeholder participation process to achieve effective buy-in. It is believed that the zonation plan proposed by this study will greatly improve both biodiversity conservation and fisheries management in and adjacent to the iSimangaliso Wetland Park and ensure better compliance with international guidelines and best practice.

Appendix 6.1: A list of pelagic gamefish and baitfish species which may be captured and retained by boat-based anglers fishing in the iSimangaliso Wetland Park. Family names are given as all species in these families may be caught. Note that these species are also subject to species-specific daily bag limits, minimum size limits and closed seasons (see current regulations [Government Gazette No. 27453] in terms of South Africa's Marine Living Resources Act [Act 18 of 1998]).

Pelagic gamefish species*

Carangidae (Kingfishes/Jacks/Trevallys)
 Coryphaenidae (Dolphinfish/Dorados)
 Istiophoridae (Sailfish, Spearfish, Marlins)
 Pomatomidae (Elf/Shad/Bluefish/Tailor)
 Rachycentridae (Cobia/Prodigal son)
 Scombridae (Tunas, Mackerels, Bonitos)
 Sphyrinae (Barracudas)
 Xiphiidae (Swordfish)

Pelagic baitfish species (includes carangids and scombrids as indicated above)

Atherinidae (Silversides)
 Belontiidae (Needlefishes/Garfish)
 Chirocentridae (Wolf herrings)
 Clupeidae (Herrings, Sardines, Pilchards)
 Engraulidae (Anchovies)
 Exocoetidae (Flyingfishes)
 Hemiramphidae (Halfbeaks)
 Scomberesocidae (Sauries)

*Note that all elasmobranchs (i.e. shark and ray species) caught within the iSimangaliso Wetland Park must be released unharmed.

CHAPTER 7: GENERAL CONCLUSION

7.1 Introduction

The overarching goal of this project was to address the question of whether the St Lucia Marine Reserve Sanctuary is providing a refuge for surf-zone angling fish species and whether the adjacent exploited areas are benefitting in terms of spillover. However, following a national ban on the use of vehicles on South African beaches in January 2002, this study also aimed to assess the potential recovery of a fish community in a previously exploited area using the no-take sanctuary area as a benchmark. Specific objectives of this study were: 1) To compare the species composition, catch-per-unit-effort (CPUE) and size composition of surf-zone fishes within the St Lucia Marine Reserve Sanctuary with that of an adjacent, previously exploited area south of Leven Point by means of research angling and to monitor the response of the fish community over time; 2) To determine movement patterns of important shore angling species on a fine spatial scale (< 100 m) by means of conventional dart tagging and to describe patterns of residency and dispersal by tagged fish and to investigate the potential occurrence of spillover from the no-take sanctuary; 3) To use tag-recapture data to investigate the growth rate of speckled snapper *Lutjanus rivulatus*; 4) To use fish movement patterns (residency and dispersal patterns) to investigate the minimum size and spacing of no-take MPAs needed to protect viable populations of shore angling species within the Delagoa Bioregion. These objectives were addressed in Chapters 3-6 of this thesis and a brief summary of the achievements is provided below:

Objective 1 (Chapter 3)

In November 2001, a project was established in the St Lucia Marine Reserve to compare surf-zone fish populations inside the no-take sanctuary zone with those in the adjacent exploited area. Surf-zone fish populations were monitored for potential recovery in the area north of Cape Vidal, as anglers could no longer easily access this area because of the prohibition of beach driving. Standardised research fishing was conducted at two sites in the previously exploited area and two sites in the no-take sanctuary. Conventional stock status indicators including trends in species composition, CPUE and size composition showed evidence of recovery in the four most common species caught in the previously exploited area, both in terms of abundance and biomass (i.e. *Pomadasys furcatus*, *Trachinotus botla*, *Lutjanus rivulatus* and *Diplodus capensis*). Generalized Additive Mixed Models (GAMMs) were used to account for the influence of targeting specific species; however, subtle differences in habitat between the sampling sites, improved angling skill over time, variability in recruitment and differential species-specific responses, complicated interpretation of results.

