MOVEMENT PATTERNS AND GENETIC STOCK DELINEATION OF AN ENDEMIC SOUTH AFRICAN SPARID, THE POENSKOP, *CYMATOCEPS NASUTUS* (CASTELNAU, 1861)

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ABSTRACT

Poenskop *Cymatoceps nasutus* (Pisces: Sparidae), an endemic South African sparid, is an important angling species being predominantly targeted by the recreational shore and skiboat sector. This species is slow-growing, long-lived, late-maturing and sex-changing, making poenskop acutely sensitive to over-exploitation. Despite interventions, such as the imposition of size and bag limits (currently 50 cm TL and one per licensed fisher per day) by authorities, catch-per-unit-effort trends reflect a severe and consistent stock decline over the last two decades.

Poenskop has been identified as a priority species for research and conservation. Although the biology and population dynamics of this species have been well-documented, little is known about the movement behaviour of poenskop. Furthermore, there is a complete lack of information on its genetic stock structure. This thesis aimed to address the current knowledge gaps concerning movement behaviour and genetic stock structure of poenskop, making use of a range of methods and drawing on available information, including available fishery records as well as published and unpublished survey and research data, and data from long-term monitoring programmes.

Analysis of available catch data (published and unpublished) revealed a decline in the number of poenskop caught as well as size of fish taken over the last two decades, ultimately reflecting the collapse of the stock (estimated to be at 20% of their pristine level). Improved catch-per-unit-effort data from the Tsitsikamma National Park Marine Protected Area (MPA), and larger poenskop being caught in the no-take areas than adjacent exploited areas of the Pondoland MPA confirmed that MPAs can be effective for the protection and management of poenskop. The current MPA network in South Africa is already well-established, and encompasses considerable reef areas, being preferable for poenskop habitation.

Conventional dart tagging and recapture information from three ongoing, long-term fish-tagging projects, conducted throughout the poenskop's distribution, indicated high levels of residency at all life-history stages. Coastal region, seasonality and time at recapture did not appear to have a significant effect on the level of movement or distance moved. However, on examining the relationship among coastal movements and fish size and ages, larger and older fish (adults) moved greater distances, with juveniles and sub-adults showing high degrees of residency. An estimation of home-range size indicated smaller poenskop to hold smaller home-ranges, while larger poenskop hold larger home-ranges. Large easterly displacements of a number of adult poenskop is in accordance with previous findings that this species may undertake a unidirectional migration up the coastline of South Africa where they possibly settle in Transkei waters for the remainder of their lives. This high level of residency makes poenskop vulnerable to localised depletion, although they can be effectively protected by suitable MPAs.

Despite considerable tagging effort along the South African coastline (2 704 poenskop tagged with 189 recaptures, between 1984 and 2010), there remains limited information on the connectivity of different regions along the South African coastline. This was addressed using mitochondrial DNA sequencing. The mitochondrial DNA control region was used due to its high substitution rate, haploid nature, maternal inheritance and absence of recombination. The mtDNA sequencing showed no evidence of major geographic barriers to gene flow in this species. Samples collected throughout the core distribution of poenskop showed high genetic diversity ($h = 0.88$, $\pi = 0.01$), low genetic differentiation among regions, no spatial structure ($\phi_{ST} = 0.012$, $p = 0.208$) and no evidence of isolation by distance.

The collapsed stock status of poenskop as well as the fact that it is being actively targeted by recreational and commercial fishers suggests that this species requires improved management, with consideration given to its life-history style, residency and poor conservation status. Management recommendations for poenskop, combined with increasing South Africa’s existing MPA network, include the possibility of setting up a closed season (during known spawning periods) as well as the decommercialisation of this species. The techniques used and developed in this study can also be adopted for other overexploited linefish species.

"When an angler lands his first large black biskop he is so impressed with the huge, bluntly-shaped, almost human head that he stands aghast at this extraordinary creation. And if the fish could only moan like the gurnard, and snort like the spotted grunter, many a new-comer to fishing would drop his line and run away!"

- Biden (1930: p 262) –

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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CHAPTER 1
GENERAL INTRODUCTION

"The blue musselcracker is found from False Bay to the north coast of Natal. In False Bay very few are caught by rock anglers, but the professional fishermen land quite a number every year as this species of musselcracker, unlike its white relative, is found in fairly deep water as well as inshore."

- Schoeman (1957: p 65) –

1.1. Study species

Poenskop *Cymatoceps nasutus* is an endemic South African sparid, being most commonly distributed along the southern and eastern coasts of South Africa, with occasional fish being recorded as far west as the south of Saldanha in the Western Cape, and as far east as Cape Vidal in northern KwaZulu-Natal (Smith and Heemstra 1986, van der Elst 1988a). This distribution is shared by the juveniles and adults, while the occurrence of larvae is unknown (Smith and Heemstra 1986, Booth 2000). The poenskop has several colloquial names and is also referred to as black musselcracker, black steenbras, blou biskop, stompkop, bank blouer, witbek and saqomolo. Known for its strong and aggressive behaviour, it is one of South Africa's iconic angling species (Smith and Heemstra 1986, Mann 2000, Heemstra and Heemstra 2004, Rouhani and Cowley 2004, Maggs 2011a) (Figure 1.1).

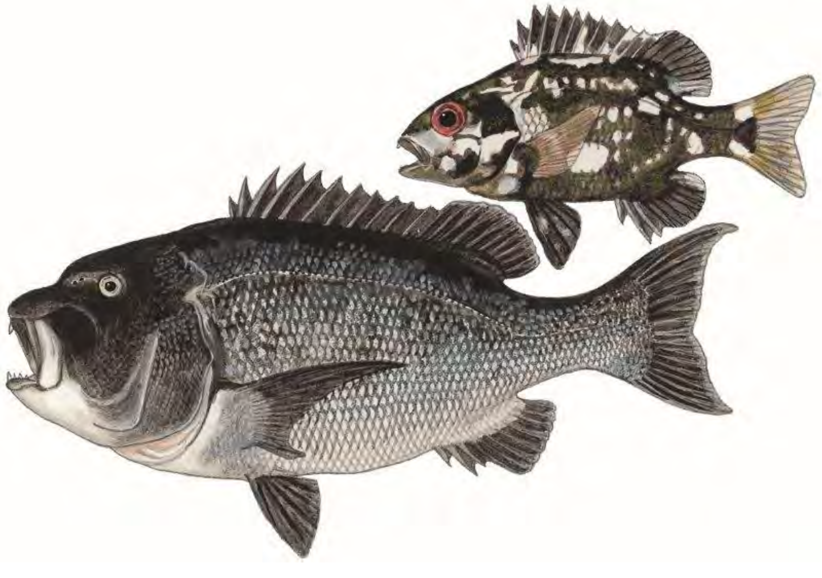

Figure 1.1: Illustration of an adult (bottom) and juvenile (top) poenskop *Cymatoceps nasutus* (Pisces: Sparidae) (Illustration from *Coastal Fishes of Southern Africa* (Heemstra and Heemstra 2004); Artist – Mrs Elaine Heemstra).

Poenskop are slow-growing and long-lived, attaining a maximum fork length (FL) of 1 089 mm, and a maximum age of 45 years (Buxton and Clarke 1989). Length-at-maturity has not been accurately determined, but based on a study done by Buxton and Clarke (1989), the length of the smallest recorded reproductively active female was 530 mm FL.

Poenskop have a generalist diet, with the most important prey groups being molluscs, crustaceans and echinoderms (Heemstra and Heemstra 2004). Buxton and Clarke (1989) found the octopus *Octopus vulgaris* and the chiton *Dinoplax gigas* to be the most important individual prey species in the poenskop's diet. Crustaceans are of considerable importance to juvenile poenskop, while gastropods and asteroids are common prey items of larger individuals (> 350 mm FL) (Buxton and Clarke 1989, Heemstra and Heemstra 2004).

Juveniles and sub-adults are resident along inshore reefs and in tidal pools, while adults are resident along inshore and offshore reefs (Buxton and Clarke 1989). Adults are also known to occur further offshore and are suspected of undertaking a unidirectional migration to the Transkei coast where they remain resident (Buxton and Clarke 1989, Booth 2000). The suspected displacement could be very similar to that undertaken by the red steenbras *Petrus rupestris*. This sparid species has similar life history characteristics to those of the poenskop. Red steenbras juveniles are extremely resident and slow-growing, making them susceptible to local depletion by fishing (Smale and Punt 1991, Brouwer 2002). The adult red steenbras undertake a migration to the Transkei coast and it is thought that the adults remain there for their entire lives (Brouwer 2002). Other South African sparids that are resident as juveniles but migrate as sub-adults to adults are the white steenbras *Lithognathus lithognathus* (Bennett 1993b) and the white musselcracker *Sparodon durbanensis* (Watt-Pringle 2009).

The poenskop is one of South Africa's most sought-after angling species (Biden 1930, Smith and Heemstra 1986). It is predominantly caught by members of the recreational shore and skiboat sector, but is also targeted by spearfishers (Coetzee and Baird 1981, Hecht and Tilney 1989, Brouwer et al. 1997, Mann et al. 1997). Poenskop are occasionally landed by commercial skiboat fishers, but are of little commercial importance due to low abundance. Poenskop appear to be of greatest abundance along the Transkei and south-east coastlines of South Africa (Smale and Buxton 1985, Booth 2000), despite catches of this species being small (Buxton and Clarke 1989). As a result of its importance as a recreational angling species, Wallace and van der Elst (1983) identified it as a priority species urgently in need of investigation.

1.2. Management of South African linefisheries

Fishing pressure has steadily increased over the last century as a result of, amongst other things, technological advancements in fishing gear. Due to the dependency on marine resources by the increasing human population, more than half of the world's fish stocks are fully exploited, and almost a third are overexploited or depleted (Bennett 2007, FAO 2010). As a result of the growing demand for marine resources, fish stocks are likely to decline further (Caddy and Griffiths 1995). A similar situation exists in South Africa, due to increases in fishing effort combined with a lack of law enforcement and compliance (Sauer et al. 2003). Some linefish stocks, many of which are reef-associated species, are considered to be collapsed. Griffiths (2000), on analysing catch-per-unit-effort data from the linefishery, showed that catch rates are much lower than those reported at the beginning of the century. Due to continued declines in catches, the Minister of the Department of Environmental Affairs and Tourism (now DEA) declared a "linefish crisis" in 2000 (Sauer et al. 2003). The linefishery was then regarded as being in a state of emergency (*Government Gazette* No. 21949 Notice 4727 of 2000) in terms of section 16 of the Marine Living Resources Act (Griffiths and Lamberth 2002).

Fishing can have an effect on biomass (Buxton and Smale 1989), stock size structure (Roberts and Polunin 1991, Buxton 1993b), growth rate (Buxton 1987), genetic structure and biotic diversity (Buxton and Smale 1989). The harvesting effect is often most apparent in reef species, due to certain life characteristics such as the late attainment of sexual maturity, lower natural mortality and greater longevity (Buxton 1993b). Because these species are less resilient to the impacts of fishing, even low levels of fishing effort would have an effect. Although fishing effects on fish stocks have been well documented (Russ 1991, Smith et al. 1991, Buxton 1993b, 1993c, Caddy and Griffiths 1995, Hall 1999, Levin and Grimes 2002, Hawkins and Roberts 2003, Götz et al. 2009a, 2009b), monitoring of population dynamics is important to provide an understanding of the implications of these effects (Buxton 1993a).

Conventional management measures, such as the imposition of size and bag limits (Attwood and Bennett 1994), and closed seasons, have often failed due to poor enforcement (Griffiths et al. 1999). As a result, fisheries managers in many countries have turned to Marine Protected Areas (MPAs) and Ecosystem Based Management (EBM) for the management and protection of reef fish stocks (Robert and Polunin 1991, DeMartini 1993, Penney et al. 1999, Russ 2002).

MPAs have been supported by numerous fisheries biologists (Buxton 1993b, Attwood and Bennett 1995, Zeller et al. 2003, Hilborn et al. 2004, Roberts et al. 2005, Mann et al. 2006, Pérez-Ruzafa et al. 2006), and are considered to be an important tool for the protection of resident invertebrates and reef-associated linefish species (Britz et al. 2001). Currently, they are amongst the most effective form of management for long-lived species exposed to intensive fishing pressure (Attwood et al. 1997a, 1997b). MPAs can also provide reference areas against which exploited areas can be compared, enabling one to assess the impacts fishing or protection has on a population (Griffiths and Wilke 2002, Hilborn et al. 2004). There are many biological benefits associated with MPAs, including (a) decreased fishing mortality (Russ 1991), (b) enhancement of resident stocks within the MPA due to direct protection (Bennett and Attwood 1991), (c) spillover of adults to adjacent fished areas facilitating the recovery of depleted stocks (Bennett and Attwood 1991, McClanahan and Mangi 2000, Berger et al. 2003, Zeller et al. 2003, Roberts et al. 2005), (d) seeding into adjacent fisheries through larval dispersal (Tilney 1993, Tilney et al. 1996), (e) improving size and age structure of the exploited populations (Buxton 1987, Buxton and Smale 1989, Russ 1991, Roberts and Polunin 1991), and (f) other benefits such as restoration of marine ecosystems (Gell and Roberts 2002).

The South African Marine Living Resources Act of 1998 called for long-term management plans for all exploited species. Included in these plans were operational management plans (OMPs) which specified clearly-defined decision rules for management action to be taken. The Linefish Management Protocol (LMP) was developed and the following information was defined for each species: (a) type of data needed to assess the stock, (b) the quantitative approach to be used, (c) appropriate biological reference points, (d) long-term goals for the stock, and (e) management actions needed to be taken to achieve these goals (Griffiths et al. 1999). Integrated Coastal Management (ICM) has also been used as a complementary measure to traditional fisheries management (Bennett 2007). The main goals of ICM include maximising social and economic benefits while focusing on optimal resource utilisation (Smith 2005); this being achieved through stakeholder participation and local knowledge. The implementation of the ecosystem approach to fisheries management was encouraged during the World Summit on Sustainable Development (WSSD) held in Johannesburg in 2002. The Ecosystem Approach to Fisheries (EAF) has similar goals to ICM in that it allows for the sustainable use of resources, meeting the needs of the users, but also maintains the ecosystem interactions and processes necessary for ecosystem functioning (Garcia et al. 2003).

The use of no-take MPAs, in conjunction with LMPs, ICMs and EAFs, is considered to be an effective complementary input management measure (Watt-Pringle 2009). Even after an MPA has been established, these conventional management measures should remain in place in the adjacent exploited areas (Russ 2002). This is particularly important when fishing becomes concentrated at the edges of an MPA (Bennett 2007).

In order to ensure effective management of a fishery species, baseline information on the species is required. Among fundamental knowledge of life-history, growth and reproductive biology, knowledge and information on the movement behaviour of a species is crucial. Additionally, information on the stock structure of the species is important.

1.3. Understanding animal movement behaviour

Understanding animal movement is fundamental to studying animal ecology and to design effective conservation and resource management strategies (Pittman and McAlpine 2001, Childs 2005). Movement is an important ecological process that determines the spatial, demographic and genetic structure of populations (Pittman and McAlpine 2001). Scales can include movement from a few centimetres to trans-oceanic movements spanning thousands of kilometres (Wilke and Griffiths 1999, Wilson et al. 2005, Chateau and Wantiez 2008). Large-scale and restricted movements require co-operative and localised management respectively. Movement has important implications for the use of no-take MPAs (Kramer and Chapman 1999, Gell and Roberts 2002). This is especially important in heavily-exploited species, in which movement information can become critical if populations are to be maintained or enhanced (Dugan and Davies 1993, Zeller and Russ 1998, Pittman and McAlpine 2001). Maintenance of long-term sustainability will then depend on understanding the relationship between animal movement patterns and management strategies (Pittman and McAlpine 2001).

1.4. Understanding stock structure

Many important recreationally exploited stocks are severely depleted (e.g. white steenbras *Lithognathus lithognathus* and red steenbras *Petrus rupestris*). Management is thus necessary to ensure sustainability and to assist in the recovery of depleted stocks (Ward 2000). Biological communities are naturally highly variable in space and time, and in addition, impacts of fishing practices are poorly understood. Biological stock structure information is often not incorporated into a stock assessment due to (a) genetic data on population structure not being available, (b) the stock bordering political and/or management boundaries, and (c) it not being economically feasible to monitor and set catch levels for each stock (Ward 2000). However, genetic studies can provide insight into the behaviour and natural history of a species, which would otherwise be impossible to identify by direct observation (Trexler 1990, Bell 2008). A variety of molecular genetics, morphological and life history characteristics have been used to determine the pattern of differentiation within and among species (Gyllensten 1985). A major challenge in any genetic analysis of population structure is to gain an understanding of the spatial and temporal scales that might be involved (Avise 2000). Information on the stock structure, combined with non-genetic data such as oceanographic data, life-history traits and movement assessments from tagging returns, can all be used to determine the most likely population structure model for the species under study (Ward 2000).

Although knowledge exists on the biology of the poenskop (Buxton and Clarke 1989), there is a deficiency of information regarding the movement behaviour and genetic stock structure of this species. Anecdotal information on the stock decline of poenskop exists, although the extent of decline has also not been assessed. Besides having important management implications, identifying the genetic diversity and structure, and movement behaviour of poenskop, as well as understanding the degree to which poenskop have declined, will greatly enhance our understanding of the ecology of this species.

1.5. Aims and objectives

The overall aim of this study was to investigate the movement behaviour and genetic stock structure of poenskop. Specific objectives were to:

(a) Evaluate the current and historic trends in catch (contribution by mass and weight (percentage) to total catch) and catch-per-unit-effort (CPUE – fish.angler-hour^{-1}) of poenskop using available fishery records, as well as published and unpublished survey and research data.

(b) Determine patterns of residency and movement of poenskop by analysing tag-recapture data from several dedicated tagging projects.

(c) Determine the genetic diversity of poenskop across its distribution, identifying possible stock substructure.

(d) Combine findings to suggest management recommendations for poenskop, as well as future research directions.

1.6. Thesis outline

This thesis is divided into six chapters.

Chapter 1 (General Introduction) provides an introduction to the study, outlining the known information on poenskop. The importance of understanding animal movement behaviour and genetic stock structure is also discussed. In this chapter, the management of the South African fisheries is also reviewed.

Chapter 2 (Materials and methods) provides a general overview of the study areas as well as the materials and methods used in this study.

Chapter 3 (Catch trends) focuses on the change in catch history of poenskop. This chapter draws information from a number of different sources including published and unpublished survey and research data, making use of total catch numbers and changes in catch-per-unit-effort (CPUE) over time.

Chapter 4 (Movement behaviour) deals with the movement behaviour of poenskop. Making use of information from several long-term tagging projects, residency patterns, direction of movement, seasonality of movement and other aspects are presented.

The genetic stock structure is discussed in Chapter 5 (Genetic stock structure), focussing on the intraspecific variation of poenskop based on the analysis of mitochondrial DNA (mtDNA) control region sequences. The aim of this chapter was to determine the genetic diversity and population structure of poenskop based on this genetic marker.

In Chapter 6 (General Discussion), the principal findings of the study are summarised in a general discussion and the contribution to the existing knowledge of this species is discussed. Management strategies and recommendations are suggested.

CHAPTER 2

MATERIALS AND METHODS

"The stompkop held many advantages. He knew every crevice and every reef, but the angler knew his tackle, knew how to handle his fish, and so long as the black biskop's head was kept up the fish stood small chance of winning the contest."

- Horne (1955: p 73) -

2.1. Introduction

In order to assess the status of fish stocks and to determine the effects fishing is having on fish resources, information in the form of either fishery-dependent or independent data needs to be collected. However, suitable methods need to be identified and adhered to in order to minimise sampling variability and to standardise results to allow comparisons to be made among different studies, monitoring programmes or monitoring areas (Sutherland 1996, ICES 2006, Bennett 2007).

This study made use of several methods (i.e. mark-recapture, molecular analyses and a desk-top study of fishery data). Data was collected throughout the distributional range of poenskop.

2.2. Methods involved in the collection of data

2.2.1. Fishery data

Fishery data (collected from the fishery itself) is an example of fishery-dependent data. This information typically includes aspects of catch, effort, gear types, fishing patterns and locations of fishing grounds, which can result in the collection of long time-series data sets (Die 1997, Penney et al. 1999, Bennett 2007). Both commercial and recreational fishery data can be collected, with commercial data being obtained from commercial catch records (Crawford and Crous 1982, Penney et al. 1999) and trawl surveys (Griffiths 2000), and recreational catch data from roving creel surveys (Brouwer et al. 1997, Cowley et al. 2002), access point surveys (Brouwer and Buxton 2002) and daily catch records (Hanekom et al. 1997, Penney et al. 1999).

Fishery-independent data, on the other hand, is typically collected through controlled research surveys (Samoilys and Gribble 1997), including acoustic surveys, underwater visual census, underwater video assessment, mark-recapture, mark-sighting and research-based controlled fishing. Fishery-independent data is considered to be more robust, accurate and representative and not biased by, among other things, false recordings (Die 1997).

In Chapter 3, fishery-dependent data from the National Marine Linefish System and fishery-independent data from marine protected areas (De Hoop Marine Reserve, Tsitsikamma National Park Marine Protected Area) were used to assess trends in poenskop catches over time. Additional information was obtained from a popular angling magazine *Stywe Lyne/Tight Lines* and personal angling records from the Transkei and Western Cape. This is covered in more detail in Chapter 3.

2.2.2. Fish movement behaviour

The study of fish movement behaviour can be extremely challenging in marine environments due to the impracticalities of observing fish underwater. Traditionally, fish movement patterns were identified by (a) observing fish above the sea surface, (b) inferring movement patterns from variation in catches over temporal and spatial scales, and (c) passing this information from generation to generation (Biden 1930, Watt-Pringle 2009). With advances in technology, movement behaviour can now be observed using a number of different methods (direct and indirect). Direct methods include SCUBA and remotely operated vehicles (ROV), as well as acoustic telemetry, while indirect methods make use of conventional tagging studies. Dingle (1996) contextualised fish movement types into station-keeping, ranging and migration, with station-keeping including movements such as foraging and territoriality. The station-keeping aspects of movement can be observed using underwater visual census (UVC) and underwater video assessment (UVA). UVC techniques have been used to estimate reef fish abundance since the 1950s (Brock 1954) and have been used to collect both qualitative and quantitative fishery-independent data, including behaviour information (Kulbicki 1998, De Girolamo and Mazzoldi 2001). UVA (including the use of a ROV) have been successfully used to assess reef fish populations (Parker et al. 1994, Willis and Babcock 2000, Stobart et al. 2007). Station-keeping movement behaviour has been identified in a number of studies making use of this method (Spanier et al. 1994, Johnson et al. 2003, Laurenson et al. 2004, Lorance and Trenkel 2006).

In terms of ranging and migration patterns (Dingle 1996), acoustic telemetry and the information obtained from mark-recapture programmes, is extremely useful. Acoustic telemetry, used to remotely track fish movements in the marine environment, typically makes use of internal tags (Zeller 1997, Eristhee and Oxenford 2001). This method has also been successfully used in a number of movement studies (Holland et al. 1993, Zeller 1998, Zeller 1999, Meyer et al. 2000, Baldwin et al. 2002, Lowe et al. 2003, Towler et al. 2003, Kerwath et al. 2005, Neat et al. 2006, Childs et al. 2008). The implanted acoustic tag emits a signal enabling the identification of a fish and its position. This signal is received via either a hydrophone operated from above or beneath the water surface, or permanent listening stations (Kerwath et al. 2007b, Childs et al. 2008, Watt-Pringle 2009). Spatial data from the tags can be obtained from data-logging archival tags on their recovery (tags can be programmed to detach and float to the surface; Gunn and Block 2001, Wilson et al. 2005) or by uploading the data to a satellite when the tag is exposed at the surface (when the fish surfaces) (Watt-Pringle 2009). Despite the advantages of acoustic telemetry, it is extremely expensive for many studies. The tag battery life and practical survey area size can also limit telemetry studies (Watt-Pringle 2009). Sea conditions can also affect the accuracy of measurements and practicality of data collection, as well as exposing sensitive equipment to environmental damage or destruction (Watt-Pringle 2009).

Mark-recapture using fish caught on hook-and-line has been extensively used to determine movement patterns of a number of different fish species (Holland et al. 1993, Attwood and Bennett 1994, Beentjies and Francis 1999, Lucas and Baras 2000, Gillanders et al. 2001, Brouwer 2002, Cowley et al. 2002, Griffiths and Wilke 2002, Brouwer et al. 2003, Moran et al. 2003, Chateau and Wantiez 2008, Smith 2008, Dagneaux et al. 2009, Escobar-Porras 2009). In order to discriminate between individuals or groups, identifiable tags, recognisable upon the recovery of the fish, are used (Moran et al. 2003, Brouwer et al. 2003). On collecting data from a sufficient number of individuals, one can make inferences about the movement behaviour of fish. This data includes the date and location of capture, as well as the date and location of recapture. Other information such as fish length and/or weight is also useful in order to determine the age of the fish, growth etc.

In Chapter 4, the movement behaviour of the poenskop is discussed in more detail. In order to determine movement patterns, information was drawn from (a) long-term monitoring projects of the De Hoop Marine Reserve, Tsitsikamma National Park Marine Protected Area and

Pondoland Marine Protected Area, and (b) the national volunteer tagging project run by the Oceanographic Research Institute. The many aspects of poenskop movement behaviour are discussed further in Chapter 4.

2.2.3. Genetic diversity and stock structure

Genetics is a valuable stock identification tool, and the resulting data can provide a direct basis for stock structuring (Ward 2000). Genetic markers, described by Okumųs and Çiftci (2003) as being a DNA sequence used to mark or track a certain locus on a particular chromosome (marker gene), can be used to identify stock structure by studying patterns of genetic variation within a certain species (Okumųs and Çiftci 2003). This information can provide insight into dispersal patterns of populations, of which the three most common approaches are (a) allozymes, (b) mitochondrial DNA (mtDNA), and (c) nuclear DNA. These approaches have been subject to a number of different reviews (Parker et al. 1998, Hallerman 2003, Galtier et al. 2009, Portnoy and Heist 2012).

