
MOVEMENT PATTERNS AND POPULATION
DYNAMICS OF FOUR CATSHARKS ENDEMIC TO
SOUTH AFRICA

Submitted in fulfilment of the
requirements for the degree of

MASTER OF SCIENCE

at

RHODES UNIVERSITY

by

JESSICA ESCOBAR-PORRAS

December 2009

ABSTRACT

Sharks are particularly vulnerable to over-exploitation. Although catsharks are an important component of the near-shore marine biodiversity in South Africa and most of the species are endemic, little is known about their movement patterns, home range and population size. With an increasing number of recreational fishers this information is crucial for their conservation. The aims of this study were threefold. Firstly, to identify and analyze existing data sources on movement patterns and population dynamics for four catshark species: pyjama (*Poroderma africanum*), leopard (*P. pantherinum*), puffadder (*Haploblepharus edwardsii*) and brown (*H. fuscus*). This highlighted a number of shortcomings with existing data sets, largely because these studies had diverse objectives and were not aimed solely at catsharks. Secondly, a dedicated study was carried out for a limited area, testing a number of methods for data collection, and where appropriate the data was analyzed to determine movement patterns and population numbers. Thirdly, the most appropriate methodology for future studies (with similar objectives) was identified, and the results of the study were used to propose a number of conservation measures.

All species of catsharks exhibited strong site fidelity and limited dispersal for extended periods. A few individuals did, however, travel distances in excess of 150 km. Significant trends in temporal abundance were not observed, nevertheless, there was some evidence for higher catches from September to December. Population estimates for the study area were low, with *P. africanum* having the smallest population size while *H. fuscus* had the highest population size within the restricted study area. Limited movements, high site fidelity and small population sizes emphasize their vulnerability and suggest that catsharks would benefit from no-take marine protected areas.

DEDICATION

This thesis is dedicated to my grandfather, Chucho Porras, who I lost while I was pursuing my dream. I am sorry I was not there.



CONTENTS

ABSTRACT	ii
DEDICATION.....	iii
CONTENTS	iv
ACKNOWLEDGEMENTS	vi
DECLARATION	viii
CHAPTER 1: GENERAL INTRODUCTION	1
1.1. Chondrichthyes.....	1
1.2. State of knowledge of South African chondrichthyans	3
1.3. Catsharks - family Scyliorhinidae	6
1.4. Aims and objectives.....	10
CHAPTER 2 GENERAL METHODS	11
2.1. Data sources and study sites.....	11
2.1.1. ORI/WWF National Volunteer Tagging Programme.....	11
2.1.2. National Marine Linefish System.....	12
2.1.3. Tsitsikamma Shore Angling Programme.....	13
2.2. Usefulness and limitations of data sources	14
2.3. Dedicated study – Study site and methods.....	15
2.3.1. Study site.....	15
2.3.2. Evaluation of different methods	17
2.3.3. Conclusion.....	23
CHAPTER 3 MOVEMENT PATTERNS OF CATSHARKS.....	25
3.1. Introduction	25
3.2. Materials and methods	26

3.2.1. Data analysis.....	26
3.3. Results	29
3.3.1. National Volunteer Tagging Programme.....	29
3.3.2. Tsitsikamma Shore Angling Programme.....	32
3.3.3. Rebelsrus.....	35
3.4. Discussion.....	39
CHAPTER 4 ABUNDANCE AND SEASONALITY	44
4.1. Introduction.....	44
4.2. Materials and methods.....	46
4.2.1. Abundance and seasonality.....	46
4.2.2. Population size estimation	48
4.3. Results	49
4.3.1. Abundance and seasonality.....	49
4.3.2. Population size and density.....	54
4.4. Discussion.....	55
CHAPTER 5.....	59
REFERENCES	64

ACKNOWLEDGEMENTS

Even though I am the author of this work, it is actually an effort from many different people that helped through the various stages of this learning process that made this work a reality. I am deeply thankful to:

- Dr. Pete Britz for blindly believing in me.
- My supervisor Warwick Sauer for constant support, understanding, patience, and acting also as a friend and even sometimes as a father. Thank you for caring.
- Cosupervisor Dr. Paul Cowley for teaching me so much not only as a scientist but also as a person. I am sorry for the hours I took you away from your family.
- Dr. Malcom Smale for comments, suggestions and for introducing me to my catsharks.
- Many field assistants Kyle, Pete, Paula, Mike, Albert, Guy, JD, Fabian, Myles and specially Phanor, Dave and Matt whom make two years of sampling the most wonderful experience.
- John Henrick for my first tagged shark and Jackie for being more than a friend in the field.
- Elaine and Phil Heemstra for becoming my South African family. I respect you both immensely as scientists, and love you endlessly as persons.
- South African Institute for Aquatic Biodiversity (SAIAB) for species images.
- DIFS friends for putting up with me through this whole process, as well as Terry Longman and Faith Faithfull.
- My mama (mother) Yolanda Porras for pushing me to reach my dream and making my live a fantasy, and Memitto for his unconditional support and advice.

- My best friend, accomplice and husband, Phanor, for loving me and standing by me through an emotional rollercoaster. Thank you for coming with me across the ocean. Tinto gracias por ser mi dosis de energia diaria.

DECLARATION

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author.

CHAPTER 1:

GENERAL INTRODUCTION

1.1. Chondrichthyes

Chondrichthyan fishes have cartilaginous skeletons and comprise of three main groups or subclasses including sharks, rays and chimaeras. The subclass Holocephalii includes chimaeras and elephantfish while the Elasmobranchii subclass includes sharks, rays and skates. One of the main differences between the two subclasses is the number of gill cover openings, with Holocephalii having only one gill cover to protect the four gills on either side, while Elasmobranchii have between five and seven paired gill openings.

Members of the subclass Holocephalii lay eggs, do not have denticles (Heemstra and Heemstra, 2004) and most of the more than 30 species worldwide are found in deep water (Compagno *et al.*, 1989). Of the three Holocephalan families, only one, Callorhynchidae, is found in the southern hemisphere (Swing and Bearez, 2006). In this family only one species, the St Joseph, *Callorhynchus capensis*, is targeted by fisheries in South Africa (Heemstra and Heemstra, 2004).

Members of the group Elasmobranchii have rough skin comprised of denticles and display three types of reproductive strategies, namely oviparity (egg laying), viviparity (live bearing) and ovoviviparity (embryos develop in egg cases inside the mother) (Compagno *et al.*, 2004; Heemstra and Heemstra, 2004), and there are more than 1000 species worldwide. This subclass is further divided into sharks and batoids (skates and rays). Sharks have flat or cylindrical bodies, long caudal fins and one to two dorsal fins. There are more than 400 species of sharks in the world found in a variety of habitats, ranging from shallow waters of estuaries and even rivers, to ocean depths of more than 700 metres. In South Africa, more than 100 shark species are found, of which 16% are endemic to southern Africa (Compagno *et al.*, 1989). The bodies of skates and rays are flat and short, with the pectoral fins attached to the side of the head (Compagno *et al.*, 2004). Most batoids are substrate dwelling and benthic feeders, with rare exceptions, for

example the *Manta birostris*, which is pelagic (Heemstra and Heemstra, 2004). The batoids group is more diverse than the sharks, with more than 500 known species worldwide, of which about 60 are found in South African waters and more than 35% are endemic to southern Africa (Compagno *et al.*, 2004, Heemstra and Heemstra, 2004).

The majority of chondrichthyans are long lived, have low reproductive rates and grow slowly. These life history characteristics make them particularly susceptible to overexploitation, with the Elasmobranchii being the most vulnerable in this respect (Tidwell and Allan, 2001; Baum *et al.*, 2003). Moreover, in the last 30 years elasmobranch populations have declined by about 70% with some shark stocks by about 90% (Compagno *et al.*, 2004). At least three species, namely the scalloped hammerhead (*Sphyrna lewini*), great white (*Carcharodon carcharias*) and thresher (*Alopias* spp.) sharks are estimated to have declined by over 75% in the past 15 years (Baum *et al.*, 2003). Verlecar *et al.* (2007) predict that as many as 20 shark species may become extinct by 2017 and suggest that urgent interventions be implemented before it is too late. The status of many species has been assessed and placed on the reviewed by the International Conservation Union (IUCN) Red List under a number of categories, rated from Data Deficient to Extinct. By 2003 more than 20% of the Red Listed species were found to be either critically endangered, endangered or vulnerable (Compagno *et al.*, 2004), another 48% of the species were found to be near threatened or data deficient (Compagno *et al.*, 2004). The most vulnerable chondrichthyans are the deep water, freshwater reliant and coastal endemic species (Compagno *et al.*, 2004). As a consequence of their life history characteristics and unknown conservation status, their preservation and management has become a global concern (Rose, 1996).

Many conservation and management strategies have been implemented worldwide over the last 40 years, such as Marine Protected Areas, closed seasons, total allowable catch (TAC's) and bag and fish size limits. However, there is a lack of data to ensure their success as all these strategies require knowledge of the biology and ecology of the species intended to be protected and information to form a basis for precautionary management is seriously lacking (Compagno *et al.*, 2004).

1.2. State of knowledge of South African chondrichthyans

Most information for the subclass Holocephalii includes brief descriptions of the species general biology (Compagno *et al.*, 1989; Heemstra and Heemstra, 2004). In the 1980s a bottom-net fishery started on the west coast of South Africa targeting the St. Joseph, *Callorhynchus capensis*, (MCM, 2002; McCord, 2005) with annual catches of more than 500 tonnes (Kroese *et al.*, 1995). This created a need for the study of the status of this fishery species (Freer and Griffiths, 1993a; Lamberth *et al.*, 1997) and a species specific study on its general biology (Freer and Griffiths, 1993b). Another study of this Holocephalii subclass included a report on a new species, *Rhinochimaera africana* (Compagno *et al.*, 1990).

In general, batoids have received less attention than the Elasmobranchii. Early studies focused on skate and ray general biology (Wallace, 1969b, a), with the family Rajidae receiving most of the attention with studies on systematics (Hulley, 1970), distribution and taxonomy (Hulley, 1972) as well as feeding ecology (Ebert *et al.*, 1991; Smale and Cowley, 1992). Later studies were on the general biology of the skates *Raja wallacei* and *R. pullopunctata* (Walmsley Hart *et al.*, 1999) and the by-catch of skates in trawl fisheries (Walmsley, 1999).

Research on Batoids focused mainly on inshore species captured by recreational anglers. For example, species specific studies addressed aspects of physiology of the eagle ray, *Myliobatis aquila* (Du Preez *et al.*, 1988) and the morphology and description of the manta ray, *Manta birostris* (Marshall *et al.*, 2008). The majority of Batoid research focussed on stingrays including the taxonomy of the dragon stingray, *Himantura draco* (Compagno and Heemstra, 1984), the biology, ecology and taxonomy of the blue stingray, *Dasyatis pastinaca* complex (Cowley, 1988), as well as studies on the general biology, feeding, reproduction and habitat utilization of the blue stingray, *Dasyatis chrysonota* (Cowley and Compagno, 1993; Cowley, 1997; Ebert and Cowley, 2003, 2008).

In South Africa, sharks have always been of great interest and research has been undertaken for different reasons. Initial research was directed towards creating protective measures for bathers from sharks as there had been more than 100 shark

attacks in less than ten years creating panic and distress among coastal communities and tourists. This led to the implementation of the first shark nets in the early 1950s and in the establishment of the Natal Sharks Board in 1964, which was created to protect bathers against shark attacks by using shark nets. This offered the opportunity to do research on sharks captured in the shark nets in KwaZulu-Natal (KZN), such as the abundance, age and growth of the Zambezi Shark, *Carcharhinus leucas* (Cliff and Dudley, 1991; Wintner *et al.*, 2002), abundance of the Dusky Shark, *Carcharhinus obscurus* (Dudley *et al.*, 2005), age and growth of the Tiger Shark, *Galeocerdo cuvier* (Wintner and Dudley, 2000) and sex ratios, maturity and length-mass relationships of the Scalloped Hammerhead Shark, *Sphyrna lewini* (De Bruyn *et al.*, 2005). Studies were also carried out on the effects of shark nets (Dudley and Cliff, 1993), shark control studies (Dudley *et al.*, 1998) and even studies on protection against shark attacks (Cliff and Dudley, 1992).

The importance of the Raggedtooth Shark, *Carcharias taurus* for the recreational fishery and sport dive industries led to a dedicated study resulting in a number of publications including an assessment of nursery areas (Smale, 2002), tag retention (Dicken *et al.*, 2006a), spatial and seasonal distribution (Dicken *et al.*, 2006c), catch and effort in coastal fisheries (Dicken *et al.*, 2006b) and abundance (Dicken *et al.*, 2008).

A number of studies have been family specific, including Carcharhinidae and Scyliorhinidae (Bass, 1972), Pseudotriakidae (Bass *et al.*, 1975), Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae (Bass *et al.*, 1976). Morphometrics of Scyliorhinid, Carcharhinid and Sphyrnid (Bass, 1973) and the physiology and predation of the Sand Shark, *Rhinobatus annulatus* have also been studied (Rossouw, 1983, 1984, 1987; Du Preez *et al.*, 1988; Harris *et al.*, 1988; Sebastian *et al.*, 2000). Other more general studies were on a perceived increase of small inshore sharks (Van der Elst, 1979) and elasmobranchs in the Eastern Cape (Compagno and Smale, 1986).

The increase in the value of shark fins, oil and meat on the European and Asian markets during the late 1980's triggered research on commercially important species. Sharks were increasingly targeted by fisheries in South Africa including the inshore shark longline fisheries operating on the west and south coasts, the inshore commercial handline fisheries, and selected vessels fishing offshore as part of the tuna longline

fisheries (MCM, 2002; McCord, 2005). The major species presently targeted in South African waters are the Shortfin Mako, *Isurus oxyrinchus*, the Blue Shark, *Prionace glauca*, the Soupfin Shark, *Galeorhinus galeus*, and the Houndsharks, *Mustelus* spp. (MCM, 2002; McCord, 2005). Tuna and Swordfish longline fisheries capture about 20 000 sharks as bycatch each year with the Blue Shark comprising about 80% of the catch (Petersen *et al.*, 2007).

Research has been conducted on the biology of the Smooth Houndshark, *Mustelus mustelus* and *M. palumbes* (Smale and Compagno, 1997), the bycatch of elasmobranchs by other commercial fisheries (Fennessy, 1994) and a general review of elasmobranch exploitation (Kroese and Sauer, 1998). Research attention then shifted to include those sharks commonly caught among recreational anglers. Studies on Hexanchoid sharks include those on the diet and reproductive biology of the Sixgill Shark, *Hexanchus griseus* (Ebert, 1994, 2002b) and the diet of the Sevengill Shark, *Notorynchus cepedianus* (Ebert, 2002a). Other studies included capture rate and sex ratios of the African Angel Shark, *Squatina africana* (Shelmerdine and Cliff, 2006), and parasites of the Lesser Guitarfish, *Rhinobatos annulatus* (Van As and Basson, 1996), as well as studies on sawfishes and guitarfish (Wallace, 1967).

Although chondrichthyan research has been carried out for many years the status of shark populations in South Africa remains largely unknown. Only the Great White Shark, *C. carcharias*, the Raggedtooth Shark, *Carcharias taurus*, the Striped Catshark, *Poroderma africanum* and the Leopard Catshark *P. pantherinum* are banned or regulated from commercial exploitation (McCord, 2005). In recent years, some research has addressed the management and conservation needs of South African chondrichthyans, with the compilation of a draft South African Shark Management Plan (Anon, 2002), but this is yet to be implemented. While certain groups and species have been well studied many species have received little attention. The catshark family (Scyliorhinidae), which has not been extensively studied, is the focus of this study.

1.3. Catsharks - family Scyliorhinidae

The family Scyliorhinidae are distributed from warm tropical to arctic waters and shallow inshore areas to depths exceeding 2 000 meters. Most species are oviparous but some are ovoviviparous such as the Broadheaded Catshark, *Bythaelurus clevai* (Compagno *et al.*, 2005). Inshore catsharks are mainly found resting in crevices during the day and feeding at night on invertebrates and small fish (Heemstra and Heemstra, 2004; Compagno *et al.*, 2005). Scyliorhinidae is the largest shark family comprising of 17 genera with more than 150 species worldwide (Heemstra and Heemstra, 2004; Compagno *et al.*, 2005). There are 17 Southern African catshark species (Human, 2006a) from eight different genera (Compagno *et al.*, 1989), of which less than half have been studied in any detail.

The family Scyliorhinidae has been mainly overlooked in South Africa. The species in this family are particularly vulnerable due to their high degree of endemism, with thirteen of the species (> 75%) endemic to Southern Africa (Human, 2006a). The few studies carried out on Scyliorhinidae in South Africa have mainly been species descriptions and distribution records (Compagno *et al.*, 1989; Compagno *et al.*, 2004; Heemstra and Heemstra, 2004; Compagno *et al.*, 2005). Some species specific studies have focused on the taxonomy (Human, 2006b), systematics and morphology (Human, 2006a, 2007a, b), general biology (Dainty *et al.*, 2001; Dainty, 2002), reproductive biology and feeding ecology (Ebert *et al.*, 1996; Roux, 2002; Ebert *et al.*, 2006). A study on parasites in two species of the genera *Haploblepharus* was also undertaken (Yeld and Smit, 2006). The only study on abundance has been for the Izak Catshark, *Holohaelurus regani* (Richardson *et al.*, 2000).

Although there is information on the general biology and taxonomy of some Scyliorhinidae species (Table 1.1), many of the species lack information on abundance, temporal variation and movement patterns.

Table 1.1: Summary of available information on Southern African catshark species (Scyliorhynidae) and their IUCN status. a = general biology, b = distribution, c = habitat, d = abundance, e = seasonality, f = population estimates, g = movement. LC: Least concern, DD: Data deficient, LR: Lower risk, NT: Near threatened, NF: Not found, V: Vulnerable. *Endemic to Southern Africa. The numbers represent the source from the reference list.

Common name	Species	IUCN status*	a	b	c	d	e	f	g
Saldanha catshark	* <i>Apristurus saldanha</i> (1,5)	LC	X	X	X				
Indian swell shark	* <i>Cephaloscyllium sufflans</i> (1,7)	LC	X	X	X	X			
Lined catshark	* <i>Halaelurus lineatus</i> (1,2,6)	DD	X	X	X	X			
Tiger catshark	* <i>Halaelurus natalensis</i> (1,2)	DD	X	X	X				
Puffadder	* <i>Haploblepharus edwardsii</i> (1,2,4,11,12,17)	LR / NT	X	X	X				
Brown shyshark	* <i>Haploblepharus fuscus</i> (1,2,11,16)	LR / NT	X	X	X				
Pyjama catshark	* <i>Poroderma africanum</i> (1,2,4,14,15,16)	LR / NT	X	X	X				
Leopard catshark	* <i>Poroderma pantherinum</i> (1,2,4,14,15,16)	NF	X	X	X				
Yellowspotted catshark	* <i>Scyliorhinus capensis</i> (1,5)	NT	X	X	X				
African sawtail	<i>Galeus polli</i> (3)	LC	X	X	X	X			
Izak	<i>Holohalaelurus regani</i> (3,8,10,13)	NF	X	X	X	X	X		
African spotted Izak	* <i>Holohalaelurus punctatus</i> (3,8,10)	NF	X	X	X				
Eastern/ Natal shyshark	* <i>Haploblepharus kistnasamyi</i> (2,8)	NF		X	X				
Dark shyshark	* <i>Haploblepharus pictus</i> (2,3,8,17)	NF	X	X	X				
No common name	* <i>Holohalaelurus favus</i> (8,10)	NF							
Smallbelly catshark	<i>Apristurus indicus</i> (3)	NF		X	X				
Smalleye catshark	<i>Apristurus microps</i> (3)	LC	X	X	X				

(1. Compagno *et al.*, 1989; 2. Compagno *et al.*, 2005; 3. Compagno *et al.*, 2004; 4. Dainty, 2002; 5. Ebert *et al.*, 2006; 6. Fennessy, 1994; 7. Heemstra *et al.*, 2006; 8. Human, 2006b; 9. Human, 2007a; 10. Human, 2007b; 11. Human, 2007c; 12. Martin, 2004; 13. Richardson *et al.*, 2000; 14. Roux, 2002; 15. Smale *et al.*, 2001; 16. Smith and Griffiths, 1997; 17. Yeld and Smit, 2006) *(IUCN, 2009)

This study attempts to contribute information on the movement and population dynamics of selected endemic species from two groups including the catsharks (*Poroderma*) and shysharks (*Haploblepharus*), for both of which very limited ecological information exists. The chosen species were *Poroderma africanum*, *P. pantherinum*, *Haploblepharus fuscus* and *H. edwardsii* (Figure 1.1).

The Pyjama or Striped Catshark, *Poroderma africanum*, is generally found in temperate waters from Saldanha Bay to East London, on the rocky substrate of the continental shelf from the coast to 100 metres seaward (Heemstra and Heemstra, 2004). The Leopard Catshark, *Poroderma pantherinum*, is mainly found from the Western Cape to the Eastern Cape and occasionally observed in KZN, it inhabits the rocky intertidal zone down to a depth of almost 250 metres (Compagno *et al.*, 1989). *P. africanum*, is the largest of the four study species and has horizontal bold dark stripes over a grey body (Heemstra and Heemstra, 2004). *P. pantherinum*, is the second largest and as the name indicates resembles a panther with black spots, rings and rosettes (Compagno *et al.*, 1989).

Shysharks comprise the other study group, they derive their name from their behaviour, as when caught, they curl into a doughnut shape covering their face with their tail (Compagno *et al.*, 1989). The two species selected from this genus were the Brown Shyshark, *Haploblepharus fuscus*, and the Puffadder Shyshark, *H. edwardsii*, which have a similar distribution from Cape Agulhas to the southern areas of KZN. However, *H. fuscus* is mainly found on shallow rocky reefs, while *H. edwardsii* is normally found close inshore over soft bottoms near rocks to depths of 130 metres (Compagno *et al.*, 1989). The larger of these shysharks is *H. fuscus* with a dark brown body and white belly, it occasionally has white or black spots (Compagno *et al.*, 2004). The smallest of the four selected species is *H. edwardsii*, only reaching 60 cm in length (Compagno *et al.*, 1989) with a light brown body with dark or reddish saddles on the dorsal area and white ventrally (Compagno *et al.*, 2004).