Objective 2 (Chapter 4)

Between 2001 and 2013, 6 613 fishes from 71 species, caught by hook and line, were tagged at four sites within and adjacent to the St Lucia Marine Reserve no-take sanctuary area. A total of 1 004 (15.2%) recaptures were made from 17 species. The majority (82.4%) of these species displayed station-keeping behaviour, whereas only three were classified as wider-ranging species and no species with discernible migratory behaviour was observed. Findings for five species with the highest recapture rates, namely *P. furcatus*, *Epinephelus andersoni*, *E. marginatus*, *Dinoperca petersi* and *L. rivulatus*, were further analysed. Recapture rates ranged from 7 to 50% and time at liberty from 0 to 3163 days. Individuals of all five species displayed station-keeping behaviour, with the 95th percentile of intra-study site movements varying between 200 and 1 025 m (linear distance). However, four of the five species also displayed some ranging behaviour and made exploratory excursions ranging from 3.5 to 125 km, in both northerly and southerly directions. The dominance of station-keeping behaviour suggests that the St Lucia Marine Reserve sanctuary zone provides an important refuge for these species, with some export to adjacent areas.

Objective 3 (Chapter 5)

The growth rate of *L. rivulatus* was investigated using data from a long-term tag-recapture study conducted in the St Lucia Marine Reserve. A total of 1 429 *L. rivulatus* were tagged and 453 (31.7%) individual fish were recaptured one or more times. Growth rates were modelled from the tag-recapture data using a maximum-likelihood approach. It was shown that *L. rivulatus* is a slow-growing species with mean growth rates of 35.4 mm.y⁻¹ at 300 mm FL and 18.2 mm.y⁻¹ at 600 mm FL, respectively. The von Bertalanffy growth parameters were calculated as $L_{\infty} = 918$ mm FL and $K = 0.06$ y⁻¹ and the growth index phi-prime (Φ) was equal to 2.69. The effects of deep-hooking and multiple captures were tested and revealed that there was no significant impact on the growth of *L. rivulatus*. The growth index was lower than that recorded in many other similar congeneric species. Slow growth, coupled with high levels of residency and site fidelity, suggest that this species is vulnerable to exploitation and that a precautionary approach towards future management is appropriate.

Objective 4 (Chapter 6)

Based on the results of the tag-recapture study conducted in the St Lucia Marine Reserve, home range size was estimated for species with sufficient recapture data. This indicated that home range size was relatively small for most surf-zone fish species, seldom exceeding 2 km, and indicated high levels of residency and site fidelity. Using home range size and best practise guidelines on the area required to protect a viable population of resident surf-zone fish species, minimum size of no-take areas (NTAs) was estimated. To ensure adequate connectivity between protected fish populations, the distance apart that such NTAs needed to be was estimated based on movement patterns of fish species displaying ranging-type behaviour, as well as best available information on the distribution of eggs and larvae.

This revealed that NTAs of 3-6 km (linear distance) with suitable surf-zone reef habitat, spaced every 15-20 km apart could provide sufficient protection and connectivity for surf-zone fish populations. The implications of these results were considered with respect to the availability of suitable surf-zone reef habitat, existing patterns of human use and the current zonation of the inshore zone within the iSimangaliso Wetland Park and recommendations for improvements were made.

7.2 Limitations and recommendations

The methods used in this project were adapted from those developed in other similar MPA monitoring projects such as De Hoop (Attwood 2002) and Tsitsikamma (Cowley et al. 2002) but were refined to enable a comparison between a no-take sanctuary area and a previously exploited area. One of the most important lessons learnt in this regard was that areas selected for comparison must be as similar as possible in terms of available habitat (Attwood 2003). As discussed in Chapter 3, the SB area in the middle of the sanctuary had the most extensive surf-zone reef habitat of the four selected sampling blocks and was also immediately inshore of a large offshore reef complex (Leadsman Shoal). Therefore, the selection of this area as a sampling block for this study complicated comparisons with other areas where surf-zone reef habitat was less prolific (see Figure 3.4).

Another important lesson learned in this study was that despite careful standardisation of the sampling protocol, the pool of research anglers gained increased local knowledge resulting in improved effective fishing effort over time (effort creep). Analytical methods for standardising catch and effort data have improved considerably over the past few years (Winker et al. 2013; 2014) and were employed in this study to remove such sources of variation not directly linked to fish abundance. However, it was difficult to account for improvement in individual angler skill. Future studies of this nature should take the phenomenon of effort creep into consideration and ensure that such variation is minimised.