Allozymes

The initial method used to determine genetic differences, based on the indirect expression of DNA loci, was followed by allozyme analysis (also known as protein electrophoresis) in the early 1970s (Utter 1994), and was mostly used to characterise population-level genetic variation in a number of fish species (Avise and Smith 1974, Allendorf et al. 1976, Utter 1991). This became the primary marker on which most genetic studies relied. The advantage of allozymes is that it is easy to apply (Park and Moran 1994, Shaklee and Bentzen 1998, Ward 2000). The speed and simplicity of this marker is one of its major advantages, and even though this technique has now been used for over 35 years, it continues to play a prominent role in the description of intraspecific genetic diversity (Okumųs and Çiftci 2003, Schlötterer 2004, Chauhan and Rajiv 2010). The use of allozymes has demonstrated that genetic markers can be useful in stock identification (Okumųs and Çiftci 2003), as well as population divergence estimation, subsequently enabling discrete fish stocks to be identified (Carvalho and Hauser 1994). Despite the advantages of using allozymes, it is now a costly method, and species with limited allozymic variation required highly polymorphic markers, which resulted in a search for markers at the DNA level (Park and Moran 1994). This, along with the molecular advances of the discovery of highly polymorphic repetitive, short nucleotide sequences (Wright 1993), and the ability to amplify genes or sequences via the polymerase chain reaction (PCR, Saiki et al. 1988), witnessed a surge of nuclear and mitochondrial DNA (mtDNA) variation studies (Park and Moran 1994, Ward and Grewe 1994, Carvalho and Hauser 1998), including studies making use of both mtDNA and microsatellite markers.

Mitochondrial DNA

This approach began in the 1980s, allowing the gene itself to be examined. MtDNA continues to hold promise in stock identification, is assumed to be more powerful than allozyme analysis for revealing population structure, and possesses several useful attributes (Ward and Grewe 1994, Shaklee and Bentzen 1998, Okumųs and Çiftci 2003). These include being maternally inherited (Hoeh et al. 1996), exhibiting only a single mitochondrial genotype (Shaklee and Bentzen 1998), being non-recombining (Shaklee and Bentzen 1998), being mainly selectively neutral (Okumųs and Çiftci 2003), and possessing a high rate of substitution (Shaklee and Bentzen 1998, Billington 2003). MtDNA is commonly used in a number of studies due to the sequences being easily accessible. The detection of nucleotide diversity in specific regions of the mtDNA genome (e.g. D-loop, NADH Dehydrogenase subunit genes) has been greatly advanced due to the availability of universal primers (Kocher et al. 1989), together with accumulating data (Karl and Avise 1993, Carvalho and Hauser 1994); this also making mtDNA a popular tool. Other attractions for using mtDNA include it having high rates of evolution, and following a clonal inheritance pattern which is well-suited to phylogenetic reconstruction (Wilson et al. 1985, Kocher and Carleton 1997). MtDNA has a smaller effective population size (together with high mutation rates), which means that differences accumulate and fix in the population more rapidly (Wilson et al. 1985, Naish 1990). The sensitivity of mtDNA in detecting intraspecific differences within a species has been demonstrated in freshwater and marine fishes (Graves et al. 1984, Avise et al. 1987, Palumbi and Wilson 1990, Magoulas et al. 1996, Hurwood and Hughes 1998, Waters and Burridge 1999, McGlashan and Hughes 2000). However, certain marine species appear to have less-variable mitochondrial genomes than freshwater or terrestrial species (Gyllensten 1985, Ovenden 1990, Ward et al. 1994).

Different regions of the mitochondrial genomes evolve at different rates, and as a result, certain types of studies have made use of certain regions of the mtDNA. Cytochrome *b* and NADH Dehydrogenase subunit genes are known to exhibit variability on the population level (Carr and Marshall 1991, Brown et al. 1993), while the control region (D-loop) has been targeted for population studies due to its variability. MtDNA variation may be analysed with three different approaches; (a) Restriction Fragment Length Polymorphism (RFLP) analysis of whole purified mtDNA obtained from fresh tissue, (b) Amplified Fragment Length Polymorphism (AFLPs) which is based on the detection of genomic restriction fragments by PCR amplification, or (c) DNA sequencing of small mtDNA segments obtained by PCR amplification (Vos et al. 1995, Okumųs and Çiftci 2003). One disadvantage of mtDNA is that the analysis of frequency distributions requires larger sample sizes (Ward 1989, Ovenden 1990, Naish et al. 1993, Carvalho and Hauser 1994). However, mtDNA can provide data sets to use (a) a frequency data set, and (b) a sequence variation data set (Wilson et al. 1985).

Nuclear DNA - Microsatellites

Polymorphic DNA sequences consist of variable-number tandem repeats (VNTRs) of nucleotide sequences; these exhibit allelic variations in the number of repeat units in a given array. Among the classes of VNTRs, the two most important for population analysis, are minisatellites and microsatellites (Tautz 1989, Wright 1993, Wright and Bentzen 1994, O'Reilly and Wright 1995, Shaklee and Bentzen 1998). Several features of VNTRs make them ideal for examining fish population structure. This includes them being non-coding regions of nuclear DNA, requiring small amounts of tissue (Carvalho and Hauser 1994, Hansen et al. 2001) and having highly variable levels of heterozygosity (Wright 1993, Wright and Bentzen 1994, Goldstein and Pollock 1997).

Microsatellites are rapidly becoming the genetic marker most used in population and fisheries biology studies. They are co-dominant nuclear markers that are inherited in a Mendelian way, making them ideal for fine-scale stock structure studies (Carvalho and Hauser 1998, Shaklee and Bentzen 1998, DeWoody and Avise 2000, Ward 2000, Hardy et al. 2003). In some instances, microsatellites have been used to detect genetic differentiation among populations where allozyme markers have been unsuccessful, most notably in marine fishes (Ruzzante et al. 1998, Shaw et al. 1999). One of the problems with microsatellite application to stock identification (and other areas), is uncertainty over the appropriate mutation model, and as a result, the appropriate measure of differentiation (Hauser and Ward 1998). Other disadvantages include (a) first requiring previous genetic information on a study species which can be time-consuming, (b) problems can be associated with PCR of microsatellites, (c) microsatellite loci can have complex mutation processes (O'Connell and Wright 1997, Parker et al. 1998), and (d) require a large amount of effort (Chauhan and Rajiv 2010). The advantages and disadvantages of the above techniques and their use for fisheries analysis are described elsewhere (see Park and Moran 1994, Ward and Grewe 1994, O'Reilly and Wright 1995, Hauser and Ward 1998, Parker et al. 1998, Okumųs and Çiftci 2003).

In Chapter 5, the genetic stock structure of poenskop was determined by analysing generated mitochondrial control region sequences. Within the vertebrate mitochondrial genome, the most useful region for studying genetic variation at the intraspecific level is the control region, owing to its extremely high rate of substitution (Meyer 1994). For this reason, and it being used in many successful studies (Lee et al. 1995, Ostellari et al. 1996, Chen et al. 1998, Donaldson and Wilson Jr. 1999), the control region was chosen to determine the genetic stock structure of the poenskop. Microsatellites were not used because no previous information on the genetic structure of poenskop exists, and the costs involved were too high. Samples, in the form of fin clips, were collected from across the South African coastline; PCR amplifications were carried out using specifically designed primers; resulting sequences were then statistically analysed to determine whether there was any variation within the poenskop stock. These approaches are described in greater detail in Chapter 5.

2.3. South African coastal marine environment and biogeography

The South African coastal zone extends approximately 3 500 km, from the Orange River (28°38'S, 16°27'E) in the west, to Kosi Bay (26°54'S, 32°48'E) in the east, and is bordered by both the Atlantic and Indian Oceans. This region covers a wide range of climatic and oceanic conditions, and as a result, supports a great diversity of flora and fauna (Harrison 2002, Harrison 2003). A large number of studies have been conducted in order to identify and qualify the biogeographic zones along the South African coast (Stephenson and Stephenson 1972, Brown and Jarman 1978; Emanuel et al. 1992, Engledow et al. 1992, Bustamante and Branch 1996, Prochazka 1998, Turpie et al. 2000, Harrison 2003, Teske et al. 2009b, Griffiths et al. 2010). It is generally agreed that the inshore marine environment of the South African coastline is comprised of three to four main biographical regions (Figure 2.1) (Hockey and Buxton 1989), namely the cool temperate region, warm temperate region, subtropical region and tropical region, with the latter not being universally accepted (Teske et al. 2009b). The cool temperate region for fishes (based on Turpie et al. 2000), which extends from Cape Point in the south, northwards to Namibia, has a low species richness, as well as low endemic species richness. In contrast to this, the subtropical region, extending from Mozambique in the north-east, southwards to approximately Port St John's, is characterised by high ichthyofaunal species richness, particularly of Indo-Pacific species (Turpie et al. 2000, Bennett 2007, Wartenberg 2011). The warm temperate region forms the transition between these biogeographical regions, and is characterised by increasing species richness from west to east (Turpie et al. 2000, Bennett 2007). This region has a particularly high richness of southern and South African endemics (Turpie et al. 2000), many of which are important to the recreational and commercial fisheries (Buxton 1993a, Attwood et al. 2002).

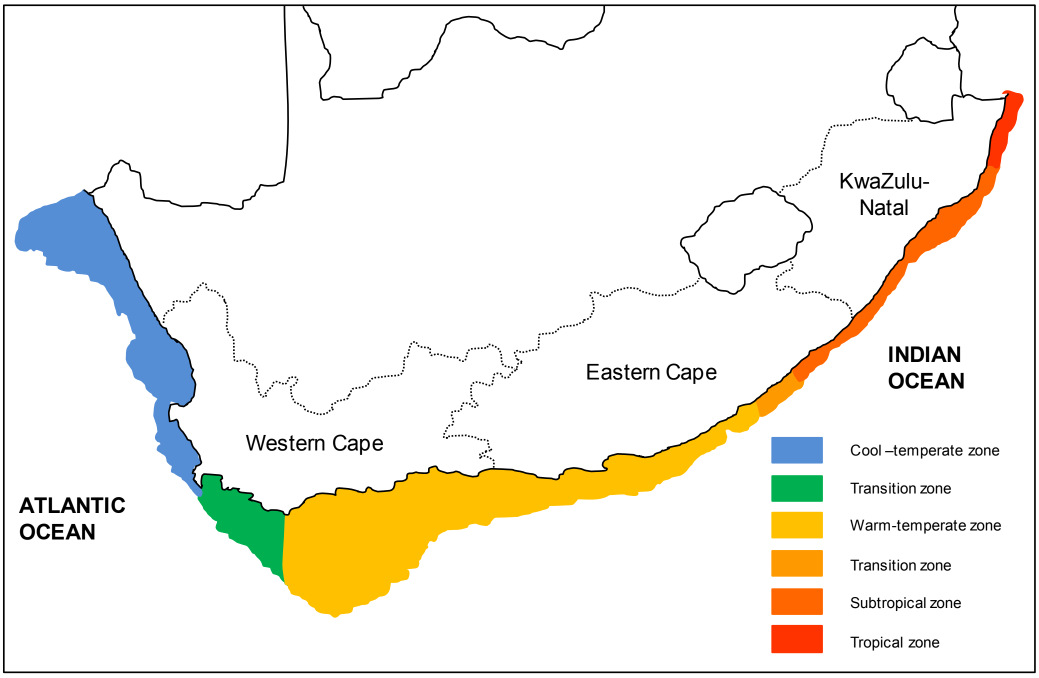

Figure 2.1: Map of South Africa showing the three main biogeographic regions (after Hockey and Buxton 1989), identified by patterns in the distribution of intertidal flora and fauna.

In contrast to these three regions, an alternative four inshore coastal bioregions have been identified by Driver et al. (2005). Bioregions are based on large-scale biological variability and biogeography, as well as large scale habitat differences related to different current systems with different temperatures and productivity (Cox and Moore 1998, Lombard et al. 2004). These include a cold Namaqua Bioregion (Sylvia Hill in Namibia to Cape Columbine), a cool-temperate South-western Cape Bioregion (Cape Columbine to Cape Point), a warm-temperate Agulhas Bioregion (Cape Point to Mbashe River) and a subtropical

Natal Bioregion (Mbashe River to Cape Vidal; Figure 2.2) (Driver et al. 2005, Götz 2005). An additional bioregion, the Delagoa Bioregion was identified by Sink et al. (2005) between Cape Vidal and Mozambique; this being distinct from the Natal Bioregion (Table 2.1).

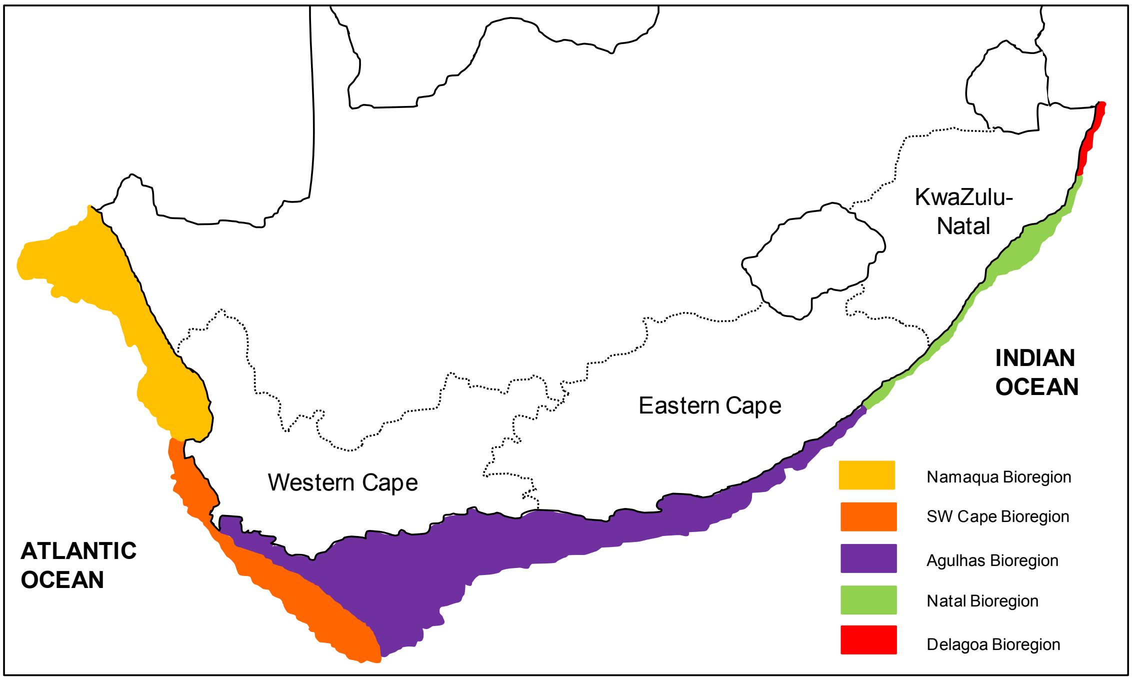

Figure 2.2: Map of South Africa showing the locations of inshore bioregions on the continental shelf.

Table 2.1: Information on the five recognised bioregions along the coastline of South Africa.

Bioregion	Coastline covered	Biogeographic zone	Species supporting break	Supporting literature
Namaqua	Syliva Hill to Cape Columbine	Cool temperate	Seaweed and invertebrate data; intertidal and subtidal habitats	Bustamante and Branch 1996 Bolton and Anderson 1997 Emanuel et al. 1992 Engledow et al. 1992
South-western	Cape Columbine to Cape Point	Cool temperate	River communities Seaweed communities Intertidal communities Rock lobster fishery	Eekhout et al. 1997 Engledow et al. 1992 Emanuel et al. 1992 Griffiths et al. 2004
Agulhas	Cape Point to Mbashe River	Warm temperate	Inshore subsurface temperature Estuarine fish communities Linefish catches Seaweed communities	Beckley and van Ballegooyen 1992 Harrison 2002 Fennessy et al. 2003 Bolton et al. 2004
Natal	Mbashe River to Cape Vidal	Subtropical	Marine community structure Seagrass and mangrove distribution patterns Tropical seabirds Cetacean species	Sink 2001 Bolton et al. 2004
Delagoa	Cape Vidal to Inhaca	Subtropical	Rocky shore habitats	Sink 2001

Poenskop are endemic to the warm-temperate and subtropical biogeographic zones, or alternatively, to the Agulhas and Natal bioregions (in which the poenskop's core distribution falls). In KwaZulu-Natal waters, poenskop are caught mostly in waters with a depth of 40 to 70 m, with catches from the shore being rare (although juvenile poenskop are known to occur inshore (Mann *pers comm.*). In the Transkei, they are caught in much shallower waters, with depth ranging from 8 to 30 m (Buxton and Clarke 1989). Poenskop are caught at a depth of 30 m or less, west of Port Elizabeth. Because the depths at which this species is found fluctuates between different regions, it is thought that poenskop remain in a preferable temperature range, living in deeper waters in KwaZulu-Natal and moving to shallower waters further westwards, often moving closer to the shore (van der Elst 1988a).

2.4. Oceanography

The coastal waters of southern Africa are influenced by two major ocean current systems, namely the Agulhas Current (south-flowing along the east coast) and the Benguela Current (north-flowing along the west coast) (Shannon 1989; Harrison 2003). The associated oceanographic conditions for each current system are thought to not only shape faunal distributions, but in many cases, the reproductive strategy of particular species (Sink et al. 2004; Watt-Pringle 2009). The Benguela Current which is characterised by cold, nutrient-rich upwellings supporting high levels of primary production, is predominantly wind-driven and flows upwards along the continental land mass (Kamstra 1985). In contrast, the Agulhas Current is a powerful western boundary current driven by the Coriolis Force – a result of the Earth's rotation. It flows in a southwesterly direction along the coast, bringing warm tropical water southwards. The Agulhas Current flows in close proximity to the South African coastline, often with greatest current velocities near the shelf break, and is largely responsible for driving inshore current patterns on the east coast (Figure 2.3).

The Agulhas Current

The east coast oceanography is dominated by the Agulhas Current, bringing warm water down the coast from the tropics (Schumann 1988, Beckley and van Ballegooyen 1992). As a western boundary current, it closely follows the continental slope south of the Delagoa Bight, becoming a detached free-flowing jet near the southern tip of the Agulhas Bank. Here it undergoes retroflection and sheds some warm rings into the South Atlantic (Roberts et al. 2010). The continental shelf varies in width, narrowing out along the Wild Coast (Beckley et al. 2002, Lutjeharms 2006), where the Agulhas Current reaches it maximum velocity (Shannon 1989, Maggs 2011a). This current also influences the inshore shelf waters between Umkomaas and Mkambati, where flow speed averages 0.75 m.sec^{-1} (Roberts et al. 2010). An upwelling cell occurs between Waterfall Bluff and Port St John's, due to the presence of a cyclonic eddy (Roberts et al. 2010). Roberts et al. (2010) also found indication of narrow counter-currents between Port Alfred and the Keiskamma River, as well as off Port St John's. The Pondoland subtidal environment consists of shelving reef complexes which run parallel to the coast (Ramsay 1994, Birch 1996, Bosman et al. 2005).

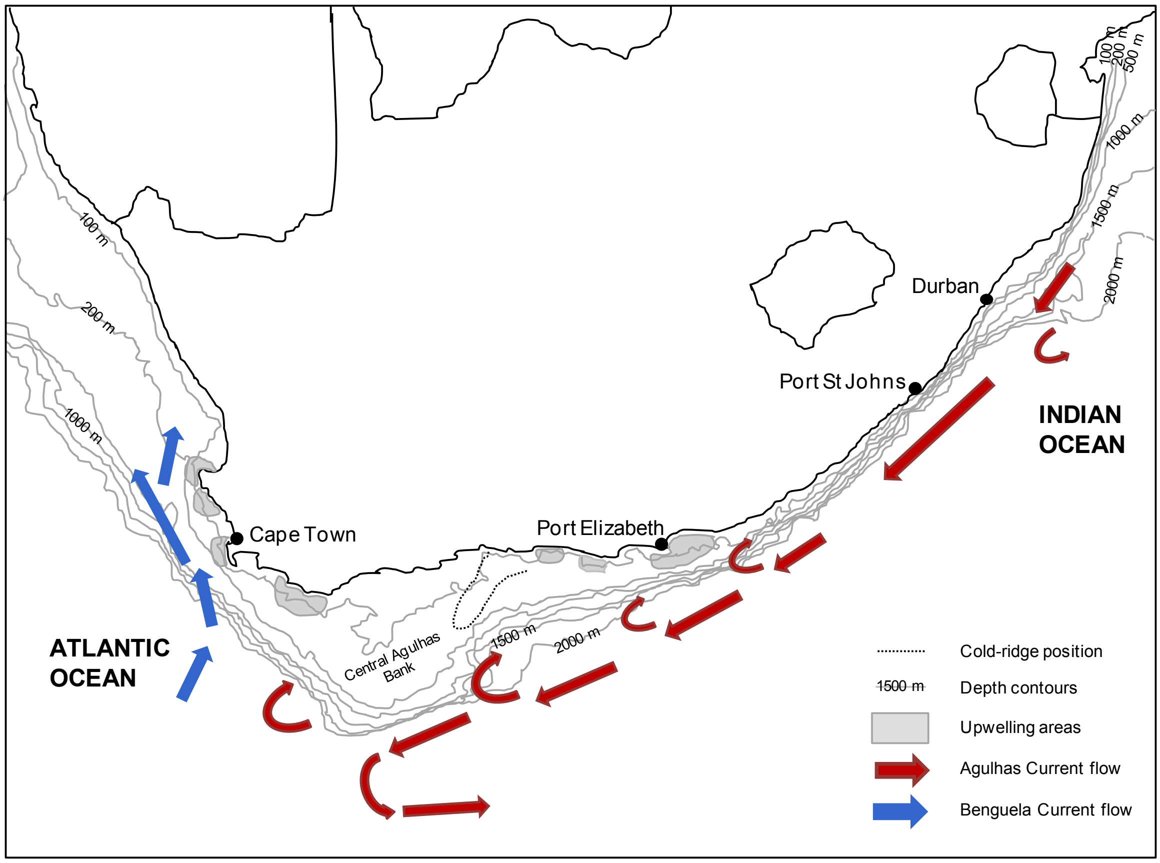

Figure 2.3: Map of South Africa showing the locations of the major current systems, and depth contours. The shelf on the east coast of South Africa is narrow, especially between Durban and Port St Johns. Upwelling areas are those described by Hutchings et al. (2002) and the location of the cold-ridge is according to Roberts and van der Berg (2005).

The characteristics of the Agulhas Current along the east coast could result in early life-history stages of marine organisms, including eggs and planktonic larvae, having the potential of being transported great distances from their place of origin (Hutchings et al. 2002). A number of fish species make use of this spawning strategy (spawning “upstream” of juvenile nursery areas). These include geelbek *Atractoscion aequidens*, red steenbras *Petrus rupestris*, shad *Pomatomus saltatrix* and white steenbras *Lithognathus lithognathus* (Hutchings *et al*. 2002).

South of East London (33°20’S, 27°55’E) the continental shelf width broadens, reducing the effect of the Agulhas Current on the nearshore environment (Watt-Pringle 2009). However, Roberts et al. (2010) identified onshore flow over the shelf edge near Port Alfred, and a narrow eastward current near the coast. The continental shelf then becomes wide and shallow in an area known as the Agulhas Banks (Lutjeharms 2006). The widest part extends 200 km offshore (Shannon 1989). Here the Agulhas Current has even less of an influence on the nearshore environment, which is now effected more strongly by coastline topography, localised wind-driven upwelling and coastal trapped waves (Schumann and Brink 1990, Schumann 1999). A prominent, semi-permanent elongated feature, referred to as the “cold-ridge”, is situated east of Plettenberg Bay and Cape Padrone (Boyd and Shillington 1994, Roberts 2005). This feature is formed when the thermocline is lifted towards the sea surface, resulting in the colder, nutrient-rich water entering the photic zone (Roberts and van der Berg 2005). Roberts (2005) showed that this cold-ridge is an upwelling filament that originates in the intense coastal upwelling zone along the Tsitsikamma coast. Tilney et al. (1996) also noticed coastal upwelling events on the South Coast, with eastward flow occurring near the seabed off the Tsitsikamma coast. Attwood et al. (2002) found that this current was more westwards, with the inshore surface current having a higher velocity. As one moves further west along the Western Cape coastline, the Benguela circulation system becomes more important (Boyd et al. 1992). The Agulhas Current changes flow direction from west south-west to south south-west between Port Elizabeth and Mossel Bay (Lutjeharms and van Ballegooyen 1988). This flow eventually meets up with the Benguela Current at the Cape Peninsula, increasing velocity at Cape Columbine (Boyd et al. 1992). Therefore, all these oceanographic and topographical features, especially those associated with the Agulhas Current, will influence the dispersal and possibly the distribution of larvae, juveniles, sub-adults and adults of poenskop.

2.5. Marine Protected Areas

2.5.1. De Hoop Marine Protected Area

The De Hoop MPA (DH), which lies adjacent to the De Hoop Nature Reserve, is situated in the Western Cape along the warm temperate South Coast (Attwood 2003) (Figure 2.4). This was declared a “no-take” MPA in 1984 under the Nature and Environmental Conservation Ordinance 19/1974 (Lemm and Attwood 2003). No fishing activities were permitted along a 51 km stretch of coastline, within a distance of 5.6 km from the shore (Attwood 2003). This MPA covers a total area of approximately 315 km^2. The shoreline consists of high-energy, broken sandy shores, interspersed with wave-cut sandstone platforms (Attwood and Cowley 2005). Other topographic features such as boulder bays, sandy beaches, subtidal rocky reefs and subtidal sandy benthos, are also present (Lemm and Attwood 2003). The surf-zone reefs are all at depths <6 m, some of which extend out 200 m from the shore (Attwood 2003).