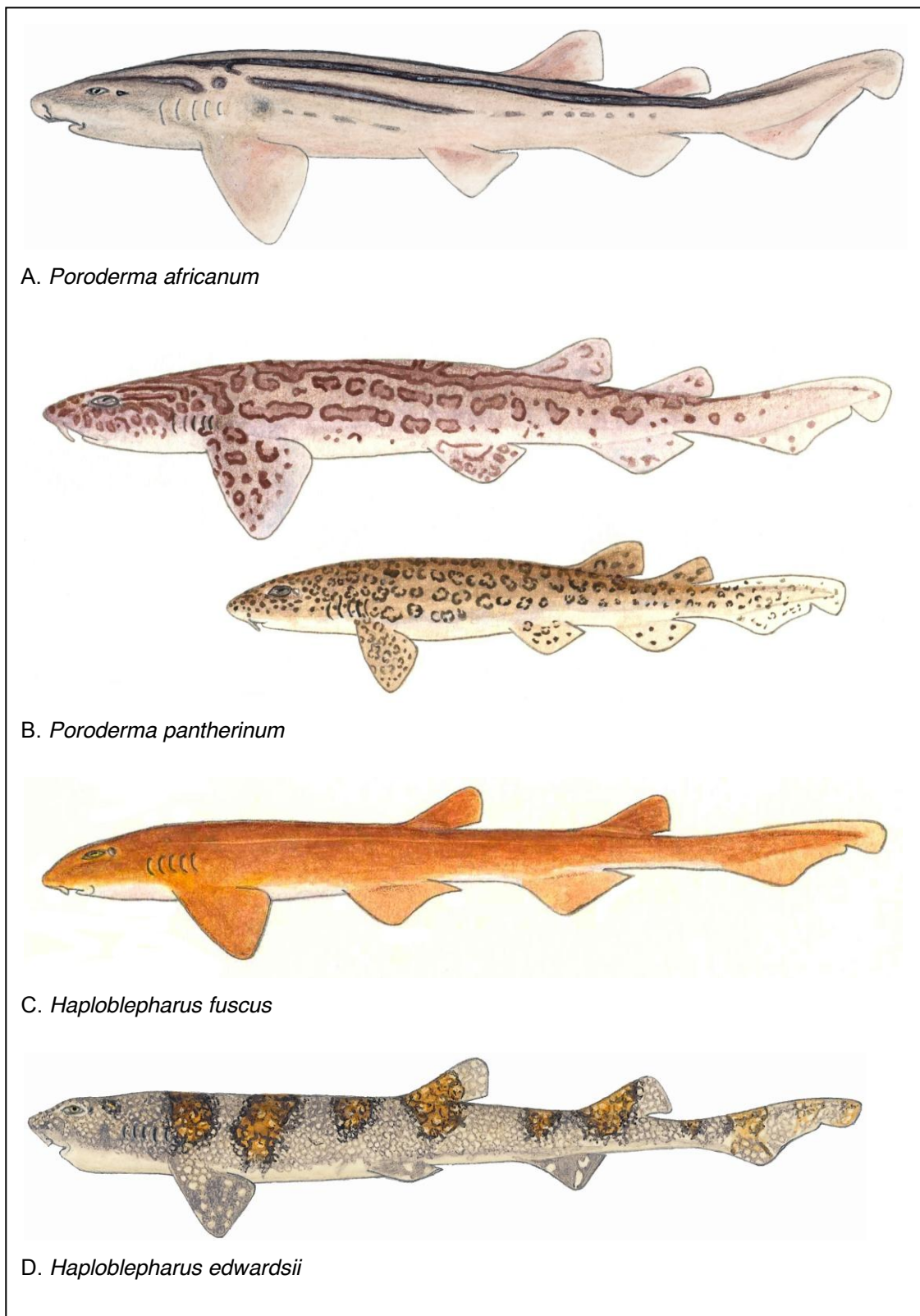


Figure 1.1: Illustrations of the study species (By E. Heemstra from the book *Coastal Fishes of Southern Africa* © SAIAB/NISC).

1.4. Aims and objectives

The aim of this study is to investigate the movement patterns, abundance and temporal variation of *Poroderma africanum*, *P. pantherinum*, *Haploblepharus fuscus* and *H. edwardsii* through (i) the identification and use of existing catch and effort and mark – recapture data sets and (ii) the implementation of a dedicated site specific mark-recapture study.

The thesis is divided in five chapters:

Chapter 1 (General Introduction), this chapter provides background to the species investigated in this study.

Chapter 2 (General Methods) provides a description of the study areas, data sources and selection of methods.

Chapter 3 (Movement Patterns) synthesises the information on movement patterns observed for the four study species from available data and the dedicated research undertaken in this study.

Chapter 4 (Abundance and Seasonality) provides estimations of abundance and monthly and diel temporal variation as well as population estimates for those species with sufficient information to apply the relevant estimation models.

Chapter 5 (General Discussion) provides a brief summary and directions for future research and conservation strategies.

CHAPTER 2

GENERAL METHODS

2.1. Data sources and study sites

All existing data sets with information relevant to this study were sourced. Three projects were identified which had collected data suitable for further analysis. These were the ORI/WWF National Volunteer Tagging Programme (NVTP), the National Marine Linefish System (NMLS) and the Tsitsikamma Shore Angling Programme (TSAP). The two national programmes collect data from the entire South African coastline, ranging from Kosi Bay in the Indian Ocean to the Orange River in the Atlantic Ocean, while the TSAP is centred in the Eastern Cape at the Tsitiskamma National Park (TNP) (Figure 2.1). The projects varied in their aims and objectives and the type of data collected, these are briefly described below.

2.1.1. ORI/WWF National Volunteer Tagging Programme

The National Volunteer Tagging Programme (NVTP) commenced in 1984 with the intention of enlisting active angler support in the tagging of specified species along the South African coastline. This programme has tagged different marine fish, both sharks and bony fish, and collected data on their movements and migrations. In addition, it provides information on growth rates, stock identity and population dynamics of important linefish species (Bullen and Mann, 2007).

The NVTP targets all marine fishes, however only fish larger than 0.5 kg are tagged (Bullen and Mann, 2007). All animals tagged and released are captured using hook and line by volunteer anglers approved by the programme. For sharks, tags are inserted in the dorsal fin and are individually identified by a numeric code with a postal address. Initially four different types of tags were used, however the type C- disc tags, originally used for sharks between 5- 25 kg, were discontinued (Bullen and Mann, 2007). The

three tags still in use are the type A tag (114 mm length, 1.6 mm diameter) used for sharks of more than 5 kg, the type B tag (161 mm length, 2.3 mm diameter) used mainly for sharks over 25 kg, and the type D tag, which is only 85 mm long and 1.6 mm in diameter, is used mainly on small sharks weighting between 0.5- 3 kg (Bullen and Mann, 2007). Type A and D tags are both spaghetti darts, while type B are darts with a stainless steel foot. All tags are made by Hallprint. Recapture information is obtained from different sources comprising line fishing from the shore, line fishing offshore and shark nets in KwaZulu-Natal (Bullen and Mann, 2007). For this study only data related to the catshark family, *Scyliorhinidae* was used. The number of sharks tagged and the date and place of capture and recapture were obtained for a 20 year period (Bullen and Mann, 2007; Pradervand *et al.*, 2007).

2.1.2. National Marine Linefish System

The National Marine Linefish System (NMLS) concentrates mainly on reporting marine fish catches along the South African coast. The aim of this system is to provide a long-term data series on South African marine fishes captured by line fishing (Pradervand, 2007). This database started in 1984, collecting information from volunteer anglers reporting their catch and effort for all marine fish species captured.

A number of different methods are used to collect the data. Catch cards are filled in by volunteer anglers under official supervision or a qualified official completes the card on behalf of the angler, tournament records are reported by angling organizations, boat inspections are carried out at launch sites where catch and effort data are recorded by KwaZulu-Natal (KZN) Wildlife officials. Finally, creel surveys or shore patrols are carried out at beaches and estuaries where catch and effort is recorded (Pradervand, 2007). Although data comes from different sites along the coast, emphasis is placed on the KZN area. Data from the NMLS used for this study was taken from recreational fisheries data from 1974 to 2007.

2.1.3. Tsitsikamma Shore Angling Programme

The Tsitsikamma Shore Angling Programme (TSAP) was started in 1995 and is an ongoing dedicated research programme based on linefish monitoring and a tagging study (Cowley and Whitfield, 2001; Cowley *et al.*, 2002). The aim of the TSAP is to record long term trends in the abundance and movement patterns of marine fishes in an area free of fishing pressure. The Tsitsikamma National Park covers approximately 80 km of coastline between Groot River West and Groot River East, but the research fishing is restricted to a five km area between the Klip and Bloukrans Rivers (Figure 2.1). The area is characterized by high profile rocky reefs with steep cliffs exposed to strong wave action.

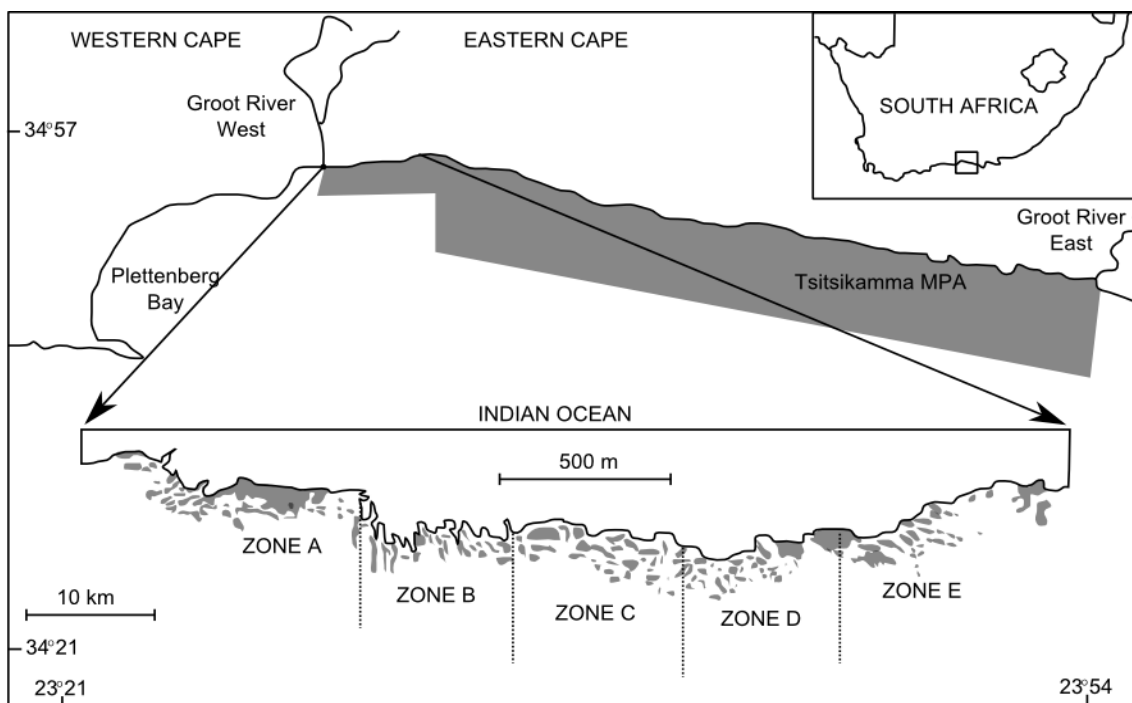


Figure 2.1: Location of the Tsitsikamma National Park on the South African coastline showing the 80 km marine area of the park and the 5 km research fishing area divided into five zones.

The research team is made up of four to eight scientifically trained anglers. Anglers use different hook sizes as well as various bait types in order to target a wide range of marine fish. For each shark captured, total length (TL) is measured in mm (Cowley *et*

al., 2002). Tags are applied to the dorsal musculature below the first dorsal fin. All sharks are tagged with the same type D plastic dart tag used by the NVTP using a metal applicator to insert the tags (Cowley *et al.*, 2002). The research team, which provides accurate high resolution spatial data for each recapture (Cowley *et al.*, 2002), reported most recaptures. From 1995 to 1997 the area was sampled during daylight hours for four to five days, six times per year (Cowley *et al.*, 2002). In 1998 the trips were reduced to four times a year and from 2005 to twice a year. The data recorded for sharks caught along the 5 km study area between 1995 and 2006 includes catch and effort, species name, length, time of capture, hook size and bait type.

2.2. Usefulness and limitations of data sources

Data from the three projects were initially assessed in terms of their usefulness to achieve the two broad objectives of this study (movement patterns and seasonal abundance).

The NMLS was not suitable for movement patterns as this programme only records capture data and no mark-recapture is carried out, however the data does allow a rough idea of the distribution of catshark species along the South African coastline on a monthly basis, even though species identification is problematic. The NVTP and TSAP are more useful, since both record data to the species level, the date of capture and recapture. However, the data were used with caution since neither of them target sharks, creating a bias. Major differences between the two data sets are in spatial resolution, the amount of biological data collected and their recapture rates (Table 2.1). Despite these differences, the two data sets (NVTP, TSAP) were found appropriate for movement analyses, described further in Chapter 3.

For abundance estimation, discussed in Chapter 4, neither NVTP nor NMLS were useful since total catch and effort data was not available. The TSAP dataset does record catch per unit effort (CPUE) and was used for calculating abundance and seasonality, taking into account that this program does not target sharks and bait changes through the different fieldtrips. For temporal variation, NMLS was only used to identify the monthly presence / absence of catsharks in catches throughout the year.

Table 2.1: Summary of movement information obtained from the two data sets used. TNP refers to Tsitsikamma National Park. DR = Distance resolution; RR = Recapture rate

Dataset	Study site	DR	Distance error	Team	Capture, recapture data	Biological data	RR (%)
NVTP	National-3000 kms	Km	5 kms	Public volunteer	Date	No reliable length	5.5
TSAP	TNP-5 kms	m	10-50 m	Scientific personnel	Date & time	Reliable length	9.0

This preliminary analysis of the data made it abundantly clear that a dedicated mark and recapture study was required to obtain better resolution data. There are a number of possible approaches and the next section describes an investigation of four methods, which were selected on the basis of suitability and financial feasibility, carried out on 2 kms of coastline near Cape St Francis in the Eastern Cape (Figure 2.2). The sampling design paid attention to the collection of (i) high resolution spatial data, (ii) correct identification at a species level and (iii) recording of localised effort for accurate calculation of CPUE.

2.3. Dedicated study – Study site and methods

2.3.1. Study site

The study area chosen (Rebelsrus) covered four bays identified as A-D in Figure 2.2. The general habitat characteristics of the area are similar to that of the Tsitsikamma National Park, with strong winds and wave action.

Bay A (Dassie Bay) is located on the western border of the study area. It has an average depth of seven to eight metres with 40% of the area deeper than 12 m. A rocky barrier at the mouth of the bay provides some protection from wave action, making it the most sheltered of the four bays. The substrate consists of a mixture of sand and rock but is mainly dominated by sand, and generally has good water visibility. In this bay two fishing points were identified from which most (70%) of the bay could be targeted.

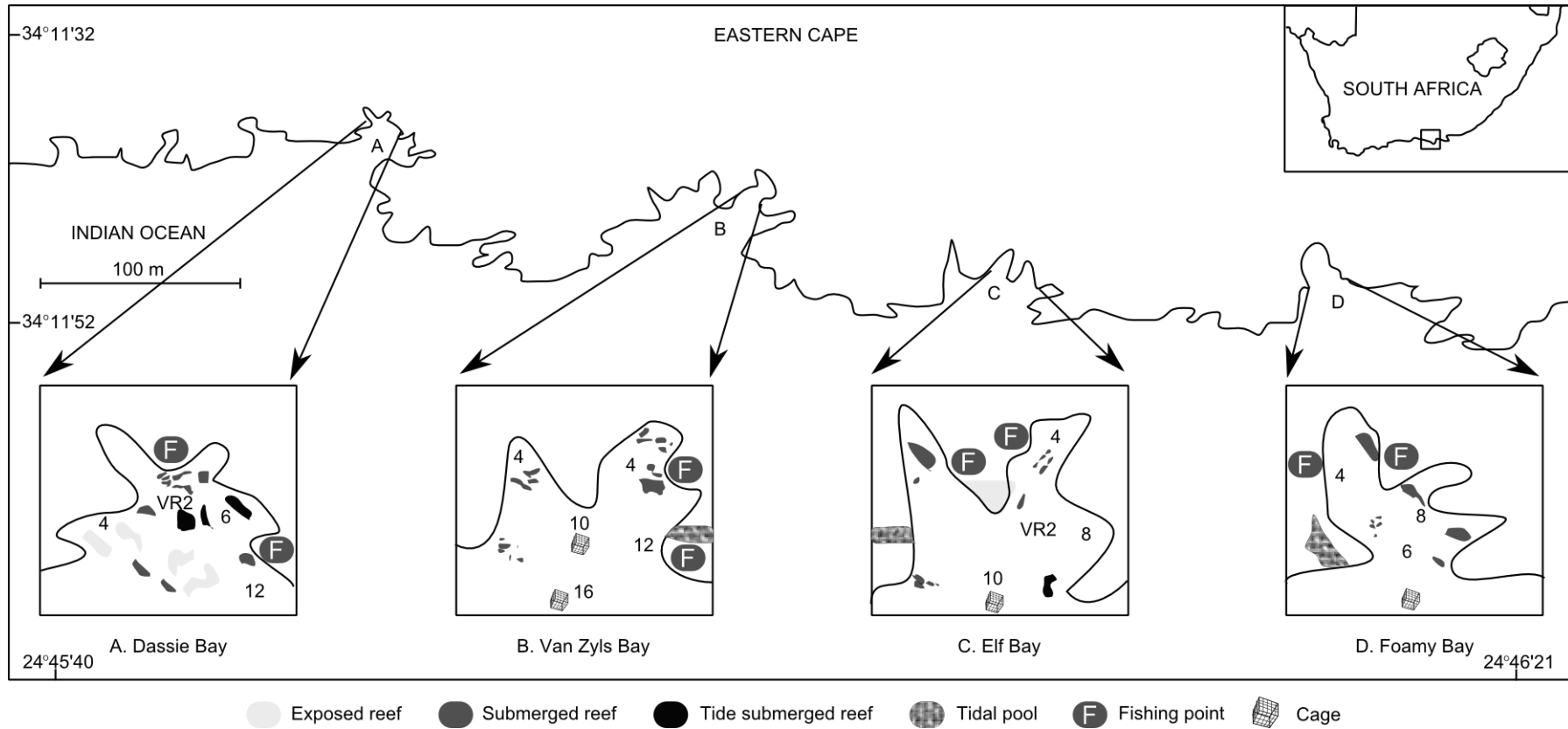


Figure 2.2: Map showing the Rebelsrus study site located near Cape St. Francis in the Eastern Cape with inserts of the four bays (A-D). Numbers given in the inserts represent depths in metres, while habitat information and fishing points are depicted by the key above. VR2 and cage positions are also shown.

Bay B (Van Zyls Bay) is the largest and deepest of the four bays with an average depth of 10 metres and reaches a maximum depth of approximately 12-15 metres towards the middle and the mouth of the bay. It comprises long sand channels between three rocky reefs. On the east side of the bay is a small tide pool that connects to Bay C at high tide. Two fishing points were located on the east side of the bay that allowed targeting of about 80% of the bay.

Bay C (Elf Bay) is more variable in depth with an average depth of eight meters, but with shallow areas of three meters. The substrate is also more variable with two high profile rocky reefs running perpendicular to the coast. The reefs end at the mouth of the bay where a sandy bottom dominates. The bay has a number of ledges suitable as fishing points covering 80% of the area.

Bay D (Foamy Bay) is on the eastern boundary of the research area. It is the shallowest of the four bays with an average depth of three meters reaching a maximum depth of six metres. It is surrounded on the west side by one to two metre ledges and mainly low profile reef with small tide pools on the west side. The bay consists of four rocky channels with sandy substratum. The east side consists of one to two metre ledges, easily accessible, with fishing targeting about 90% of the bay.

2.3.2. Evaluation of different methods

This study investigated four possible methods of data collection including fish traps, underwater visual census, acoustic telemetry and research angling, spanning a period of 20 months, from March 2006 to November 2007. Monthly surveys were carried out for five to seven days.

2.3.2.1. Fish traps

Methods:

Baited fish traps were designed to be tested both within bays and just offshore of the mouths of bays. The trap design was based on traps used for targeting panga,

Pterogymnus laniarus, which caught catsharks as a bycatch (Gray *et al.*, 2007). The traps were modified to accommodate the average size of catsharks and to cope with the rough ocean conditions of the study area. The cage frame was made from steel, reinforced with 10 mm bars and covered with hexagonal wire mesh. The dimensions were 2m x 1m x 0.70m, with a mouth opening of 20cm x 20cm on one side. The opposite side had a frame of steel 0.70m x 1m covered in wire mesh which was used as the door to retrieve the sharks and re-bait the trap. The cages were secured to 40kg concrete blocks of 50cm x 50cm with stainless steel shackles. Traps were baited daily and left overnight, resulting in a minimum soaking time of 12 hours. The position of each trap was marked with a surface buoy (inshore) or a GPS position (offshore). It was planned that cages be used twice a month (20 times in total) over four bays for a total of 40 times per bay.

A cage was placed inshore by divers only in Bay B (Van Zyls), 10 metres from the shore on sandy substrate (Figure 2.2). The trap was tested in this bay first since it is the deepest and the most sheltered. Offshore, a vessel was used to deploy the cages. Cages were placed 160m, 180m and 240m, from the shoreline of bays B (Van Zyls), C (Elf) and D (Foamy) respectively (Figure 2.2). All cages were placed on a mix of sandy/rocky substrate. Inshore and offshore divers retrieved the sharks and re-baited the cages. Sharks were placed in a net bag and taken back to either shore or the boat where they were measured, sexed and tagged. A spaghetti tag (114 mm length, 1.6 mm diameter) was inserted using an applicator in the base of the first dorsal fin. Females were tagged towards the front of the first dorsal fin while males were tagged towards the back of the fin. Sharks were then released directly at the GPS position of the cage. On occasions where misidentification could occur, photographs were taken for later species confirmation. This tagging procedure was used for all methods.