Targeting of specific fish species was another difficult aspect of this project to account for in terms of directed angler effort. Effort targeting of “large fish” (e.g. *Caranx ignobilis*, *Carcharhinus limbatus*, *Rhynchobatus djiddensis*) and “small fish” (e.g. *Lutjanus rivulatus*, *Trachinotus botla*, *Pomadasys furcatus*), was split by using hook size > 7/0 as the threshold criterion. However, it was not possible to further quantify deliberate targeting of certain species or species groups, even in terms of the cluster analysis undertaken (He et al. 1997; Winker et al. 2013). The large diversity of fish species found in the study area and the ability of anglers to “read” the water and target species likely to occur in that particular area, meant that anglers could change their target species on every cast simply by changing the hook size, bait type and/or the habitat type they cast into. The practice of allowing two hooks per trace was used to target different species. For example, by using a smaller top hook (1/0 or

2/0) baited with squid or prawn and a larger bottom hook (4/0 or 5/0) baited with fish bait, different species could be targeted on an individual trace (e.g. *T. botla* or *P. furcatus*) on the top hook and *L. rivulatus* or *E. marginatus* on the bottom hook. To better define targeting in future studies of this nature, it is recommended that the trace should be limited to only one hook. Since the tagging study (movement data) was of more interest to participating anglers, it motivated them to target larger fish suitable for tagging (i.e. fish ≥ 30 cm FL). This was a potential bias as considerably more fish could have been caught if anglers had only targeted smaller fish using smaller hooks. While such practice was discouraged in terms of standardising the project protocols, consideration should be given to limiting hook sizes to a narrower range (e.g. 2/0 to 6/0) in future projects of this nature.

It was hypothesised that the surf-zone fish communities within the previously exploited area between Cape Vidal and Leven Point would recover over time once fishing had ceased. While this study provided strong evidence for the recovery of at least four of the most commonly caught shore-angling fish species, it was not unequivocal. The complex patterns of natural variation driven by processes such as recruitment success, competition and succession between species, seasonal fluctuations in fish abundance, and subtle differences in habitat availability between sampling sites, masked clear signals of recovery in both fish abundance and mean size. Furthermore, many of the species concerned are slow growing and require a long time to recover after exploitation (Jennings et al. 1999). Again this emphasises the need for careful project design and implementation. It also speaks to the importance of conducting such studies over a long period of time (at least 10 years). Sampling should also be conducted throughout the year (or at least seasonally) to enable such natural variability to be accounted for. The use of a variety of indicators such as those used in this study (species composition, CPUE, size composition and fish movement data) is also recommended to enable the detection of other masking factors in such long-term monitoring programmes.

The gradation in shore fishing effort exerted by members of the angling public, being highest in close proximity to the beach access point at Cape Vidal and gradually decreasing further away, made detection of clear differences between the sanctuary area and the previously exploited area less conspicuous, especially in the EB sampling block (4 km from the sanctuary). Lower historical angling effort and spillover from the proximate sanctuary area (edge effect) made signals of recovery less easy to detect in the EB sampling block in comparison to EA (12 km from the sanctuary). Such phenomena also need to be taken into account when designing projects that aim to assess recovery in fish populations and communities in different areas over time, especially when using a sanctuary area as a benchmark.

Somewhat surprisingly, there have been very few projects implemented to monitor the recovery of shore-angling fish populations after the introduction of the beach vehicle ban in South Africa in

January 2002. As such this project provided some important insights into the recovery that may have taken place in other resident surf-zone angling fish populations in areas that were previously only accessible to shore anglers by means of driving along the beach. While the introduction of this legislation has undoubtedly been beneficial to many such remote fish populations by providing a natural refuge, cognisance needs to be taken of the resultant shift in shore angling effort (Mann et al. 2008; Dunlop and Mann 2012, Parker et al. 2013) which is now focused with greater intensity at beach access points. It has also resulted in fishing effort shifting to more accessible areas such as estuaries (Cowley et al. 2013), which provide important nursery areas to many marine fish species and are vulnerable to overfishing. Furthermore, considering the degree of coastal development along the South African coast, particularly in KZN, and the associated network of roads and vehicle tracks that have been developed within the coastal zone, there are in fact relatively few areas (outside terrestrial protected areas or private land) that are not accessible to shore anglers. Implementation of the legislation banning driving on the beach should thus not be seen as a substitute or replacement for the implementation of a well-designed network of no-take MPAs along the South African coast.