Data used in Chapter 3 and 4 is the result of a controlled shore-angling project which was initiated at Koppie Alleen to study galjoen *Dichistius capensis* in 1984. The project then became the only allowed fishing activity within the MPA (Attwood and Cowley 2005). The main research angling areas, Koppie Alleen (34°28.65’S, 20°30.70’E) and Lekkerwater (34°26.92’S, 20°39.15’E), both have a length of 3.4 km and are situated 11 km apart (Attwood 2003), being 40 km and 25 km west of Cape Infanta respectively (Bennett and Attwood 1993). These two research sites have different exploitation histories. Prior to 1984, Koppie Alleen was heavily exploited by recreational anglers, while Lekkerwater, whose shore used to be privately owned, was lightly exploited (Attwood 2003). However, by 1991, the Koppie Alleen population had recovered to a density that was indistinguishable from that at Lekkerwater (based on fishery-independent CPUE catch and release data) (Bennett and Attwood 1991). Because poenskop catches are limited in the De Hoop MPA (only 36 poenskop caught in 13 years), tagging information used in Chapter 4 has been combined with the ORI Tagging Project.

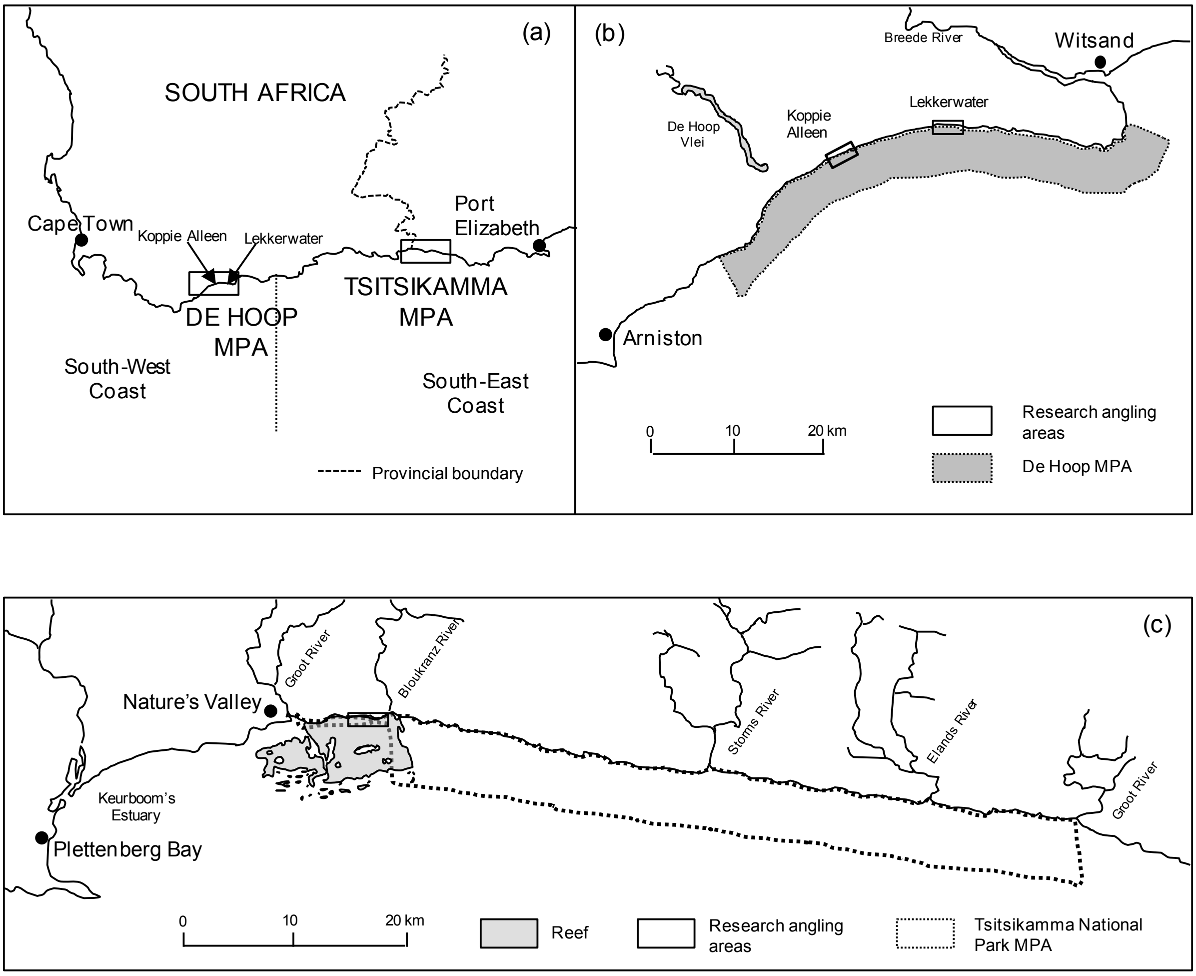

Figure 2.4: Maps showing (a) the locations of the De Hoop and Tsitsikamma National Park Marine Protected Areas, (b) the De Hoop MPA on the south-western Cape coast showing locations of the research angling areas at Koppie Alleen and Lekkerwater, and (c) the Tsitsikamma National Park MPA showing locations of the research angling areas. The shaded and unshaded regions indicate reef and sand areas in the study area, respectively (from Wood et al. 2000).

2.5.2. Tsitsikamma National Park Marine Protected Area

The Tsitsikamma National Park (TNP), situated in the warm temperate region of South Africa, was established in 1964 and is Africa's oldest "no-take" marine protected area (MPA) (Guenette et al. 2000, Wood et al. 2000). It is situated along an exposed part of the South African southern coast between Groot River West (33°59'S, 23°34'E) and Groot River East (34°04'S, 24°10E), extending approximately 72 km alongshore with a narrow terrestrial component incorporating the shoreline and cliff (Tilney et al. 1996). The park has a seaward boundary of 5.6 km offshore between Groot River East and Bloukranz River, but decreases to 0.9 km at Die Punt at Nature's Valley, covering a total area of approximately 350 km^2 (Cowley et al. 2002). The majority of this stretch of coastline is exposed to strong wave action, with the topography being rugged with high rocky cliffs. The intertidal gullies amongst the rocky shoreline are usually filled with boulders or sand (Hanekom et al. 1989, Cowley et al. 2002, Attwood and Cowley 2005) providing excellent habitat for reef-associated fish populations (Faasen and Watts 2007). The main research angling area, consisting of ± 5 km of predominantly rocky coastline, lies close to the western boundary of the MPA between the Klip and Bloukranz Rivers (Figure 2.4). At the Bloukranz site, there are a number of subtidal habitats including rocky (includes deep, high-profile reef rocky gullies, and shallow, low-profile reef or boulder beds), sandy (near the river mouths) and transitional habitats (Watt-Pringle 2009).

Shore-angling in the TNP has been prohibited since 1978, and after the declaration of the "linefish crisis" in 2000, a small 3 km open fishing area bordering the main restcamp at Storms River, was also closed to fishing (Hanekom et al. 1997, Cowley et al. 2002). As a result of this closure, the entire TNP became a no-take MPA. The tagging information analysed in Chapter 4, is from an ongoing tag and release project conducted in a small research fishing area (approximately 5 km) in the TNP, with catch per unit effort (CPUE) data (used in Chapter 3) also being collected during this project (Cowley et al. 2002) (Figure 2.4).

2.5.3. Pondoland Marine Protected Area

The Pondoland MPA, situated on South Africa's east coast between the Mzamba (31°04.8'S, 30°11.7'E) and Mzimvubu Rivers (31°37.7'S, 29°32.9'E), is approximately 90 km in length and is part of the greater region called the Wild Coast (Maggs 2011a). The majority of the Pondoland coast is rural with a rugged shoreline, being rocky with small sandy bays and estuary mouths (Mann et al. 2003, Maggs 2011a). The Pondoland MPA (Figure 2.5), proclaimed in 2004, includes approximately 1 300 km^2 of marine environment and replaced the Mkambati MPA which was originally proclaimed in 1992 under the Environmental Conservation Decree (under the previous Transkei government) (Maggs 2011a, BQ Mann, Oceanographic Research Institute, *pers comm.*). This MPA, which is the largest MPA in South Africa, includes 90 km of coastline, extending 10-15 km seawards to the 1 000 m depth contour (Tunley 2009). Due to the richness of the marine biodiversity in this region, the Pondoland MPA was considered to be an important gap in the network of MPAs along the South African Coast (Attwood et al. 1997b, Turpie et al. 2000, Mann et al. 2006, Celliers et al. 2007, Tunley 2009). This MPA is situated within the Natal Bioregion. Elements of both sub-tropical and warm temperate regions exist, indicating that the MPA is part of a transition zone (Tunley 2009). Pondoland MPA includes a large off-shore no-take area (40 km stretch of coastline from Sikombe River to Mboyti River, representing 6.8% of the Natal Bioregion), and exploited areas (Figure 2.5). Shore-based fishing, spear-fishing and boat-based linefishing are permitted in certain areas within the MPA. The MPA is considered to be one of the best places to view the sardine run (O'Donoghue et al. 2010).

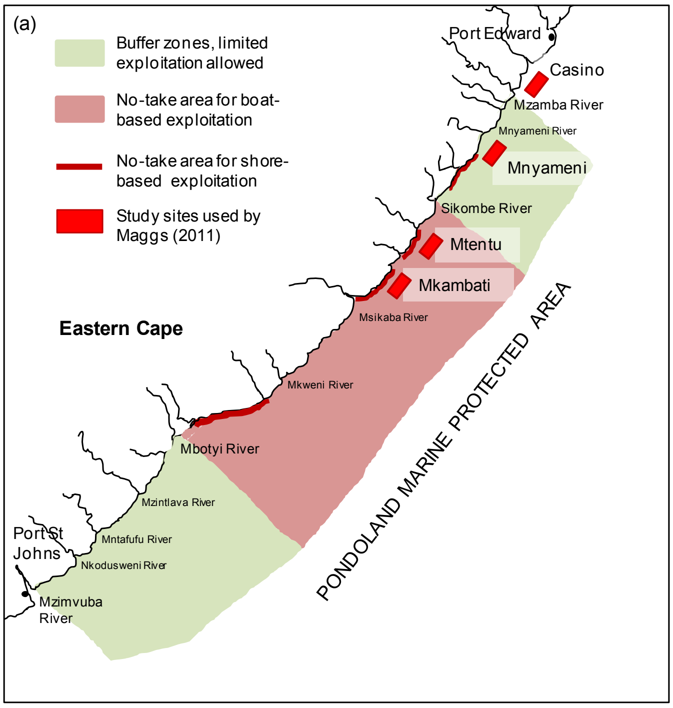

Figure 2.5: Map of South Africa indicating (a) the Pondoland MPA, and (b) the study sites in Pondoland MPA used by Maggs (2011a). Two exploited (Casino and Mnyameni) and two no-take areas (Mtentu and Mkambati) were used. Maps adapted from Maggs (2011a).

The tagging information used in Chapter 4, was collected as part of the Pondoland MPA reef fish monitoring project, initiated in 2006. This information was collected from two sites occurring within the no-take area (Mtentu and Mkambati) and two within the exploited area (Casino and Mnyameni) (Figure 2.5).

CHAPTER 3

CHANGES IN CATCH: OVERFISHING AND THE DECLINE OF POENSKOP

"Personally, I think that our waters are being fished out. Sixty years ago, at Voëlklip, Heroldsbay, fish were so plentiful that a poenskop of 25 kg was considered to be on the small side."

- Jan Stander (1976: May edition *Stywe Lyne/Tight Lines*) -

3.1. Introduction

Fish stocks worldwide have been over-exploited and, according to Attwood et al. (2000), the South African marine environment is also showing symptoms of this over-exploitation and degradation. These authors suggested that the pressure on marine resources is likely to increase in the foreseeable future. Fishing has both direct and indirect effects on the ecosystem; direct effects being changes in fish abundance, demographic changes in individual populations (including changes in size frequency distribution and sex ratios), with indirect effects including alterations to the benthic environment, changes to community structure, changes to gene pools (e.g. loss of genetic diversity as a result of a severe reduction in population size, Hauser et al. 2002, Hutchinson et al. 2003), alterations to biology (e.g. earlier onset of reproduction), and incidental mortality of non-target species (Attwood et al. 2000).

Recent evidence suggests that the global catch of wild marine fish, after reaching its peak in 1996, has been gradually declining, and that, at present, almost 88% of individual fish stocks are fully- to over-exploited (Ye and Cochrane 2011). Pauly et al. (2005) recorded that fishery resources are over-exploited, and may lead to a point of collapse or even extinction. Many examples of overfishing exist in the commercial sector, such as the collapse of the Peruvian anchovy *Engraulis ringens* fishery (Pauly et al. 2002), the cod *Gadus morhua* fishery off Newfoundland (Ruzzante et al. 2001), and the collapse of the orange roughy *Hoplostethus atlanticus* (Clark et al. 2000) and Patagonian toothfish *Dissostichus eleginoides* (Bialek 2003) fisheries. This scenario, however, is not confined to species exploited in the commercial sector, but also applies to those targeted by recreational anglers, particularly involving those species shared with the commercial sector. This situation is relevant to South Africa, as a growing body of evidence suggests that a number of important shore-angling species are over-exploited or are in a process of decline. Species such as white steenbras *Lithognathus*

lithognathus and dusky kob *Argyrosomus japonicus* have been exploited down to less than 20% and 10% of their pristine stocks, respectively (Bennett 1993a; Griffiths 1997a; Cowley et al. 2002). Other examples include the red steenbras *Petrus rupestris* (Smale and Punt 1991) and seventy-four *Polysteganus undulosus* (Chale-Matsau et al. 2001), which are now both considered to be economically extinct.

Poenskop have been targeted for 1000s of years with remains of this species even being found in caves near False Bay (Rooiels and Smitwinkelbaai) dating back to 3 000 years and 1 175 years before present, respectively (Poggenpoel and Robertshaw 1981, Smith 1981). Despite the increasing evidence of decreasing poenskop catches, South Africa's growing marine recreational sector (shore angling and ski-boat angling) are still known to actively target this premier sport fish (Figure 3.1).

Figure 3.1: Front cover images of *Stywe Lyne/Tight Lines* angling magazines, depicting the popularity of poenskop as a recreational sport fish.

In terms of distribution, Smith and Heemstra (1986) reported the distribution of poenskop to extend from the Western Cape to KwaZulu-Natal. Van der Elst (1988a) described the distribution of poenskop from Cape Agulhas on the Cape south coast up to St Lucia on the KwaZulu-Natal north coast, with some fish reported reaching as far north as Maputo (van der Elst 1993). Heemstra and Heemstra (2004) recorded poenskop being distributed from the south of Saldahna to Cape Vidal. Despite these conflicting reports in distribution, the core distribution is suggested to be along the southern and eastern coasts of South Africa, having a relatively high abundance along the Transkei coastline. However, Smith and Heemstra (1986) described this fish species as being nowhere abundant along the coastline.

Booth (2000) and Rouhani and Cowley (2004) alluded to the residency shown by juvenile poenskop, as well as some of the adults, suggesting that poenskop may be territorial and hold small home-ranges. This potentially makes poenskop particularly vulnerable to exploitation, while their life history – slow-growing, long-lived and late-maturing, with a reproductive biology that includes protogynous hermaphroditism (Buxton and Clarke 1989) – makes the species acutely sensitive to over-exploitation. Despite various interventions, such as the imposition of size and bag limits (currently 50 cm TL and one per licensed fisher per day applying to both recreational and commercial fishers) by government authorities, CPUE trends reflect a severe and consistent stock decline over the last two decades (Booth 2000). Griffiths and Lamberth (2002) also recorded the stock status of poenskop as being collapsed, with only an estimated 20% of pristine stock remaining.

The aim of this chapter was to review and evaluate the current and historic trends in catch and catch-per-unit-effort (CPUE) of poenskop. This was achieved by making use of published and unpublished survey and research data. Additionally, long-term trends relative to historical management measures, in the relevant fishery sectors, were elucidated.

3.2. Fisheries management in South Africa

The first legislative attempt to manage the linefishery was the Sea Fisheries Act in 1940, through the introduction of minimum size limits for a few selected species. However, a shortage of life-history information led to these regulations being determined on an arbitrary basis (Griffiths et al. 1999). Since 1948, a series of amendments to the Sea Fisheries Acts witnessed the imposition of a number of controls and restrictions for both the commercial and recreational linefishery (e.g. licensing, permit requirements) (Hutton and Pitcher 1998). Prior to 1973, anglers had open access to marine resources, which, combined with increasing commercial effort, ultimately lead to overfishing and overharvesting of stocks (Hutton and Pitcher 1998). It was then recommended that participation be restricted in order to control effort exerted on resources. The Sea Fisheries Act, passed in 1940, was then replaced by amended Acts in 1973 and 1988. The first legislation passed, aiming to improve protection of species showing stock declines, was the Linefish Management Framework, implemented in 1985 (*Government Gazette* No. 9543, December 1984). One of the main objectives behind the framework was to steer fishing effort away from vulnerable reef fishes to the more resilient shoaling species (Griffiths et al. 1999). Various other regulatory measures such as closed seasons and the proclamation of MPAs were also introduced over the years, all of which aimed to further decrease effort. The Marine Living Resources Act (MLRA, Act No. 18 of 1998, *Government Gazette* No. 18930), promulgated in 1998, aimed to provide equitable access to and sustainable utilisation of living marine resources (Witbooi 2006). The MLRA also provided details for permit allocations and quotas, as well as setting of catch and effort restrictions.

Governance in the recreational sector consists of a series of catch restrictions on licensed anglers, including minimum legal size and maximum daily bag limits, and area and seasonal closures. In the past, many regulations failed to protect target species (Griffiths 2000). This was due to the absence of suitable biological information, where regulations were based on perception rather than scientific evaluation (Griffiths 2000). Management regulations pertaining to the recreational linefishery, with those important to the protection of poenskop, are presented in Table 3.1. However, few attempts have also been made to assess the effectiveness of management measures introduced for linefish species (Attwood 2003).

3.3. Fishery sectors

In South Africa, inshore commercial and recreational linefisheries are major contributors to the local economy of many coastal areas (Brouwer and Buxton 2002). A decade ago, these fisheries employed approximately 131 500 people and the shore angling sector alone had an estimated 412 000 participants. This fishery exploits over 200 demersal and pelagic species, of which 95 are economically important (Griffiths et al. 1999, Griffiths and Lamberth 2002), and has been shown to contribute 1.3% of the gross domestic product of local economies (McGrath et al. 1997).

Table 3.1: Management regulations pertaining to the recreational fishery and MPA declarations important for the protection of poenskop.

Year	Regulation	Source
1964	Proclamation of Tsitsikamma MPA	Government Gazette No. 936
1973	Linefish catch regulations promulgated	Sea Fisheries Act No. 58
1984	Implementation of linefish management framework	Government Gazette No. 9543
	- Minimum legal size limit set at 25 cm TL	Government Gazette No. 9543
	- Maximum daily bag limit set at 2 pppd	Government Gazette No. 9543
1984	Proclamation of De Hoop MPA	Government Notice No. 1429
1988	Replacement of linefish catch regulations	Sea Fisheries Act No. 12
	- Minimum legal size limit set at 50 cm TL	Sea Fisheries Act No. 12
1992	Revision of linefish catch regulations	Government Gazette No. 14353
1992	Proclamation of Dewa-Cwebe MPA	Transkei Environmental Conservation Decree
1998	Marine Living Resources Act	Government Gazette No. 18930
2002	Ban on recreational use of vehicles in the coastal zone	Government Gazette No. 22960
2004	Proclamation of Pondoland MPA	Government Gazette No. 26430
2005	Most recent amendments to linefish catch regulations	Government Gazette No. 27453
	- Maximum daily bag limit set at 1 pppd	Government Gazette No. 27453
2008	Proclamation of Stillbaai MPA	Government Gazette No. 31517
2012	Current restrictions: 1 pppd ≥ 50 cm TL	

The South African linefishery comprises three main sectors, namely the commercial, recreational and subsistence fisheries. Of these, the recreational sector encompasses several facets including estuarine shore and boat-based fishing, spearfishing, skiboat fishing and rock and shore angling. In the past, poenskop contributed considerably (by mass) to total catches of the commercial skiboat fishery. Currently, poenskop are mostly targeted by members of the recreational fishery (Table 3.2).

3.3.1. Spearfishery

The spearfishery is the smallest facet of the sport fishery, with an estimated 7 000 participants. Little information exists for this fishery but, based on a study by Mann et al. (1997) and Lloyd et al. (2012), there has been little change in CPUE, as well as no significant changes in species composition between 1984 and 2007. However, one point of concern is that many of the target species recorded in spearfishing catches are particularly vulnerable to over-exploitation. This is largely due to these fishes' life history which includes endemicity, slow growth, residency and sex change (Mann et al. 1997). These include reef fish such as many of the sparid and serranid species. Amongst the most vulnerable of these species include the red steenbras *P. rupestris* and poenskop *Cymatoceps nasutus* (Mann et al. 1997). Despite the notion that spearfishing can deplete local stocks, it is the most regulated sector of the South African linefishery (Cook 1990).

Table 3.2: The South African linefishery divided into three main sectors, indicating additional facets. The facets from which poenskop are predominantly caught are indicated with a cross (X). A question mark (?) indicates that poenskop may be caught but are not necessarily targeted.

Sector	Facet	Poenskop caught
Commercial	Skiboat	X
	Trawling	
	Long-line	
	Seine and gillnet	
	Estuary gillnet	
Recreational	Skiboat	X
	Shore-based	X
	Spearfish	X
	Estuary shore- and boat-based	
Subsistence	Shore-based	?
	Estuary-based	

3.3.2. Offshore recreational skiboat fishery

The development of the offshore skiboat, following World War II, had a dramatic effect on the recreational fishery and now provided anglers the opportunity of actively participating in the nearshore fishery (Penney et al. 1999). The further development of inflatable semi-rigid crafts ("rubber ducks") during the 1990s, resulted in increased recreational participation and fishing effort (Penney et al. 1999). Where fishing from the shore was once the only option, anglers were now able to focus effort on offshore reefs (Penney et al. 1999). Improvements in fishing gear, including geared reels, nylon line and fibreglass rods have improved the overall efficiency of boat anglers (Bennett 1990). Technological advances which were initially developed to aid commercial fisheries have also been increasingly used by participants in the recreational fishery (Cooke and Cowx 2006). These advances allowed anglers to locate fish more rapidly (e.g. global positioning systems (GPS), echo sounders, depth-finder technologies) (Leadbitter 2000).

Skiboat angling is primarily a weekend recreational activity, and is considered to be economically important in terms of equipment outlay (± R 17 million) and running expenses (± R 1.65 million) (Smale and Buxton 1985). Just over a decade ago, this sector had an estimated 12 800 participants and some 3 500 boats (Griffiths et al. 1999). Recreational skiboaters are known to compete with commercial line fishermen for certain target species but the overlap with the trawl fishery is minimal (Smale and Buxton 1985). A good example of this competition is found in KwaZulu-Natal, where many recreational skiboaters operate on a commercial basis (i.e. illegally sell their catch) (Sauer et al. 1997). This activity is intensified when migratory, shoaling linefish species (e.g. geelbek) become available. Brouwer and Buxton (2002) recorded a similar competition between the recreational and commercial skiboat fishery in the Eastern Cape.

Many aspects of the recreational skiboat fishery have been investigated (Smale and Buxton 1985, Sauer et al. 1997, Fennessy et al. 1999, Brouwer and Buxton 2002, Fennessy et al. 2003, Pradervand and van der Elst 2008). These include assessment of species composition and CPUE in the Eastern Cape (Smale and Buxton 1985), management measures and attitudes towards management in South Africa (Sauer et al. 1997), estimation of effort and catch rates of commercial vs. recreational skiboats in the Transkei (Fennessy et al. 1999, 2003), and a socio-economic assessment of the charter-boat fishery in KwaZulu-Natal (Pradervand and van der Elst 2008). A study by Smale and Buxton (1985) showed that the Port Elizabeth Deep-Sea Angling Club increased their annual effort by a factor of 1.6 between 1975 to 1982. Brouwer and Buxton (2002) revealed that CPUE in the skiboat fishery along the South African Eastern Cape coast declined markedly, despite an increase in effort. Changes in the catch composition were also recorded.

3.3.3. Shore angling fishery

Shore angling has been a popular pastime for at least 100 years, but over the past few decades has developed into an important recreational pursuit in South Africa, and is also increasing in economic importance (Clarke and Buxton 1989, Coetzee et al. 1989, Bennett 1990, Brouwer et al. 1997, McGrath et al. 1997). It is also the most accessible to the general population and is, therefore, the most popular angling discipline (Guastella and Nellmapius 1992). Bennett (1991) estimated this fishery to have 380 000 participants in 1990, increasing at rate of 6% per annum. McGrath et al. (1997) estimated the recreational shore fishery to have approximately 412 000 participants, increasing at a rate of 2.1% per annum. Bennett (1991) suggested that the fishery would have over one million participants by 2011. However, recent estimates in KZN suggest that there has been very little change in participation since the 1990s (Dunlop 2011). The development of off-road vehicles in the 1960s further enabled easy access to large stretches of the coastline, previously only accessible on foot. This resulted in a marked increase in effort by shore anglers, resulting in an implicit marked decline in catches of some species, specifically more resident, reef-associated teleosts (Bennett et al. 1994, Brouwer et al. 1997, Hutton and Pitcher 1998, Brouwer and Buxton 2002).