Results:

Initial inshore results showed sea conditions to be unsuitable after only two occasions. On both occasions the cage had moved and was resting on its side and no sharks were caught. However offshore was more successful with four deployments over nine days, the weather conditions did however preclude daily checking of the cages, and vessel use

was prohibitively expensive. The fish traps yielded a CPUE of 0.16 sharks per hour per cage. The total catch was composed of four *H. fuscus* and *H. edwardsii*, three *P. pantherinum* and two *P. africanum*. Interestingly, *H. edwardsii* was only captured offshore.

Due to variable weather conditions and fuel expenses fish traps were discarded as a suitable method for this study.

2.3.2.2. Underwater visual census

Methods:

Underwater visual census (UVC) was planned for three surveys per month (daylight periods) for each bay over a 20 months period. Each survey consisted of 30-40 minute sessions, where two divers swam in a zigzag pattern covering the bay while searching for sharks. One diver carried a sock baited with pilchard attached to a one metre long rope. The other diver was in charge of catching (by hand) the sharks encountered, placing them in a net-bag and taking them to shore to be measured and tagged. Additionally, mapping of the bays was carried out during the first survey using a water proof slate for drawing and a dive computer to measure depth.

Results:

Only 12% of the planned dives for the first seven months could be carried out due to unsuitable sea conditions. During good visibility, although the bays were surveyed thoroughly, few sharks were located. Only three sharks were observed in total, two *H. fuscus* and one bronze whaler, *Carcharhinus brachyurus*. The three sharks were found in Bay C (Elf) swimming around the reefs and not in crevices as expected for the catsharks. Although this method was suitable for determining a rough outline of the ocean floor, suitable replicates were not possible and this method was discarded.

2.3.2.3. Acoustic telemetry

Method:

This method was explored in order to record the presence / absence periods of catsharks within two bays, over a period of three months. Two stationary single channel acoustic receivers (Vemco, Ltd.VR2s) with a memory of 2MB, an expected battery life of 15 months and a capacity to record over 300 000 detections, were used. They were placed in Bay A (Dassie) and Bay C (Elf) (Figure 2.2). Receivers attached to a buoy were swum out to a 40 kg concrete block. Each receiver was then attached to a stainless steel shackle at one end and hooked to a steel ring on the concrete block and secured with cable ties. The receivers were positioned 15cm above the sandy substrate in November 2006 and recovered in March 2007. The receivers identified coded transmitters and recorded time and date of sharks that swam within the reception range of the VR2.

Although it was recognised that in the shallow bays the range of the receivers would vary considerably, a rough estimate of range was obtained during moderate sea conditions by submerging a transmitter (Vemco V9) at fixed points (every metre) along three perpendicular 10 metre transects, originating at the concrete block (Figure 2.3). As expected the reception range was poor with a maximum of only nine metres, limiting the usefulness of this method.

Five *Poroderma pantherinum*, captured by hook and line, were tagged with coded acoustic transmitters (Vemco, Ltd. V8) on 4 November 2006. Prior to surgery, the sharks were placed in an anaesthetic solution of marine water with 0.7 ml.l⁻¹ 2-phenoxyethanol. The transmitters were surgically implanted by making a 1-2 cm incision on the ventral side and then closing it with two stitches. The sharks were also marked with spaghetti tags, sexed and measured (Table 2.2). After the surgery, which lasted five to seven minutes, the sharks were placed in a portable pool filled with marine water to allow them to recover, after which they were released.

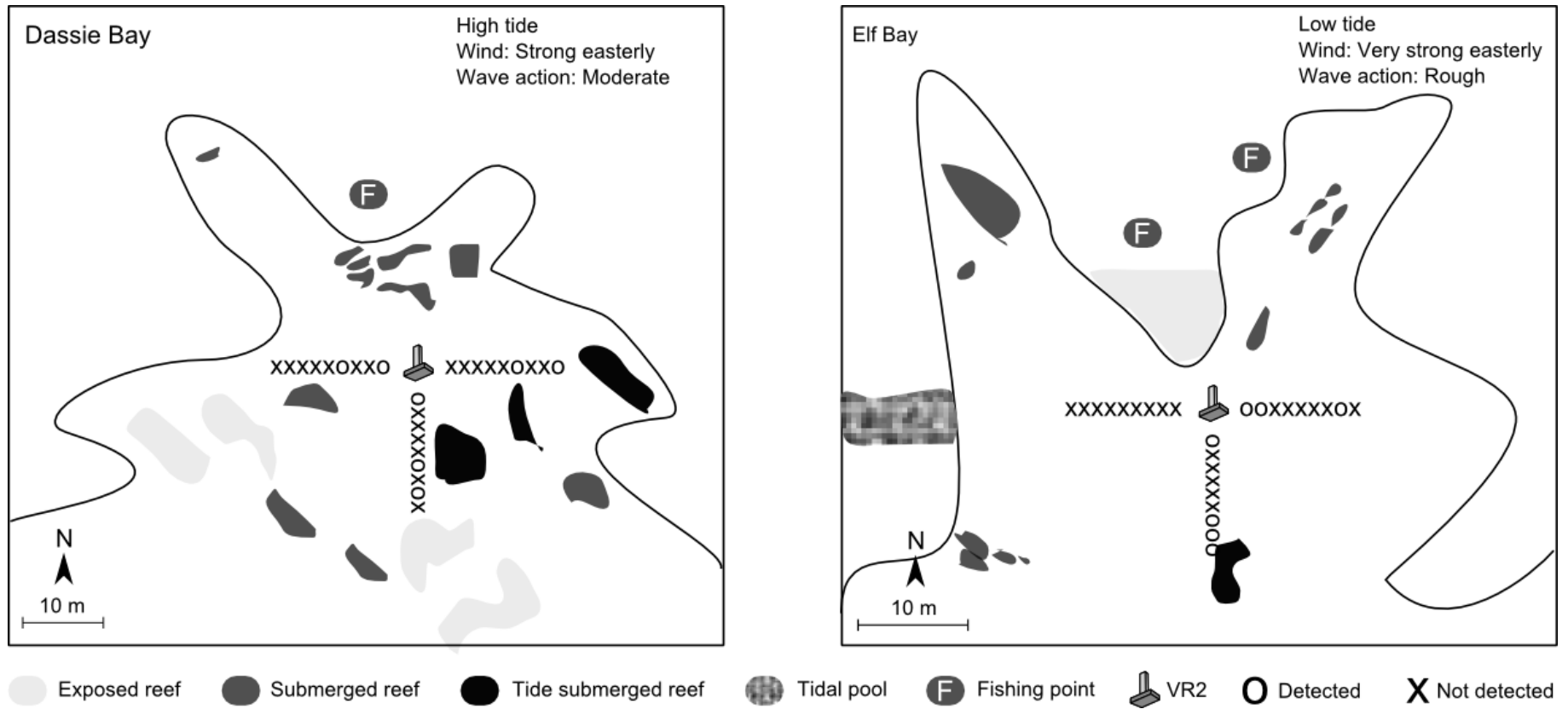


Figure 2.3: Results of reception range tests using a V8 transmitter and a VR2 receiver conducted at Rebelsrus on 15 November in Elf Bay and 11 November 2006 in Dassie Bay. Each transect was 10 metres long and signal reception tested at every metre. (X denotes Not detected and O denotes Detected).

Table 2.2: Summary of tagging information for the *Poroderma pantherinum* tagged with V8 transmitters. All sharks were tagged on 4 November 2006. D TAG refers to the spaghetti tag color (W= white, G= green) and number attached in the dorsal fin. Sharks with information received in the VR2 (*).

Code	D TAG	Sex	TL (mm)	Surgery duration (min)	Captured/ Released	Detections (number)
248*	W 561	Female	620	05:27	Bay C	1
249	W 562	Female	684	06:44	Bay C	0
250*	W 563	Male	720	07:20	Bay C	19
251	W 564	Male	696	06:35	Bay A	0
252*	G 097	Male	716	07:43	Bay A	444

Results:

The receivers yielded data for three sharks, one male and one female in Bay C and one male in Bay A. All data points were recorded at night between 18:36 and 04:44. At the same time all data points were recorded in the same bay where the sharks were initially released. The VR2 in Bay C was dislodged during a storm in early March 2007 and later retrieved on the shoreline.

Due to poor reception range, low detection rate and marginal sea conditions this method was discarded after the three month trial.

2.3.2.4. Research angling

Method:

The last method explored was research angling. It was planned to sample each bay every month for a period of 20 months. Each fishing session consisted of three hours, split into two 90 minutes periods with a fishing break of 30 minutes. There were three sessions planned each day: in the morning (5:00-8:30), at mid-day (11:00-14:30) and at night (17:00-20:30). Two to four anglers, fishing simultaneously, carried out each sampling session.

Research angling surveys were conducted over four to five day trips on a monthly basis within the bays, chosen randomly for each fishing session but ensuring similar effort

between bays. Two fishing sites were identified within each bay to ensure maximum coverage of the area (Figure 2.2). In each session, all sharks were targeted using size 6/0 and 7/0 barbless hooks. Several bait types were used including octopus (*Octopus vulgaris*), squid (*Loligo reynaudii*), strepie (*Sarpa salpa*) and pilchard (*Sardinops sagax*).

Results:

This method proved to be optimal during most weather conditions. By this method alone 124 sharks were captured, which includes 22 recapture events within the bays and one shark recaptured offsite. A total of 96 sharks were tagged and 17 individuals recaptured within the bays, with effort distributed uniformly between the bays (Table 2.3). Recapture rates were highly variable ranging between 18% and 29%. Research angling proved to be successful with adequate data for further analysis.

Table 2.3: Summary of research angling results over a 20 month period at Rebelsrus. These numbers represent all the shark captured, including multiple recapture events, completed only through angling within the bays.

Bay	Actual effort (hours)	<i>P. africanum</i>	<i>P. pantherinum</i>	<i>H. fuscus</i>	Total caught	Total recapture
A	177	3	6	22	31	4
B	175	2	9	12	23	7
C	180	8	21	18	47	8
D	178	0	4	14	18	3

2.3.3. Conclusion

Four methods were evaluated to achieve the objectives of this study (Table 2.4), of which three were found to be unsuitable for reasons given in the preceding paragraphs. Consequently only one method (research angling) was adopted for the entire 20 month period. This allowed for a first quantification of movement patterns, abundance, seasonality and population size estimation.

Table 2.4: Summary of methods tried in the field and their success.

Method	Planned surveys	Actual surveys	Bays surveyed (#)	Sharks captured (#)	Method discarded / accepted
Cages	1728 hours	72 hours	3	13	X
Diving	216 hours	26.2 hours	4	3	X
Telemetry	3 months	4 months	2	5 tagged	X
Research angling	1440 hours	710 hours	4	124	√

Existing data sets only provide a limited amount of information with a number of biases and limitations. The dedicated study also clearly revealed the limitations of working in a highly dynamic inshore environment and only catch and release fishing provided the depth of data required for attempting to answer the objectives of this study.

CHAPTER 3

MOVEMENT PATTERNS OF CATSHARKS

3.1. Introduction

Mark-recapture studies on elasmobranchs have been conducted worldwide since the 1920s and have been used extensively to gain information about growth, mortality, mixing of stocks, migration patterns, among many other biological concepts (Kohler and Turner, 2001). According to these authors, the United States, Australia, New Zealand and South Africa are leaders in tag and release programmes, many of which rely on voluntary participation by recreational anglers. Such mark-recapture studies have two main advantages, in that large numbers of fish can be tagged and awareness of conservation is created among fishermen (Kohler and Turner, 2001; Latour, 2004). However, one of the main disadvantages of public participation is the lack of accuracy in the data collected and uncertainty of fish identification (Sumpton *et al.*, 2003).

In South Africa, the National Voluntary Tagging Programme (NVTP), hosted by the Oceanographic Research Institute (ORI) relies on recreational angler participation to tag fish along the South African coast as well as provide recapture information (Bullen and Mann, 2007). Since its inception in 1984, more than 200 000 fish representing 355 species have been tagged, with an overall recapture rate of 4.97% (Bullen *et al.*, 2008). Although a number of catshark species have been tagged, data were often reported and logged at a family level (i.e. catsharks) due to difficulties associated with species identification. If identified and reported at the species level, the data was captured accordingly. Despite this shortcoming the long-term database provides general insights on the movement patterns of catshark species and aid the development of dedicated studies from which further inferences can be made.

The Tsitsikamma National Park (TNP) was proclaimed as a marine protected area in 1964 and in 1995 a research based shore angling programme was initiated to monitor inshore linefishing. By December 2007, the Tsitsikamma Shore Angling Programme

(TSAP) had tagged 12 180 fish and recaptured 560 (4.6%) fish (Bullen *et al.*, 2008). The data collected have been used to analyse the movement of several teleost species, e.g. bronze bream *Pachymetopon grande*, white steenbras *Lithognathus lithognathus* (Cowley, 1999), blacktail *Diplodus capensis*, (Cowley *et al.*, 2002), roman *Chrysolephus laticeps*, (Kerwath *et al.*, 2007) and galjoen *Dichistius capensis* (Attwood and Cowley, 2005). Although a number of shark species have been tagged in the TSAP, no analysis of the data has been attempted previously.

Recognising the inherent drawbacks in the existing data sets (NVTP and TSAP) where sharks were not specifically targeted, a dedicated study was carried out at Reblersrus, near St. Francis Bay. The broad objective of this chapter is to investigate movement patterns of four endemic species of catsharks: *Poroderma africanum*, *P. pantherinum*, *Haploblepharus fuscus* and *H. edwardsii*. Tag-recapture data collected from the NVTP, TSAP and the dedicated Reblersrus study were used to investigate movement behaviour in relation to 1) time at liberty, 2) size and 3) sex.

3.2. Materials and methods

A general description of the methods and study sites for the NVTP, TSAP and the Reblersrus study are given in Chapter 2.

3.2.1. Data analysis

Since NVTP and TSAP data sets differed in spatial resolution and type of data collected they were analyzed separately (See Chapter 2, Table 2.1). The NVTP capture localities were recorded as a distance (in km) from south of the South African/Mozambique border to the site of capture (Bullen and Mann, 2007). However, Kerwath (2005) questioned this stated accuracy and suggested that a resolution of 4 - 5 km was more appropriate, so 5 km resolution was applied in this study. Although length was reported for 57% of the recaptured sharks in the NVTP, the type of length measured was not indicated. Consequently, movement was correlated to size in fewer than 50% of the recaptured individuals.

Movement analysis for the TSAP data was recorded at a much finer spatial resolution as the entire research fishing area was geo-referenced and mapped (See chapter 2). Research anglers recorded localities according to names given to each of the fishing spots. Movement distance of recaptured sharks was measured in metres and taken as the shortest route between release point and site of recapture (Figure 3.1). Tag recoveries of long-shore movements (> 30 km) made outside the research fishing area were reported by recreational anglers with a spatial resolution similar to the NVTP. Distance travelled was correlated to total length measured for each species at time of capture and recapture. Total length was measured in millimetres and reported in 99% of the records.

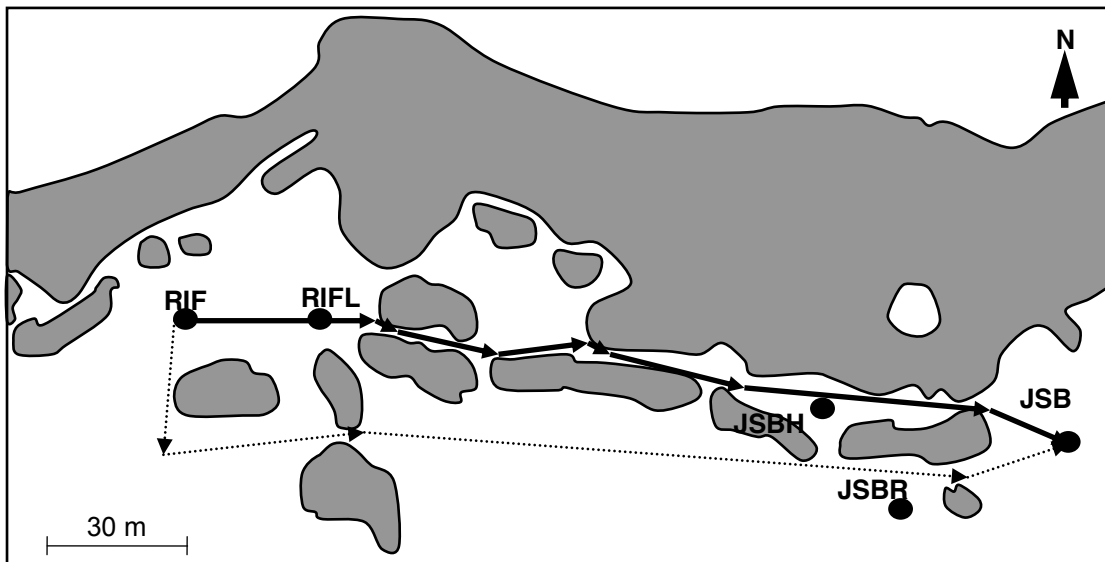


Figure 3.1: Mapped section of the TNP study site demonstrating the calculation of the distance moved using the measurement tool in ARCVIEW GIS 3.2. In the example shown, a shark, *H. edwardsii*, tagged at Rif (RIF) was recaptured at Jan Se Bank (JSB). The thick line indicates the shortest possible route (a distance of 235.2 m), while the dotted line represents an alternative longer route.

In both the above mentioned data sets movement was correlated with time at liberty for each of the studied species. However, movement could not be correlated with sex as this was not recorded in the NVTP, while in the TSAP data only 5% of the sharks captured were sexed.

Movement data from Rebelsrus was obtained for three of the four studied species, namely *Poroderma africanum*, *P. pantherinum* and *Haploblepharus fuscus*. *H. edwardsii* was only caught during the offshore cage experiments which were discontinued as outlined in Chapter 2.

Movement was analyzed in two different ways: 1) movement between bays, where zero distance was recorded when sharks were recaptured in the same bay, and 2) movement within bays, which were recorded as movements between quadrants for each bay and displacement recorded as same quadrant or adjacent quadrant (Figure 3.2). Movements between bays were measured as the shortest distance between the capture and recapture sites using the same protocol as used for TSAP. Movement analysis within the bays was identified as 0 if the shark was recaptured in the same quadrant of initial capture and 1 when the shark was recaptured in any adjacent quadrant (Figure 3.2). Movement was correlated with days at liberty, length and sex for all three species.

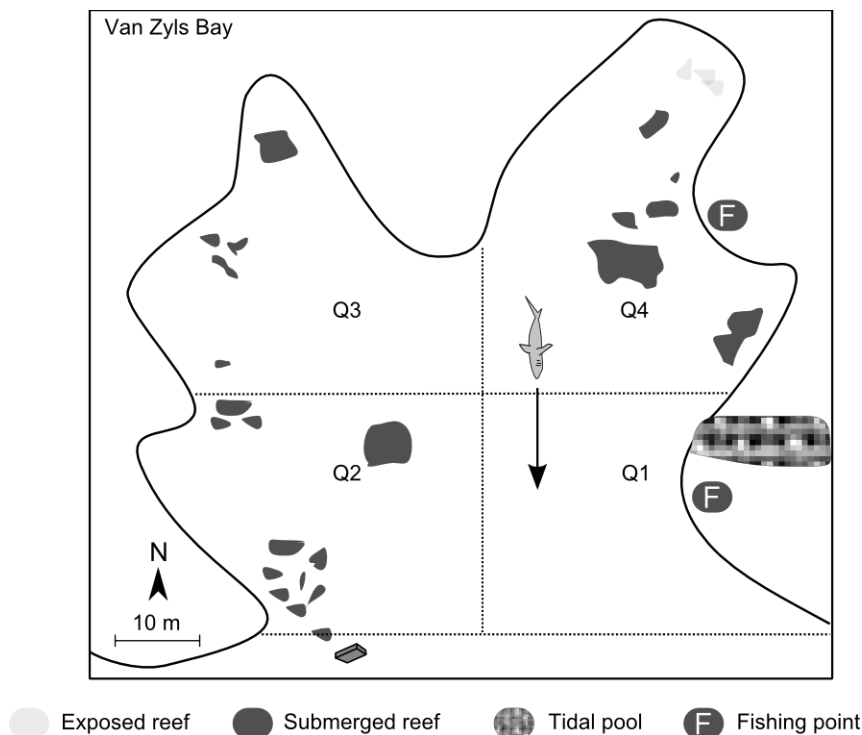


Figure 3.2: Bay A (Van Zyls) as an example of the quadrant division done in every bay.

Results from all three data sets (NVTP, TSAP, Rebelsrus) were analyzed for normality and since its assumptions were not met, Kruskal-Wallis (H) ANOVA and Spearman Rank correlation were used to evaluate movements in relation to time at liberty and size of the sharks. STATISTICA 8.0 was used for all analyses and significance was determined when P values were less than 0.05. Results from all three data sets were then summarized to determine dispersal and site fidelity of the four species.

3.3. Results

3.3.1. National Volunteer Tagging Programme

A total of 1603 catsharks, including seven species not part of this study, were tagged between 1984 and 2008, with an overall recapture rate of 5.93% ($n = 95$). Of the study species, *Poroderma africanum* yielded most recaptures, followed by *P. pantherinum*, *Haploblepharus edwardsii* and *H. fuscus*. The recapture rates for the study species ranged from 3 to 9% (Table 3.1). The maximum distance covered by an individual was 722 km and the maximum time at liberty was 4431 days (Table 3.1).

Table 3.1: Summary statistics of the four studied species tagged and recaptured between 1984 and 2008 in the NVTP (Bullen and Mann, 2007; Bullen *et al.*, 2008). Distance moved (km) and time at liberty (days) are reported as the range min-max and average (in parenthesis). *Poroderma pantherinum* data excludes data recorded as *Poroderma marleyi*, although this is likely to be the same species (Human, 2006a). ZDT = Zero distance travelled; DM = Distance moved; DaT = Days at liberty.

Species	No. tagged	No. recaptured	Recapture rate (%)	ZDT (%)	DM Min-max (Average)	DaT Min-max (Average)
<i>P. africanum</i>	761	39	5.1	76.9	0-381 (13.0)	0-2096 (364)
<i>P. pantherinum</i>	338	23	6.8	68.2	0-722 (40.9)	1-4431 (660)
<i>H. fuscus</i>	203	6	2.9	83.3	0-10 (1.7)	0-933 (445)
<i>H. edwardsii</i>	113	10	8.8	90.0	0-20 (2.0)	1-483 (79)
Total	1415	78	5.5	76.6	0-722 (14.4)	0-4431 (387)

The majority (> 76%) of recaptured individuals for each of the studied species showed no movement from their initial release site (Figure 3.3). Fewer than 16% of all recaptured individuals moved more than 10 km (Figure 3.3).