The tagging study provided new insights into the movement patterns of surf-zone angling fish species found in the Delagoa Bioregion. The dominance of station-keeping behaviour and the high degree of site fidelity, even for species which are less reef-associated, such as *T. botla* and *Rhabdosargus sarba*, was surprising given the dynamic nature of the surf-zone environment. The original decision to limit the four sampling areas to two kilometres in length was potentially restrictive as for the first 10 years virtually no research fishing was conducted between the four sampling blocks and, other than fish caught and reported by members of the angling public, there was no possibility of the research team recapturing fish that had moved greater distances (unless the fish had moved into another sampling block). However, home range size was later validated when the size of the sampling blocks was increased from 2 km to approximately 10 km in November 2011. This meant that the entire length of coastline between Cape Vidal and the middle of the sanctuary area was being sampled. Subsequent testing of home range size estimates for species such as *L. rivulatus* in the larger sampling blocks found no significant difference compared to the original 2 km sampling blocks. While angling effort of four anglers fishing along a 10 km stretch of coast on one day is understandably greatly diluted compared to fishing in a 2 km stretch, the same highly-productive fishing areas (areas with good surf-zone reef structure) were frequently selected within each 10 km sampling area. Although such changes in sampling strategy would understandably reduce the random nature of sampling and increase bias, after 10 years (November 2001 to July 2011) and 50 sampling trips, it was decided that the objectives of this project needed to shift away from the original focus on recovery of the previously exploited area and concentrate more on the movement behaviour of surf-zone fish communities, particularly to investigate the potential for spillover from the sanctuary area. It is believed that this change in sampling strategy was therefore justified.

The lack of research fishing effort north of the middle of the sanctuary area (SB22) and the paucity of tag returns from members of the angling public in areas open to shore-fishing both north and south of the sanctuary area (Dunlop et al. 2013) was a weakness of the tagging study. This was despite attempts to create greater awareness among recreational and subsistence fishers of the importance of reporting the capture of tagged fish through the erection of posters at Cape Vidal and Sodwana Bay, placing articles in angling magazines and through direct communication with subsistence fishery monitors working in the area during dedicated training courses. It is anticipated that more ranging-type movements of fish moving out of the sanctuary area will be documented in time by the subsequent extension of the current project. Since February 2015, four areas namely Cape St Lucia to Maphelane, Cape Vidal to the middle of the sanctuary, middle of the sanctuary to Sodwana Bay and Dog Point to Kosi Bay have been sampled using the same methods and the same team of anglers. While limited to one field trip to each site per year, this extended sampling design along a greater stretch of the coastline of the iSimangaliso Wetland Park should provide better information on ranging movement behaviour and enable better quantification of the export of sub-adult and adult fish from the sanctuary area. It will also provide better information regarding latitudinal changes in surf-zone fish species composition, especially south of the known biogeographic break at Cape Vidal (Sink et al. 2012).

Determination of the growth rate of *L. rivulatus* using tag-recapture methods was an important achievement in this study as no fish were deliberately killed. Such non-destructive methods of fish sampling should generally be encouraged in MPAs. However, the effect of tagging on growth rate (Attwood and Swart 2000) could not be quantitatively assessed. In this regard, it is only through sacrificial sampling and removal of fish otoliths that more empirical age estimates can be made. It is therefore recommended that a future study should be conducted whereby a limited number of *L. rivulatus* from a representative range of size classes are sacrificed to enable completion of an age and growth study using otoliths. This will enable direct comparison with growth rates determined from the tagging study.