A number of studies, assessing aspects of the South African shore angling fishery, such as catch composition, CPUE, abundance and catch trends, have been undertaken (Joubert 1981, Clarke and Buxton 1989, Coetzee et al. 1989, Hughes 1989, Bennett 1990, Bennett 1991, Guastella and Nellmapius 1992, Taylor 1993, Bennett et al. 1994, Guastella 1994, Brouwer et al. 1997, Brouwer and Buxton 2002, Mann et al. 2003, Pradervand and Hiseman 2006, Pradervand et al. 2007, Beckley et al. 2008). In the majority of these studies, catch has declined in terms of numbers caught, the size of the fish caught and, in most instances, there has been a shift in species composition. Angling patterns also changed, as the more sought-after species have dwindled and anglers have been forced to change to less popular species (Bennett 1990). The sparids are the fish species which have been most susceptible to overfishing. Early reports of overfishing in the Cape (Biden 1930), indicated that catches of red steenbras *P. rupestris* and geelbek *Atractoscion aequidens* were not as good at that time as they had been in earlier years, and red steenbras had already become scarce in False Bay by 1910. Smith (1935) also stated that catches of galjoen *Dichistius capensis* had declined in certain areas as a result of overfishing (Bennett 1990). Clarke and Buxton (1989) showed that anglers in the Eastern Cape perceived catches of some species, including the poenskop, to have declined dramatically both in terms of numbers and in the size of fish taken. Bennett et al. (1994) also showed that overall catch rate in False Bay had declined drastically from 1938 – 1992. Species composition was dominated by blacktail *Diplodus capensis* and white stumpnose *Rhabdosargus globiceps* prior to 1950, changing to yellowtail *Seriola lalandi* and geelbek *A. aequidens* during the 1950s, with blacktail *D. capensis* becoming important once again after 1960. Brouwer et al. (1997), on interviewing fishers from the entire South African coastline, found that most interviewees reported a decline in shore angling catches taken along the coast. Griffiths and Lamberth (2002) recorded that a large number of stock assessments done in South Africa showed recreational shore anglers to be directly responsible for the depletion of a number of species, including members of the Sparidae (Bennett 1993a), Dichistiidae (Bennett 1988) and Sciaenidae (Griffiths 1997b). Despite varying methods and different study sites, all these studies have similar conclusions - that overfishing has resulted in a decline in catches and the size of fish caught, and changed the species composition of fish caught. As a result of these declining trends, the South African linefishery, in 2000, was declared to be in a state of emergency (*Government Gazette* No. 21949 Notice 4727 of 2000).

The species most affected by overfishing are those from the family Sparidae, including species such as red steenbras *P. rupestris*, seventyfour *P. undulosus* and poenskop. These species once comprised more than 60% of the offshore linefish catch but more recently contribute less than 10% (van der Elst 1993). There have been a number of references made to the declining poenskop stocks. Stander (1976) reported that the size of poenskop in the Western Cape was decreasing, stating that poenskop caught during the early 1900s were plentiful and that a poenskop of 25 kg was considered to be small.

3.4. Methodology and data sources

National Marine Linefish System

Efforts to collect catch and effort data from the various sectors of the South African linefishery were intiated in the early 1970s, with the resultant development of catch and effort data-collection systems in the Cape (for the commercial fishery by the Sea Fisheries Research Institute) and in KwaZulu-Natal (for the recreational sector by the Oceanographic Research Institute) (Pradervand and Govender 1999). These efforts progressed independently until 1982, when the two systems were merged to form the National Marine Linefish System (NMLS); a catch and effort database under the Chief Directorate: Sea Fisheries Administration (Penney 1993, Sauer et al. 1997). Since 1984, monthly submission of commercial linefishing catch and effort data has been mandatory. Although the recreational fishery was far more diverse and fragmented, catch and effort data collection was achieved by enlisting the voluntary support of recreational anglers. As a result, this system presently documents vast numbers of recreational angler outings each year with greatest coverage occurring in KwaZulu-Natal (Maggs 2011b). The NMLS covers four recreational fishing sectors, namely a) rock- and surf-angling, b) shore- and boat-based estuarine angling, c) marine boat-based angling and d) spearfishing (Sauer et al. 1997). In order to optimize the collection of data from these different linefishing activities, a number of different strategies have been developed by researchers (to improve the NMLS), including shore patrols (roving creel surveys) and skiboat inspections (access point surveys) conducted by compliance officers from Ezemvelo KwaZulu-Natal Wildlife (EKZNW), this being supplemented by catch cards and tournament records (Maggs 2011b). NMLS data sources include a) catch records cards, mostly voluntarily completed by anglers, b) tournament records obtained from angling organisations, c) vehicle- or foot-based shore patrols/roving creel surveys along the beaches and estuaries of KZN, and d) boat inspections/access point surveys involving inspections at popular launch sites along the KZN coast (Maggs 2011b). Information collected, in addition to species and numbers caught, include the weight of the fish (kg), date, the type of gear used, number of anglers fishing and the hours they spent fishing, locality and distance from the shore.

Personal angling records

Recreational angling is becoming increasingly popular and if anglers record all their personal catches over a long period of time, this data can be useful as a monitoring tool (Platten 2004). Platten (2004) found that some fishers in the Gladstone region in Queensland, Australia, had been fishing at particular sites over extended time periods and maintained records of their catches, thereby providing useful trend data. Platten (2004) also stated that in many cases recreational catch data may sometimes be the only reliable long-term data available which can be used to show change over time. Pollock et al. (1994) found that these personal angling records (called angler diary programmes) are generally accepted as the most economically viable method of collecting angler-provided data (Cooke et al. 2000). Personal angling records also offer the potential for indexing long-term trends in relative abundance of a particular target species (Cooke et al. 2000). This study makes use of personal angling records obtained from the Transkei. Information collected includes the date, species caught, bait used and weight of the fish (lbs). No data to assess effort was recorded and no unsuccessful fishing outings were recorded.

Stywe Lyne/Tight Lines

This popular angling magazine, first published in 1960, generally provides catch information on popular angling species, such as poenskop. In most instances, only the weight (first in pounds, changing to kilograms in 1972) and location of the catch were recorded. All issues of *Stywe Lyne/Tight Lines* were accessed, with information including the date, weight and location of the catch, being recorded. No data to assess effort was recorded.

Robberg Diaries

The Robberg Diaries (Thesen 2000) is a collection of personal and fishing entries made from one hut from 1931 to 1986. All records are made from the Robberg Peninsula; a long rugged coastline with topography ranging from sea cliffs to more sheltered bays (at Plettenberg Bay). In 1924, the peninsula was under control of the Knysna divisional Council. Robberg was then transferred to the Cape Provincial Administration, falling under the jurisdiction of Provincial Nature Reserves in 1982. All leases were then terminated and subsequently, by 1986, the hut was vacated and the last diary entry was recorded. The Robberg Peninsula then fell into the Robberg Marine Protected Area. Subsequent to the termination of the leases, ORI has continued to receive some catch cards from Robberg intermittently since 1984. These records have been captured on the NMLS. Information recorded included the date, weight, species caught, bait used, location of catch, tide, time of day and general weather conditions.

3.5. Trends in catch, effort and catch-per-unit-effort

3.5.1. Fishery surveys

Numerous studies have been conducted to assess the catch, effort, species composition and value of the shore and skiboat fisheries, along different parts of the coastline (see Coetzee and Baird 1981, Coetzee et al. 1989, Bennett 1990, Hecht and Buxton 1993, Hanekom et al. 1997, Penney et al. 1999, Griffiths 2000, Brouwer and Buxton 2002). Unfortunately, differences in survey techniques, analyses, time periods and angler behaviour (e.g. competitive vs. recreational) do not allow for direct comparison between these studies (Bennett and Attwood 1993). However, the results allow one to assess catch and effort trends over time. The results of a number of studies were used to determine the percentage contribution (numerical and gravimetrical, where possible) of poenskop to overall catch between 1977 and 2010. Where possible, CPUE (fish.angler-hour^{-1}, unless otherwise specified) for different sections of the coastline was determined (Table 3.3). Most studies made use of roving creel surveys, assessing the shore fishery at a regional and national level. Information from the recreational skiboat fishery and research programmes (mainly in MPAs) has been included in this assessment.

A number of different coastal regions were described in these studies. This, combined with the changing of provincial boundaries in recent years, makes the interpretation of these studies rather complex. For the purpose of this chapter, five coastal sections were defined:

- South-west coast: ranging from Strand to Cape Infanta
- Southern coast: ranging from Duiwenhoks/Puntjie to St Francis Bay
- South-east coast: ranging from the Kromme River to Kei River
- Transkei: ranging from Qolore River to Mtentwana River
- KwaZulu-Natal: ranging from Umtamvuna River to Kosi Bay (Figure 3.2).

South-west coast

Limited data exists on poenskop catches for this stretch of coastline. Historically, mentions of the poenskop's decline have been made in numerous books and articles (Biden 1930, Horne 1955, Schoeman 1957). Biden (1930) recorded boatmen and netters not knowing of poenskop at any point between Table Bay and Walvis Bay, and therefore suggested that poenskop belong entirely to the Indian Ocean. However, Schoeman (1957) recorded poenskop being caught by rock anglers in False Bay. Even though mentions are made of poenskop being caught south of Saldanha, this stretch of coastline is thought to be outside the limits of its distributional range.

The south-west coast, as defined for this analysis, encompasses, amongst others, an existing MPA, namely the De Hoop MPA. Bennett (1991), on analysing catch data obtained from Bloukrans (now De Hoop Marine Reserve), found that mean annual total catch of reef fish, including poenskop, had declined markedly since 1965. CPUE data (fish.angler-hour-1) from the De Hoop inshore fish tagging project also showed an overall decline between 1987 and 2009.

Table 3.3: Survey locations, dates and catch, CPUE (fish.angler-hour^{-1}, unless otherwise specified), and contribution (% number, % mass) data of poenskop for studies that assessed shore- and boat-angling (research, recreational and competitive), and commercial boat-angling along different regions of the coastline of South Africa. Abbreviations used include Res = research, Rec = recreational and Comp = competition.

Region	Locality	Period	Form	Shore or skiboat	CPUE	% (N)	% (kg)	Source
SWC	Bloukrans	1932 - 1979	Recreational	Shore	-	-	-	Bennett (1991)
SWC	De Hoop MPA	1987 - 2009	Research	Shore	-	0.08	-	CG Attwood (unpub.)
SWC, SC, SEC	Cape Point – Kei River	1994 - 1995	Spearfishery		-	1.79	-	Mann et al. (1997)
SWC, SC, SEC	Stillbaai – Kei Mouth	1994 - 1996	Recreational	Skiboat	-	3.13	-	Brouwer and Buxton (2002)
SC	Struisbaai – Plettenberg Bay	1931 - 1933	Research	Shore	0.004	0.05	-	Griffiths (2000)
SC	Struisbaai – Plettenberg Bay	1987 - 1993	Research	Shore	0.003	0.13	-	Griffiths (2000)
SC	Tsitsikamma MPA	1989 - 1995	Res + Rec	Shore	-	2.15	3.15	Hanekom et al. (1997)
SC	Tsitsikamma MPA	1995 - 2009	Research	Shore	1.05	6.01	-	PD Cowley (unpub.)
SC	Tsitsikamma MPA	1998 - 2005	Research	Shore	0.11	11.05	-	Götz et al. (2008)
SC	Plettenberg Bay	2003 - 2004	Research	Shore	<0.01	0.1	-	King (2006)
SC	Tsitsikamma MPA	2003 - 2004	Research	Shore	0.1	10.1	-	King (2006)
SC	Rebelsrus	2003 - 2004	Research	Shore	0.09	9.4	-	King (2006)
SC, SEC	Robberg – Great Fish River	1978 - 1982	Competition	Shore	0.24 kg.ang-wk^{-1}	1.24	0.64	Coetzee et al. (1989)
SC, SEC	Robberg – Great Fish River	1979 – 1982	Competition	Shore	0.47 kg.ang-wk^{-1}	0.83	0.37	Coetzee et al. (1989)
SEC	Port Elizabeth	1979 - 1980	Recreational	Skiboat	0.002	0.25	1.39	Smale and Buxton (1985)
SEC	Port Elizabeth	1985 - 1986	Rec + Comp	Shore	0.002 kg.ang-hr^{-1}	0.74	0.67	Clarke and Buxton (1989)
SEC	Port Elizabeth region	1986	Commercial	Skiboat	-	-	0.1	AJ Penney (unpub.)
SEC	Flat Rocks and Schoenmakerskop	1985 – 1986	Recreational	Shore	1.72 g.ang-hr^{-1}	0.9	0.9	Clarke (1988)
SEC	Cape St. Francis – Port Elizabeth	1985 - 1987	Spearfishery		0.019	1.4	2.2	Clarke (1988)
SEC	Algoa Bay	2006 - 2008	Research	Skiboat	-	0.28	-	Chalmers (2011)
TKI	Coffee Bay – Mtamvuna River	1995 – 1999	Commercial	Skiboat	-	0.6	4.4	Fennessy et al. (1999, 2003)
TKI	Coffee Bay – Mtamvuna River	1995 – 1999	Recreational	Skiboat	-	3.0	14.7	Fennessy et al. (1999, 2003)
TKI	Coffee Bay	1949 - 1970	Recreational	Shore	-	7.30	25.17	Historical angling records
TKI	Coffee Bay	1984 - 1992	Commercial	Skiboat	-	3.46	-	Hecht and Buxton (1993)
TKI	Coffee Bay	1995 – 1999	Commercial	Skiboat	-	2.2	10.8	Fennessy et al. (1999)
TKI	Coffee Bay	1995 – 1999	Recreational	Skiboat	-	17.0	44.1	Fennessy et al. (1999)
TKI	Kei River	1995 – 1999	Commercial	Skiboat	-	0.5	0.8	Fennessy et al. (2003)
TKI	Kei River	1995 – 1999	Recreational	Skiboat	-	2.3	9.9	Fennessy et al. (2003)
TKI	Kei River – Mtamvuna River	1997 - 1998	Recreational	Shore	-	<1	4.08	Mann et al. (2003)
TKI	Kei River – Port Edward	1997 - 1998	Recreational	Shore	-	<1	-	McDonald et al. (1999)
TKI	Pondoland MPA	2006 - 2010	Research	Skiboat	0.26	4.57	8.5	Maggs (2011a)
TKI, KZN	Scottburg – Ballito	1989 - 2007	Spearfishery		-	0.15	0.67	Lloyd et al. (2012)
KZN	Mbashe River – Kosi Bay	1977 - 2000	Competition	Shore	-	<0.1	<0.1	Pradervand et al. (2007)

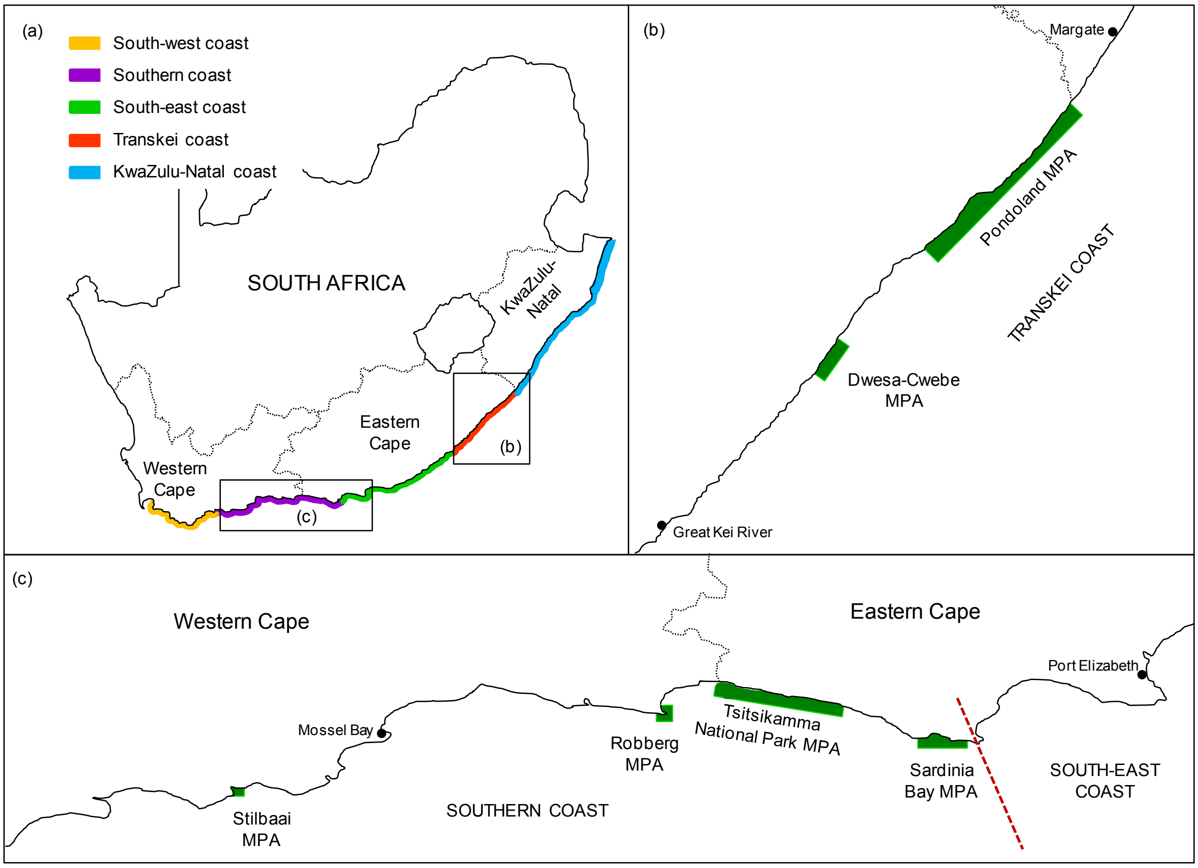

Figure 3.2: (a) Map of South Africa showing the different coastal regions used to describe the local fisheries, with inserts showing the localities of MPAs, along the (b) Transkei and (c) southern coastlines, important for the protection of poenskop.

Poenskop accounted for 0.08% of all fish caught during this period, alluding to this stretch of the coastline being at the southern limits of the poenskop's distribution range (CG Attwood, L Swart, unpublished data). However, the majority of the De Hoop MPA shoreline is sandy with small areas consisting of both sand and rock. Poenskop generally occur along inshore and offshore reefs, therefore the surf-zone within the De Hoop MPA may not be suitable habitat for poenskop.

Southern coast

This stretch of coastline incorporates a number of MPAs, including the Tsitsikamma National Park MPA (TNP), within which dedicated research angling has been conducted since 1995. The TNP, established on 4 December 1964, is Africa's oldest "no-take" MPA (Wood et al. 2000). Initially, a limited 3 km stretch of coastline was open to recreational fishing, but after the declaration of the "linefish crisis" in 2000, the entire TNP became a no-take MPA (Cowley et al. 2002). Hanekom et al. (1997) reported that poenskop caught in the TNP between 1989 and 1995, contributed 1.7% and 2.6% of the total catch. In contrast, the TNP inshore fish monitoring project (PD Cowley, unpublished data), the poenskop's contribution to total catch was 6.01% between 1995 and 2009, being the fifth most abundant species caught (Figure 3.3). Abundance was similar to that obtained by Götz et al. (2008), who found that poenskop contributed 5.6% to the total catch in the TNP between 1998 and 2005.

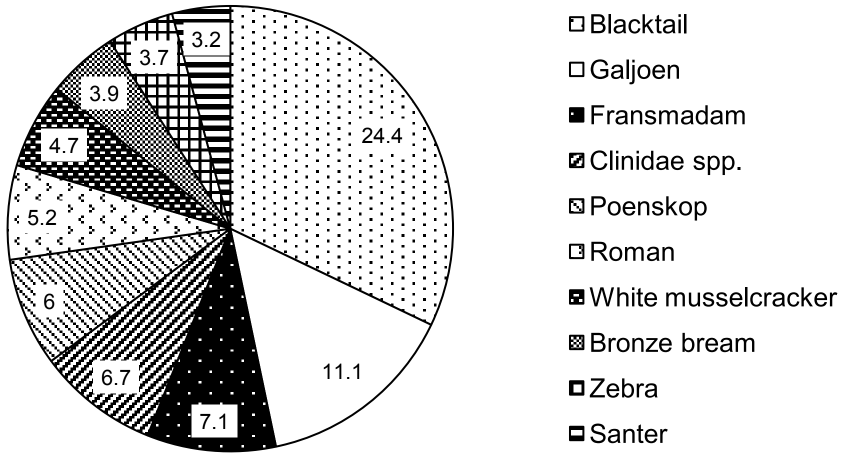

Figure 3.3: Percentage catch composition of fishes caught in the Tsitsikamma National Park Marine Protected Area between 1995 and 2009 (PD Cowley, unpublished data).

Mean CPUE for poenskop within the MPA between 1995 and 2009 was 1.05 fish.angler-hr^{-1} (PD Cowley, unpublished data). Interestingly, there was an increase in the mean CPUE between 1995 and 2009, suggesting that the abundance of poenskop in the TNP is increasing (Figure 3.4).

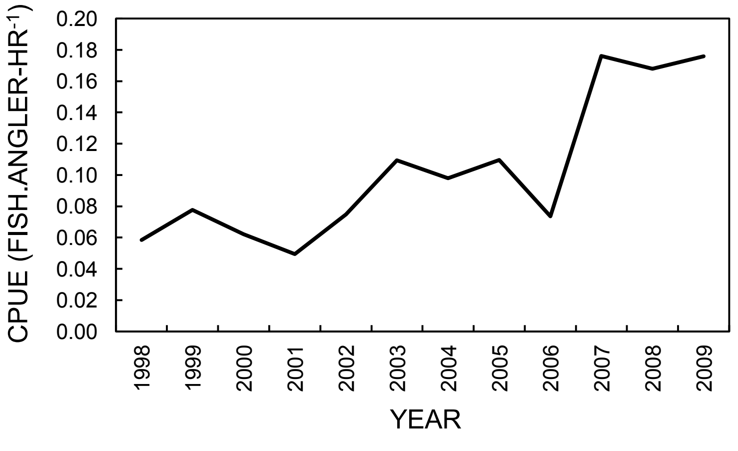

Figure 3.4: Increasing trend in mean annual CPUE (fish.angler-hour^{-1}) for poenskop recorded during research angling in the Tsitsikamma National Park MPA over the period 1998 to 2009 (PD Cowley, unpublished data).

According to anecdotal records provided in the "Robberg Diaries", catches of poenskop in Plettenberg Bay were common, with at least one poenskop being landed on each fishing trip (Thesen 2000). However, King (2006) suggested that the poenskop population around the Robberg Peninsula has been over-exploited. On comparing the catch compositions of teleosts in Plettenberg Bay with those caught in the TNP, reef fish species were more prevalent in TNP, with poenskop being amongst the top five species in the TNP (King 2006). On comparing the effect fishing pressure had on life history traits, King (2006) found that, despite CPUE being similar for poenskop in Rebelsrus (an area near Cape St Francis with moderate fishing pressure) and TNP (no fishing pressure), poenskop in the TNP were larger in terms of average weight and maximum size. In 2004, poenskop contributed 10.1% by number to the total catch made in the TNP (King 2006). Percentage composition was marginally lower in the moderately exploited Rebelsrus (9.4%) (King 2006). This contribution to the TNP's total catch increased to 16.5% in 2007 (King 2006).

Despite limited information existing on South Africa's spearfishery, Clarke (1988) analysed catches made between 1985 and 1987 during the National Spearfishing Championships. The locality of the competition would regularly change in order to prevent "home ground" advantages. In March 1987, the Championships were held in Knysna. Poenskop contributed 0.5% by number and 1.7% by mass to total catch. The recorded CPUE for poenskop was 0.035 kg.angler-hour^{-1} and 0.005 fish.angler-hour^{-1}. Schoeman (1957) recorded large numbers of poenskop being caught in the Knysna area earlier, however, at present, poenskop are not abundant along this coastline. A handful of large poenskop catches from Knysna have been recorded in the popular angling magazine *Stywe Lyne/Tight Lines*, including two poenskop weighing 16 kg and 24 kg, taken in 1971and 1988 respectively.

South-east coast

In a study of the recreational skiboat fishery in the Eastern Cape, Smale and Buxton (1985) showed that catches of poenskop were small. Even though a total of 163 captured poenskop were recorded between 1979 and 1980 (at a rate of 0.002 fish.angler-hour^{-1}), poenskop only contributed 0.25% to the total catch. Clarke and Buxton (1989) on surveying the recreational rock-angling fishery at Port Elizabeth between 1985 and 1986, found that poenskop contributed 0.98% and 0.5% to the recreational and competitive shore fishery, respectively. CPUE of poenskop caught recreationally (0.002 kg.angler-hour^{-1}) was also marginally higher than that of the competitive recreational fishery (0.001 kg.angler-hour^{-1}; Clarke and Buxton 1989). Clarke (1988) showed that poenskop contributed 0.9 and 2.2% by mass to the Eastern Cape recreational rock-angling and spearfisheries, respectively. Commercial catches of poenskop in this area were also low, accounting for only 0.1% by mass to the total teleost catch in the Eastern Cape in 1986 (Buxton and Clarke 1989). Clarke (1988) recorded a CPUE of 0.002 kg.angler-hour^{-1} and 0.001 kg.angler-hour^{-1} for non-club anglers and club anglers respectively between 1985 and 1986. Information obtained during the National Spearfishing Championships between 1985 and 1987 in the Eastern Cape revealed an average CPUE of 0.06 kg.angler-hour^{-1} and 0.019 fish.angler-hour^{-1}.

Competition shore-angling data from the south-east coast showed that poenskop is generally not a large contributor in these catches. Competition information was provided by Coetzee et al. (1989). This included catch card returns made by individual anglers during shore-based angling competitions, between Robberg and the Great Fish River, between 1959 and 1982. Poenskop were not represented in the catch-card returns. Coetzee et al. (1989) also presented competition shore angling data for the same region for the annual competition known as “Angling Week” between 1978 and 1982, as well as information from postal competitions between 1979 and 1982. In Angling Week, teams of anglers fished for a set period of one week in February each year (Coetzee et al. 1989). Postal competitions saw teams of anglers fishing for a single eight-hour period, with nine competitions being held annually (Coetzee et al. 1989). In both competitions, estimates of CPUE were obtained. Overall, Coetzee et al. (1989) found that poenskop contributed 1.24% of total catch by number, with a CPUE of 0.24 kg.angler-week^{-1} in the Angling Week catches, and 0.83% by number with a CPUE of 0.47 kg.angler-week^{-1} in the postal competitions (Coetzee et al. 1989).

Mandatory commercial catch data from the south-east coast (and KwaZulu-Natal) were most abundant in the NMLS. Gear type for all poenskop catches was recorded as linefishing. No distinction between shore and boat-based fishing was indicated. Based on records for the south-east coast between 1985 and 2010, CPUE for poenskop (Figure 3.5) appears to have declined. Overall poenskop make a low contribution to total catch (seen from the low CPUE). This trend is similar to a number of other sparid species, including white steenbras *L. lithognathus* (Bennett 2012) and red steenbras *P. rupestris* (Smale 1988).