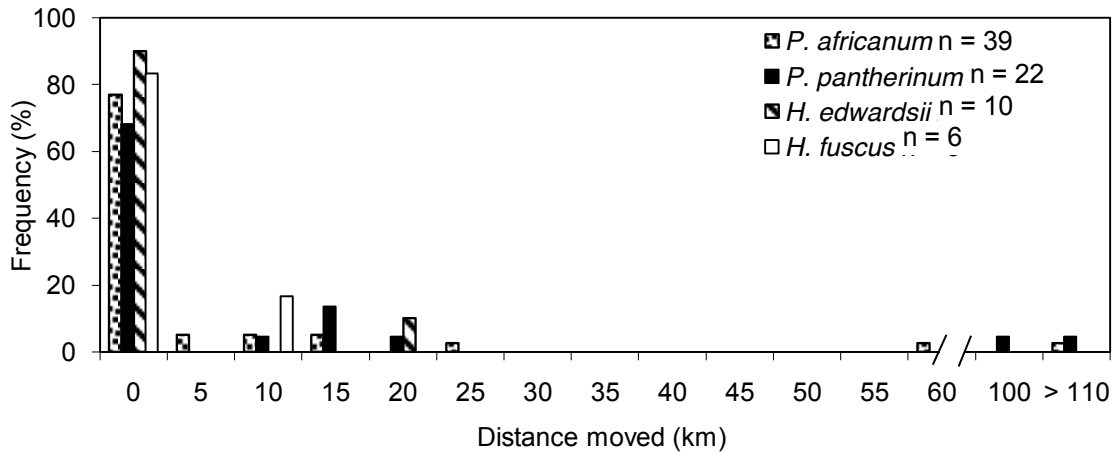


Figure 3.3: NVTP recapture data showing the proportion of recaptures made in 10 km intervals from the tagging location. Two individuals from the genus *Poroderma* moved more than 110 km; one *P. africanum* moved 380 km and one *P. pantherinum* moved 720 km.

Tagged sharks included both immature and mature individuals and ranged from 660 mm to 820 mm, 353 mm to 1120 mm, 632 mm to 670 mm and 930 mm to 580 mm TL for *P. pantherinum*, *P. africanum*, *H. edwardsii* and *H. fuscus* respectively. Although only a small number of sharks were measured prior to tagging, recaptured individuals were represented in almost all size classes (Figure 3.4). No trends were evident between distance moved and shark size (Figure 3.5). The only species (*P. africanum* n=13) with enough data points for correlation showed a negative correlation between movement and total length, but it was not statistically significant ($r_s = -0.21$, $P > 0.05$).

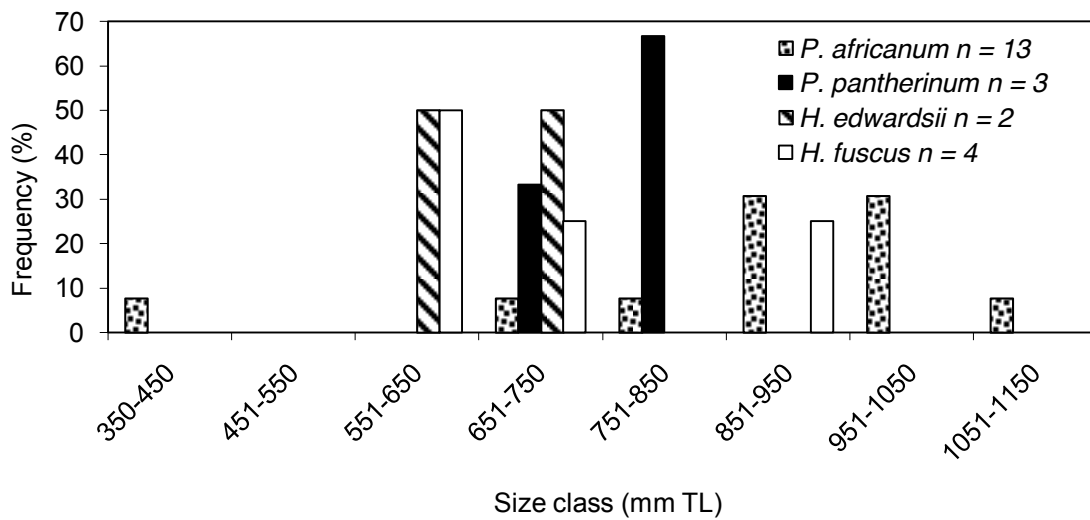


Figure 3.4: NVTP recaptures of sharks where total length (TL) was measured.

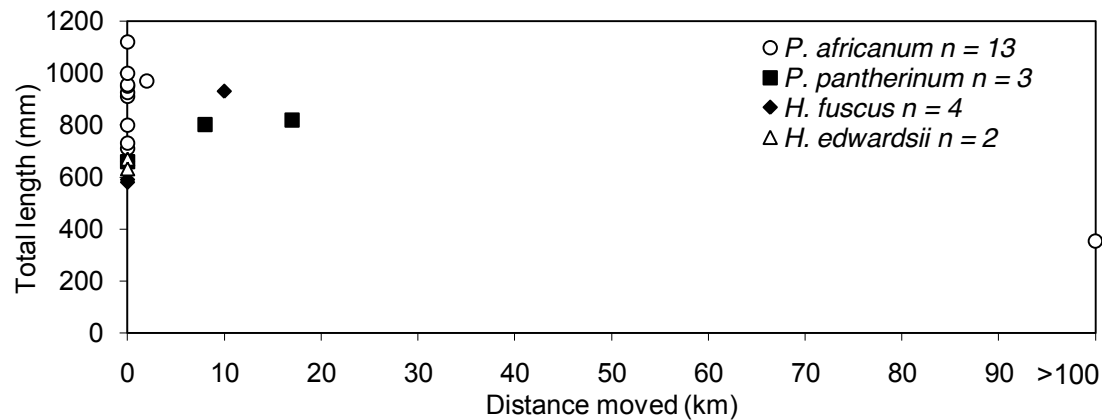


Figure 3.5: Relation between distance moved and shark length from NVTP.

Poroderma pantherinum was the only species to show a relationship between distance travelled and days at liberty but this was not significant ($P > 0.05$) (Figure 3.6). The majority (76%) of recaptures for all four species occurred within 300 days at liberty. Four *P. africanum* and three *P. pantherinum* were the only ones to be recaptured after 1000 days (Figure 3.7).

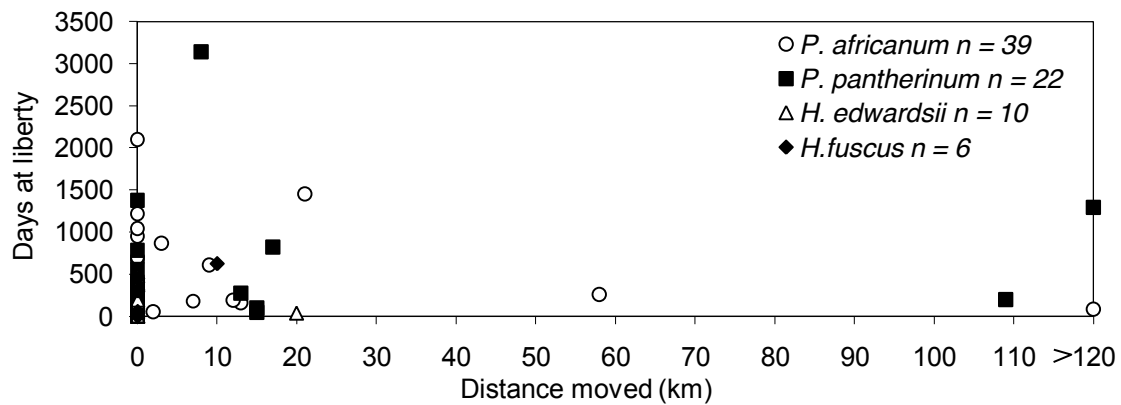


Figure 3.6: Relationship between days at liberty and distance travelled for all four species from NVTP.

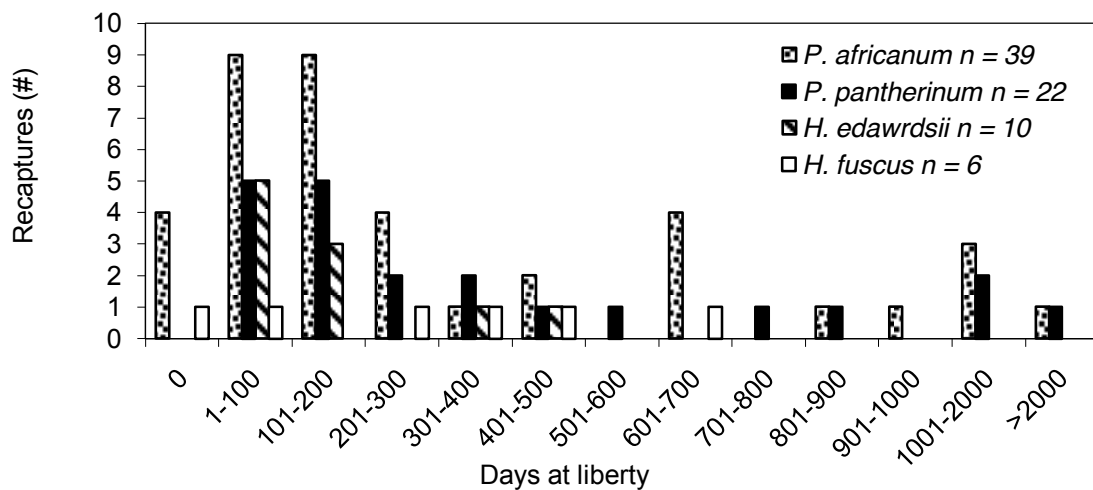


Figure 3.7: NVTP recaptures for all four species in relation to days at liberty. One *P. africanum* was recaptured after 2 096 days, and one *P. pantherinum* after 3 139 days.

3.3.2. Tsitsikamma Shore Angling Programme

A total of 545 catsharks were captured, of which 277 were tagged between 1995 and 2006 with an overall recapture rate of 9.03% ($n = 25$). At the species level, *H. edwardsii* had the highest recapture rate, followed by *P. africanum*, *P. pantherinum* and *H. fuscus*. The recapture rates for the studied species ranged from 8.3% to 12% (Table 3.2). *H. fuscus* showed the highest recapture rate and site fidelity. The maximum

distance covered by an individual was 300 km and the maximum time at liberty was 1220 days (Table 3.2).

Table 3.2: Summary statistics of the four studied species tagged and recaptured between 1995 and 2006 in the TSAP. Distance moved (m) and time at liberty (days) are reported as the range min. – max. and average (in parenthesis).

Species	No. tagged	No. recaptured	Recapture rate (%)	Zero distance travelled (%)	Distance moved Min-max (Average)	Days at Liberty Min-max (Average)
<i>P. africanum</i>	88	8	9.1	12.5	0-30 000 (4034)	6-1220 (408)
<i>P. pantherinum</i>	60	5	8.3	40.0	0-2016 (564)	27-414 (172)
<i>H. fuscus</i>	25	3	12.0	100.0	0	195-385 (290)
<i>H. edwardsii</i>	104	9	8.6	55.6	236 (1474)	1-483 (176)
Total	277	25	9.0	44.0	0-30 000 (1208)	1-1220 (261)

More than 80% of the recaptured individuals showed movements of less than 500 m from their initial release site. Only 16% of all recaptured individuals moved more than 1000 m (Figure 3.8). The genus *Poroderma* showed the least site fidelity with only 12% of the recaptures having zero movement.

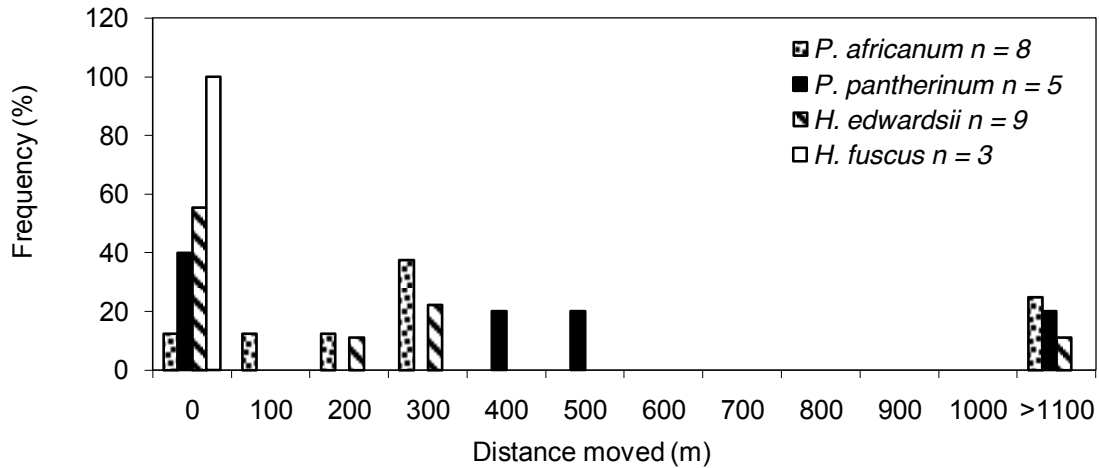


Figure 3.8: TSAP recapture data showing the proportion of recaptures made in 100 m intervals from the tagging location. Three individuals from the genus *Poroderma* moved more than 1100 m; two *P. africanum* moved 30 km and 1306 m, and one *P. pantherinum* moved 2016 m. One *H. edwardsii* moved 1474 m.

Both immature and mature sharks were tagged, ranging in size from 485 mm to 606 mm, 720 mm to 1000 mm, 485 mm to 709 mm and 602 mm to 704 mm TL for *P. pantherinum*, *P. africanum*, *H. edwardsii* and *H. fuscus*, respectively. Overall, a low number of recaptures was obtained with no discernible trend for distance moved with size (Figure 3.9). However, the largest *P. africanum* individual showed the most movement and the three *H. edwardsii* individuals that moved were larger than 600 mm total length (TL).

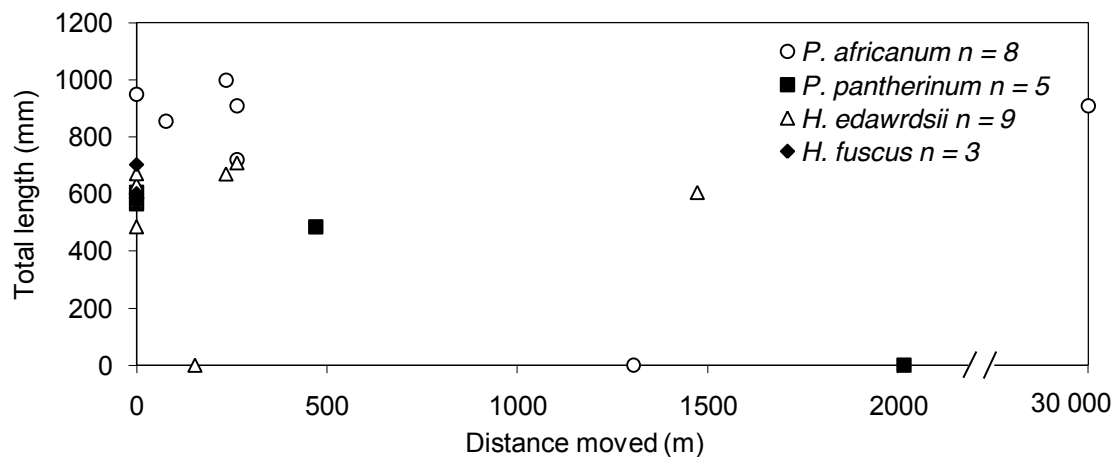


Figure 3.9: Relationship between distance moved (m) and shark length (mm TL) from individuals recaptured in TSAP.

Poroderma pantherinum was the only species to show an increase in distance travelled as the days at liberty increased, but no significant ($P > 0.05$) correlation was observed (Figure 3.10).

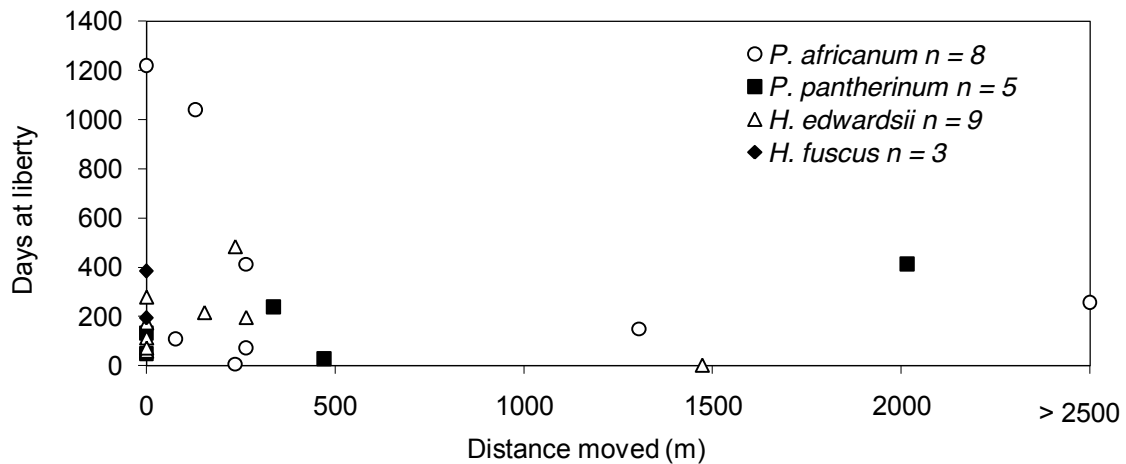


Figure 3.10: Relationship between days at liberty and distance travelled for all four species from TSAP.

As a result of the relatively low overall number of recaptures obtained from TSAP, the relationship between distance and sex could not be evaluated.

3.3.3. Rebelsrus

During the dedicated study at Rebelsrus between March 2006 and November 2007, a total of 138 catsharks were caught. This number includes all recaptures events (23), tagged sharks (108), and seven catsharks too small (< 30 cm) for tagging. The overall recapture rate was 21.3% ($n = 23$). The maximum distance covered by an individual was 130 km and the maximum time at liberty was 596 days (Table 3.3). At the species level, *P. pantherinum* and *H. fuscus* had the same number of recaptures (10), while *H. edwardsii* had none (Table 3.3).

Table 3.3: Summary statistics of the four studied species tagged and recaptured between March 2006 and November 2007 in Rebelsrus. Distance moved (m) and time at liberty (days) are reported as the range min. – max. and average (in parenthesis).

Species	No. tagged	No. recaptured	Recapture rate (%)	Zero distance travelled (%)	Distance moved Min-max (Average)	Days at Liberty Min-max (Average)
<i>P. africanum</i>	14	3	21.4	33.3	0-130 000 (65000)	35-596 (315)
<i>P. pantherinum</i>	35	10	28.6	80.0	0-632 (126)	1-298 (108)
<i>H. fuscus</i>	56	10	17.9	100.0	0 (0)	0-300 (211)
<i>H. edwardsii</i>	3	0	0.0	0.0	0	0
Total	108	23	21.3	82.6	0-130 000 (21708)	0-596 (211)

A large majority (80%) of recaptured individuals showed no movement, with only 8.7% moving more than 500 m (Figure 3.11). Only four sharks showed some movement between the bays.

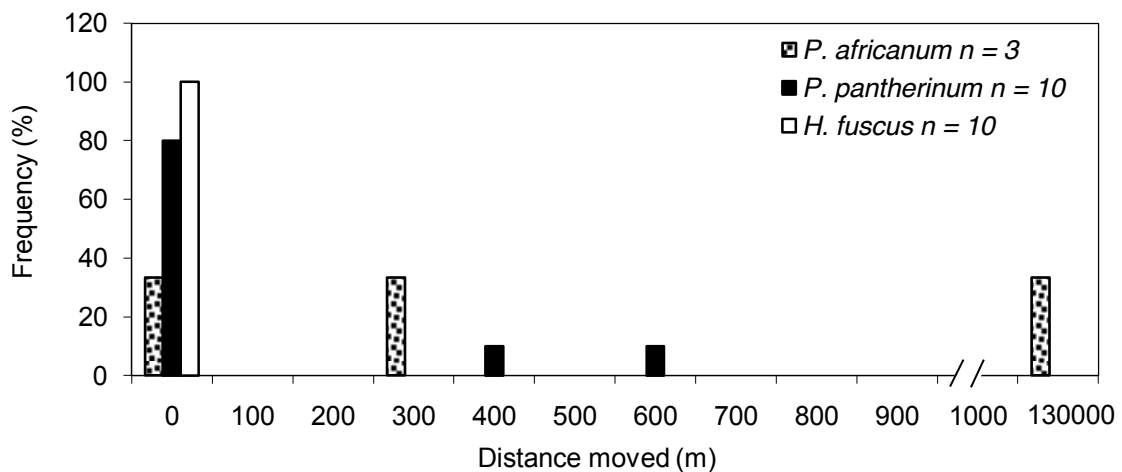


Figure 3.11: Rebelsrus recapture data showing the proportion of recaptures made in 100 m intervals from the tagging location. One *P. africanum* moved 130 km.

The size of sharks tagged ranged from 925 mm to 941 mm, 450 mm to 716 mm, 575 mm to 725 mm and 420 mm to 435 mm TL for, *P. africanum*, *P. pantherinum*, *H. fuscus* and *H. edwardsii* respectively. Recaptured individuals were represented in only four size classes (Figure 3.12). Low sample size precluded an analysis of distance moved versus size in *P. africanum*, *H. fuscus* and *H. edwardsii* (Figure 3.13). However, *P. pantherinum* showed a trend of increase in distance travelled with an increase in size, this was not statistically significant ($r_s = 0.31$, $P > 0.05$).