While growth rates of the majority of important surf-zone angling fish species sampled during this study have already been determined in previous ageing studies using otoliths [e.g. *T. botla* (Parker and Booth 2014); *R. sarba* (Radebe et al. 2002); *D. capensis* (Mann and Buxton 1997); *E. marginatus* (Fennessy 2006); *E. andersoni* (Fennessy 2000)], the growth rates of two important surf-zone fish species have not yet been determined, namely *P. furcatus* and *D. petersi* (Mann 2013). Given the high recapture rate (20%), a future study on the growth rate of *D. petersi* using a similar tag-recapture approach to that used for *L. rivulatus* in this study is recommended. However, with regard to *P. furcatus*, the fact that only specimens ≥ 30 cm FL were tagged which represents the upper size range

of this species, and the fact that they showed a relatively high degree of tag shedding, it is believed that a tag-recapture growth study on this species would not provide useful data as at this size, growth rate has already likely reached an asymptote. As they are locally abundant, an age and growth study using otoliths would therefore be a better approach for this species.

This thesis has literally only “skimmed the surface” in terms of the amount of data collected over the past 12 years. Opportunity therefore still exists to investigate a wide range of interesting phenomena including time of catches related to fish foraging behaviour (e.g. Watt-Pringle 2009), the effects of bait type and hook size on catches, correlating physical parameters (e.g. water temperature, swell height, wind speed and direction, etc.) with catches and estimating mortality rates of key species caught in the no-take sanctuary area (e.g. Götz et al. 2008). In addition, linking the results of this study with those from similar studies conducted in other MPAs around the South African coast (e.g. Solano-Fernández et al. 2012), provides an opportunity to showcase the magnitude of MPA research conducted locally compared to many other parts of the world.

7.3 Contributions towards improved conservation

Perhaps the most useful product of this study from a conservation perspective was the finding with regard to optimal reserve size and spacing based on fish movement data. The findings suggested that relatively small no-take areas (NTAs) of suitable surf-zone reef habitat of 3-6 km in length should be sufficient to protect viable populations of resident fish species. Placing such NTAs every 15-20 km along the coast would ensure sufficient connectivity between protected fish communities through egg and larval dispersal and by ranging movement behaviour of sub-adult and adult fish. This assumes that spawning occurs within these NTAs and/or that they are connected with protected deeper-spawning habitat for those species which move offshore as they mature. Being a rough guideline, this configuration of NTAs (i.e. 20-30% full habitat protection) agrees well with that recommended by other local and international studies (Attwood and Bennett 1995; Botsford et al. 2003; Gaines et al. 2010; Green et al. 2015). The proposed implementation of a surf-zone NTA network along the entire length of the iSimangaliso Wetland Park was presented in Chapter 6. The optimal network included the existing NTAs and identified the need for including two additional areas (i.e. in the vicinity of Nine-Mile Reef and Lala Nek) based on identified gaps (see Figure 6.4). Notwithstanding that the three NTAs in the extreme north (i.e. Dog Point to Boteler Point, Beacon 13 to Beacon 30, north of Kosi Mouth to the RSA/Mozambique border) and the one in the extreme south of the Park (i.e. Railway Ledges) are not fully-fledged because subsistence linefishing by members of the local community occurs in the surf-zone, the conceptual layout of the proposed NTA network requires attention by the local management authority.

An exciting and relatively novel idea introduced in this study with regard to MPA management in South Africa is the concept of having catch-and-release areas (CARAs) as buffer zones on either side of NTAs (see Chapter 6). While catch-and-release fishing can incur species-specific fishing mortality (Bartholomew and Bohnsack 2005; Cooke and Wild 2007), the success of this project in demonstrating the recovery of fish populations in the previously exploited area south of Leven Point using catch-and-release fishing provides testimony of the feasibility of introducing CARAs (also see Cooke et al. 2006). Furthermore, the results of the growth study on *Lutjanus rivulatus* (Chapter 5) provided strong evidence to suggest that deep-hooking and multiple captures did not significantly affect the growth rate of this species. It is therefore believed that with the development of suitable guidelines and training in fish handling and responsible fishing (Cooke and Suski 2005), introduction of CARAs for shore-based recreational angling within the iSimangaliso Wetland Park would be an important development in terms of improved fisheries conservation, increasing angler opportunities and awareness, and securing additional visitor revenue for the Park.