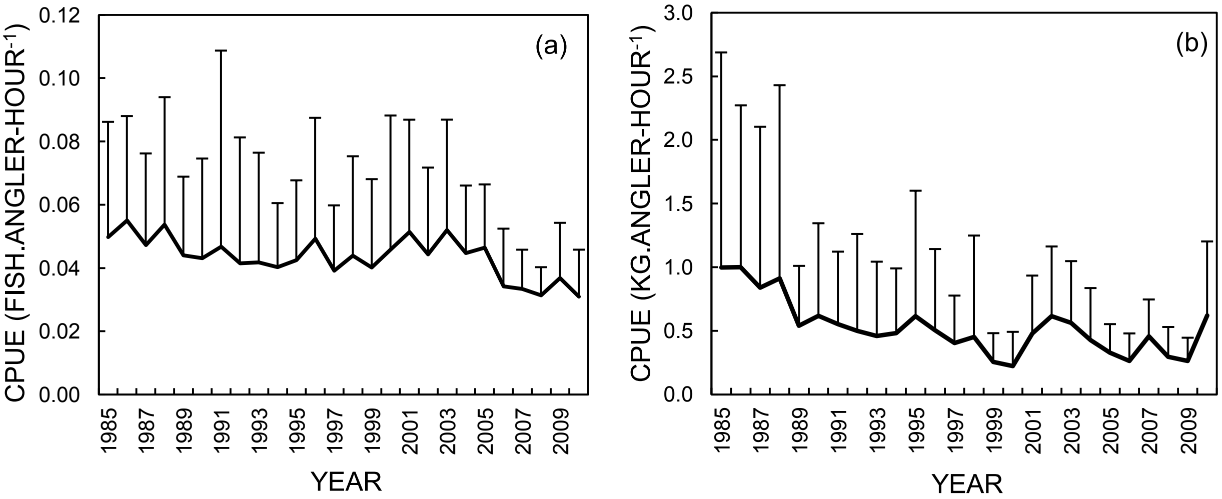

Figure 3.5: Mean (+SD) annual CPUE ((a) fish.angler-hour^{-1} and (b) kg.angler-hour^{-1}) of poenskop caught by the commercial fishery along the south-east coast of South Africa, as recorded in the National Marine Linefish System.

Transkei

This study also considered personal angling records from the Transkei coastline between 1949 and 1970. Records of catches by an unknown recreational shore angler were meticulously kept, with information collected including the date, species caught, bait used and weight of the fish (lbs). Unfortunately, no effort (fishing hours) data was recorded (in terms of fishing hours). Poenskop was the fifth most abundant species recorded in these personal angling records, and contributed 7.3% by number, and 25.2% by mass to the total catch (Figure 3.6).

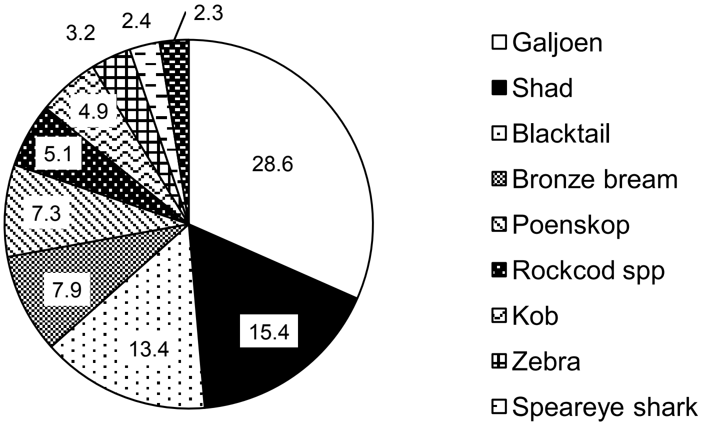

Figure 3.6: Percentage catch composition of fishes recorded in personal shore angling records from the Transkei between 1949 and 1970. Numerical contribution to the total catch is expressed as a percentage.

Hecht and Buxton (1993) analysed catches made by a commercial linefishery at Coffee Bay (Transkei) between 1984 and 1992. In 1984 and 1985, poenskop catches were high, with this species contributing 10 – 16% by number to the total catch. At this time commercial fishermen in the area believed that poenskop were seriously threatened by overfishing. As a result, commercial fishermen agreed to a voluntary cessation of the catching of poenskop (Hecht and Buxton 1993), accounting for no poenskop being caught in 1986 (Figure 3.7). Subsequent to this cessation, poenskop catches in the commercial linefishery remained relatively low, contributing an average of approximately 1.5% by number to the total catch. Poenskop were also caught in lower numbers between 1997 and 1998. It was one of two species targeted by both the recreational shore-anglers and members of the Transkei skiboat fishery (Mann et al. 2003). Even though poenskop were caught in low numbers, they contributed just over 4% to the total weight of all fish caught.

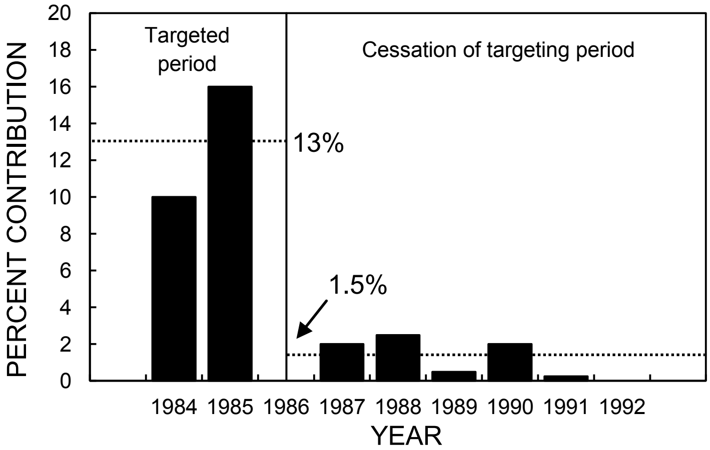

Figure 3.7: The percent contribution of poenskop to the total commercial landings in the Coffee Bay linefishery (from Hecht and Buxton 1993).

A national survey evaluating participation in and the management of the South African linefishery was conducted between 1994 and 1996 (Brouwer et al. 1997, Lamberth et al. 1997, Mann et al. 1997, Sauer et al. 1997). However, due to the Transkei coast (between Mtamvuna and Kei Rivers) not falling within South Africa's borders, it was not surveyed during between 1994 and 1996. This former homeland was then re-incorporated into the Eastern Cape and a decision was made to complete the survey in this area, thereby allowing evaluation of linefish management along the entire South African coast (Fennessy et al. 1999). Fennessy et al. (1999, 2003) assessed both the recreational and commercial skiboat fishery in the Transkei between 1995 and 1999. A total of 75 interviews, each with an associated catch inspection, were conducted between 1995 and 1998, with most interviews being focussed on recreational anglers. Additional field trips were undertaken in the northern (Port Edward, Mzamba, Mkambati, Mbotyi, Port St. Johns' and Mngazana River mouth) and southern Transkei (Coffee Bay and Kei Mouth) between March 1997 and April 1999. Poenskop made relatively small contributions in number to total recreational catch in the northern Transkei (3.0%) and Kei Mouth (2.3%). In contrast, poenskop contributed 17.0% by number to total catch in Coffee Bay. The contribution to total catch by mass was relatively high in both the recreational and commercial fisheries, and northern and southern Transkei, with poenskop contributing a staggering 44.1% to the total catch by mass landed in Coffee Bay by the recreational skiboat fishery between 1995 and 1999 (Fennessy et al. 2003).

Maggs (2011a) conducted a study determining the effects of protection on important fishery species in the Pondoland MPA between 2006 and 2010. Poenskop contributed 4.57% by number and 8.5% by mass to the total catch, with a mean CPUE of 0.26 fish.angler-hour^{-1}. Besides the CPUE recorded in the TNP, this was the highest CPUE recorded for poenskop from all studies and areas.

KwaZulu-Natal

Information of the KZN commercial linefishery, collected since 1910, showed that poenskop and other large endemic sparids (such as seventy-four and red steenbras) were heavily exploited in the 1920s, accounting for more than half the annual catch between 1922 and 1933 (van der Elst 1989). Based on limited information from KwaZulu-Natal, total catch of poenskop has declined considerably (Penney et al. 1999). Catch rates in KwaZulu-Natal (commercial skiboat sector) have declined from approximately 500 kg.boat-year^{-1} (1930 - 1933) to 100 kg.boat-year^{-1} (1986 - 1987); this represents a reduction of 80% (Buxton and Clarke 1989). Up until 1998, poenskop were placed in the "critical" category regarding management regulations (from Chief Director Sea Fisheries 1996).

Pradervand et al. (2007) on analysing the long-term trends in the competitive shore fishery along the KZN coast between 1977 and 2000, found that poenskop contributed <0.1 % by both number and mass to the total catch. This suggests that the abundance of poenskop in KZN is lower than other regions along the South African coastline. This could also be a result of this region being towards the northern limit of the poenskop's distribution.

The geographic coverage of commercial and recreational returns recorded in the NMLS differs markedly (Penney 1993). Only 9% of all commercial returns submitted between 1985 and 1990 came from KZN. In contrast, a staggering 96% of all recreational returns submitted for the same time period were from KZN (Penney 1993). This return bias is a result of the relatively large size of the recreational skiboat fishery in KZN (in comparison to the commercial fishery) and, more importantly, reflects the system of recreational skiboat inspections undertaken by EKZNW staff and captured on to the NMLS since 1984. One compliance officer every two kilometres was found to be present in KZN (0.53 compliance officers per kilometre of coastline). This is in sharp contrast to the Eastern Cape where only 0.03 inspectors per kilometre were present (Griffiths and Lamberth 2002). Therefore, the catch data recorded in the NMLS for KZN is most representative of actual catches made. As with records for the south-east coast, gear type for all poenskop catches was recorded as linefishing. Based on records for KZN from the NMLS, between 1985 and 2010, CPUE (Figure 3.8) for poenskop caught by recreational skiboat fishermen has remained relatively constant.

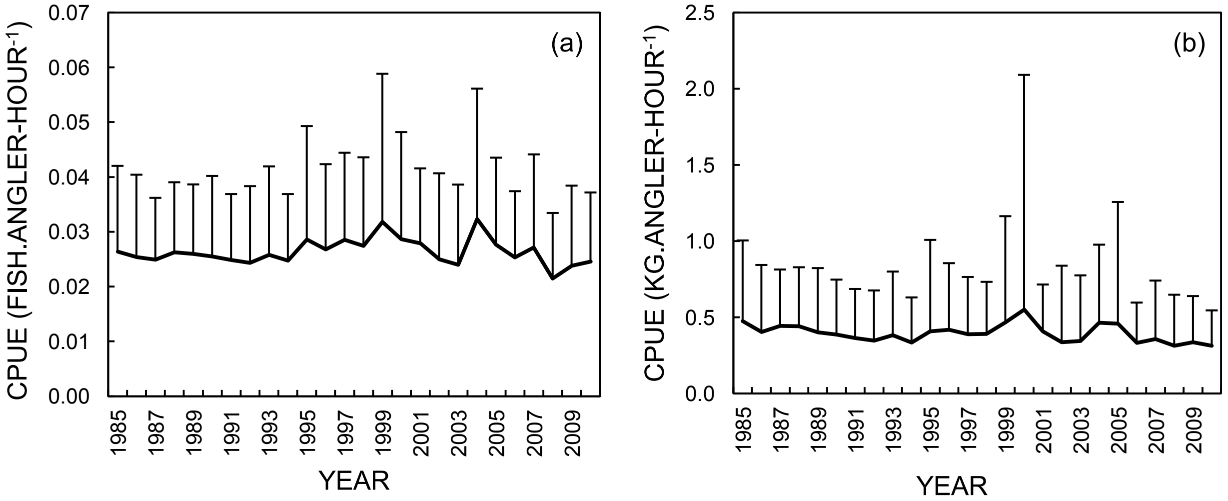

Figure 3.8: Mean (+SD) annual CPUE ((a) fish.angler-hour^{-1} and (b) kg.angler-hour^{-1}) of poenskop caught by recreational skiboat anglers along the KwaZulu-Natal coast, as recorded in the National Marine Linefish System (Maggs 2011b).

Summary at a national level

CPUE data in the results of the studies presented were scarce; however, for studies that presented these results, CPUE was generally higher within MPAs. CPUE was highest in the TNP, followed by CPUE in the Pondoland MPA. Based on the percentage contribution by mass to total catch, poenskop made the highest contribution within the Transkei, specifically the recreational skiboat and shore-based fishing sectors. The commercial skiboat sector in the Transkei also contributed a high proportion of poenskop by mass to the total catch. Catches in the south-west coast, south-east coast and in KZN were considerably lower than those made along the southern coast and in the Transkei (Figure 3.9).

The poenskop's representation in catches along the south-east coast was expected to be higher, as this region represents the core of its distribution range. As a consequence there are a large number of angling competitions in this region that specifically target poenskop. Even though this species is highly-sought after (Coetzee et al. 1989) competition anglers also tend to target elasmobranchs (sharks, skates and rays) (Clarke 1988). This is largely due to their mass, which contributes considerably to overall catch (Coetzee et al. 1981).

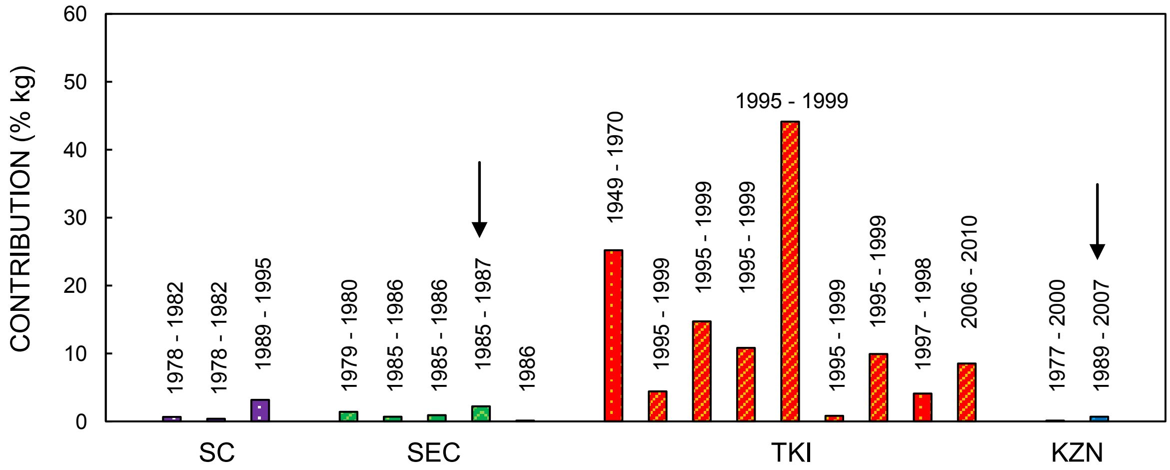

Figure 3.9: Poenskop percentage contribution by mass (kg) to total catch, recorded or inferred from recreational shore and skiboat fishery surveys along different regions of the South African coastline (SC - southern coast, SEC - south-east coast, TKI - Transkei, KZN - KwaZulu-Natal). Results are plotted in geographical order from west to east. Dotted bars represent shore-based fishing, diagonal lines represent skiboat fishing, and spearfishing is indicated by an arrow.

Catch data for KZN, with the exception of the NMLS data, is relatively scarce. Pradervand et al. (2007) found poenskop in KZN to contribute less than 0.1% gravimetrically to total catch. Brouwer et al. (1997) estimated total shore-angling effort of 3 238 921 angler days per year, with the greatest proportion of this effort being expended along the KZN shoreline. However, based on tagging information from the Oceanographic Research Institute Tagging Project, tagging effort in KZN accounts for 10% of national tagging effort since the inception of the project. Because high levels of effort are recorded for this area, the lack of poenskop caught could be a direct result of this effort. Northern KZN also represents the limit of the distributional range of poenskop. The number of poenskop in KZN is also thought to be lower than other stretches along the South African coastline.

The proclamation of the Tsitsikamma MPA in 1964 was the first marine regulation to affect the linefishery directly (both recreational and commercial sectors), resulting in decreased effort in that area. The TNP MPA has been shown to protect a number of important linefish species, with higher CPUE in the protected area than adjacent open areas (Hanekom et al. 1997, Cowley 1999). In 1992 and 2004, the Dwesa-Cwebe and Pondoland MPAs in the Transkei were proclaimed, respectively. The highest poenskop catches are still made along the Transkei coastline, therefore it is likely that these MPAs are affording critical protection for this species.

3.6. Discussion

Decreases in CPUE as an index of a decline in the abundance of species has been recorded in a number of different studies (see Hecht and Buxton 1993, Pilfold and Pampallis 1993, Penney et al. 1999, Hsu 2007, Mann and Pradervand 2007). Of particular concern is the decline of species which have K-selected life histories, such as sparid species. Griffiths (2000) found that resident reef fish that live longer than 15 years and are susceptible to being caught by hook and line are vulnerable to overexploitation by various linefisheries. Griffiths (2000) also described species which were resilient to overfishing having characteristics including nomadic movement patterns (resulting in unpredictable distribution) and shorter lifespans (less than 15 years). Poenskop, however, display high levels of residency (see Chapter 4) and can reach ages in excess of 45 years, thus making them extremely vulnerable to overfishing. The poenskop is threatened by both the recreational shore- and skiboat fishery, despite catches of poenskop being low. Even though they are considered to be of little commercial importance due to their low relative abundance, high recreational catches are still taken in the Transkei (Booth 2000).

A number of stock assessments have revealed that South African recreational anglers have been directly responsible for the decline of several species, including representatives of the Sparidae (Bennett 1993a, Garratt 1996, Chale-Matsau et al. 2001), Dichistiidae (Bennett 1988) and Sciaenidae (Griffiths 1997a). Griffiths and Lamberth (2002), on analysing catch contributions, found that recreational shore and boat anglers have contributed substantially (20 - 80% decrease in abundance) to the catches of at least nine collapsed stocks (including the poenskop), in KZN. The south-east coast data from the NMLS also indicate a substantial decline in CPUE in terms of fish.angler-hour^{-1} and kg.angler-hour^{-1}. Even though the KZN CPUE data from the NMLS showed poenskop catches to have remained relatively constant between 1985 and 2010, this could also be a result of a number of different factors. Other recreationally targeted fish such as kingfish *Caranx* spp. and pompano *Trachinotus* spp. may be more abundant in KZN waters increasing the probability of catching these species instead of a poenskop. Furthermore, migratory fish moving to KZN waters following the sardine run, such as shad *Pomatomus saltatrix* and leervis *Lichia amia* that are actively targeted, may further decrease the probability of catching a poenskop. Addtionally, regional differences in habitat use may make poenskop less accessible in KZN. Even though poenskop are present in KZN waters, they may not necessarily be targeted by both shore and skiboat recreational anglers.

Brouwer and Buxton (2002), on studying catch and effort of the shore and skiboat linefisheries along the Eastern Cape coast, found that fishers in these sectors blamed trawlers, pollution and other linefishing fishing sectors for the decline in catches (Brouwer et al. 1997, Sauer et al. 1997). Sauer et al. (1997) recorded overlap occurring between the commercial and recreational skiboat sectors. In addition, Penney et al. (1999) found that a number of recreational anglers in KZN sold their catch which further increased the competition between these sectors. In contrast to this, Griffiths and Lamberth (2002) found that this conflict is a result of perceived rather than actual competition. However, a number of other reasons (in addition to multi-sector targeting and competition) could have contributed to the declining poenskop stock as well as other sparid species. This includes (a) the development of the skiboat (Mara and Rorke 1986, Penney et al. 1999), (b) improvements in fishing gear (Bennett 1990, Leadbitter 2000, Cooke and Cowx 2006), (c) lack of compliance and enforcement (Bennett et al. 1994, Attwood 1997b, Griffiths and Lamberth 2002, Fennessy et al. 2003, Wood 2004, Murray 2009), (d) natural species fluctuations (Cribb 1994, Penney et al. 1999, Brouwer and Buxton 2002, Cooke and Cowx 2006), and (e) more participants and increased fishing effort in these sectors.

Penney et al. (1999) recorded recreational catches of a number of reef-dwelling sparids and serranids fluctuating in opposition to species such as kob and king mackerel. Sparid and serranid catches would increase as a result of poor catches of these other species, and decrease during good runs of kob and king mackerel (Penney et al. 1999). This trend was similar to that noticed by Cribb (1994), where in the case of declining fish stocks, fishing does not cease but rather different species are targeted, with the reduced fish species only being caught occasionally (Brouwer and Buxton 2002).

Cooke and Cowx (2006) found that recreational anglers (shore and skiboat) tended to respond to changes in catch rates by shifting their location in order to either maintain or increase catch rates. The development of the skiboat allowed anglers to focus fishing effort on undiscovered reefs that had previously not been exploited and were likely to be functioning as natural harvest refugia for resident reef fish speices (Penney et al. 1999). The spread of fishing effort resulted in a number of reefs being "fished out", as recorded around Durban by Mara and Rorke (1986). Poenskop are known to be dogged fighters when hooked and, with the continuing improvement in fishing gear, the probability of landing a poenskop is greatly increased. Increased fishing effort in both the recreational shore- and skiboat angling sectors and the commercial linefishing sector, coupled with the inability of the poenskop stock to sustain high levels of fishing effort is considered to be the the most likely reason for the decline in poenskop catches seen during the 20th Century.

Data from this chapter have shown that poenskop catches, with the majority of them being caught by fishers in the recreational sector, have been steadily declining in terms of number of fish caught. Various technological developments have also increased the probability of landing a poenskop (besides other species). The size of fish caught has steadily declined with almost all fish caught, at present, being less than 5 kg. Again, this is likely to be a direct result of overfishing.

Robust data on long-term CPUE trends for poenskop are scarce. Poenskop are also not well represented in catches, as discussed from the literature. Furthermore, possible biases or sources of error may have influenced some conclusions made. Percentage catch composition (Figure 3.3 and 3.6) may not necessarily be the most appropriate indicator of relative abundance. Instead, the contribution could indicate the species targeted and present in the area during that time. These results could also be the influence of selective fishing, once again with certain species being targeted that may not necessarily include poenskop. Another major bias could involve the regional differences in habitat use which in turn could influence catch rates and hence regional comparisons. Despite these obstacles, all available data were collected and analysed as best as possible. Anecdotal records of poenskop catches in *Stywe Lyne/Tight Lines*, the Robberg Diaries and personal angling records suggest that poenskop were once considerably more abundant. Fish of a larger size were caught more regularly. Clarke and Buxton (1989) on surveying the recreational shore-based fishery in Port Elizabeth found that anglers reported poenskop catches to have declined dramatically, both in terms of both the number and size of fish taken. Buxton and Smale (1989) assessed the abundance and distribution patterns of roman *C. laticeps*, dageraad *C. cristiceps* and red steenbras *P. rupestris* in exploited and unexploited areas off the southern Cape coast between 1984 and 1986. These authors recorded these sparid species to be more abundant in the unexploited area within the TNP. Size frequency distribution of all three species also showed a decrease in the proportion of larger fish and a smaller maximum size in the exploited area (Buxton and Smale 1989). These effects are classic symptoms of fishing pressure (Weatherley 1972), and the differences recorded between the two areas was attributed to exploitation by line- and spearfishermen (Buxton and Smale 1989). The percent contribution (by number and mass) of poenskop to total catch by the various fishing sectors has also decreased.

CPUE values for poenskop were highest in the MPAs. This could attest to the effectiveness of MPAs for protecting resident reef fish such as poenskop. Halpern (2003) showed that the density, biomass, organism size and diversity of protected animals increased within MPAs, irrespective of reserve size. Additionally, there was a 90% increase in biomass and an 80% increase in average body size of fish species within MPAs. Maggs (2011a), on studying effects of protection on important fishery species in Pondoland MPA between 2006 and 2010, found that overall CPUE in the no-take area was significantly greater than in the exploited area, with weight displaying a similar trend. The CPUE of slinger *Chrysoblephus puniceus*, scotsman *Polysteganus praeorbitalis*, and yellowbelly rockcod *Epinephelus marginatus* were all higher in the no-take area compared to the adjacent exploited area. These fish species also had a larger mean size in the no-take area, with mean sizes of each showing upward trends during the four-year study period (Maggs 2011a). Götz et al. (2008), on studying selected fishery and population parameters of eight shore-angling species in the TNP, including poenskop, found the CPUE for poenskop to have increased from 1998 to 2005. Götz et al. (2009a), on evaluating the functioning of the Goukamma MPA by means of a boat-based fishing study, found that protected roman *C. laticeps* were more abundant and of a larger mean size than in nearby heavily exploited areas. Juvenile poenskop and a large proportion of adults are known to be highly resident (Chapter 4). The above studies clearly show that MPAs are more than capable of protecting resident species. Therefore MPAs could be the most effective management tool for the protection of poenskop.

CHAPTER 4

MOVEMENT BEHAVIOUR AS INFERRED FROM LONG-TERM TAGGING PROJECTS

"The fish's habitat ranges from north of Natal to False Bay. It is not sufficiently common to trace from place to place in its course of migration, but probably follows the same littoral course as most of the sparids according to the flows of inshore warmer currents."

- Biden (1930: p 263) -

4.1. Introduction

Animal movement is an important ecological process that determines the demographic, spatial and genetic structure of populations (Pittman and McAlpine 2001). Ecological and evolutionary responses to environmental heterogeneity are reflected in the movement paths of individuals (Southwood 1977, Cohen and Levin 1991, Pittman and McAlpine 2001). Highly mobile species, such as many fish, exhibit complex and sometimes predictable movement patterns. These movement patterns can be associated with home-range activity (movement and relocation), ontogenetic shifts, spawning migrations and dispersal of eggs and larvae (Pittman and McAlpine 2001). Therefore, understanding animal movement in both time and space is important for the study of ecology, effective conservation design and resource management strategies, aimed at the protection of a species (Pittman and McAlpine 2001, Attwood et al. 2007).