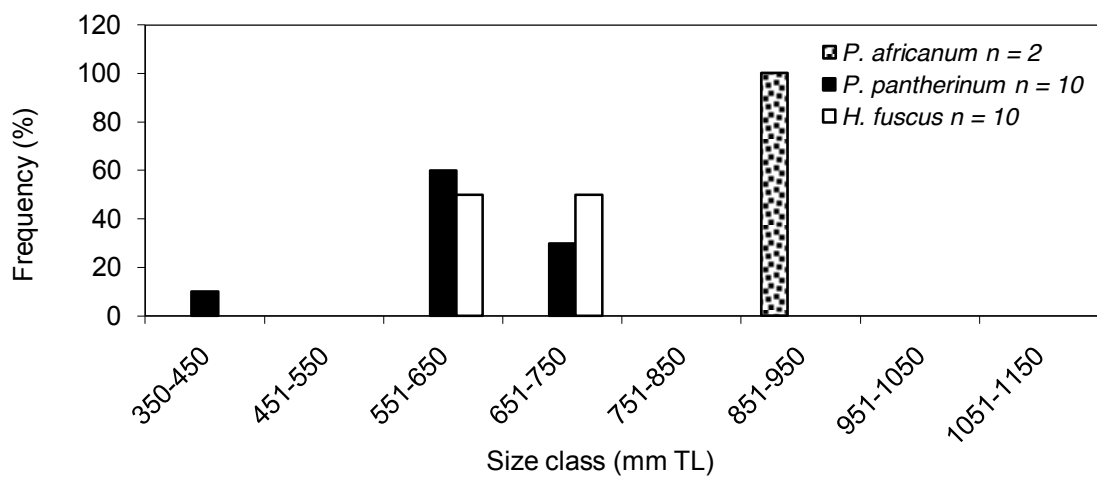


Figure 3.12: Rebelsrus recaptures of sharks where total length (TL) was measured.

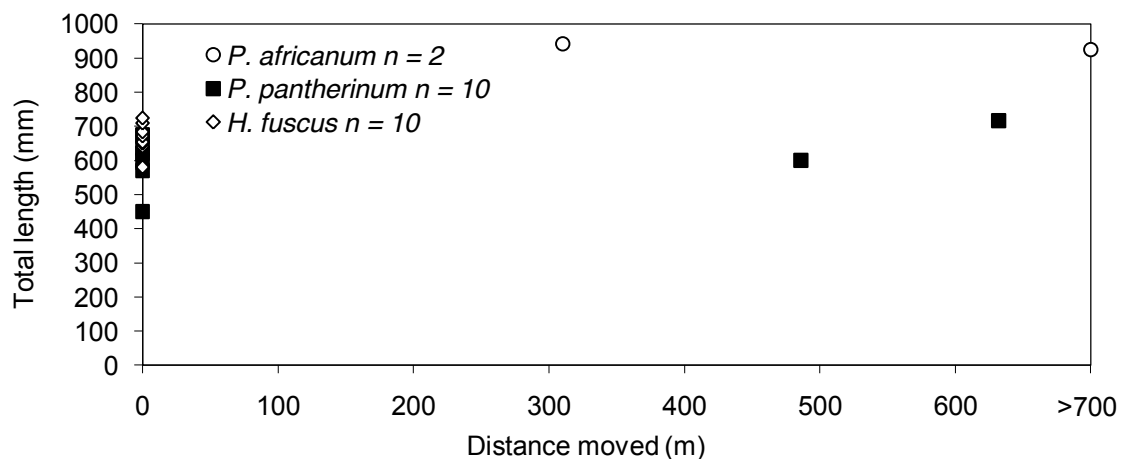


Figure 3.13: Relation between distance moved (m) and shark length (mm) from Rebelsrus. *P. africanum* only had two recaptures with total length measured.

No discernible trends were identified between days at liberty and distance travelled for any of the species. Most recaptures occurred within six months after initial capture (Figure 3.14), with no trends observed among males and females in relation to distance travelled (Table 3.4).

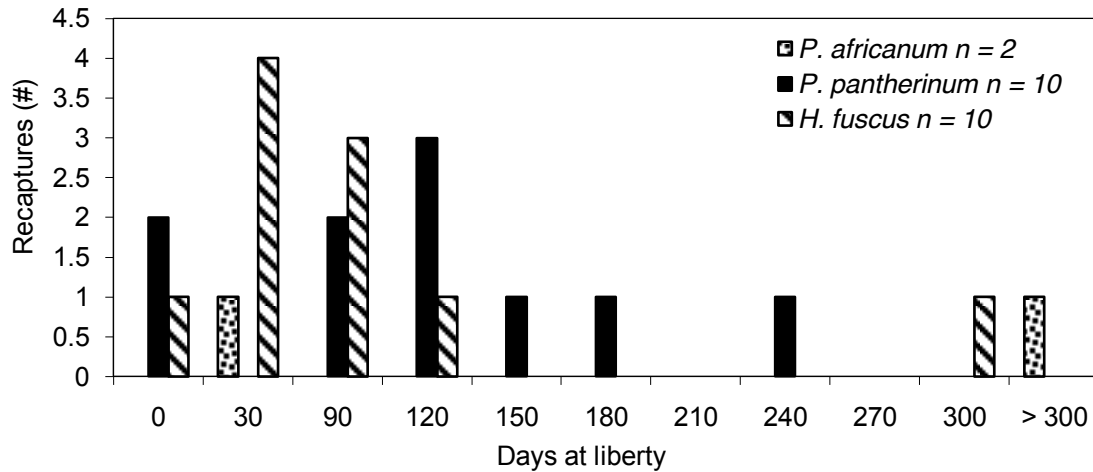


Figure 3.14: Recaptures for three species in relation to days at liberty. One *P. africanum* was recaptured after 596 days and *H. edwardsii* had no recaptures.

Table 3.4: Summary of number of females and males recaptured for each of the species and the distance travelled (m) from Rebelsrus.

Distance Travelled (m)	<i>P. africanum</i>		<i>P. pantherinum</i>		<i>H. fuscus</i>	
	F	M	F	M	F	M
0	1		1	7	4	6
300		1				
450			1			
>500	1			1		

Discerning movement between different quadrants within a bay at Rebelsrus was hampered by low sample sizes. However, the majority of *H. fuscus* recaptures occurred within adjacent quadrants to the capture quadrant, while *P. pantherinum* had the same number of recaptures between same and adjacent quadrants (Figure 3.15).

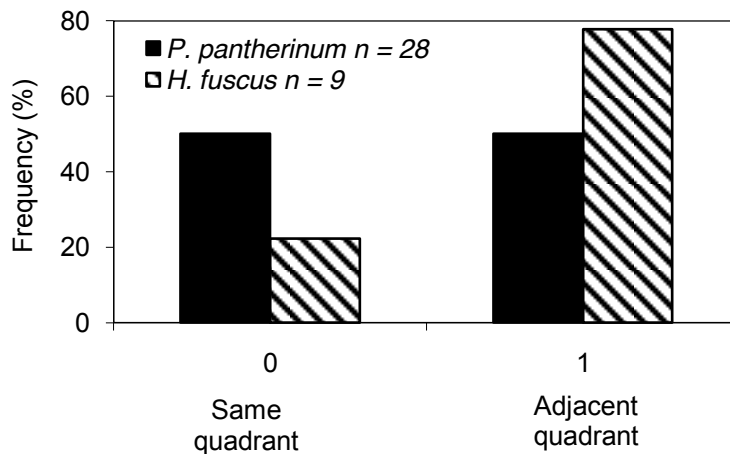


Figure 3.15: Rebelsrus recapture data of two species showing the proportion of recaptures made in same (0) or different (1) quadrant of initial capture.

3.4. Discussion

Generally recapture rates differed among the projects and increased as the spatial resolution increased. NVTP incorporated 3000 km of coastline and had a recapture rate of 5.5%, while the 5 km TSAP study site had a 9% recapture rate and Rebelsrus (2 km) had a 21.3% recapture rate. The NVTP recapture data are considered to be imprecise, as distances reported as zero could be as much as five km (Kerwath *et al.*, 2005). The low recapture rates obtained from the NVTP are difficult to interpret and can be ascribed to poor tagging or handling skills resulting in increased mortality and low reporting rates (Brouwer *et al.*, 2003). This is exacerbated by inaccurate reporting from the volunteer anglers both tagging and recapturing the fish (Latour, 2004). In the case of TSAP and the dedicated study at Rebelsrus, movement was reported in metres instead of kilometres. In addition, fish identification and reporting was more reliable in this method as a group of scientific anglers collected the data. A drawback of the TSAP was that research anglers targeted a wide range of species and often used tackle and bait not suitable for the capture of catsharks, which explains the lower recapture rate in comparison to Rebelsrus. High recapture rates at Rebelsrus can be ascribed to targeting effort, only using baits favoured by catsharks (pilchards, squid, octopus and fish fillets), fishing effort, with fishing being concentrated within a small area (1.98 km) and that research angling was conducted on a monthly basis. As a result a higher recapture rate was obtained from the TSAP and Rebelsrus compared to the NVTP. However,

Rebelsrus did not offer enough movement data for *Haploblepharus edwardsii*, showing zero recaptures, this suggests that the focused study site did not cover the habitat of this species as it was only captured during the offshore cage experiments (Chapter 2).

Combining all the available data from the three tagging projects, from 1980 to 2008, a total of 1 800 catsharks were tagged and 127 were recaptured (7.05%). Data from all three studies did show limited dispersal and high site fidelity in all four species. More than 65% of all recaptures for all four species revealed zero displacement, while limited longshore movements were recorded. Results show catsharks make limited movements along the coast. It also suggests that *Poroderma pantherinum* restricts its movement to portions of the bay, while *Haploblepharus fuscus* moves within the entire bay. This is similar to the results of a study on the Spotted Catshark, *Scyliorhinus canicula*, which revealed a limited home range (Sims *et al.*, 2001; Sims *et al.*, 2006). Small home ranges are also found for a number of teleost species in South Africa, e.g. Galjoen *Dichistius capensis* (Attwood and Cowley, 2005) and Roman *Chrysoblephus laticeps* (Kerwath *et al.*, 2007). This is also evident with the Snapper *Pagrus auratus* where 85% of the recaptures occurred less than a kilometre from the initial release site (Sumpton *et al.*, 2003).

Some individuals showed strong site fidelity, as is evident by the high recapture rates at Rebelsrus within a limited two year sampling period. This study highlights the strong site fidelity of three of the four species. Furthermore, the short telemetry survey carried out at Rebelsrus (See Chapter 2) showed three *P. pantherinum* sharks with high site fidelity, visiting the same bay on a regular basis for a period of three months. However other shark movement studies showed no site fidelity and higher movement rates. For example, adult Leopard Sharks, *Triakis semifasciata* (Ackerman *et al.*, 2000) and adult Bonnethead Sharks, *Sphyrna tiburo* (Parsons, 1990). In contrast, strong site fidelity for part of the year was recorded for juvenile Sandbar Sharks, *Carcharhinus plumbeus*, which only utilized two bays during summer (Grubbs and Musick, 2007).

None of the three data sets showed a significant correlation between distance movement and time at liberty, size or sex. For example in the NVTP, it was observed that even after more than 2000 days at liberty an individual was recaptured within five kilometres of the initial capture site. Similarly in TSAP a *P. africanum* was recaptured in the same

site (zero metres) after 1220 days at liberty. Despite this apparent long-term residency, diving surveys carried out at Rebelsrus (see Chapter 2) showed that during the day catsharks may be absent from the bays (per. obs.) and shark detections by the VR2s occurred only at night. It has been suggested that as time at liberty increases so does the opportunity for fishes to travel long distances, i.e. the chances of diffusion increase (Okubo, 1980). This study suggests that the site fidelity may be independent of time at liberty, with extreme residency being displayed by several members of each study species for extended periods. In the case of Galjoen, *Dichistius capensis* about 80% of the fish showed high site fidelity, with few individuals undergoing specific migrations (Attwood and Cowley, 2005). However, studies in Australia on the Snapper, *Pagrus auratus*, showed high dispersal along the shelf after a number of years at liberty (Moran *et al.*, 2003). One should therefore be careful when interpreting results and a long-term inshore / offshore tagging programme dedicated and designed only for catsharks should be implemented to answer this question in the family Scyliorhinidae.

In none of the projects (NVTP, TSAP & Rebelsrus) was there a significant correlation between movement and total length of the catsharks. However, on the few occasions where a catshark travelled a significant distance (> 30 km), these individuals were adults. It has been proposed that larger fish will travel or move more often than smaller fish (Attwood and Cowley, 2005). This is confirmed by the dedicated study at Rebelsrus where two of the “travellers” that covered the longest distance were the largest, a *P. africanum* of 925 mm TL travelled 130 km and a *P. pantherinum* of 716 mm TL travelled 630 m. Despite this, a correlation between size and distance travelled was not significant.

Movement in relation to gender was only evaluated in the Rebelsrus study. Neither *P. africanum* nor *H. fuscus* showed a significant correlation. However, *P. pantherinum* displayed a higher number of males recaptured in the same bay of initial capture than females, however the differences were not statistically significant. It should also be noted that a *P. africanum* female covered the longest distance of 150 km. Females travelling greater distances is not uncommon, as shown by Ackerman, *et al.* (2000), who found that Leopard Shark, *Triakis semifasciata*, females travelled the longest distances.

Although limited dispersal and strong site fidelity were observed, the combined data showed that catsharks have the capacity to travel long distances. Having the capacity to travel long distances poses the question; why do these “travellers” or “movers”, as called by Attwood and Cowley (2005), undertake the journey? In this regard it is important to know whether they will eventually return to their original capture site. A return trip was observed in TSAP, where one *P. pantherinum* was first captured at Jan Se Bank (JSB), later recaptured at Rif (RIF) and 11 months later recaptured back at JSB, which suggests that catsharks do return to the original site. Carlson, *et al.* (2008) showed that juvenile *Rhizoprionodon terraenovae* maintained a small home range and recaptures occurred in their initial capture site even after four years at liberty. In their study only few individuals travelled long distances, the reasons for which are still unknown. One explanation is that the initial shock of being caught and tagged may trigger movement and for this reason many studies disregard movement directly after release (Francis, 1988). It has also been suggested that these few “travellers” undergo long trips in order to maintain a continuous genetic stock of the species (Crossland, 1982). Whatever the reasons for these “travellers”, it is imperative that further studies be undertaken on these few individuals to analyze the effects of limited dispersal observed in most of the individuals.

Limited dispersal and high site fidelity has advantages and disadvantages. This behaviour, especially in endemic species such as the catsharks, Galjoen (Attwood and Cowley, 2005) and Roman (Kerwath *et al.*, 2007) can have a number of disadvantages in terms of their conservation. Limited dispersal makes them more vulnerable to localised fishing pressure either as a target species or as bycatch in a fishery. Fishing also directly affects the number of offspring produced (Gruber *et al.*, 2001), which can further decrease their numbers. Another concern of this extreme site fidelity is that of inappropriate coastal development and point source pollution, which adversely impacts the local environment.

One advantage of site fidelity is “energy saving” for mating and feeding. Studies on Snappers related localised movement to feeding and spawning processes (Crossland, 1982). Energy spent looking for mates can be better used in reproduction or egg laying. It is possible that sharks also use the shallow bay environment to avoid large predators

(Compagno *et al.*, 2005). In Brazil, juvenile Lemon Sharks, *Negaprion brevirostris*, stayed in large groups and on shallow reefs in order to avoid adult Lemon Sharks who have show cannibalism (Wetherbee *et al.*, 2007).

Due to their station - keeping behaviour (limited dispersal and site fidelity) these catshark species will most likely benefit from no take Marine Protected Areas (MPAs) as a conservation strategy. However, knowledge on the extent of their home range, particularly the seaward boundary, is important to ensure that these species are adequately protected. It is also important to acquire knowledge on their temporal variation in abundance, reproductive biology, and population sizes to develop a more appropriate, holistic conservation plan.

CHAPTER 4

ABUNDANCE AND SEASONALITY

4.1. Introduction

At a global level, most chondrichthyans are vulnerable to overexploitation and there is a general lack of knowledge on abundance, temporal variation and population size for many species. This information is used to assess the status of a species population and later to implement conservation strategies. The recommendations of the International Union for Conservation of Nature (IUCN) are commonly followed to manage and protect organisms, but when a species lacks the basic information for its assessment, the species is categorized as “data deficient”. Attention is often focussed on those organisms considered “critically endangered” or “vulnerable”, while those for which data is not available are ignored. For this reason it is important to undertake studies that provide the basic data required to assess the status of chondrichthyans.

As pointed out in the introduction (Chapter 1), abundance estimates are often made for commercially important or charismatic tourism-related species, with little attention paid to those species that may be vulnerable and have little commercial or aesthetic value. Abundance estimates are readily available for commercial shark species such as the Soupfin *Galeorhinus galeus* (Punt and Walker, 1998; Lucifora *et al.*, 2004), Gummy shark *Mustelus antarcticus* (Pribac *et al.*, 2005) and the Blue shark *Prionace glauca* (Aires-Da-Silva *et al.*, 2008), and for charismatic species including the Basking shark *Cetorhinus maximus* (Francis and Duffy, 2002), Ragged-tooth shark *Carcharias taurus* (Lucifora *et al.*, 2002) and Tiger shark *Galeocerdo cuvier* (Wirsing *et al.*, 2006).

The spatial and temporal variation in abundance of chondrichthyans is important in designing conservation areas and determining closed seasons. In Portugal *Raja undulata*, is abundant in shallow waters while the small spotted catshark *Scyliorhinus canicula* is more abundant in deeper waters (Coelho *et al.*, 2005). In Norway *R. undulata* is generally abundant in waters shallower than 300 metres, but in winter, it

will move to deeper waters (Skjæraasen and Bergstad, 2000). This spatial and temporal information could be use in the implementation of marine protected areas or closed seasons. In South America, the Sand Tiger shark, *Carcharias taurus*, is known to be vulnerable during the mating season (January - February), prompting the introduction of conservation measures (Lucifora *et al.*, 2002).

In South Africa, there is a general lack of biogeographical and ecological data on many species of chondrichthyans, partly as a result of limited targeting and concomitant lack of interest and funding from management agencies. Recently, abundance data has been calculated for a commercially exploited species, the smooth hound shark, *Mustelus mustelus*, using available catch rates (Da Silva, 2007), and for the ragged-tooth shark, which is important as an attraction for tourist diving operations, using catch rates from angling clubs (Dicken *et al.*, 2006b) and mark-recapture data (Dicken *et al.*, 2008).

Catch rates have been used not only to identify abundance, but also spatial and temporal variation. For example spatial variation was found between juvenile and adult raggedtooth sharks, with sexually mature individuals using different regions in the Eastern and Western Cape (Smale, 2002). Temporal variation, on the other hand can be obtained from yearly, monthly or daily catch rates. The Whale shark, *Rhincodon typus*, is more abundant in South African waters during summer months and the Tiger shark *Galeocerdo cuvier*, frequents the South African coast during winter (Heemstra and Heemstra, 2004). Temporal trends have been explored for various elamosbranch species such as inter-annual trends in *Raja annulatus* and *Gymnura natalensis* (Pradervand, 2003a), while monthly trends were found for *Carcharhinus obscurus* (Pradervand, 2004), and Hammerhead shark *Sphyrna spp.* (Pradervand, 2003b).

Abundance can be inferred from catch rates, but population size estimates are mainly determined from mark- recapture data with adequate recapture rates (>10%), as was the case for some of the species in the present study. A number of population models, with associated assumptions and biases exist, and in South Africa various models have been used. The Jolly-Seber, an open population model, assumes that capture probability changes over time, immigration and emigration occurs, and models both non-captured and recaptured individuals. This method has been used for marine mammals such as the Humpback dolphin, *Sousa chinensis* (Karczmarski *et al.*, 1999). Closed population

models had been used mainly to estimate the population size of species found in estuaries such as the Cape stumpnose, *Rhabdosargus holubi* (Cowley and Whitfield, 2001), the Southern mullet, *Liza richardsonii*, and the gobie, *Glossogobius callidus*, among many others (Lukey *et al.*, 2006). These models tend to be simpler and assume that the study population remains unchanged for the duration of the study.

Where a number of species are targeted, and adequate recapture rates are available for at least one species, it is possible to obtain some idea of population size for species with low or zero recapture rates, using a derived method (Cowley and Whitfield, 2001). In this case the species with the highest recapture rate is used as the control for the other species. The basic assumptions of this method include that all species have the same probability of being captured and all the species being estimated have the same distribution as the control species. In estuaries, the population sizes of various species including the Groovy mullet, *Liza dumerili*, White steenbras, *Lithognathus lithognathus* and the Strepie, *Sarpa salpa* have been estimated through this method (Cowley and Whitfield, 2001).

Currently the study by Richardson *et al.* 2000 is the only study where abundance has been estimated for a South African catsharks species. These authors calculated the abundance of the offshore species *Holohalaelurus regani* from stratified trawl capture data. Some data are available on temporal abundance for mature *Poroderma africanum* and *P. pantherinum* catsharks (Roux, 2002), however no population estimates exist. This chapter examines catch and recapture data to investigate the general distribution range and temporal variation in abundance of four species of catsharks, and provides preliminary estimates on population numbers for selected species.

4.2. Materials and methods

4.2.1. Abundance and seasonality

The general distribution range and temporal variation of the species were inferred from the results of the National Marine Linefish System (NMLS) data, and is presented as the mean capture rate within each biogeographical zone (Subtropical, Cool and Warm

temperate) (Figure 4.1). Since the NMLS dataset does not incorporate effort data it was not possible to calculate trends in abundance. Simultaneously, capture records for cool-temperate region were not available for analysis.