Based on the ideas advocated in Chapter 6, a more comprehensive system of inshore zonation for the iSimangaliso Wetland Park (Figure 7.1) was recently (May 2016) proposed to the iSimangaliso Wetland Park Authority and the Department of Environmental Affairs in response to the call for public comment on the proposed offshore and southward extension of the Park (Government Gazette No. 39646, Regulation No. 118, p. 196-221). This proposal recommended the implementation of four Controlled Zones at major beach access points within the Park namely at Bhanga Nek between Beacon 13 and Boteler Point (IICZ1), 5 km north and south of Sodwana Bay (IICZ2), 5 km north and south of Cape Vidal (IICZ3) and between 5 km north of St Lucia and 3 km south of Mapelane (IICZ4). Permitted recreational shore anglers and subsistence shore fishers would be able to harvest fish caught from the shore within these controlled zones according to existing fisheries regulations (i.e. size limits, daily bag limits and closed seasons). This effectively provides consumptive access to most shore anglers within reasonable walking distance of major beach access points.

The recommendation then proposes the implementation of 10 Restricted Zones (CARAs) within the Park namely 0.5 km north and south of Kosi Mouth (IIRZ1), Dog Point to Lala Nek (IIRZ2), 3 km south of Lala Nek to 2 km north of Nine-Mile beach (IIRZ3), 2 km south of Nine-Mile Beach to 5 km north of Sodwana Bay (IIRZ4), 5 km south of Sodwana Bay to Red Cliffs (IIRZ5), Leven Point to 5 km north of Cape Vidal (IIRZ6), 5 km south of Cape Vidal to just north of South Ledges (IICZ7), Mziki Path to First Rocks (IIRZ8), 3 km south of Mapelane to Railway Ledges (IIRZ9) and from the wreck of the Jolly Rubino to Cape St Lucia (IIRZ10). These Restricted Zones would essentially act as CARAs for recreational shore anglers and all fish caught would have to be released. They would have access to these areas either on foot or bicycle but the potential also exists for permitted concessionaires with vehicles to offer catch-and-release fishing in these areas. In these areas strict

guidelines would need to be developed to control catch-and-release shore angling (Cooke and Suski 2005). However, local permitted subsistence fishers who live in close proximity to these Restricted Zones would still be allowed to harvest fish in these areas in order to sustain their livelihoods.

Six existing and two new no-take Sanctuary Zones (NTAs) are then proposed namely from the RSA/Mozambique border to 0.5 km north of Kosi Mouth (IISZ1), 0.5 km south of Kosi Mouth to Beacon 13 (IISZ2), Boteler Point to Dog Point (IISZ3), Lala Nek to 3 km south (IISZ4), 2 km north and 2 km south of Nine-Mile Beach (IISZ5), Red Cliffs to Leven Point (IIWZ1)², north of South Ledges to Mziki Path (IISZ6) and from Railway Ledges to the wreck of the Jolly Rubino (IISZ7). Implementation and effective enforcement of these NTAs would make a significant contribution towards the improved conservation and sustainable use (through spillover) of the surf-zone fish communities and associated marine biodiversity found within the iSimangaliso Wetland Park.

² For the purposes of marine zonation a Wilderness Zone (WZ) is the same as a no-take Sanctuary Zone but is simply immediately adjacent to a terrestrial Wilderness Area.