Fish movement studies generally take two basic approaches – short-term studies or long-term studies. Short-term studies, typically using technologically-advanced techniques, are intensive and involve a small number of individuals that allow fine-scale movement patterns to be studied. Long-term studies, on the other hand, usually making use of less-specialised techniques, are conducted on many individuals, and yield information that provides an understanding of population movements. Watt-Pringle (2009) studied the movement behaviour of three inshore coastal fishery species (blacktail *Diplodus capensis*, zebra *Diplodus hottentotus* and white musselcracker *Sparodon durbanensis*) and found that the most suitable method to assess their movement patterns was to rely on external marks that were visible upon recapture. These external marks were in the form of plastic dart tags which have been used successfully in numerous other studies (Barrett 1995, Holland et al. 1996, Griffiths and Wilke

2002, Kerwath et al. 2007a). The strength of this technique is in the low cost and ease of application, allowing high numbers of fish to be tagged.

Residency is a common behavioural pattern seen in both temperate and tropical reef fish species (Roberts and Polunin 1991, Brouwer 2002, Brouwer et al. 2003). Although many South African sparids show residency throughout their lives (Buxton and Allen 1989, Cowley et al. 2002, Kerwath et al. 2007a), some species have predictable migrations (Griffiths and Hecht 1995, Brouwer 2002), while others disperse unpredictably (Attwood and Bennett 1994, Brouwer et al. 2003). A number of South African sparids which are resident as juveniles but migratory as sub-adults and adults include the white steenbras *Lithognathus lithognathus* (Bennett 1993b), red steenbras *Petrus rupestris* (Brouwer 2002) and white musselcracker *Sparodon durbanensis* (Watt-Pringle 2009). The poenskop is a reef-associated species with a similar life-history to the red steenbras and white musselcracker. Therefore, this suggests that poenskop will display similar movement behaviour.

Despite low recovery rates, long-term datasets utilising dart tags can provide thorough assessments of fish movement patterns. In South Africa, there are a number of long-term fish tagging monitoring programmes. These include the Oceanographic Research Institute's National Voluntary Tagging Project (van der Elst and Bullen 1993) and two dedicated research tagging projects associated with marine protected areas (MPAs), namely the Tsitsikamma National Park (Cowley et al. 2002), and the Pondoland MPA (Maggs 2011a) Fish Tagging Projects. These two MPA projects make use of tags supplied by the ORI Tagging Project. These projects have been recording fish movements along the South African coastline since 1984, 1995 and 2006, respectively. Even though information obtained from such long-term mark-recapture programmes only records two positions occupied by a fish during the course of its life (unless multiple recaptures of the same fish are made), they are still able to provide a general idea of the movement patterns undertaken by a specific fish species.

The overall aim of this chapter was to assess the movement behaviour of poenskop. Specific objectives were to:

(a) Describe movement using data collected from three dedicated long-term conventional dart tagging projects;

(b) Evaluate the effects of (i) geographic location, (ii) time at liberty, (iii) size/age of movement, and (iv) seasonality on recapture locality;

(c) Compare movements and home-range size estimates within inshore and offshore MPAs.

4.2. Material and methods

4.2.1. Data sources

Conventional dart tagging and recapture data for assessment of movement patterns of poenskop were obtained from three ongoing, long-term coastal fish-monitoring projects, conducted at different spatial scales; the first covered the entire South African coastline (Oceanographic Research Institute), and two were research-based projects in marine protected areas (Tsitsikamma National Park (TNP) and Pondoland MPA (PLD) linefish tagging projects), aiming to assess residency within the specific MPAs (Figure 4.1).

The two MPA-based tagging projects occur within poenskop's core distribution, and the ORI Tagging Project spans the majority of the poenskop's entire distribution range. The widespread operation along most of the coastline and the high level of effort exerted in the South African linefishery provided a high level of recapture effort for the national tagging project. The long-term nature of the ORI Tagging Project (started in 1984) allowed for assessment of movement patterns over long periods of time. Tagging and recapture data in the MPAs were recorded by researchers, allowing for trustworthy and accurate position recording, fish measurement and species identification (Attwood and Cowley 2005).

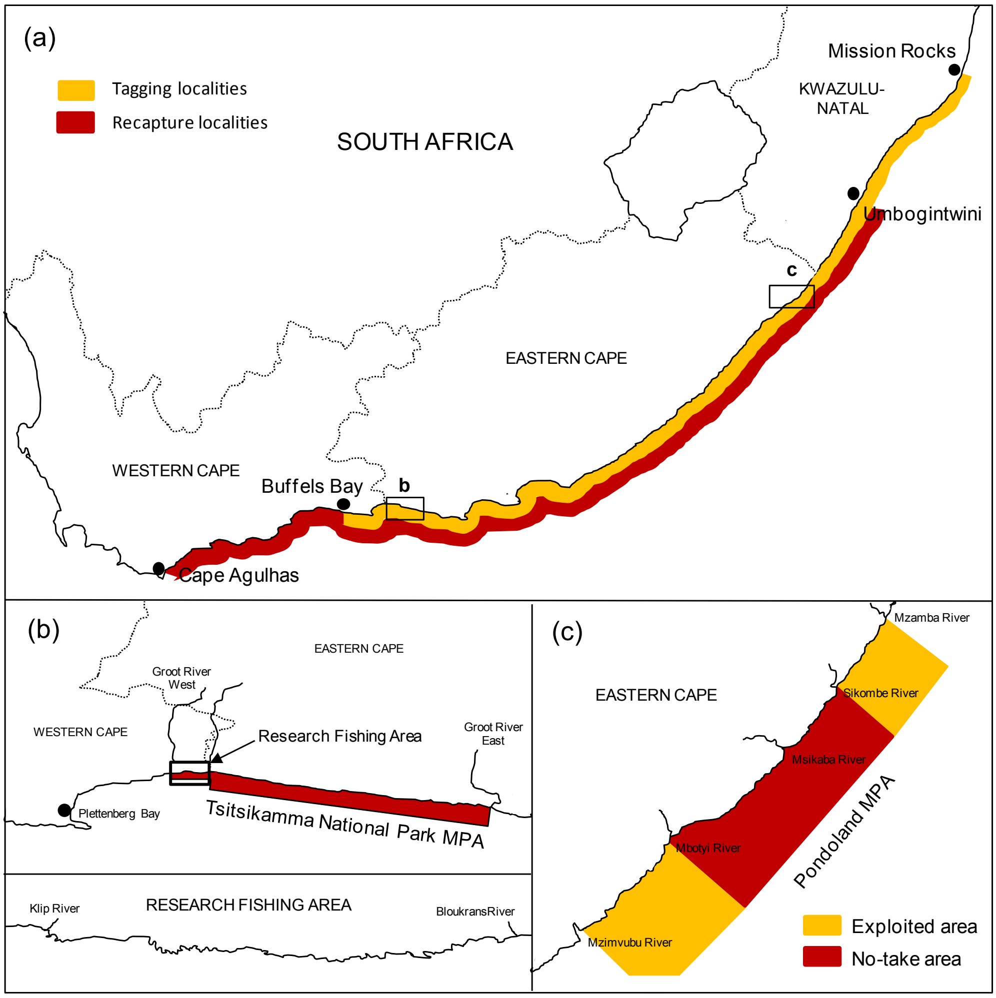

Figure 4.1: Study areas of (a) the ORI Tagging Project that spans the entire South African coastline and two research-based tagging projects: (b) Tsitsikamma National Park (TNP) and (c) Pondoland (PLD) MPAs.

A number of differences exist between the available data (Table 4.1). The data obtained from the MPA projects were fine-scale high resolution data with a precision of 15 to 100 m, while the information from the ORI Tagging Project was large-scale low resolution data where localities reported were on a scale of > 1 km. For analyses of all the tagging projects, distances were first converted to kilometres. Furthermore, due to the resident nature of many reef-associated fish species (including poenskop), most recaptures within the MPA projects were made by researchers (who were the only anglers allowed to fish within the MPAs), while reporting of recaptures in the ORI project relied on the participation of the angling public. Information for the species under investigation was obtained from both inshore (shore-angling) and offshore (boat-based angling) records in the ORI Tagging Project. The TNP provided inshore tagging effort, while the PLD fish were only tagged offshore. Together, these data provide a good platform on which to base the analyses of poenskop movement patterns.

Table 4.1: Summary information on the data sets derived from the Oceanographic Research Institute (ORI), Tsitsikamma National Park (TNP) MPA and Pondoland (PLD) MPA tagging projects.

Dataset	**Study site**	**Distance Resolution**	**Distance error**	**Information recorded**	**Inshore/ offshore**
ORI	Entire South African coast (± 3650 km)	Km	1 - 5 km	Tag number Date Location	Inshore Offshore
TNP	Tsitsikamma National Park MPA (5km research site)	M	10 - 50 m	Tag number Date Location Angler effort Water Temperature	Inshore
PLD	Pondoland MPA (four 1 x 2 km sites)	M	15 - 100 m	Tag number Date Location Angler effort	Offshore

ORI Tagging Project

The ORI Tagging Project, initiated in 1984 and administered by the South African Association for Marine Biological Research, is a nationwide tagging programme. This project differs from the MPA projects in that it enlists the help of volunteer recreational anglers (fishing with hook and line) who voluntarily join as members and agree to tag and release fish along the entire South African coastline. The high number of participants allows for high numbers of fish, from a wide range of species, to be tagged and recaptured. The recreational fishery also allows for geographically-widespread angling effort for tagging and recapture. The tagging of fishes takes place opportunistically, with tagging effort generally being excluded from inaccessible areas (e.g. protected, private or remote areas), while higher tagging effort takes place in areas with easier accessibility (e.g. holiday resorts, close to urban centres, etc.) (Watt-Pringle 2009). The number of active ORI participants varied from 300 to 600 per year (Bullen et al. 2008) and few were specifically trained in fish handling and tagging techniques (Govender and Bullen 1999). A request for the available data on poenskop was requested from ORI, who provided a data summary report (Dunlop and Mann 2011) that was used in the current analyses.

Tsitsikamma National Park Tagging Project

The Tsitsikamma National Park tagging project, initiated in 1995, aimed to determine the level of residency of important fishery species within, and the level of dispersal from, the MPA. The assessment of long-term catch-per-unit-effort (CPUE) within the MPA was also an aim. The project was started by researchers from the Department of Ichthyology and Fisheries Science (Rhodes University) and administered by Dr Paul Cowley (South African Institute for Aquatic Biodiversity) from 1996 to 2010, and subsequently by Dr Warren Potts (Rhodes University). The project initially comprised six five-day field trips annually, which decreased to four trips annually from 1997 until 2005. From 2006 until 2010, there were two trips annually (summer and winter), but this increased again to quarterly trips in 2011. The study area, situated between the Bloukrans and Klip Rivers, includes 5 km of coastline towards the western end of the TNP. The topography of the MPA is described in Chapter 2. All angling and tagging is conducted by experienced research anglers who have been trained to handle and tag fish.

Pondoland MPA Tagging Project

The Pondoland MPA, proclaimed in June 2004, is a multi-use MPA, consisting of two controlled zones allowing boat-based exploitation, and a restricted no-take area closed to all forms of fishing. The tagging project, initiated in 2006, aimed to elucidate movement patterns of important linefish species and examine the level of spillover into the adjacent exploited area (Figure 4.1). The project was started by researchers from the Oceanographic Research Institute (ORI) and administered by Mr Bruce Mann (ORI) from 2006 until present. The project saw two exploited sampling sites (Casino and Mnyameni) and two no-take sampling sites (Mkambati and Mtentu) within the MPA being visited quarterly for a period of two days (Maggs 2011a). Each sample site was effectively fished for three hours each day, and each fishing station within a sample site was actively fished for a maximum of one hour and a minimum of 15 minutes. The topography of the MPA is described in Chapter 2. The fishing was conducted by three anglers fishing off a ski-boat using standardized bait and tackle including the use of barbless circle hooks. A fourth person on the ski-boat was used to record information such as catch and effort data and tagging data. In addition to the fish recaptured by the research team at the study sites, recaptures were also reported by the public.

Figure 4.2: (a) A tagged juvenile poenskop, (b) a tagged sub-adult poenskop with a fouled tag and, (c) an adult poenskop being tagged by Dr Colin Attwood in the De Hoop MPA.

Dart tagging

Fish handling and tagging procedures in the TNP and PLD projects were consistent. Captured fish were placed on a wet flexible PVC vinyl sling with a central rigid baton and an attached measuring tape. Fish were measured to the nearest mm fork length (FL) and/or total length (TL), and tagged with a uniquely numbered plastic dart tag. Two types of plastic dart tags (Hallprint^{TM}, Australia) were used; namely Type-A and Type-D plastic barb tags. Type-A tags, having a length of 114 mm and a diameter of 1.6 mm, were generally used for larger fish (i.e. > 3 kg and/or > 60 cm). Type-D tags, having a shorter length of 85 mm and a diameter of 1.6 mm, were used for the tagging of smaller fish (i.e. 0.5 – 3 kg and/or 30 – 60 cm). Tags were inserted into the dorsal musculature of the fish, being anchored between two inter-neural spines, using a hollow stainless steel applicator. Fish tagged during the MPA projects were released at their capture localities.

Members of the public (recreational anglers) volunteer to tag fish as part of the ORI Tagging Project. Despite guidelines for the correct handling and tagging of fish being provided, the standardisation of this process cannot be guaranteed. However, because of the number of fish tagged and recaptured in the ORI project, and the comparable recapture rates obtained for most fish species (i.e. comparable to scientific tagging studies), suggest that this is a suitable and reliable method to provide a large sample size.

The dart tags used in all the tagging projects are enclosed in a sealed transparent sheath to prevent the abrasion of the numerical code as has been experienced with many other tag types (Dunlop and Mann 2011). Information from recaptured fish was returned to ORI via post, telephone or email; this information included the angler's name, tag number, species, recapture date, locality, fish length (and/or weight) and whether the fish was re-released or not.

4.2.2. Tagging data analysis

Recapture distances

The tagging and recapture localities for the ORI Tagging Project are based on a series of 1 km "coastal localities" between the northern border of Mozambique (in the east), and the Namibian border (in the west) (van der Elst and Penney 1995). However, not every 1 km stretch of coastline is uniquely defined. Attwood and Cowley (2005) questioned the accuracy (1 km precision) of both the capture and recapture locations reported to ORI, reporting that some positions may be out by as much as five kilometres. Therefore, it is possible that two localities may be separated by more than 1 km, and a recapture taken between two localities is recorded as the nearest locality defined by the ORI project. This results in a potential decrease in the resolution and accuracy of the data (Attwood and Cowley 2005). The error in position estimation has been suggested to be rarely more than 1 or 2 km. Therefore, this error is sufficiently low for studying the movement behaviour of poenskop, especially over larger spatial scales. The distances between capture and recapture localities, are thus calculated as the distances between coastal localities. As a result, movements were grouped into 5 km "bins", which was deemed to be more appropriate for analysis of spatial resolution.

The tagging and recapture positions of fish tagged in the Tsitsikamma and Pondoland MPA were recorded using "GPS accuracy". This provided high-resolution data, and distances between capture and recapture events were calculated as the distance along the coastline between the two positions. The precision of locations within the MPA projects was 15 - 100 m. For the purpose of this study, movements were grouped into 100 m bins.

Effect of coastal region on the level of movement

The South African coastline within the distribution range of poenskop was divided into five coastal regions, namely KwaZulu-Natal, Transkei, south-east coast, southern coast and south-west coast (Figure 4.3). KwaZulu-Natal and Transkei regions were defined based on provincial and political boundaries respectively. The other three coastal regions were in keeping with those defined in Chapter 3. The proportions of fish in each region that were recaptured in the same region or that moved to another coastal region were calculated. This was done in order to determine the level of residency and movement on a regional scale. Only the ORI Tagging Project data was used for this purpose, due to its wide coverage.

Effect of time at liberty on distance moved

The distances between capture and recapture locations for fish were statistically compared to the time at liberty between the two events for each fish, using linear regression (Statistica version 10) to determine whether the distance between tag and recapture localities was a function of time at liberty.

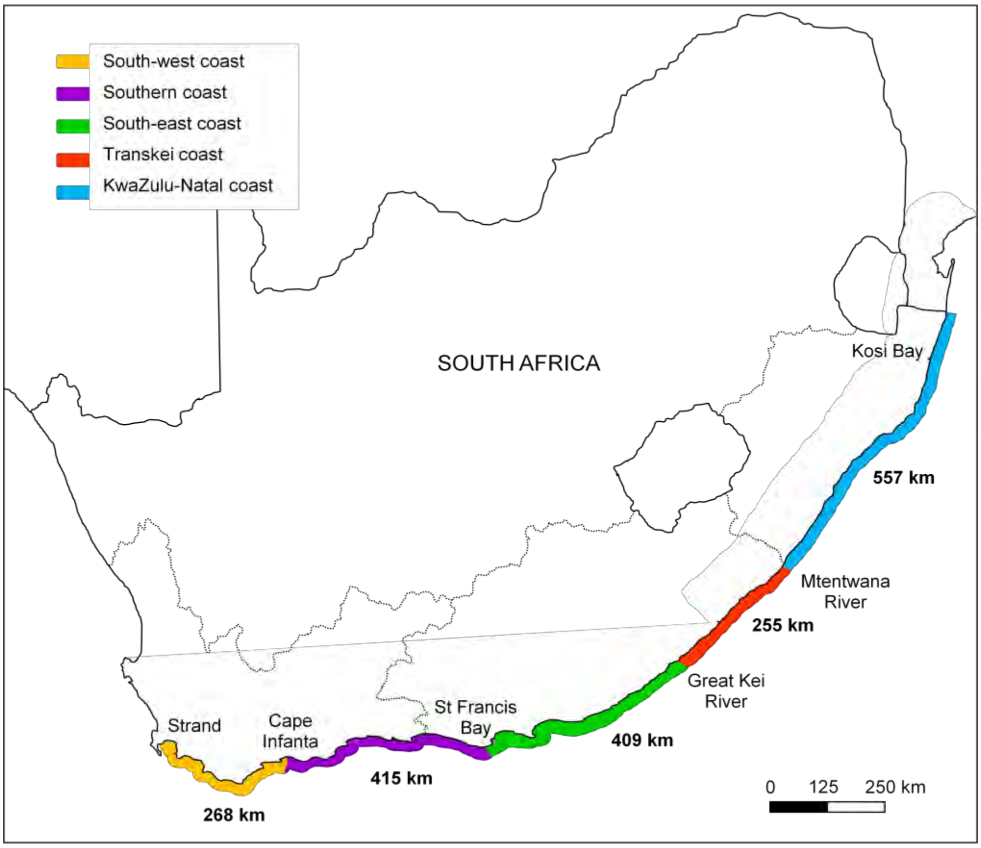

Figure 4.3: Map of the South African coastline, showing the different coastal regions and their lengths (km) as defined in the analyses, from the south-west coast to KwaZulu-Natal.

Effect of size (age) at recapture on distance moved

Recapture distances for all fish measured at the time of recapture were compared to size and age of the fish, using a Kruskal-Wallis ANOVA. This was performed to determine whether fish size or age influenced the distances moved. For this analysis, fork lengths were converted to ages, by means of an age-length equation. In the case of poenskop, the equation reads as follows:

$$age(years) = \frac{\ln\left(1 - \frac{FL}{1089.5}\right)}{-0.0502} - 2.885$$

According to Buxton and Clarke (1989), the smallest reproductively active female had a recorded length of 530 mm FL. This was therefore assumed to be the length-at-maturity in the absence of better information. Juveniles were therefore defined as those less than 530 mm FL. All fish below 700 mm FL were considered to be female and all poenskop above 700 mm FL were considered to be male. Buxton and Clarke (1989) found evidence of poenskop changing sex at this length.

Effect of season on recapture location

The effect of seasonality on movements was assessed in two ways. Firstly, proportions (%) of recaptures made monthly in each defined coastal region were calculated. Poenskop have been suspected of undertaking large-scale movements to the Transkei coastline during the winter months (Buxton and Clarke 1989). Therefore, this analysis was conducted in order to determine whether trends in these proportions would support this theory. Secondly, the monthly proportions of movements that were made in each direction from the tagging site (i.e. east or west) and the proportion that remained resident were determined. Attwood and Cowley (2005) suggested that assessment of seasonal movements (to detect seasonal effects) should be based on short times at liberty. Therefore, recaptures of poenskop that were at liberty for less than six months (Attwood and Cowley 2005) were extracted for this analysis.

Inshore vs. offshore environments

The inshore recapture data from TNP was compared to the offshore data from PLD by determining whether there was an effect of size at recapture on distance moved. This analysis was identical to that performed for the ORI dataset.

Home-range estimation

Home-range size for poenskop in the Pondoland MPA was estimated by Maggs (2011a). This was done to further quantify the degree of residency shown by poenskop. In order to calculate home-range (area), at least three points are required. However, in this study and that conducted by Maggs (2011a), the linear distance of a fish's home-range was calculated to determine whether fish movements go beyond the MPA boundaries. The linear distance of a home-range was estimated for poenskop by taking the 95th percentile of tag-recapture movements (linear distance between tag-release and tag-recapture). The resulting home-range length estimate is referred to as the single linear distance (SLD). Multiple recaptures (when a fish is tagged, released and subsequently recaptured on more than one occasion, creating a two-dimensional polygon), although scarce, were used to estimate home-range size by taking the 95th percentile of the greatest linear distance (GLD) across the interior of the polygon. In addition to SLD and GLD, Kramer and Chapman (1999) suggested the following equation for the calculation of home-range length:

$$Home - range\ length\ (m) = 0.000178\ (\text{fork length (mm)})^{2.35}$$

The estimations from TNP and PLD for SLD and GLD were then compared to the home-range length predicted by Kramer and Chapman (1999).

Of all recaptured poenskop, 34 were either recorded in mm total length (TL), or no length at recapture was recorded. Fish lengths reported as TL were converted to fork length (FL) prior to analysis. This was done by using the length relationship given by Buxton and Clarke (1989).

$$mm\,FL = \frac{mm\,TL}{1.1252} + 1.2376$$

Where no recapture length was recorded, estimates of FL were derived from the poenskop's von Bertalanffy growth equation.

4.3. Results

Tag longevity

In movement studies utilising dart tags, it is important to have an indication of the lifespan of a tag, as well as having an approximation of the number of recaptures likely to retain tags after a specific period of time. Overall, a total of 189 fish were recaptured from the combined tagging projects (Figure 4.4). By plotting the proportion of recaptures made every six months, and fitting a power curve to the graph ($R^2 = 0.859$), the life-span of a tag was able to be calculated. For example, after approximately three months at liberty, 100% of recaptures should still have their tag. The possibility of a poenskop holding its dart tag reduces with an increase in time. Therefore, after six months at liberty, only 50% of poenskop should retain a tag. Even though this calculation could prove useful to other studies, it should be used tentatively. Poenskop have been recaptured after more than 10 years at liberty with the dart tag still intact.

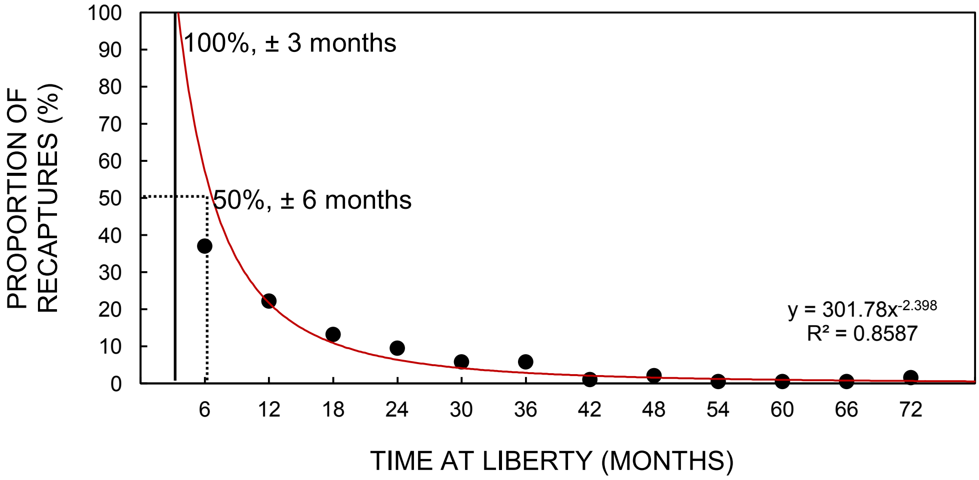

Figure 4.4: The proportion of poenskop recaptures made every six months in all three tagging projects. The solid line represents the proportion of recaptures at which 100% of recaptures are likely to still have an intact dart tag. The dotted line represents the proportion of recaptures at which 50% of recaptures are likely to still have an intact dart tag.

Analysis of recaptures

At the time of analyses, 2 704 poenskop had been captured and tagged with conventional dart tags, of which 189 (6.99%) were recaptured. Most fish (n = 1 935) were tagged in the ORI project, while 556 were tagged in the Tsitsikamma MPA and 213 in the Pondoland MPA research projects (Table 4.2).

Table 4.2: Summary of recapture data obtained for poenskop tagged along the South African coast between 1984 and 2010.

Tagging Project	No. tagged	Recaptures		Distance travelled (km)			Days at liberty		
		No.	%	Mean	Min	Max	Mean	Min	Max
ORI	1 935	74	3.82	24	0	483	430	0	3 295
TNP	556	73	13.13	0.04	0	0.25	393	0	2 407
PLD	213	42	19.72	0.12	0	0.64	468	59	1 390
Total	*2 704*	*189*	*6.99*	*9*	*0*	*483*	*424*	*0*	*3 295*

Recaptures were made from Cape Point to KwaZulu-Natal, spanning the core distribution of the species. Recapture rates were high in the MPAs (Table 4.2), while the recapture rate for the ORI project was considerably lower. In total, twenty-two fish were recaptured twice, three poenskop were recaptured three times, and one individual from the Pondoland MPA was recaptured five times.

ORI Tagging Project recaptures

By the end of 2010, 1 935 poenskop had been tagged from Buffels Bay in the west to Mission Rocks (just north of St Lucia) in the east, of which 74 (3.82%) were recaptured (Figure 4.4). Recaptures were made from Cape Agulhas (in the Western Cape) to Umbogintwini, near Durban, in KwaZulu-Natal, spanning approximately 1 300 km of coastline. Based on the frequency distributions of distances from the ORI project, the majority of recaptures (74%) were made within 5 km of the tagging sites (Figure 4.5). Considerably fewer recaptures fell into the other distance bins. These recaptures were made from Cape Agulhas to Ramsgate (near Margate). Four poenskop (6%) were recaptured 5-10 km from the tagging site, while eight (11%) and seven (9%) fish, respectively, were recaptured between 10 and 100 km, respectively, and more than 100 km, from the tagging locality (Figure 4.5). Three fish were recaptured twice, all at the tagging site.