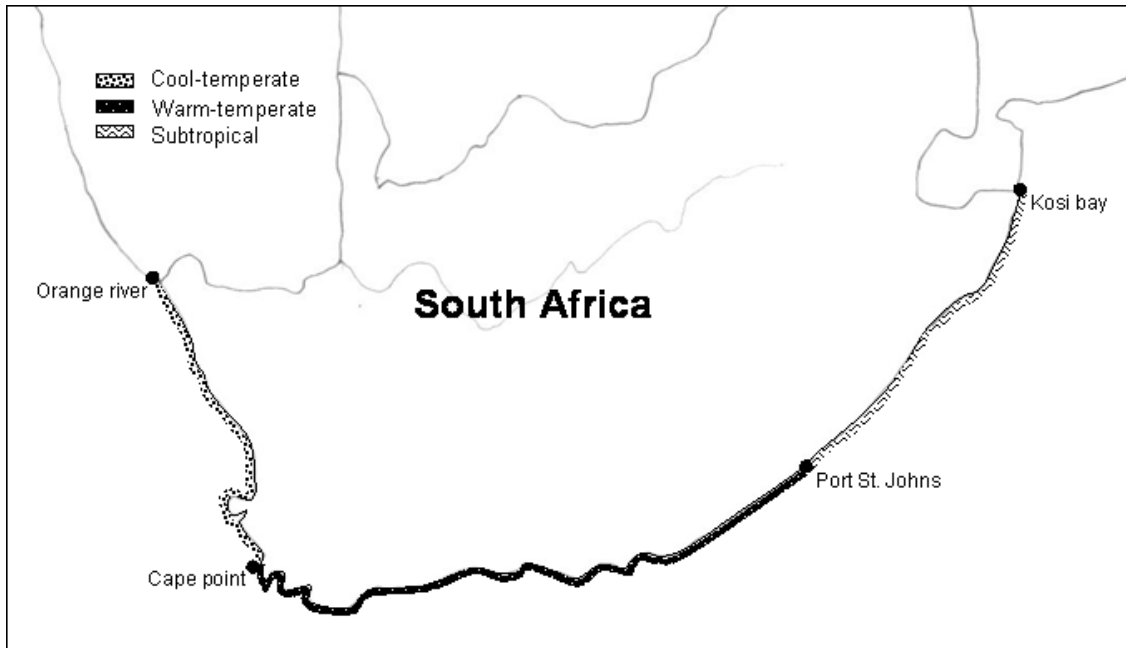


Figure 4.1: Eco-regions boundaries in the South African coast for NMLS dataset.

Abundance on a monthly basis was calculated separately using catch per unit effort (CPUE) data from TSAP and Rebelsrus. CPUE was estimated by calculating the number of sharks captured each month divided by the total monthly effort (angler. hour). Average CPUE was then obtained by dividing by the number of months sampled in the case of TSAP and by the number of days sampled in each month for Rebelsrus.

Diel changes in abundance were only calculated from the Rebelsrus study since TSAP surveys took place only during daylight hours, from sunrise to sunset at different hours depending on the season. Sharks captured at Rebelsrus between 04h00 to 09h00 were categorized as dawn captures, from 11h00 to 15h00 were considered noon captures and from 16h00 to 21h00 dusk captures. The survey times at Rebelsrus remained constant irrespective of the season.

Data was not normally distributed and a non-parametric Kruskal-Wallis ANOVA by ranks was used at a α - level of significance of 0.05 to test for differences between mean catch rates at the relevant temporal scale. Replicates consisted of the overall monthly CPUE in each year for the TSAP data, while for Rebelsrus, individual research angling sessions served as replicates for the relevant month or time-of day category. All analyses were performed with STATISTICA 8.0 (Statsoft Inc.).

4.2.2. Population size estimation

The Rebelsrus dataset was suitable for population size estimation with adequate recapture rates for three species, (*Poroderma pantherinum* 29%, *P. africanum* 21% and *Haploblepharus fuscus* 18%), with high site fidelity and limited dispersal (See Chapter 3). Due to the characteristics (high recapture > 10% and limited dispersal) of these three species a closed population model was chosen as the most appropriate. The Schnabel method with a 95% confidence interval (Ricker, 1975; Seber, 1982) was used to obtain some preliminary estimates, using the following equation:

$$N = \frac{\sum_{i=2}^n n_i M_i}{\sum_{i=2}^n r_i}$$

N = Total population size
 i = Sampling day i_{th}
 n_i = Total of sharks on the i_{th} sampling day
 r_i = Total of recaptures on the i_{th} sampling day
 M_i = Total number of tagged fish in the study area before i_{th} sampling day.

The Schnabel close population model assumes that no recruitment, emigration, mortality, nor tag loss occurs during the study, and that the probability of capture of tagged and untagged fish is the same, with random mixing of tagged and untagged individuals.

The derived method that has been used for species with low or no recaptures (Cowley and Whitfield, 2001; Lukey *et al.*, 2006) was not applied to *Haploblepharus edwardsii*, as they were only captured offshore, therefore did not meet the required assumptions.

An estimate of the size of the study area, taken as the area of the four bays (Rebelsrus) was calculated using SigmaScan Pro 5.0. Density for each species was calculated by dividing the population size estimated by the area, calculated in km².

4.3. Results

4.3.1. Abundance and seasonality

In the NMLS dataset all species were found in both biogeographical regions, except for *P. africanum* that was absent in the subtropical region. However, temporal variation was observed between regions, except for *P. africanum*, which was captured throughout the year. *P. pantherinum* was only absent during January in the warm-temperate region and present all year in the subtropical region. Shysharks on the other hand were absent in subtropical region during four months of the year, but present in all months at the warm temperate region (Figure 4.2). It is important to point out that the mean capture rate used is meaningless since total effort was never reported and as a result the calculated rates are overinflated. Capture rates were estimated with the only purpose to show presence / absence of catsharks in each month of the year in the different eco-regions.

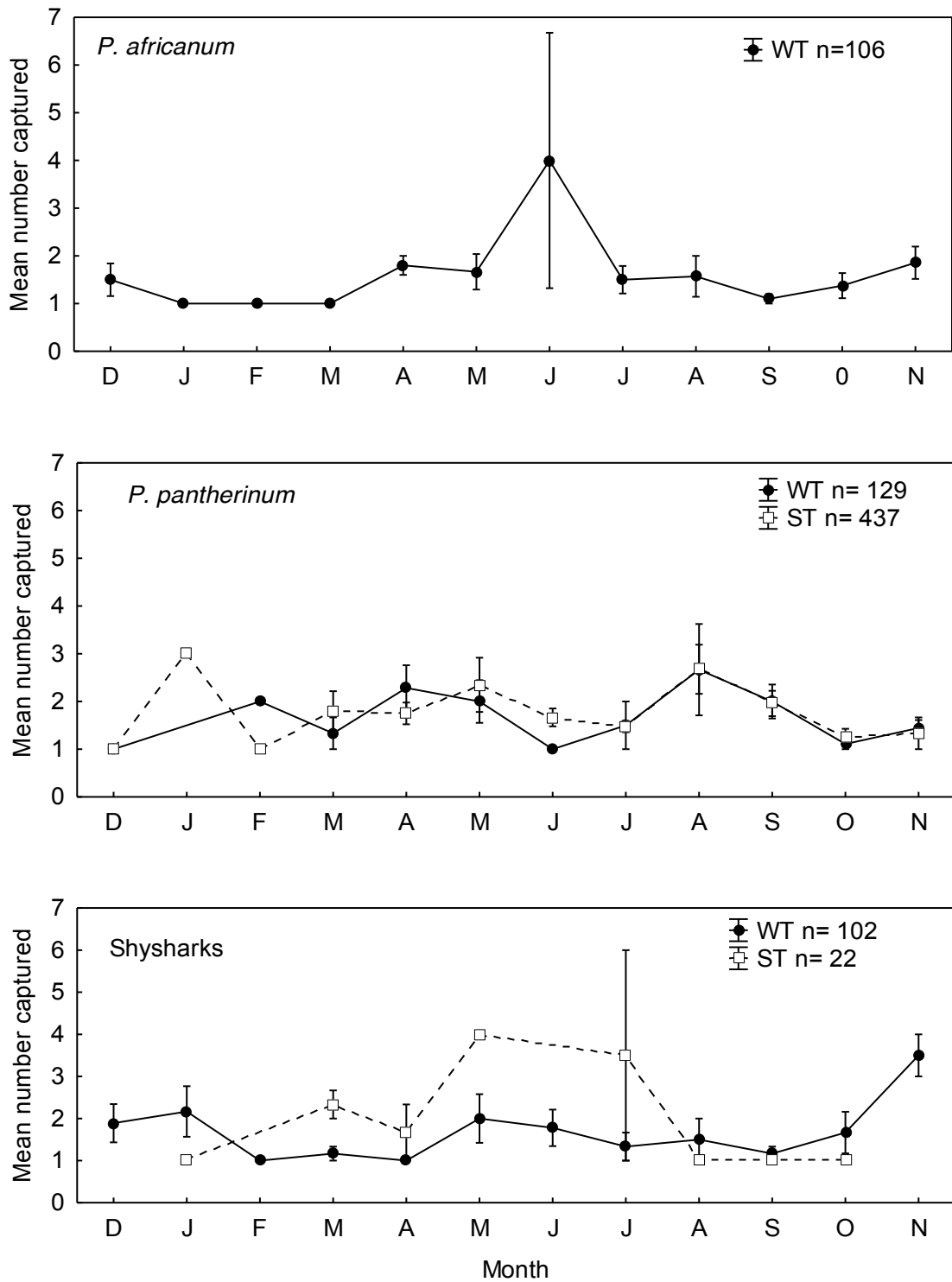


Figure 4.2: NMLS average (\pm SE) monthly number catsharks captured in the sampled regions in South Africa from 1984 to 2007. N= represents the total number of sharks captured, WT= warm-temperate and ST= subtropical.

In the Tsitsikamma Shore Angling Program (TSAP) and Rebelsrus, both within the warm temperate region, abundance varied among species, with overall higher catch rates at Rebelsrus (Table 4.1). Interestingly no *Haploblepharus edwardsii* were caught during the Rebelsrus study, while there were abundant in catches from the TSAP.

Table 4.1: Summary of CPUE (No.Ang.hr⁻¹) trends from TSAP and Rebelsrus studies, both within the warm-temperate region. TSAP data was collected over a 10 year period, while Rebelsrus over 20 months.

Species	TSAP		Rebelsrus	
	CPUE Mean	CPUE Range	CPUE Mean	CPUE Range
<i>P. africanum</i>	0.010	0.0 – 0.05	0.019	0.0 – 1.0
<i>P. pantherinum</i>	0.010	0.0 – 0.07	0.056	0 – 1.85
<i>H. edwardsii</i>	0.025	0.0 – 0.09	0.0	0.0
<i>H. fuscus</i>	0.005	0.0 – 0.03	0.088	0 – 2.5

Temporal variation in CPUE was only significant (KW-H (11, 56) = 20.8, $P = 0.035$) for *P. africanum* in TSAP, with peaks in December and a decrease from May to September (Figure 4.3). Although some fluctuation in abundance was also observed for *P. pantherinum* this was not significant. For the Rebelsrus dataset, *P. africanum* abundance peaked in December but this species was absent seven months of the year, while *P. pantherinum* peaked in November and was only absent in January. Shyshark monthly CPUE varied between the two species, however this was found to be not significant. *H. edwardsii* was captured all year peaking in April and absent only in January (Figure 4.4). In contrast, *H. fuscus* peaked in July and was less abundant for most of the year in TSAP. At Rebelsrus, although large abundance fluctuations were observed for *H. fuscus*, this was not significant. Although also not significantly different, the individual species CPUE tended to peak a month apart towards the end of the year and an interesting overlap was observed in March for *P. africanum* and *H. fuscus*.

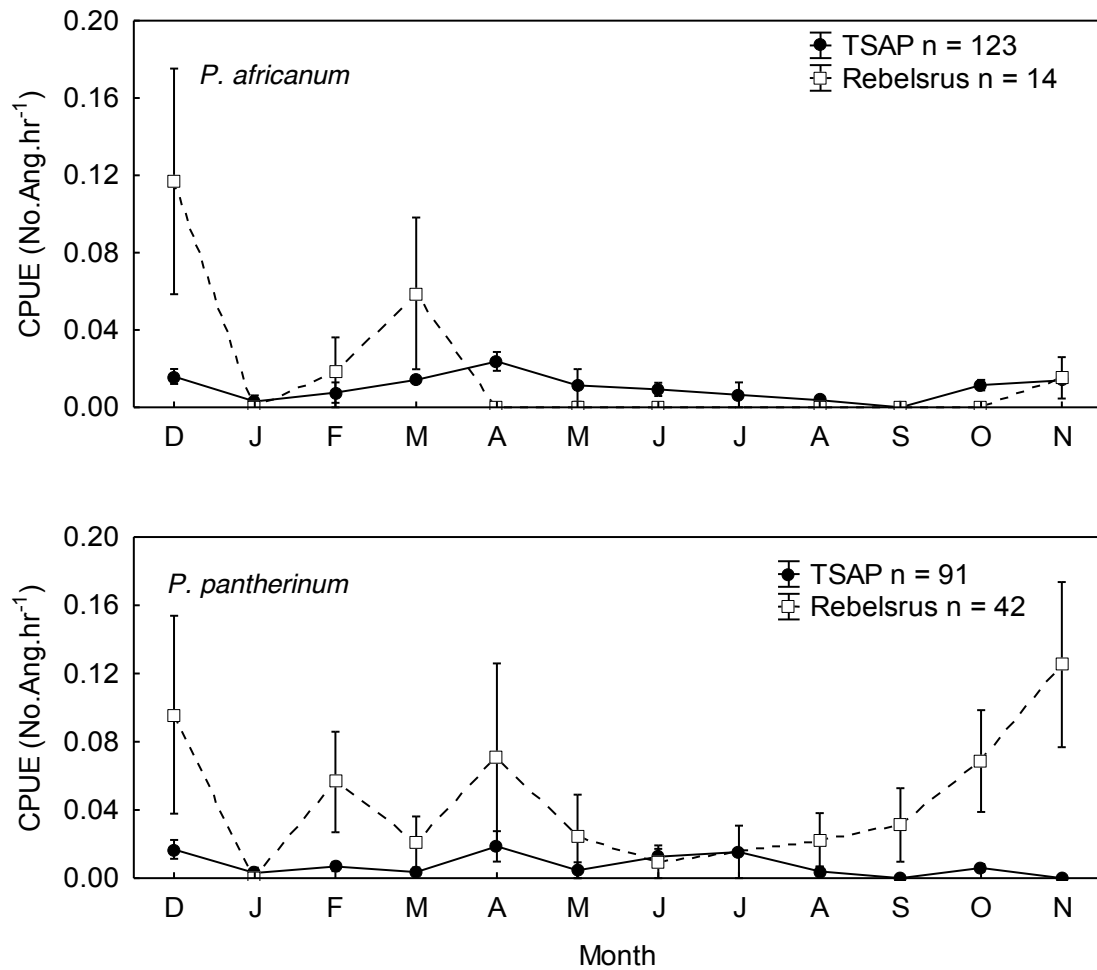


Figure 4.3: Average (\pm SE) monthly CPUE for *Poroderma* sp. in TSAP and Rebelsrus. N = represents the total number of sharks captured. Data were collected over a 20 month period at Rebelsrus and from 1995 to 2006 in TSAP.

Diel CPUE variation was evaluated only from the Rebelsrus dataset. The three species caught showed higher catches during the dusk research angling sessions (Figure 4.5). Abundance of *P. africanum* was the lowest among the three species, and was not significantly different between time categories. However the abundance of *P. pantherinum* (KW-H (2, 221) = 15.3, $P = 0.0005$) and *H. fuscus* (KW-H (2, 221) = 7.65, $P = 0.022$) was significantly greater during dusk than morning and afternoon (Figure 4.5).

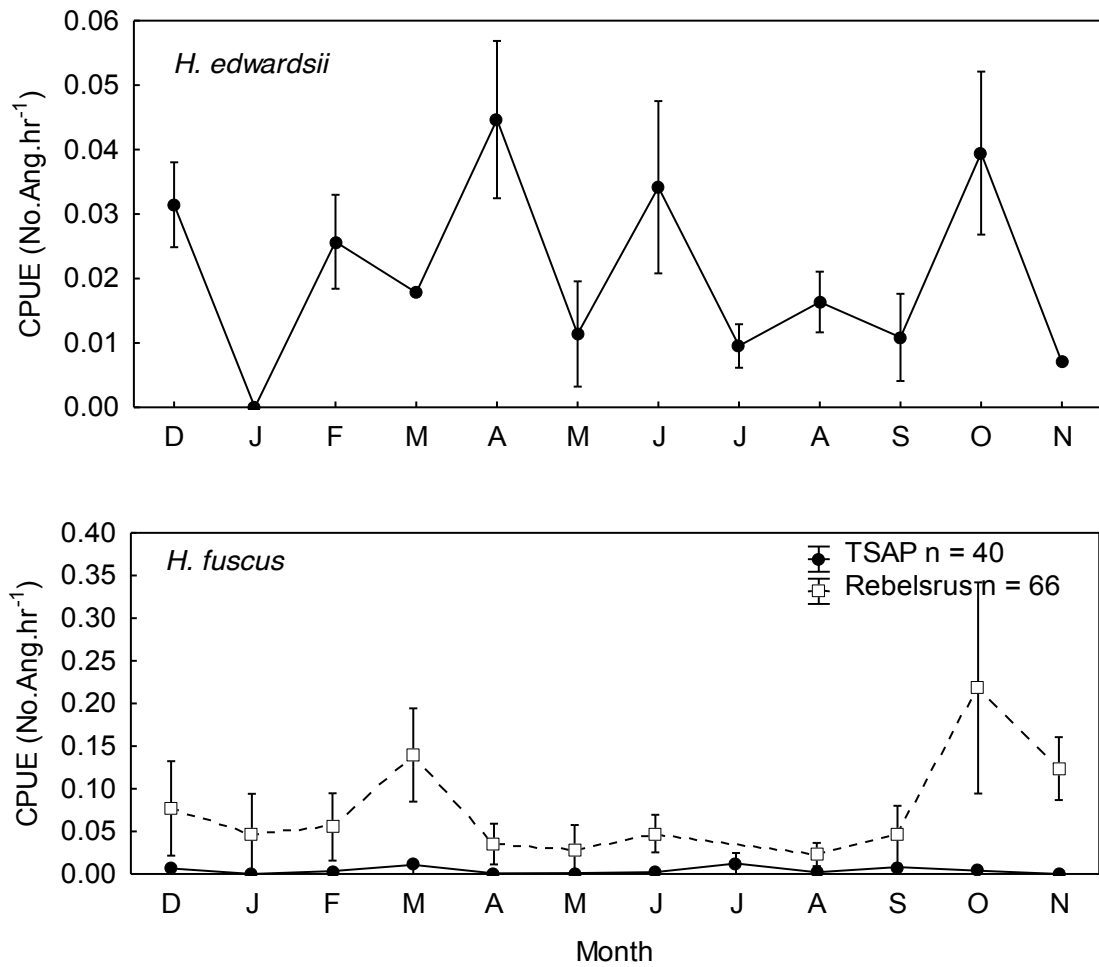


Figure 4.4: Average (\pm SE) monthly CPUE for *Haploblepharus* in TSAP and Rebelsrus. N = represents the total number of sharks captured. *H. edwardsii* was only capture by research angling in TSAP with an n = 290.

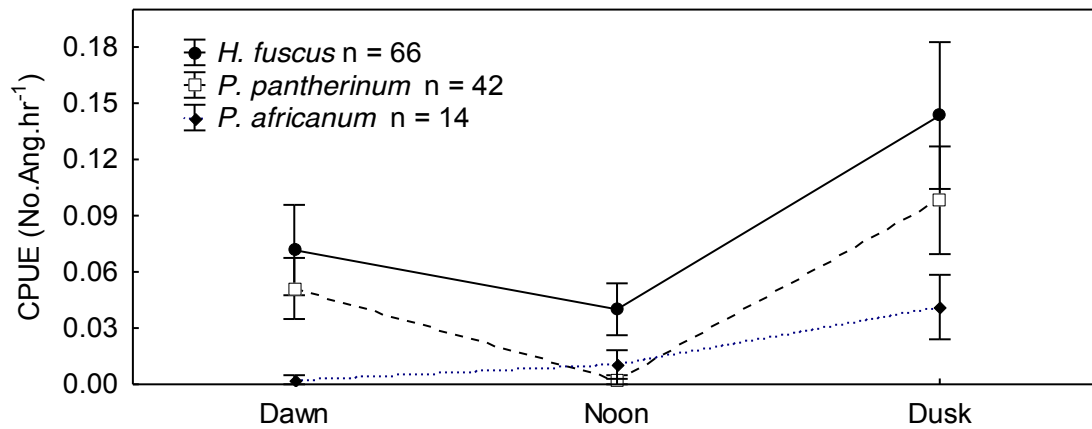


Figure 4.5: Average (\pm SE) CPUE for *Poroderma africanum*, *P. pantherinum* and *Haploblepharus fuscus* for the different research angling sessions at Rebelsrus. Total N= 221 (Dawn N = 67, Noon N = 72, Dusk N = 82).

4.3.2. Population size and density

Rebelsrus population size estimates were lowest for *P. africanum*, followed by *P. pantherinum* and highest for *H. fuscus* (Table 4.2). However, confidence in these estimates was low due to the low sample size for each of the species.

Table 4.2: Summary of species tagged, recaptured, population size estimate and 95% confidence intervals (CI) at Rebelsrus. The total number of sharks tagged in the Rebelsrus study was 108, however this table excludes *H. edwardsii* captures (3).

Species	Number tagged	Number recaptured	Recapture rate (%)	Population size	95% CI
<i>P. africanum</i>	14	3	21.43	47	19 - 268
<i>P. pantherinum</i>	35	10	28.57	80	37 - 560
<i>H. fuscus</i>	56	10	17.86	181	75 - 453

The study area was calculated as 1.032 km². Density estimates were the lowest for *P. africanum* with 45 sharks/km², followed by *P. pantherinum* (77 sharks/km²) and *H. fuscus* with the highest density (175 sharks/km²).

4.4. Discussion

Members of the family Scyliorhinidae, with more than 150 species worldwide, occur over a wide range of habitats. For example catsharks can be found from the temperate inshore waters of the Pacific Ocean (red-spotted catshark, *Schroederichthys chilensis* (Farina and Ojeda, 1993), to the Mediterranean Sea in the case of the Small-spotted catshark *Scyliorhinus canicula* (Donghia *et al.*, 1995). Some are endemic, such as *Halaelurus dawsoni* in New Zealand (Francis, 2006) and the Tiger catshark, *Halaelurus natalensis* in southern Africa (Heemstra and Heemstra, 2004). The four catshark species studied in this study are all endemic to southern Africa, and, with the exception of *P. africanum*, they are found across all three bio-geographical regions (subtropical, cool and warm-temperate). *P. africanum* is only recorded in the warm-temperate region of South Africa, which extends from Langebaan to Port St. Johns. The warm-temperate region of South Africa is characterized by water temperatures ranging from 15° C to 21° C (Hanekom *et al.*, 1989), which is in the preferred range for this species (Compagno *et al.*, 1989), and temperature is likely to be one of the factors limiting the distribution of this species. The effect of water temperature in limiting the distribution of animals has been observed in other species such as the Shortfin mako shark *Isurus oxyrinchus* (Casey and Kohler, 1992) and young Sandbar sharks *Carcharhinus plumbeus* (Merson and Pratt, 2001).