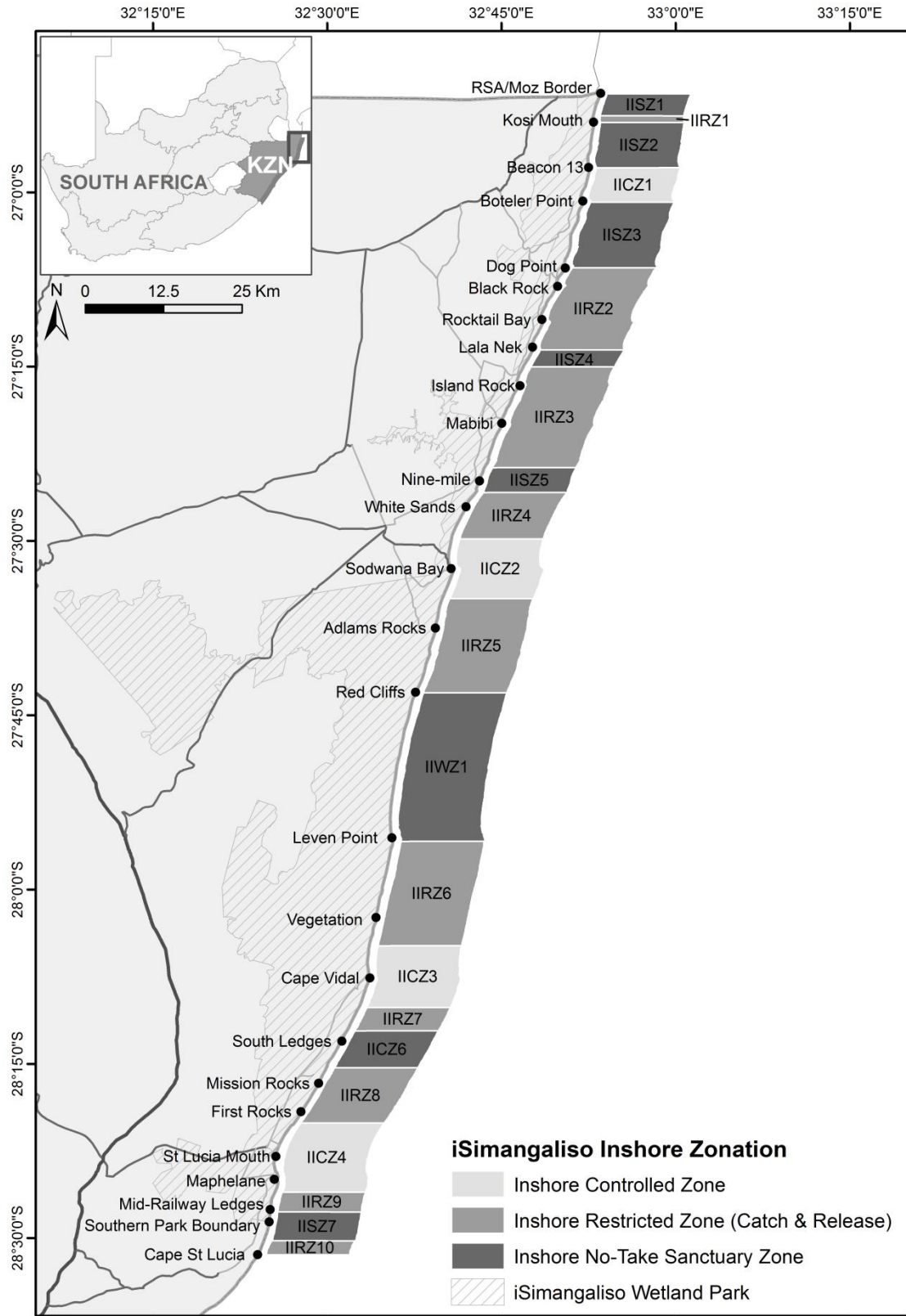


Figure 7.1. Recently proposed inshore (shore-based) zonation for the iSimangaliso Wetland Park (IICZ = iSimangaliso Inshore Controlled Zone; IIRZ = iSimangaliso Inshore Restricted Zone; IISZ = iSimangaliso Inshore Sanctuary Zone; IIWZ = iSimangaliso Inshore Wilderness Zone).

Finally, the 12-year duration of this project has been a real adventure. Every one of the 59 field trips was eagerly awaited, from the precooking of meals to the collection of bait and preparation of tagging equipment and fishing tackle. The excitement and camaraderie associated with giving a team of volunteer anglers the opportunity to fish in a no-take sanctuary area that has been protected for the past 30 plus years is unsurpassed (Figure 7.2). As a consequence it is my belief that one of the most important achievements of this project was proving to anglers that MPAs work. As the cliché states “seeing is believing”. Many of the anglers that have participated in this and other similar projects have gone on to become “ambassadors” for MPAs within their own communities and circles of friends. The distribution of field trip reports to all participants, presentation of talks to fishing clubs and other interest groups, publication of popular articles in fishing magazines and screening of a number of documentaries about this project on television have also helped to explain the value of MPAs to a wider audience. Communicating the conservation value of protected areas has been an extremely important component of this project that should ultimately benefit future attempts to establish a more comprehensive MPA network around the South African coast.



Figure 7.2: The author (left) fishing with two good friends Pat Garratt (middle) and Simon Chater (right) in the St Lucia Marine Reserve Sanctuary (November 2010) (Photo: M. Karon).

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