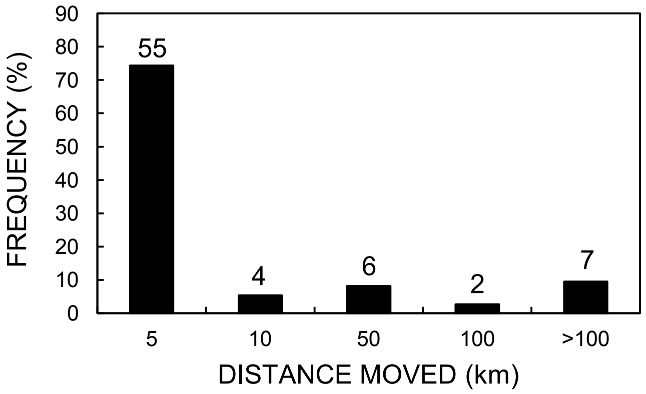

Figure 4.5: Frequency distribution of distances moved (km, values represent the upper limit of distance bins) for poenskop tagged in the ORI Tagging Project. Sample sizes are presented above each bar.

Large-scale movements (> 100 km) were recorded in the Eastern Cape (n = 6) and KwaZulu-Natal (n = 1) provinces, of up to 483 and 148 km, respectively. There was also evidence of connectivity among different coastal regions, between Storms River (southern coast) and Kromme River (south-east coast), between Port Alfred (south-east coast) and Mazeppa Bay, Bulungula Mouth and Mnyameni River (Transkei coast), and Mzamba River (Transkei coast) and Umbogintwini (KwaZulu-Natal coast). No long distance displacements were recorded crossing the south-west and southern coasts (Figure 4.6). Tagging and recaptures were not equally distributed along the coastline, with the majority (n = 1 059, 55%) of poenskop being tagged and released along the south-east coast. A total of 412 (21%) poenskop were tagged in the Transkei, and a further 253 (13%) along the southern coast.

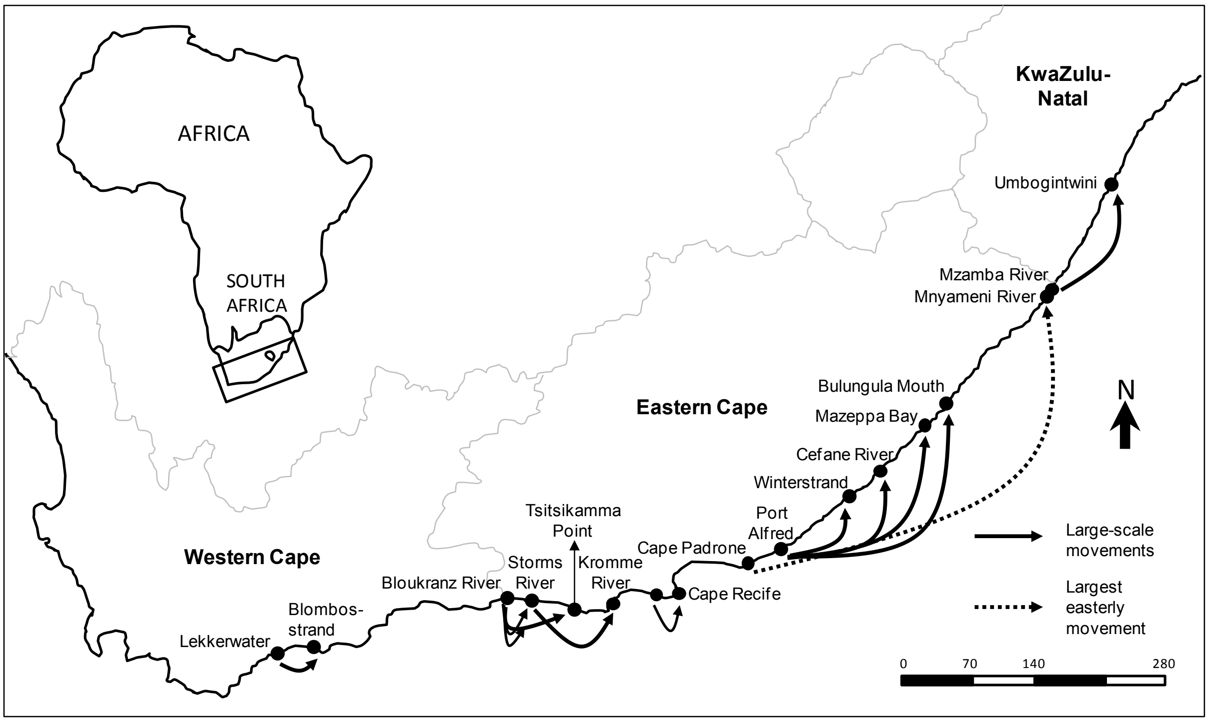

Figure 4.6: Long-distance movements (> 15 km) of recaptured poenskop along the South African coastline recorded in the ORI Tagging Project. Arrows connect tagging and recapture locations.

TNP MPA recaptures

Most recaptures made within the Tsitsikamma MPA were made at the tagging site. Eleven multiple recaptures were made, with all recaptures, once again, being made at the tagging site. The greatest distance moved by a single fish was 250 m. The results from the TNP showed the majority of recaptures were made at the tagging sites (63%), with all recaptures being made within 250 m of the tagging sites (Figure 4.7). Fifteen percent of recaptures moved between 10 and 50 m from the tagging site, 19% moved between 100 – 200 m, and 3% being recaptured 250 m from the tagging site (Figure 4.8).

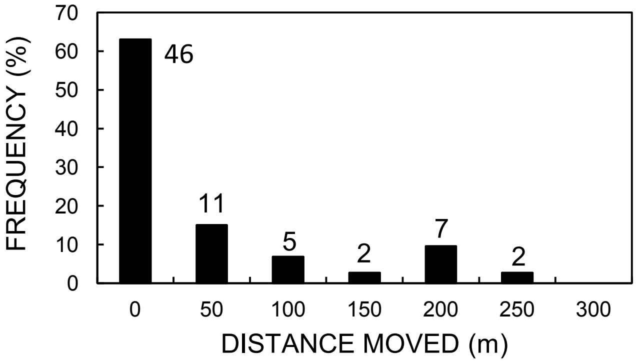

Figure 4.7: Frequency distribution of distances moved (m, values represent upper limit of distance bins) for poenskop tagged in the Tsitsikamma tagging project. Samples sizes are presented above bars.

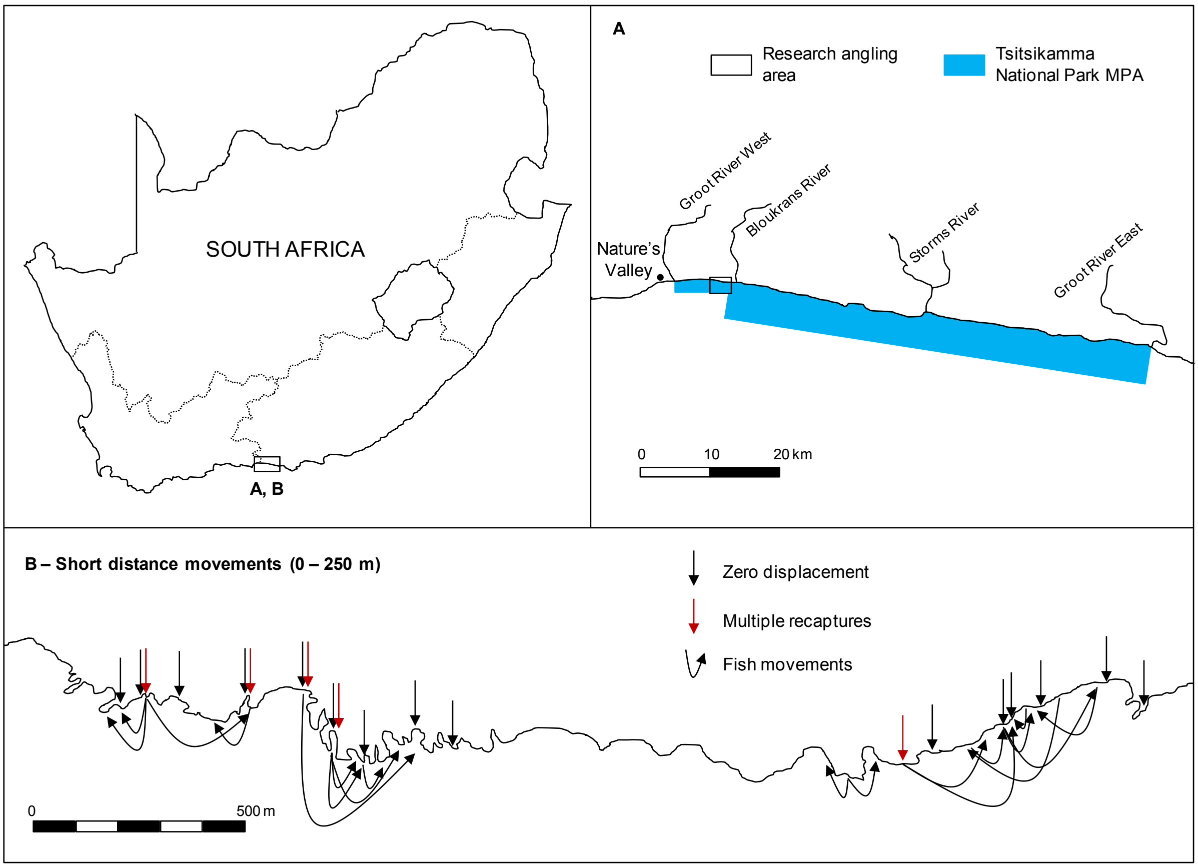

Figure 4.8: Short-distance movements (0 – 250 m) of poenskop recaptured in the Tsitsikamma National Park MPA. Arrows connect tagging and recapture locations; red arrows indicate multiple recaptures from the same location.

Pondoland MPA recaptures

Of the 213 poenskop tagged in the Pondoland MPA tagging project, 42 were subsequently recaptured (19.7% recapture rate). Of all recaptures made, only two individuals were recaptured at the tagging site, while 10 (24%) poenskop moved between 10 – 50 m, 25 (60%) were recaptured between 51 and 200 m, and five individuals (12%) moved distances greater than 250 m. Fifty-seven percent of all poenskop caught in the PLD were recaptured within 100 m of the tagging locality (Figure 4.9). The greatest distance moved by an individual was 636 m. No recaptures were made outside the MPA. Eight multiple recaptures were made, with all recaptures being made in zone in which they were tagged, although all displayed movement (between 10 and 350 m) (Figure 4.10).

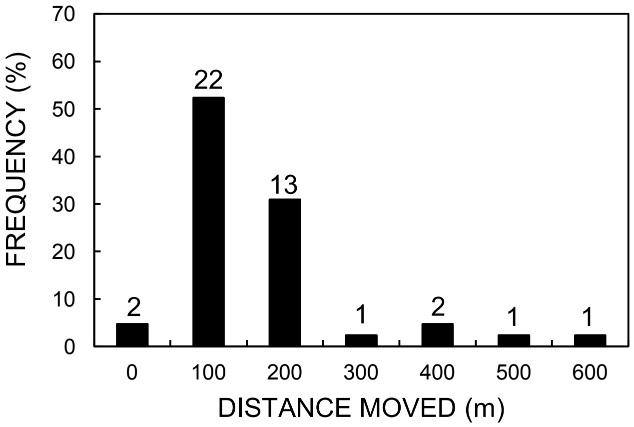

Figure 4.9: Frequency distribution of distances moved (m, values represent the upper limit of distance bins) for poenskop tagged in the Pondoland tagging project. Sample sizes are given above bars.

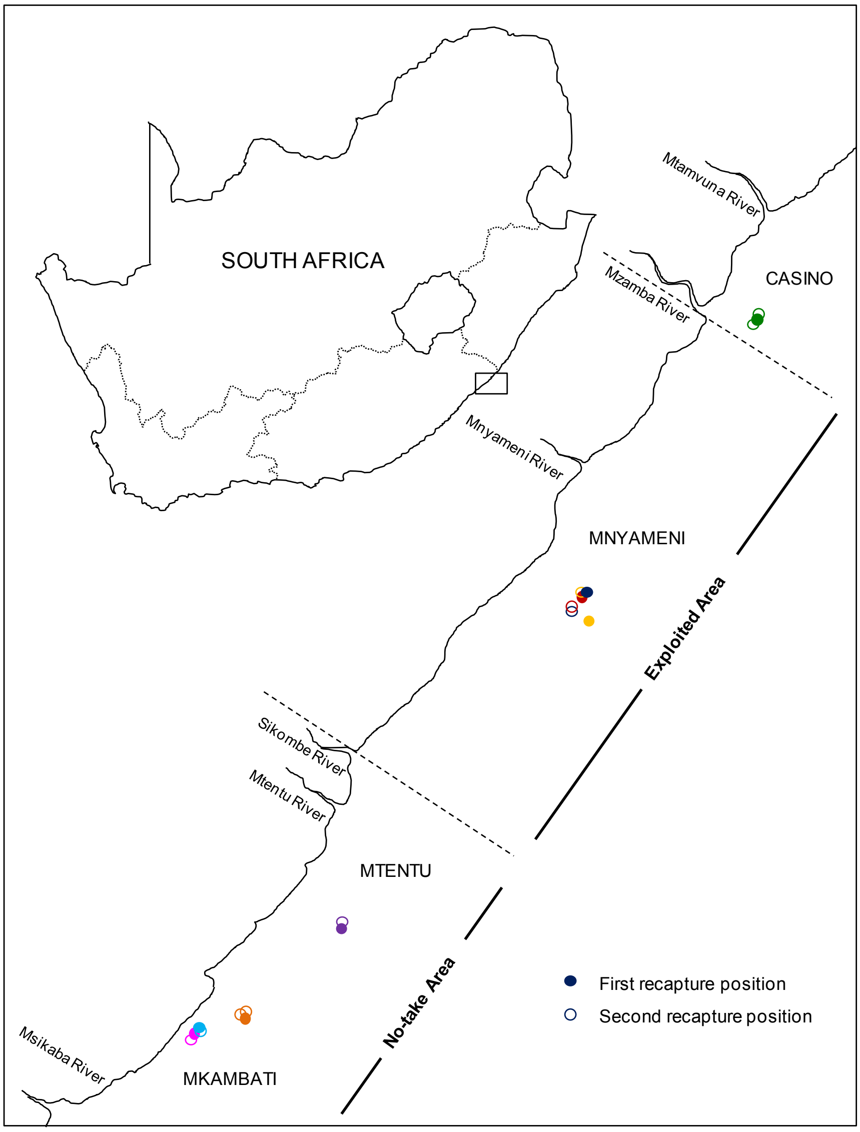

Figure 4.10: Movement of poenskop (n = 8) recaptured on more than one occasion in the Pondoland MPA.

Recapture distances and direction of movement

Habitat type and the resolution at which tagging and recapture localities were recorded could have an influence on the proportions of recaptures falling into the lowest recapture distance bins (i.e. 0 to 5 km). The frequency distributions of distances for all recaptures in the three tagging projects were thus compared graphically (Figure 4.11).

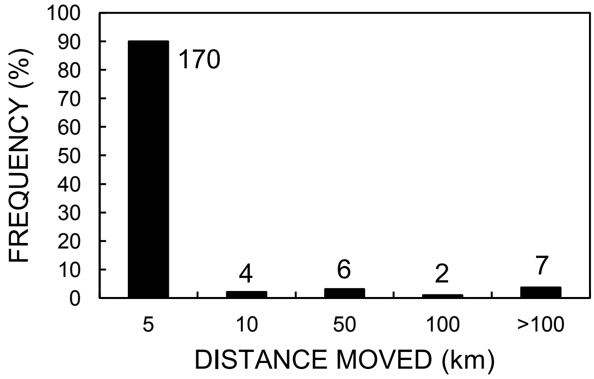

Figure 4.11: Frequency distributions of distances moved (km) for all fish (n = 189) recaptured from the three tagging projects, showing 0 to 5 km and > 5 km recapture distances combined. Sample sizes are presented next to and above each bar.

Although the majority of recaptures (± 90%) were made within five km of the tagging site (Figure 4.11), large-scale movements, up to 483 km, were recorded for some individuals. The frequency and magnitude of these movements were greater in an eastward direction from the tagging site (Figure 4.12).

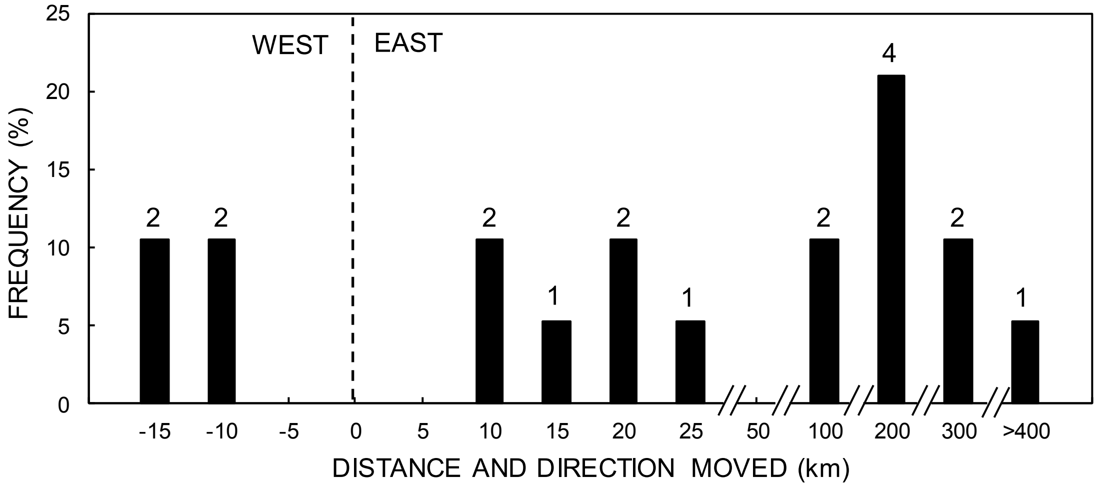

Figure 4.12: Frequency (%) distribution of distances for poenskop that moved > 5 km (n = 19), including direction of movement along the coast (all projects). Negative and positive values represent displacement in a westerly and easterly direction respectively. Sample sizes are given above each bar.

Effects of coastal region on fish size and the level of dispersal

Size of fish at tagging

The sizes of poenskop that were measured at the time of tagging in the ORI Tagging Project (n = 1 935) in each coastal region reflected the size distribution of those at recapture for the three projects combined. The majority of fish tagged were < 500 mm FL (i.e. sub-adults). Only 303 (16%) adult fish were tagged (Figure 4.13a). There was no significant difference in the size of fish tagged within each coastal region (ANOVA, $p = 0.11$) (Figure 4.13b).

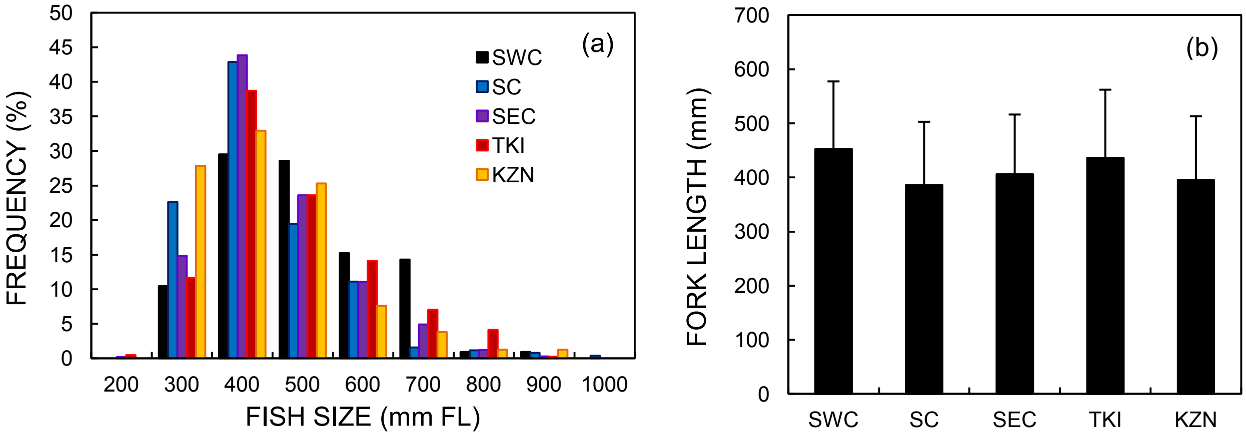

Figure 4.13: Sizes of poenskop (mm FL) that were measured at the time of tagging in the ORI Tagging Project (n = 1 935), showing (a) size frequency (%) distribution by coastal region, and (b) mean size (± SD) by region (SWC – south-west coast, SC – southern coast, SEC – south-east coast, TKI – Transkei, KZN – KwaZulu-Natal).

Effect of coastal region on levels of dispersal and residency

A high proportion of fish tagged in the ORI project in each coastal region were recaptured within the same tagging region, providing strong evidence of residency on a regional level (Figure 4.14). Fish seldomly bypassed a coastline region. All fish that were tagged in KwaZulu-Natal and along the south-east coast were recaptured within the same coastal regions. At least 85% of fish tagged within the south-west coast, southern coast and Transkei coastal regions were recaptured within the same region (Figure 4.14). The Transkei had the greatest proportion of “dispersal”, with 19% of recaptures being made outside the region.

The mean distance moved by fish recaptured within each region showed no trend. This may be due to the low number of recaptures attained for each coastal region, and the recaptures predominantly displaying zero movement.

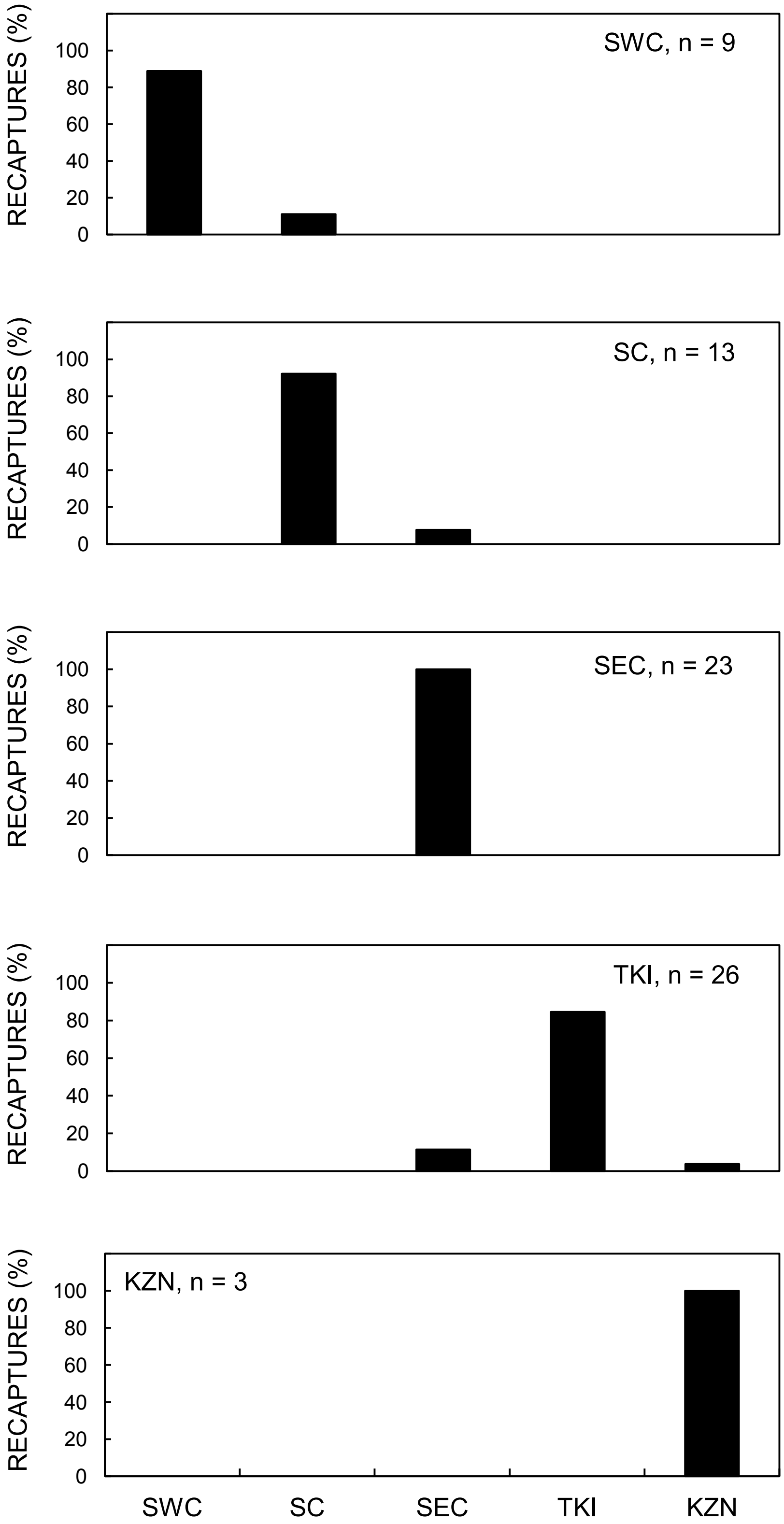

Figure 4.14: The regional distribution (%) of recaptures (n = 74) from the ORI Tagging Project for poenskop tagged in the different coastal regions (SWC – south-west coast, SC – southern coast, SEC – south-east coast, TKI – Transkei, KZN – KwaZulu-Natal).

Effect of fish size and age on distance moved

Lengths of recaptured fish ranged from 204 to 920 mm FL. Most of the recaptures in each of the three projects (70 to 97%) and overall (85%) were juveniles or sub-adults, smaller than the size-at-maturity (± 530 mm FL) (Figure 4.15).