Other aspects of the environment are also likely to play a role in the distribution patterns and seasonal abundance of the study species. For example, within the warm-temperate region *H. edwardsii* and *H. fuscus* were found in the TSAP while only *H. edwardsii* was captured at Rebelsrus, and only on the offshore reefs using the fish traps. The coastal shelf along the Tsitsikamma coast is a mix of smooth sediment substratum and continuous bedrocks covered by sediment (Martin and Flemming, 1986), and the inshore depths where experimental fishing took place is often deeper than 10 metres. On the other hand rocky reefs dominate at Rebelsrus and the average depth of the bays ranges between five and eight metres. *H. edwardsii* is known to prefer soft substrates in depths up to 130 m while *H. fuscus* prefers shallow rocky reefs (Compagno *et al.*, 1989). Microhabitat separation between *H. edwardsii* and *H. fuscus* has in fact also been observed in the Southeastern cape region, where *H. fuscus* were found associated with

inshore rocky areas while *H. edwardsii* preferred deeper sandy substrates (Bass *et al.*, 1975; Compagno, 1984).

Not unexpectedly the results of this study indicate a high degree of residency with no evidence of a seasonal migration. From both the diving and fishing data at Rebelrus they do, however, only appear to spend limited time inshore, being most abundant in the bays during the night, likely related to nocturnal feeding behaviour, with resting periods during the day. Nocturnal behaviour has also been observed in the Swellshark *C. ventriosum*, and the bamboo sharks *C. punctatum* and *Hemiscyllium ocellatum*, where these species rest under corals during the day (Compagno, 1984). Night feeding is advantageous for these relatively small sharks who feed mainly on invertebrates and bony fishes (Compagno *et al.*, 1989; Compagno *et al.*, 2005), and are probably incapable of pursuing day - active prey (Compagno, 1984). As limited long-shore distribution of the study of these species was apparent, it is more likely that an inshore – offshore movement occurs, most probably on a daily basis. Although the reasons are unknown, inshore - offshore movement has been reported for hound sharks, *Mustelus asterias*, *M. lenticulatus* (Compagno, 1984) and in *M. norrisi* (Heemstra 1973).

Although found not to be statistically significant, some indication of temporal variation in abundance inshore was identified for all of the study species. In both the TSAP and Rebelrus data sets, and for both *P. africanum*, and *P. pantherinum*, CPUE decreased considerably during the autumn and winter months. In contrast, the shyshark, *H. edwardsii*, displayed no differences throughout the year, for the TSAP dataset. A difference in abundance may be attributed to a number of factors, e.g. feeding competition, avoidance of predators or reproductive behaviour, as suggested for *P. pantherinum* by Roux (2002). In this study the smallest species (*H. fuscus*) was most abundant in October, followed by *P. pantherinum* in November and lastly by *P. africanum*, the largest of the three species, in December. As all of the study species feed primarily on invertebrates and bony fishes (Compagno *et al.*, 2005), there may be some competition for food. In addition, *P. africanum* is known to feed on smaller sharks (Compagno *et al.*, 2005), and the smaller species may be more abundant inshore during periods of lower abundance of *P. africanum*. Predator-prey dynamics have been analyzed extensively in previous studies, suggesting that predators sharing a common

prey will probably adjust their behaviour (temporal change) in order to avoid competition (Arditi and Ginzburg, 1989). Reproduction may also play a role in the drop in numbers inshore in March for *P. pantherinum*, as they have been postulated to lay eggs on the offshore reefs (Roux, 2002).

Abundance estimates for sharks show a wide range, depending on the species, and life history characteristics. For example in South Africa, although with high confidence intervals, annual abundance estimates of Ragged-tooth (*Carcharias taurus*) range from 9 000 (1985-86) to 23 500 (1991-92) (Dicken *et al.*, 2008) while that of White sharks (*Carcharodon carcharias*) suggests an annual catch of 80 sharks with a preliminary population estimate of 655 and a range of 508 to 836 sharks between Cape Point to Natal (Cliff *et al.*, 1993). The only information from South Africa pertinent to the present study, shows the abundance of the Izak catshark *Holohalaelurus regani* to have increased from 1 606 tonnes in 1986 - 1993 to 3 012 tonnes in 1994 - 1999 (Richardson *et al.*, 2000). Outside of South Africa, the abundance of the Small-spotted catshark *Scyliorhinus canicula* has been estimated in Portugal from semi-pelagic long-lines of 2.17 per 1000 hooks and in trammel net of 0.17 per 1000 m (Coelho *et al.*, 2005), however the different methods of assessment preclude any direct comparison with this study.

This study was the first attempt to calculate population size for the catshark species *P. pantherinum*, *P. africanum* and *H. fuscus*, and as a result there is no literature available for comparison. Although preliminary it is likely that most of the model assumptions were met. For example, it is likely that there was limited recruitment during the study period, particularly as small sharks (less than 35 cm) were not tagged. Fishing mortality was also likely to be low as the area is isolated and does not experience much fishing pressure from recreational fisherman. Although a previous tag retention study on Ragged-tooth sharks showed high tag loss (Dicken *et al.*, 2006a), the high recapture rate for this study, with tags in good condition after more than 500 days at liberty, suggests that tag loss was minimal. Only a single tagged shark was caught outside of the area, and this recapture occurred after completion of the study, suggesting little or no immigration. However, the possible inshore – offshore daily movements of these species may have influenced the results, suggesting that they were not always available

for capture. Certainly a higher sample size is required to reduce the wide confidence interval of the estimates. In addition further studies assessing mortality rates, recruitment and tag-retention will be useful to further test the assumptions of the model.

The results, however suggest that shark numbers are fairly low in the study area, compared to other species such as the sparid roman *Chrysolephus laticeps* who shares similar life history characteristics (i.e. late maturity, slow growth, high site fidelity) (Kerwath *et al.*, 2007). In this study the population size was highest (180) for the species with the lowest recapture rate (*H. fuscus*), and lowest (47) for *P. africanum*, (a total of 75 catsharks per hectare) compared to red roman (in a marine protected area) with a density of 346 fish per hectare (Gotz, 2005; Kerwath, 2005).

Further studies to estimate population size will have to contend with the patchy distribution of the species and the changing topography of the coastline. Catshark estimates have been carried out at the family level in United States, with estimates of 75 sharks per hectare obtained from remotely operated vehicle (ROV) video transect census (Adams *et al.*, 1995), however such surveys are likely to be unsuccessful in inshore areas in South Africa due to the environmental conditions. It is interesting that during this study Adams *et al.* (1995), found that population estimates were always higher during video transects than trawl estimates.

The relatively low numbers coupled with the high degree of residency suggest that these species are vulnerable to localized depletion. Therefore, conservation strategies such as the designation of limited Marine Protected Areas (MPAs) may be useful in the conservation of these species. The nocturnal feeding behaviour may, however make these sharks less susceptible to inshore recreational fishers, who mainly fish during daylight hours.

CHAPTER 5

GENERAL DISCUSSION

As a group, chondrichthyans are vulnerable to overexploitation, and many species are under threat (Walker, 1998; Stevens *et al.*, 2000; Baum *et al.*, 2003; Myers *et al.*, 2007). A major reason for a lack of a conservation strategy for coastal sharks in South Africa and elsewhere can be ascribed to the lack of suitable information (Cavanagh *et al.*, 2003; Zhou and Griffiths, 2008). Although basic biological traits of chondrichthyan species are important it is now recognized that population dynamics, movement patterns and temporal abundance are also crucial to developing sound management and conservation frameworks.

Funding for research projects on non-commercial elasmobranch species in South Africa, is rare or non-existent. One has, therefore, to rely on scant and often flawed information from government agencies and volunteer programs. Programs such as the National Volunteer Tagging Program (NVTP), the National Marine Linefish System (NMLS) and the Tsitsikamma Shore Angling Program (TSAP) provide information on abundance, movement and catch rates of many marine species. Although these programs have drawbacks (i.e. misidentification, low recapture rates, a multi species scientific study etc) they do provide a valuable framework for developing species specific studies.

For this study the available databases (Table 5.1) provided information on distribution and some evidence for high site fidelity for catsharks and shysharks. This provided base line information with which to plan the dedicated study at Rebelsrus working in a limited area, and exploring various data collection techniques.

Table 5.1: Summary of data sets used for this study; catch rates for the NMLS, mark recapture data for the other three data sets.

Data sets	Movement	Abundance	Temporal variation	Population size
NMLS	X	√	√	X
NVTP	√	X	X	X
TSAP	√	√	√	X
Rebelsrus	√	√	√	√

The South African south east coast provides a considerable challenge to undertaking fieldwork. The dedicated study at Rebelsrus clearly revealed the limitations of working in a highly dynamic inshore environment, and frequent rough seas precluded a number of promising methods for data collection. For example the fish traps were unsuccessful but the technique itself has merit, and may be able to be adapted in the future to withstand the turbulent conditions inshore, and allow a less expensive method of deployment and retrieval offshore. Although acoustic telemetry was ineffective, it may prove useful in the offshore environment in deeper and calmer waters, and should be explored. Underwater visual census cannot be reliably undertaken on a regular basis, and therefore has limited value. Research angling provided the depth of data required for attempting to answer the objectives of this study (Table 5.2).

Table 5.2: Summary of the success or failure of data collection methods explored during the dedicated study at Rebelsrus.

Method	Inshore	Offshore
Fish traps	X	√
Acoustic telemetry	X	√
Underwater visual census	X	X
Research angling	√	√

Although limited, the investigation of the various data sets and methods did provide a range of information useful to our understanding of the movement of the study species. There are many reasons for animals to move around, it could be to find food, shelter, mates, breeding habitat, etc. This creates different categories into which movement can

be classified. For example, an animal can move within its home range in which case the movement can be classified as station keeping or commuting. Dingle and Drake (2007) described these two types as foraging movement between food resources in a repetitive mode, with the difference that commuting is a “round trip” behavior between spatially separated resources. In contrast the individual can move outside its home range in which case its movement can be classified as ranging or migrating. For ranging the individual may actively search for a new home in which to settle, while migration is movement without “distraction” (Dingle and Alistair Drake, 2007).

Movement of catsharks is difficult to classify since their home range has never been determined. High site fidelity and limited dispersal, particularly long shore, suggest “station keeping”. The limited information obtained from the diving surveys, the CPUE data, and the tag recapture data, however, suggest that the sharks only spent limited periods within the bays, and it appears that the home range may extend directly offshore of the bays, which could also suggest “commuting”.

Individuals appear to visit the bays during the night while moving to offshore areas during the day. This may be driven by foraging behavior inshore, with the offshore areas providing shelter and protection during the day.

Limited dispersal could prove disadvantageous for endemic species, making them an easy target for fishermen. However the nocturnal behavior of the study species may make these species less vulnerable as little fishing activity occurs directly offshore, and the maximum period of vulnerability appears to be during dusk and periods of darkness, when recreational fishing activity is limited.

Determining seasonal behavior, and having a better understanding of its triggers, could contribute in the generation of conservation strategies of endemic species. Although tenuous, the study did reveal some interesting seasonal trends. Decreased abundance from May to October, in at least three species, may be a response to abiotic factors such as water temperature, which has been shown for other species (Bass *et al.*, 1975; Compagno, 1984). The differential abundance of the species inshore during the year may be a response to competition and predator avoidance. Competition between these catshark species is likely to occur since they have similar habitat (coastal reefs) and

feeding preferences (Compagno *et al.*, 1989; Compagno *et al.*, 2004). Competition for food is likely, since prey items are similar, comprising small bony fishes, crustaceans and mollusks (Compagno, 1984; Compagno *et al.*, 2005; Ebert *et al.*, 2006). When species occur in the same space and share feeding resources they tend to have temporal adaptations in order to secure the resource, avoiding competition (Odum, 1971; Arditi and Ginzburg, 1989). This may lead to the exclusion of some species and smaller individuals (Odum, 1971). Predator avoidance is also likely for some species, for example *P. africanum* is known to feed on smaller sharks and on shark egg cases (Compagno *et al.*, 2004), and the presence of larger numbers of this species may preclude the abundance of smaller species such as *H. fuscus*. Although not the topic of the present study reproductive biology is also likely to play a role. Roux (2002) suggested, based on egg diameter, that *P. africanum* reproduces year round, while *P. pantherinum* has a peak during the autumn months (March-May). Other resident catshark species such as Nursehound shark, *Scyliorhinus stellaris*, show reproductive seasonality (Compagno, 1984).

Reef topography and depth of water appears to play a role in the distribution of the study species alongshore, this is highlighted by the differences in catches between Rebelsrus and Tsitsikamma (about 110 km apart). One species (*H. edwardsii*) was not found in the shallow bays at Rebelsrus, but was present directly offshore of the bays, while in the Tsitsikamma study it was found in large numbers inshore.

The factors presented above present a challenge when estimating population numbers for the study species, and the results must be considered with caution and should be considered as a rough first estimation. These are, however, the only data available, and can be used as base line information for management purposes. In future, detailed topographical information may assist in estimating numbers within the greater biogeographical zone.

The limited home range and low numbers of the study species inshore has implications for their conservation. A fairly small Marine Protected Area may be adequate for the protection of adults although it is unclear how far offshore this should extend. In order to decrease fishing pressure during spring and summer seasons, recreational fishing could be prohibited between dusk and dawn. Concomitantly it is also important that

there is an awareness campaign to educate recreational fishers and commercial boat fishers of the importance of the endemic shark species, and the need to return these alive. These conservation strategies need to be complemented with future research that focuses on inshore - offshore movement, reproductive strategies, and estimating population numbers.

REFERENCES

- Ackerman, J. T., Kondratieff, M. C., Matern, S. A. & Cech Jr, J. J. (2000). Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. *Environmental Biology of Fishes* 58, 33-43.
- Adams, P. B., Butler, J. L., Baxter, C. H., Laiding, T. E., Dahlin, K. A. & Wakefield, W. W. (1995). Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. *Fishery Bulletin* 93, 446-455.
- Aires-Da-Silva, A. M., Hoey, J. J. & Galluci, V. F. (2008). A historical index of abundance for the blue shark (*Prionace glauca*) in the western North Atlantic. *Fisheries Research* 92, 41-52.
- Anon (2002). Towards a South African shark management plan. *Fishing Industry News Southern Africa* August, 8.
- Arditi, R. & Ginzburg, L. R. (1989). Coupling in Predator-Prey Dynamics: Ratio-Dependence. *Journal of theoretical biology* 139, 311-326.
- Attwood, C. G. & Cowley, P. D. (2005). Alternate explanations of the dispersal pattern of galjoen *Dichistius capensis*. *African Journal of Marine Science* 27 (1), 141-156.
- Bass, A. J. (1972). The carcharhinid and scyliorhinid sharks of the east coast of southern Africa. Thesis. Durban: University of Natal. 269 pp.
- Bass, A. J. (1973). Analysis and Description of Variation in the Proportional Dimensions of Scyliorhinid, Carcharhinid and Sphyrnid Sharks. South African Association for Marine Biological Research. Durban: Oceanographic Research Institute. 28 pp.
- Bass, A. J., D'Aubrey, J. D. & Kistnasamy, N. (1975). Sharks of the east coast of southern Africa, II: The families Scyliorhinidae and Pseudotriakidae. Investigative Report. Oceanographic Research Institute. 1-64 pp.
- Bass, A. J., D'Aubrey, J. D. & Kistnasamy, N. (1976). Sharks of the east coast of southern Africa, 6: The families Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae. Investigative Report. Oceanographic Research Institute 1-103 pp.
- Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J. & Doherty, P. A. (2003). Collapse and Conservation of Shark Populations in the Northwest Atlantic. *Science* 17299 (5605), 389-392.
- Brouwer, S.L., Griffiths, M. H. & Roberts, M. J. (2003). Adult movement and larval dispersal of *Argyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area. *African Journal of Marine Science* 25 (1), 395-402.
- Bullen, E. M. & Mann, B. Q. (2007). Summary of tag and recapture data on catsharks (Family: Scyliorhinidae) from 1984-2006. Locality: Kosi Bay to Orange River. ORI Data Report. Durban: Oceanographic Research Institute. 18 pp.
- Bullen, E. M., Mann, B. Q. & Everett, B. (2008). Tagging News. Durban: Oceanographic Research Institute. 12 pp.
- Carlson, J. K., Heupel, M. R., Bethea, D. M. & Hollensead, L. D. (2008). Coastal Habitat Use and Residency of Juvenile Atlantic Sharpnose Sharks (*Rhizoprionodon terraenovae*). *Estuaries and Coasts* 31, 931-994.

- Casey, J. G. & Kohler, N. E. (1992). Tagging Studies on the Shortfin Mako Shark (*Isurus oxyrinchus*) in the Western North Atlantic. *Australian Journal of Marine and Freshwater Research* 43 (1), 45-60.
- Cavanagh, R. D., Kyne, P. M., Fowler, S. L., Musick, J. A. & Bennett, M. B. (2003). The Conservation Status of Australasian Chondrichthyans: Report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop. Brisbane, Australia: 182 pp.
- Cliff, G. & Dudley, S. F. J. (1991). Sharks Caught in the Protective Gill Nets Off Natal, South-Africa. 4. The Bull Shark *Carcharhinus-Leucas* Valenciennes. *South African Journal of Marine Science* 10, 253-270.
- Cliff, G. & Dudley, S. F. J. (1992). Protection against Shark Attack in South-Africa, 1952-90. *Australian Journal of Marine and Freshwater Research* 43 (1), 263-272.
- Cliff, G., Van der Elst, R. P., Witthuhn, T. K. & Bullen, E. M. (1993). Tagging of Great White Sharks *Carcharodon carcharias* on the South African coast provides a first estimate of population size. *Aide Memoire of the Great White Shark Workshop*. Sea Fisheries Research Institute May 3, 1993.
- Coelho, R., Erzini, K., Bentes, L., Correia, C., Lino, P. G., Monteiro, P., Ribeiro, J. & Gonçalves, J.M.S. (2005). Semi-pelagic Longline and Trammel Net Elasmobranch Catches in Southern Portugal: Catch Composition, Catch Rates and Discards. *Journal of Northwest Atlantic Fisheries Science* 35, 531-537.
- Compagno, L. J. V. & Heemstra, P. C. (1984). *Himantura draco*, a new species of stingray (Myliobatiformes: Dasyatidae) from South Africa, with a key to the Dasyatidae and the first record of *Dasyatis kuhlii* (Muller & Henle, 1841) from Southern Africa. *J L B Smith Institute of Ichthyology, Special Publication* 33, 17.
- Compagno, L. J. V. & Smale, M. J. (1986). Recent records of four warm-water elasmobranchs from the Eastern Cape Province, South Africa. *South African Journal of Marine Science* 4, 11-15.
- Compagno, L. J. V., Ebert, D. A. & Smale, M. J. (1989). *Guide to the sharks and rays of Southern Africa*. Cape Town: Struik. 160 pp.
- Compagno, L. J. V., Stehmann, M. & Ebert, D. A. (1990). *Rhinochimaera africana*, a new longnose chimaera from Southern Africa, with comments on the systematics and distribution of the genus *Rhinochimaera* Garman, 1901 (Chondrichthyes, Chimaeriformes, Rhinochimaeridae). *South African Journal of Marine Science* 9, 201-222.
- Compagno, L. J. V., Marks, M. A. & Fergusson, I. K. (1997). Threatened fishes of the world: *Carcharodon carcharias* (Linnaeus, 1758) (Lamnidae). *Environmental Biology of Fishes* 50, 61-62.
- Compagno, L. J. V., Dando, M. & Fowler, S. L. (2004). *A field guide to the Sharks of the world*. London. UK.: Collins. 370 pp.
- Compagno, L. J. V., Dando, M. & Fowler, S. L. (2005). *Sharks of the world*. New Jersey, USA: Princeton University Press. 368 pp.
- Compagno, L.J.V. (1984). FAO species Catalogue. Sharks of the World Part 2: Carcharhiniformes. *FAO Fisheries Synopsis* 4 (125), 251-655.
- Cowley, P. D. (1988). The biology, ecology and taxonomy of the blue stingray *Dasyatis pastinaca* (Linnaeus 1758). Research Report Series Grahamstown: Rhodes University Department of Ichthyology and Fisheries Science. 1-5 pp.

- Cowley, P. D. (1997). Age and growth of the blue stingray *Dasyatis chrysonota chrysonota* from the South-Eastern Cape coast of South Africa. *South African Journal of Marine Science* 18 (1), 31-38.
- Cowley, P. D. (1999). Preliminary observations on the movement patterns of white steenbras *Lithognathus lithognathus* and bronze bream *Pachymetopon grande* (Teleostei: Sparidae) in the Tsitsikamma National Park. In *3rd southern African Marine Linefish Symposium*, pp. 106-108. Arniston: South African Network for Coastal and Oceanographic Research Occasional Report.
- Cowley, P. D. & Compagno, L. J. V. (1993). A taxonomic re-evaluation of the blue stingray from Southern Africa (Myliobatiformes: Dasyatidae) *South African Journal of Marine Science* 13 (1), 135-149.
- Cowley, P. D. & Whitfield, A. K. (2001). Fish population estimates from a small intermittently open estuary in South Africa, based on mark-recapture techniques. *Marine and Freshwater Research* 52, 283-290.
- Cowley, P. D., Brouwer, S.L. & Tilney, R. L. (2002). The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern Cape coast of South Africa. *South African Journal of Marine Science* 24, 27-35.
- Crossland, J. (1982). Movements of tagged snapper in the Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research* 16, 1-15.
- Da Silva, C. (2007). The status and prognosis of the smoothound shark (*Mustelus mustelus*) fishery in the southeastern and Southwestern Cape coasts, South Africa. MSc Thesis. Grahamstown: Rhodes University. 162 pp.
- Dainty, A. M. (2002). Biology and ecology of four Catshark species in the Southwestern Cape, South Africa. Thesis. Cape Town: University of Cape Town. pp.
- Dainty, A. M., Marks, M. A., Griffiths, C. L. & Compagno, L. J. V. (2001). Age, growth and consumption rate analyses of four catshark species in the southwestern Cape, South Africa. In *6th Indo-Pacific Fish Conference*, pp. 21-22.
- De Bruyn, P., Dudley, S. F. J., Cliff, G. & Smale, M. J. (2005). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 11. The scalloped hammerhead shark *Sphyrna lewini* (Griffith and Smith). *African Journal of Marine Science* 27 (3), 517-528.
- Dicken, M. L., Booth, A. J. & Smale, M. J. (2006a). Preliminary observations of tag shedding, tag reporting, tag wounds and tag biofouling for ragged-tooth sharks (*Carcharias taurus*) tagged of the east coast of South Africa. *ICES Journal of Marine Science* 63, 1640-1648.
- Dicken, M. L., Smale, M. J. & Booth, A. J. (2006b). Shark fishing effort and catch of the ragged-tooth shark *Carcharias taurus* in the South African competitive shore-angling fishery. *African Journal of Marine Science* 28 (3-4), 589-601.
- Dicken, M. L., Smale, M. J. & Booth, A. J. (2006c). Spatial and seasonal distribution patterns of the ragged-tooth shark *Carcharias taurus* along the coast of South Africa. *African Journal of Marine Science* 28, 603-616.
- Dicken, M. L., Booth, A. J. & Smale, M. J. (2008). Estimates of juvenile and adult ragged-tooth shark (*Carcharias taurus*) abundance along the east coast of South Africa. *Canadian Journal of Fisheries Aquatic Science* 65, 621-632.
- Dingle, H. & Alistair Drake, V. (2007). What is migration? *Bioscience* 57 (2), 113-121.

- Donghia, G., Matarrese, A., Tursi, A. & Sion, L. (1995). Observations on the depth distribution pattern of the small-spotted catshark in the North Aegean Sea. *Journal of Fish Biology* 47 (3), 421-426.
- Dudley, S. F. J. & Cliff, G. (1993). Some Effects of Shark Nets in the Natal Nearshore Environment. *Environmental Biology of Fishes* 36 (3), 243-255.
- Dudley, S. F. J., Haestier, R. C., Cox, K. R. & Murray, M. (1998). Shark control: experimental fishing with baited drumlines. *Marine and Freshwater Research* 49, 653-661.
- Dudley, S. F. J., Cliff, G., Zungu, M. P. & Smale, M. J. (2005). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 10. The dusky shark *Carcharhinus obscurus* (Lesueur 1818). *African Journal of Marine Science* 27 (1), 107-127.
- Du Preez, H. H., Mclachlan, A. & Marais, J. F. (1988). Oxygen consumption of two nearshore marine elasmobranchs, *Rhinobatos annulatus* (Muller and Henle, 1841) and *Myliobatus aquila* (Linnaeus, 1758). *Comparative Biochemistry and Physiology. Part A: Molecular & Integrative Physiology* 89A (2), 283-294.
- Ebert, D. A. (1994). Diet of the six gill shark *Hexanchus griseus* off Southern Africa. *South African Journal of Marine Science* 14, 213-218.
- Ebert, D. A. (2002a). Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). *Marine and Freshwater Research* 53, 517-523.
- Ebert, D. A. (2002b). Some observations on the reproductive biology of the sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) from Southern African waters. *South African Journal of Marine Science* 24, 359-363.
- Ebert, D. A. & Cowley, P. D. (2003). Diet, feeding behaviour and habitat utilisation of the blue stingray *Dasyatis chrysonota* (Smith, 1828) in South African waters. *Marine and Freshwater Research* 54, 957-965.
- Ebert, D. A. & Cowley, P. D. (2008). Reproduction and embryonic development of the blue stingray, *Dasyatis chrysonota*, in southern African waters. *Journal of the Marine Biological Association of the United Kingdom*, 1-7.
- Ebert, D. A., Cowley, P. D. & Compagno, L. J. V. (1991). A preliminary investigation of the feeding ecology of skates (Batoidea : Rajidae) off the west coast of southern Africa. *South African Journal of Marine Science* 10, 71-81.
- Ebert, D. A., Cowley, P. D. & Compagno, L. J. V. (1996). A preliminary investigation of the feeding ecology of catsharks (Scyliorhinidae) off the west coast of Southern Africa *South African Journal of Marine Science* 17, 233-240.
- Ebert, D. A., Compagno, L. J. V. & Cowley, P. D. (2006). Reproductive biology of catsharks (Chondrichthyes: Scyliorhinidae) off the west coast of southern Africa. *ICES Journal of Marine Science* 63, 1053-1065.
- Farina, J. M. & Ojeda, F. P. (1993). Abundance, activity, and trophic patterns of the redspotted catshark, *Schroederichthys chilensis*, on the pacific temperate coast of Chile. *Copeia*(2), 545-549.
- Fennessy, S. T. (1994). Incidental capture of elasmobranchs by commercial prawn trawlers on the Tugela Bank, Natal, South Africa *South African Journal of Marine Science* 14 (1), 287-296.
- Francis, M. P. (1988). Movement patterns of rig (*Mustelus lenticulatus*) tagged in southern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 22, 259-277.

- Francis, M. P. (2006). Distribution and biology of the New Zealand endemic catshark, *Halaelurus dawsoni*. *Environmental Biology of Fishes* 75, 295-306.
- Francis, M. P. & Duffy, C. (2002). Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. *Marine Biology* 140, 831-842.
- Freer, D. W. L. & Griffiths, C. L. (1993a). Estimation of age and growth in the St. Joseph *Callorhynchus capensis* (Dumeril). *South African Journal of Marine Science* 13, 75-81.
- Freer, D. W. L. & Griffiths, C. L. (1993b). The fishery for, and general biology of, the St. Joseph *Callorhynchus capensis* (Dumeril) off the South Western Cape, South Africa *South African Journal of Marine Science* 13, 63-74.
- Gotz, A (2005). Assessment of the effect of Goukamma Marine Protected Area on community structure and fishery dynamics. PhD Thesis. Grahamstown: Rhodes University. 239 pp.
- Gray, M. S., Hecht, T. & Sauer, W. H. H. (2007). On the feasibility of a directed trap-fishery for panga *Pterogymnus laniarius* (Sparidae) in South Africa. *African Journal of Marine Science* 29 (3), 465-472.
- Grubbs, R. D. & Musick, J. A. (2007). Spatial delineation of summer nursery areas for juvenile sandbar sharks in Chesapeake Bay, Virginia. In *American Fisheries Society Symposium*.
- Gruber, S. H., Marignac, J. R. C. & Hoenig, J. M. (2001). Survival of Juvenile Lemon Sharks at Bimini, Bahamas, Estimated by Mark-Depletion Experiments. *Transactions of the American Fisheries Society* 130, 376-384.
- Hammerschlag, N., Martin, R. A. & Fallows, C. (2006). Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environmental Biology of Fishes* 76 (2-4), 341-350.
- Hanekom, N., Hutchings, L., Joubert, P.A. & Van Der Byl, P.C.N. (1989). Sea temperature variations in the Tsitsikamma Coastal National Park, South Africa, with notes on the effect of cold conditions on some fish populations. *South African Journal of Marine Science*(8), 145-153.
- Harris, S. A., Bennett, B. A. & Branch, G. M. (1988). An assessment of the role of the sand shark *Rhinobatos annulatus* as a predator in Langebeen Lagoon. *South African Journal of Marine Science* 7, 153-159.
- Heemstra, P.C. (1973). A revision of the shark genus *Mustelus* (Squaliformes Carcharhinidae). Ph.D. Thesis, University of Miami.
- Heemstra, P. C. & Heemstra, E. (2004). *Coastal Fishes of Southern Africa*. Grahamstown, South Africa: SAIAB - NISC. 488 pp.
- Hulley, P.A. (1970). An investigation of the Rajidae of the West and South Coasts of Southern Africa. *Annals of The South African Museum* 55 (4), 151-220.
- Hulley, P.A. (1972). The origin, interrelationships and distribution of Southern African Rajidae (Chondrichthyes, Batoidei). *Annals of The South African Museum* 60 (1), 1-103.
- Human, B. A. (2006a). Size-corrected shape variation analysis and quantitative species discrimination in a morphologically conservative catshark genus, *Poroderma* Smith, 1837 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) *African Natural History* 2, 1-15.

- Human, B. A. (2006b). A taxonomic revision of the catsharks genus *Holohalaelurus* Fowler 1934 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae), with descriptions of two new species. *Zootaxa* 1315, 1-56.
- Human, B. A. (2007a). Size-corrected shape variation analysis and quantitative species discrimination in a morphologically conservative catshark genus, *Haploblepharus* Garman, 1913 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *African Natural History* 3, 59 - 73.
- Human, B. A. (2007b). Size-corrected shape variation analysis and quantitative species discrimination in a morphologically conservative catshark genus, *Holohalaelurus* Fowler, 1934 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *Online journals* 3, 75-88.
- IUCN (2009). IUCN Red List of Threatened Species.
- Karczmarski, L., Winter, P. E. D., Cockcroft, V. G. & McLachlan, A. (1999). Population analyses of Indo-Pacific Humpback dolphins *Sousa chinensis* in Algoa Bay, Eastern Cape, South Africa. *Marine Mammal Science* 15 (4), 1115-1123.
- Kerwath, S. E., Gotz, A., Cowley, P. D., Sauer, W. H. H. & Attwood, C. G. (2005). A telemetry experiment on spotted grunter *Pomadasys commersonnii* in African estuary. *African Journal of Marine Science* 27 (2), 389-394.
- Kerwath, S. E., Gotz, A., Attwood, C. G., Cowley, P. D. & Sauer, W. H. H. (2007). Movement pattern and home range of roman *Chrysolephus laticeps*. *African Journal of Marine Science* 29, 93-104.
- Kerwath, SE (2005). Empirical studies of fish movement behaviour and their application in spatially explicit models for marine conservation. PhD:Science Thesis. Grahamstown: Rhodes University. 227 pp.
- Kohler, N. E. & Turner, P. A. (2001). Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes* 60, 191-223.
- Kroese, M. & Sauer, W. H. H. (1998). Elasmobranch exploitation in Africa. *Marine and Freshwater Research* 49, 573-577.
- Kroese, M., Sauer, W. H. H. & Penny, A. J. (1995). An overview of shark catches and by-catches in South African Fisheries. In *The 14th Regular Meeting of the Commission for the Conservation of Atlantic Tunas*, p. 23. Madrid, Spain.
- Lamberth, S.J., Sauer, W. H. H., Mann, B. Q., Brouwer, S.L., Clark, B.M. & Erasmus, C. (1997). The status of the South African Beach-seine and gill-net fisheries. *South African Journal of Marine Science* 18, 195-202.
- Latour, R. J. (2004). Chapter 4: Tagging methods and associated data analysis. In *Elasmobranch Fisheries Management Techniques*. (Musick, J. & Bonfil, R., eds.), pp. 285-381.
- Lucifora, L. O., Menni, C. R. & Escalante, A. H. (2002). Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. *ICES Journal of Marine Science* 59, 553-561.
- Lucifora, L. O., Menni, R. C. & Escalante, A. H. (2004). Reproductive biology of the school shark, *Galeorhinus galeus*, off Argentina: support for a single south western Atlantic population with synchronized migratory movements. *Environmental Biology of Fishes* 71, 199-209.
- Lukey, J. R., Booth, A. J. & Froneman, P. W. (2006). Fish population size and movement patterns in a small intermittently open South African estuary. *Estuarine, Coastal and Shelf Science* 67, 10-20.

- Marshall, A. D., Pierce, S. J. & Bennett, M. B. (2008). Morphological measurements of manta rays (*Manta birostris*) with a description of a foetus from the east coast of Southern Africa. *Zootaxa*(1717), 24-30.
- Martin, A. K. & Flemming, B. W. (1986). The Holocene shelf sediment wedge off the south and east coast of South Africa. Shelf sands and sandstones Canadian Society of Petroleum Geologists, Memoir. 27-44 pp.
- Martin, R. A. (2004). Natural mortality of puffadder shysharks due to Cape fur seals and black-backed kelp gulls at Seal Island, South Africa. *Journal of Fish Biology* 64, 711- 716.
- Martin, R. A., Hammerschlag, N., Collier, R. S. & Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of the Marine Biological Association of the United Kingdom* 85 (5), 1121-1135.
- McCord, M. E. (2005). Aspects of the ecology and management of the Soupfin shark (*Galeorhinus galeus*) in South Africa. Master Thesis. Grahamstown: Rhodes University. 122 pp.
- MCM (2002). Draft: Shark Management Plan. Cape Town: Marine and Coastal Management, Department of Environmental Affairs and Tourism & Rhodes University. 79 pp.
- Merson, R. R. & Pratt, H. L. Jr. (2001). Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. *Environmental Biology of Fishes* 61, 13-24.
- Moran, M., Burton, C. & Jenke, J. (2003). Long-term movement patterns of continental shelf and inner gulf snapper (*Pagrus auratus*, Sparidae) from tagging in the Shark Bay region of Western Australia. *Marine and Freshwater Research* 54, 913-922.
- Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. & Peterson, C. H. (2007). Cascading effects of the loss of Apex predatory sharks from a Coastal ocean. *Science* 315, 1846- 1850.
- Odum, E. P. (1971). *Fundamentals of ecology*. Mexico: W.B. Saunders Company. 574 pp.
- Okubo, A. (1980). *Diffusion and Ecological Problems: Mathematical Problems*. Berlin: Springer-Verlag. 294 pp.
- Parsons, G. R. (1990). Metabolism and swimming efficiency of the bonnethead shark *Sphyrna tiburo*. *Marine Biology* 104, 363-367.
- Petersen, S. L., Nel, D. C. & Ouardien, A. (2007). Towards an Ecosystem Approach to Longline Fisheries in the Benguela: An assessment of impacts on seabirds, sea turtles and sharks. WWF Report series. pp.
- Pradervand, P (2007). National Marine Linefish System: An inventory of catches of Scyliorhinids (catsharks) in selected regions of South African shore fishery. ORI Data Report. Durban: Oceanographic Research Institute. 6 pp.
- Pradervand, P. (2003a). National Marine Linefish System: Temporal trends in catches of dominant elasmobranch species in the shore-based competition fishery along the KwaZulu-Natal coast. ORI Data Report. Durban: Oceanographic Research Institute. 7 pp.
- Pradervand, P. (2003b). National Marine Linefish Systems: Assessment of catches of hammerhead shark (*Sphyrna spp.*) in the competitive shore fishery along the

- Transkei and KwaZulu-Natal coasts. ORI Report. Durban: Oceanographic Research Institute. 3 pp.
- Pradervand, P. (2004). National Marine Linefish System: Temporal trends in catches of *Carcharhinus obscurus* in the shore-based competition fishery along the KwaZulu-Natal and Transkei coasts. ORI Report. Durban: Oceanographic Research Institute. 3 pp.
- Pradervand, P., Mann, B. Q. & Bellis, M. F. (2007). Long-term trends in the competitive shore fishery along the KwaZulu-Natal coast, South Africa. *African Zoology* 42 (2), 216-236.
- Pribac, F., Punt, A. E., Taylor, B. L. & Walker, T. I. (2005). Using Length, Age and Tagging Data in a Stock Assessment of a Length Selective Fishery for Gummy Shark (*Mustelus antarcticus*). *Journal of Northwest Atlantic Fisheries Science* 35, 267-290.
- Punt, A. E. & Walker, T. I. (1998). Stock assessment and risk analysis for the school shark (*Galeorhinus galeus*) off southern Australia. *Marine and Freshwater Research* 49, 719-731.
- Richardson, A. J., Maharaj, G., Compagno, L. J. V., Leslie, R. W., Ebert, D. A. & Gibbons, M. J. (2000). Abundance, distribution, morphometrics, reproduction and diet of the Izak catshark. *Journal of Fish Biology* 56, 552-576.
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* 191 (191), 382.
- Rose, D. A. (1996). An Overview of World Trade in Sharks and Other Cartilaginous Fishes. *Traffic International*, 106.
- Rossouw, G. J. (1983). The biology of the sandshark *Rhinobatus annulatus* in Algoa Bay with notes on other elasmobranchs. Ph. D. Thesis. Port Elizabeth: University of Port Elizabeth. 180 pp.
- Rossouw, G. J. (1984). Age and growth of the sand shark, *Rhinobatos annulatus*, in Algoa Bay, South Africa. *Journal of Fish Biology* 25 (2), 213-222.
- Rossouw, G. J. (1987). Function of the liver and hepatic lipids of the lesser sand shark, *Rhinobatos annulatus* (Müller & Henle). *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* 86 (4), 785-790.
- Roux, C. (2002). Aspects of the reproductive biology of two catsharks, *Poroderma africanum* and *P. pantherinum* off the Eastern Cape coast, South Africa. Honours project. Grahamstown: Rhodes University. 30 pp. Unpublished
- Sebastian, C. R., Field, J. G., Sauer, W. H. H. & Smale, M. J. (2000). Status of the shark fishery: Rhinobatidae. *Southern African Marine Linefish Status Reports* 2000 (7), 218-219.
- Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters*. New York: Macmillan. 654 pp.
- Shelmerdine, R. L. & Cliff, G. (2006). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 12. The African angel shark *Squatina africana* (Regan). *African Journal of Marine Science* 28 (3-4), 581-588.
- Sims, D. W., Nash, J. P. & Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine Biology* (139), 1165-1175.
- Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G. C., Righton, D., Metcalfe, J. D., Nash, J. P. & Morritt,

- D. (2006). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology* 75, 176-190.
- Skjæraasen, J.E. & Bergstad, O.A. (2000). Distribution and feeding ecology of *Raja radiata* in the northeastern North Sea and Skagerrak (Norwegian Deep). *ICES Journal of Marine Science* 57, 1249-1260.
- Smale, M. J. (2002). Occurrence of *Carcharias taurus* in nursery areas of the Eastern and Western Cape, South Africa. *Marine and Freshwater Research* 53, 551-556.
- Smale, M.J., Sauer, W.H.H. and Roberts, M.J. (2001). Behavioural interactions of predators and spawning chokka squid off South Africa: towards quantification. *Marine Biology* 139, 1095-1105.
- Smale, M. J. & Cowley, P. D. (1992). The feeding Ecology of skates (Batoidea : Rajidae) off the Cape south coast, South Africa. *South African Journal of Marine Science* 12, 823-834.
- Smale, M. J. & Compagno, L. J. V. (1997). Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* Smith, 1957 (Pisces: Triakidae) *South African Journal of Marine Science* 18 (1), 229-248.
- Smith, C. & Griffiths, C. (1997). Shark and skate egg-cases cast up on two South African beaches and their rates of hatching success, or causes of death. *South African Journal of Zoology* 32 (4), 112 - 117.
- Stevens, J. D., Bonfil, R., Dulvy, N. K. & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476-494.
- Sumpton, W. D., Sawynok, B. & Carstens, N. (2003). Localised movement of snapper (*Pagrus auratus*, Sparidae) in a large subtropical marine embayment. *Marine and Freshwater Research* 54, 923-930.
- Swing, K. & Bearez, P. (2006). First record of an elephant fish (Chondrichthyes, Holocephali) in Ecuadorian waters during an ENSO event. *Revista de Biología Marina y Oceanografía* 41 (1), 107-109.
- Tidwell, J. H. & Allan, G. L. (2001). Fish as food: aquaculture's contribution. *European Molecular Biology Organization* 2 (11), 958-963.
- Van As, J. G. & Basson, L. (1996). An endosymbiotic trichodinid, *Trichodina rhinobatae* sp n (Ciliophora: Peritrichia) found in the lesser guitarfish, *Rhinobatos annulatus* Smith, 1841 (Rajiformes: Rhinobatidae) from the South African coast. *Acta Protozoologica* 35 (1), 61-67.
- Van der Elst, R. P. (1979). A proliferation of small sharks in the shore-based Natal sport fishery. *Environmental Biology of Fishes* 4 (4), 394-362.
- Verlecar, X. N., Desai, S. S. R. & Dhargalkar, V. K. (2007). Shark hunting – an indiscriminate trade endangering elasmobranchs to extinction. *Current Science* 92 (8), 5.
- Walker, T. I. (1998). Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* 49, 553-572.
- Wallace, J. H. (1967). The batoid fishes of the east coast of southern Africa. Part I: sawfishes and guitarfishes. Investigative Report. Oceanographic Research Institute. 1-32 pp.
- Wallace, J. H. (1969a). Final report on the skate and ray project. *South African Association for Marine Biological Research Bulletin* 7 (7), 24-26.

- Wallace, J. H. (1969b). Notes on some interesting batoid fishes. *South African Association for Marine Biological Research Bulletin* 7 (7), 26-30.
- Walmsley Hart, S. A., Sauer, W. H. H. & Buxton, C. D. (1999). The biology of the skates *Raja wallacei* and *R. pullopunctata* (Batoidea: Rajidae) on the Agulhas Bank, South Africa. *South African Journal of Marine Science* 21, 165-179.
- Walmsley, S. (1999). The biology of two important by-catch skate species on the Agulhas Bank, South Africa. Research Report Series Science, Department of Ichthyology and Fisheries Science. Grahamstown: Rhodes University 82-86 pp.
- Wetherbee, B. M., Gruber, S. H. & Rosa, R. S. (2007). Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. *Marine Ecology Progress Series* 343, 283-293.
- Wintner, S. P. & Dudley, S. F. J. (2000). Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of South Africa. *Marine and Freshwater Research* 51, 43-53.
- Wintner, S. P., Dudley, S. F. J., Kistnasamy, N. & Everett, B. (2002). Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Africa. *Marine and Freshwater Research* 53, 557-566.
- Wirsing, A. J., Heithaus, M. R. & Dill, L. M. (2006). Tiger shark (*Galeocerdo cuvier*) abundance and growth in subtropical embayment: evidence from 7 years of standardized fishing effort. *Marine Biology* 149, 961-968.
- Yeld, E. M. & Smit, N. J. (2006). A new species of Trypanosoma (Kinetoplastida: Trypanosomatidae) infecting catsharks from South Africa. *Journal of the Marine Biological Association of the United Kingdom* 86, 829-833.
- Zhou, S. & Griffiths, S. P. (2008). Sustainability Assessment for Fishing Effects (SAFE): A new quantitative ecological risk assessment method and its application to elasmobranch bycatch in an Australian trawl fishery *Fisheries Research* 91, 56-68.