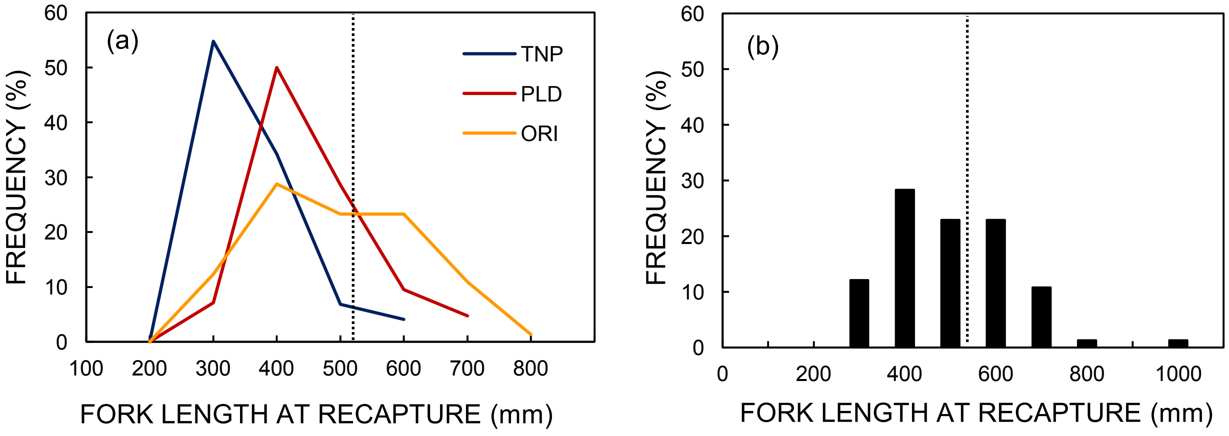

Figure 4.15: Fork length (mm) for poenskop measured at the time of recapture, for (a) each tagging project, and (b) all projects combined (n = 189). The dotted line indicates approximate size at sexual maturity.

Poenskop moving greater distances were characterised by greater mean sizes (mm FL) and ages at time of recapture (Table 4.3). A single adult fish (920 mm FL being approximately 34.2 years old) was removed from the 0-1 km category providing a clearer pattern of movement based on size and age.

Table 4.3: Mean (± SD) lengths (mm FL), length ranges, mean (± SD) ages (years) and age ranges of poenskop recaptured within various distance bins (n = 189).

Distance moved (km)	Number measured	Mean (± SD) size (mm FL)	Size range (mm FL)	Mean (± SD) ages (years)	Age range (years)
0 – 1	164	373 (± 109)	220 – 690	5.7 (± 3.4)	1.2 – 17.1
> 1 – 10	10	414 (± 74)	307 – 526	6.7 (± 2.2)	3.7 – 10.2
> 10 – 100	8	388 (± 117)	250 – 579	6.1 (± 3.5)	2.3 – 12.2
> 100	7	650 (± 58)	562 – 740	14.8 (± 2.7)	11.6 – 19.8

Three size classes were selected (juveniles: < 300 mm FL, sub-adults: 300 – 530 mm FL, adults: > 530 mm FL) to determine whether distances moved were significant among the selected size classes. After analysis, it was found that distances moved differed significantly among size classes (Kruskal-Wallis ANOVA, $p < 0.001$) (Figure 4.16). Distances moved by the two smaller size classes were not significantly different ($p > 0.05$). Adult poenskop undertook significantly greater movements (mean distance moved: 55 ±111.85 km) than either juveniles (mean distance moved: 1.8 ±7.76 km) or sub-adults (mean distance moved: 0.7 ±3.49 km) ($p < 0.001$).

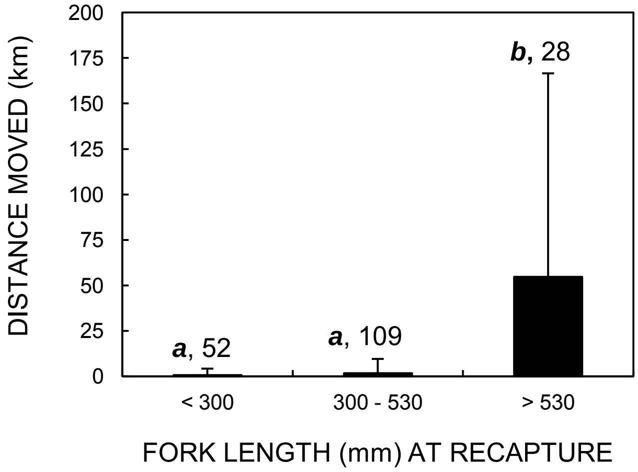

Figure 4.16: Mean (± SD) distance moved (km) by size class (mm FL) for all recaptures in all projects (n = 189). Different letters (*a*, *b*) indicate those size classes that are significantly different. Sample sizes are presented above each bar.

Effect of time at liberty on distance moved

Times at liberty between tagging and recapture ranged widely (Figure 4.17), with some fish being recaptured on the same day as tagging (as in the Tsitsikamma and ORI tagging projects), and ranging up to 3 295 days (ORI Tagging Project). The mean days at liberty were similar among all projects (ranging from 393 to 468 days). The mean numbers of days at liberty were similar between coastal regions, with recaptures along the south-east having the highest average and KwaZulu-Natal having the lowest average number of days at liberty.

On examining the time at liberty for all fish recaptured (n = 189) against distance moved (km), no clear trend was evident. One fish showed zero displacement after being at liberty for 3 295 days. However, linear regression showed a weak, but significant ($R^2 = 0.049$, $p < 0.005$), positive correlation between distance moved (km) and the number of days at liberty for all recaptured fishe from all tagging projects (Figure 4.18).

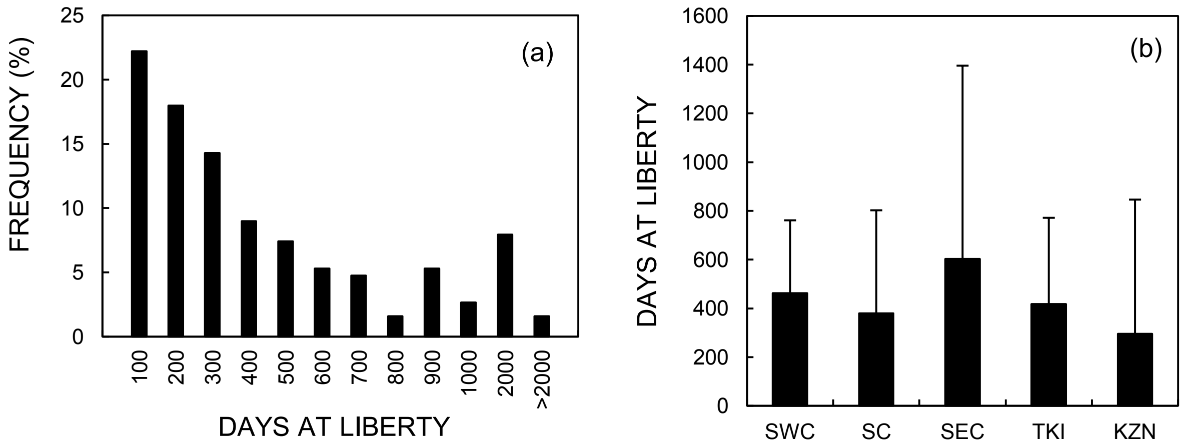

Figure 4.17: Time at liberty (days) for all poenskop recaptured from all tagging projects (n = 189), expressed as (a) a frequency (%) distribution, and (b) mean days at liberty (± SD) by coastal region (SWC – south-west coast, SC – southern coast, SEC – south-east coast, TKI – Transkei, KZN – KwaZulu-Natal).

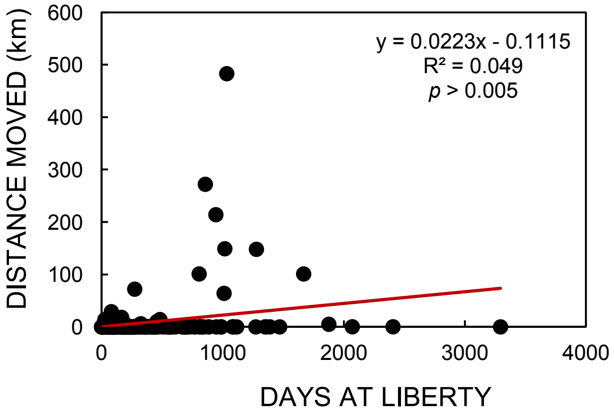

Figure 4.18: Time at liberty (days) plotted against recapture distance (km) for all recaptures (n = 189) showing a linear regression analysis of recapture distance against time at liberty (days).

Effect of seasonality on recapture location

Monthly proportions (%) of recaptures made in each of the coastal regions showed no seasonal trend, although peaks in certain regions could be identified. Over the summer months (December – February), fishing effort along the South African coastline tends to increase (see Chapter 3). This trend was clearly evident among recaptures made along the southern and south-east coastal regions (Figure 4.19). Only five recaptures were made in KwaZulu-Natal (in February, May, August and November).

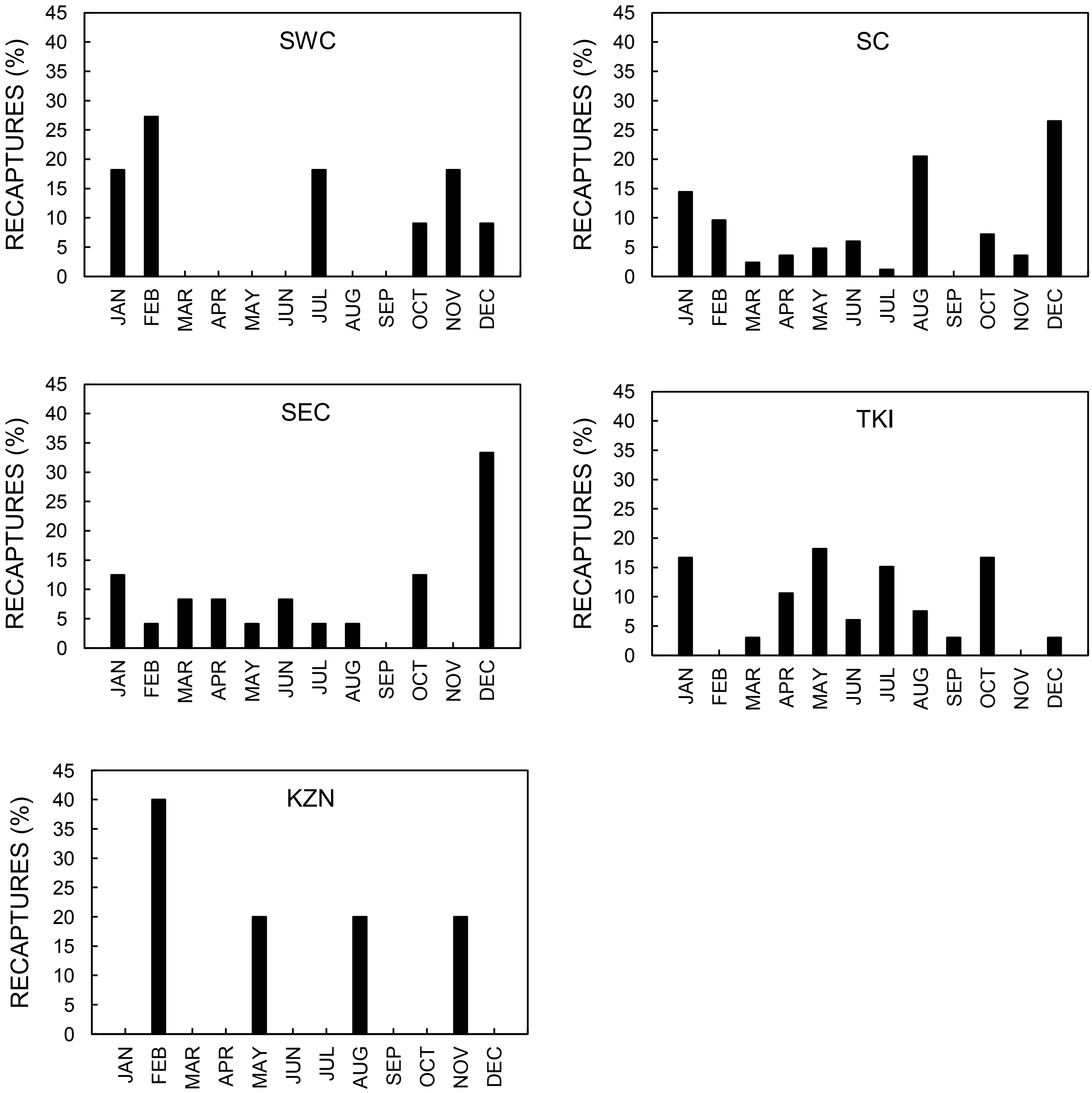

Figure 4.19: Monthly proportions (%) of recaptures made in each of the different coastal regions (SWC – south-west coast: n = 11, SC – southern coast: n = 83, SEC – south-east coast: n = 24, TKI – Transkei: n = 66, KZN – KwaZulu-Natal: n = 5).

Monthly proportions of movement directions (west, east or zero displacement) for fish at liberty for up to six months were investigated (Figure 4.20). The proportion of fish recaptured in December was highest for those showing no movement (Figure 4.20). Poenskop moving in a westerly or easterly showed no preferred month for movement. The vast majority (85%) of fish tagged and recaptured were juveniles and sub-adults. Therefore, the data is not reflective of movements undertaken by adult fish. From Figure 4.19 and Figure 4.20, it can be concluded that there was no seasonality in recaptures.

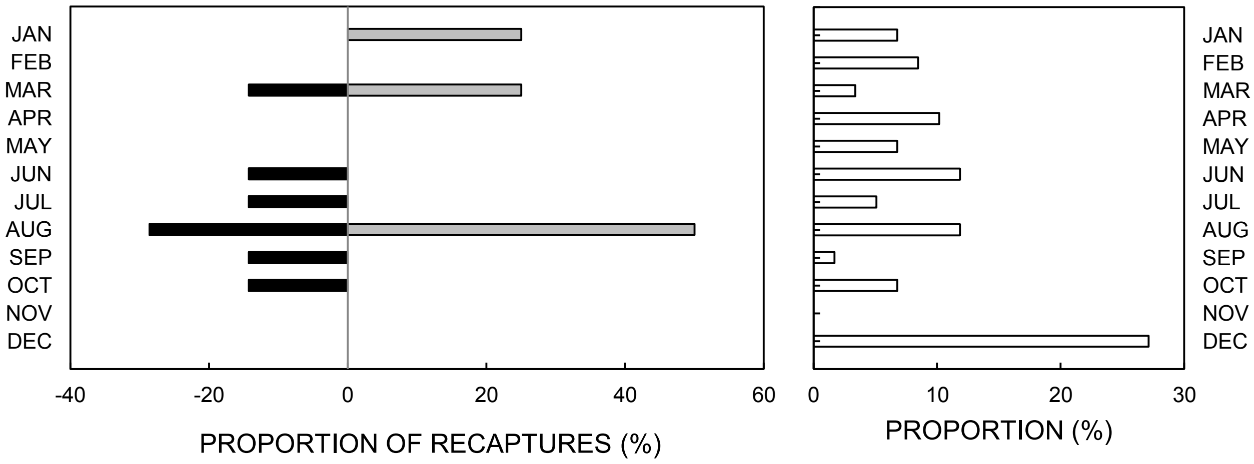

Figure 4.20: Monthly proportions of recaptures (from all projects) for poenskop at liberty for up to six months (n = 70) for fish that moved in a westerly (negative proportions) and easterly (positive proportions) direction, or showed zero displacement. Black bars represent westward proportions, grey bars represent eastward proportions and white bars represent fish that remained stationary.

Inshore vs. offshore environments

Of the 115 poenskop recaptured in the Tsitsikamma and Pondoland MPA, all fish were reliably measured, with length being recorded in mm FL. The majority of poenskop recaptured in the TNP (55%) were juveniles (< 300 mm FL), while 83% of poenskop recaptured in the PLD were sub-adults (300 to 530 mm FL) (Figure 4.21).

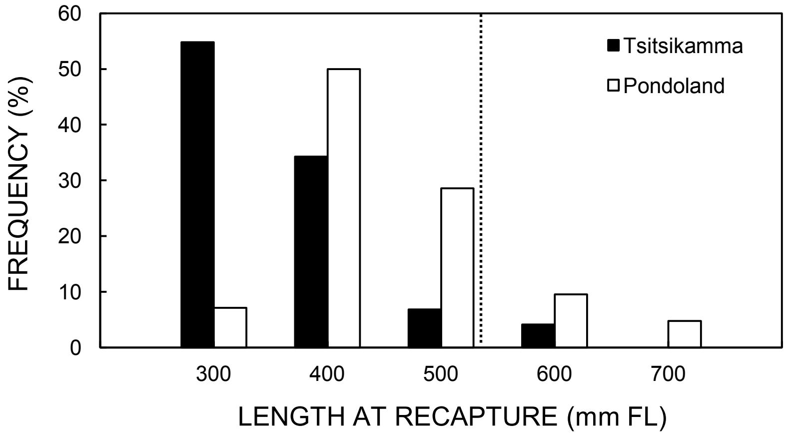

Figure 4.21: Fork length (mm) of recaptured poenskop for the Tsitsikamma and Pondoland tagging projects. The dotted line indicates approximate size at sexual maturity.

Distances moved differed significantly among size classes (Kruskal-Wallis ANOVA, $p < 0.001$) (Figure 4.22). In both the TNP and PLD, adults (> 530 mm FL) undertook significantly greater movements than juveniles (< 300 mm FL) and sub-adults (300 to 530 mm FL). Distances moved by the two smaller size classes were not significantly different ($p > 0.05$). Adult fish in the TNP also moved, on average, greater distances than adults in the PLD. In contrast to this, juvenile poenskop in the TNP moved, on average, smaller distances with poenskop in the PLD moving larger distances (Figure 4.22).

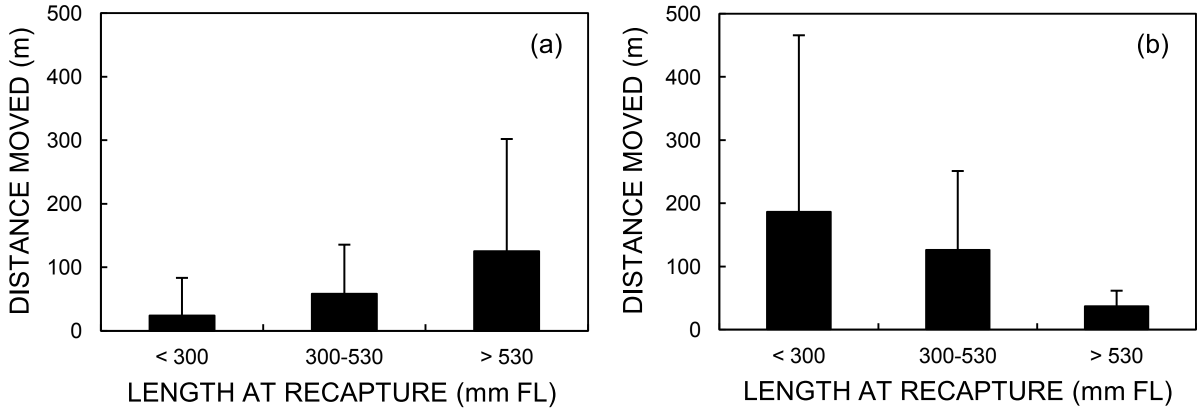

Figure 4.22: Mean (± SD) distance moved (m), by size class (mm FL), for all recaptures made in the (a) Tsitsikamma and (b) Pondoland tagging projects (n = 115).

Home-range estimation

Overall, the estimation of home-range size in the TNP was smaller than home-range size in PLD. The single linear distance (SLD) value was considerably higher than the calculated greatest linear distance (GLD) value in the TNP and PLD, but the value obtained using the equation by Kramer and Chapman (1999) was the highest value (Table 4.4). Maggs (2011a) calculated the home-range of poenskop in the Pondoland MPA to be 162 – 390 m (GLD and SLD respectively) with the Kramer and Chapman (1999) equation estimating a home-range length of 835 m. The estimated home-range size for the poenskop recaptured in the Tsitsikamma National Park was smaller than that in the Pondoland MPA. The home-range estimate for TNP calculated using the Kramer and Chapman (1999) equation, was almost half of the estimate obtained for PLD. This could be related to the size of poenskop tagged in each of these MPAs i.e. smaller poenskop hold smaller home-ranges.

Table 4.4: A summary of single linear distance (SLD) and greatest linear distance (GLD) estimates of home-range size (calculated using the 95th percentile following Maggs (2011a)) compared with the value obtained using the equation by Kramer and Chapman (1999). All values provided for both the Tsitsikamma National Park MPA and the Pondoland MPA are recorded as metres (m).

Region	SLD	GLD	Kramer and Chapman
Tsitsikamma National Park MPA (inshore)	211	70	492
Pondoland MPA (offshore)	390	162	835

4.4. Discussion

Despite varying spatial resolutions, this study made use of information obtained from three long-term tagging studies, one of which exceeds five years, and two which exceeded 10 years in duration, and collectively covering the core distributional range of poenskop. This allowed for a good assessment of the movement behaviour of this endemic South African sparid. Recapture rates were high, especially those from the MPA tagging projects (Table 4.2). All recaptures (100%) were made and reported by researchers within the MPAs. These recapture rates were similar to those recorded for red steenbras *P. rupestris* [17.5% in the TNP (Brouwer 2002), 20.7% along central Agulhas Banks (Griffiths and Wilke 2002)], santer *Cheimerius nufar* (13.2%, Griffiths and Wilke 2002) and carpenter *Argyrozona argyrozona* (11.0% - inshore, Griffiths and Wilke 2002). The lower overall recapture rate for the ORI Tagging Project (Table 4.2) must be a result of some other factors, such as the project covering a larger area as well as it having lower tagging effort per unit area. There are a number of reasons which may prevent a fish from being recaptured. These include immediate capture-induced mortality of the fish, delayed mortality, tag shedding, and non-reporting by the public (Lamberth 1997, Gilbert et al. 2001, Gillanders et al. 2001, Shirakihara and Kitada 2004, Attwood and Cowley 2005, Maggs 2011a). Non-reporting of tag-recoveries has been recorded in a number of studies conducted in South Africa (Attwood and Bennett 1994, Brouwer 1997, Lamberth 1997, Attwood and Cowley 2005, Kerwath 2005). Dunlop (2011), on surveying the KwaZulu-Natal recreational line-fishery, found that the public did not report at least 42% of tagged fish caught. Brouwer et al. (1997) recorded a non-reporting rate of 44% of fishes recaptured along the South African coast. Similarly, Lamberth (1997) estimated that only 58% of recaptured fish caught by the public were successfully reported. Reports of recaptures may also vary between regions. Dicken et al. (2006) found that tag-reporting rates of ragged-tooth sharks *Carcharias taurus* varied among provinces. Non-reporting could be accredited to (i) fear of prosecution for illegal fishing activities, (ii) wanting to keep fishing spots unknown to others, or (iii) forgetting to report recapture information to ORI (Watt-Pringle 2009).

Despite the lowest poenskop recapture rate being recorded in the ORI Tagging Project, the recapture rate was similar to those obtained in a number of different studies (Table 4.5). Even though it may be a result of non-reporting, the low recapture could also be a result of un-quantified levels of recapture effort, due to this project relying predominantly on volunteer anglers to tag and recapture fish (Maggs 2011a). In contrast, the MPA projects (TNP and PLD) use experienced scientific personnel (Attwood and Cowley 2005), have standardised recapture effort and 100% reporting rate (except when fish moved out of the sampling area), and as a result, should have higher recapture rates.

Table 4.5: Recapture information on a number of different sparid species tagged and recaptured along the South African coastline. RR (%) refers to the recapture rate, resident refers to the percentage (%) captured within 1 km of the tagging site, fork length (FL) refers to the mean mm fork length of tagged individuals, DH – De Hoop MPA, TNP – Tsitsikamma National Park MPA, GAENP – Greater Addo Elephant National Park, CAB – Central Agulhas Banks, ORI – ORI Tagging Project.

Species	RR (%)	Resident	Study period	Study area/ data source	Source
Blacktail *Diplodus capensis*	2.6	91	1984 - 2007	DH, TNP, ORI	Watt-Pringle (2009)
Zebra *Diplodus hottentotus*	2.7	85	1984 - 2007	DH, TNP, ORI	Watt-Pringle (2009)
White musselcracker *Sparodon durbanensis*	3.4	66	1984 - 2007	DH, TNP, ORI	Watt-Pringle (2009)
Carpenter *Argyrozona argyrozona*	5.0	90	1997 – 2000	TNP	Brouwer et al. (2003)
White steenbras *Lithognathus lithognathus*	5.1	62	1984 – 2010	DH, TNP, GAENP, ORI	Bennett (2012)
Roman *Chrysoblephus laticeps*	5.9	74	1987 – 1993	CAB	Griffiths and Wilke (2002)
Carpenter (offshore) *Argyrozona argyrozona*	6.3	84	1997 – 1999	CAB	Griffiths and Wilke (2002)

Residency is one of the most common behaviours in reef fishes and is prevalent among other local sparids. For example, 90% of adult carpenter *A. argyrozona* recaptures were made in the same location within the Tsitsikamma MPA (Brouwer et al. 2003), and 96 to 100% of recaptures of blacktail *D. capensis*, zebra *D. hottentotus* and bronze bream *Pachymetopon grande* were made within a short section of coastline within the Tsitsikamma MPA (Cowley et al. 2002). Similar high levels of residency (85%) were displayed in roman *Chrysoblephus laticeps* within the Goukamma and Tsitsikamma MPAs, and juvenile white musselcracker *S. durbanensis* in the De Hoop and Tsitsikamma MPAs (Watt-Pringle 2009). Poenskop also appeared to display limited movement over extended periods of time, showing extreme residency throughout all life-history stages (Figure 4.11). However, even though most juvenile/sub-adult poenskop were very resident (Figure 4.16), a few showed fairly extensive movements (up to 483 km, Figure 4.6). As a general trend, larger mature poenskop moved greater distances. It should be noted that most tag-recapture data only record two positions that a fish occupied at specific times in its life. Hence, knowledge on the movement of the fish between captures is unavailable (Attwood and Cowley 2005). In order to clarify movement patterns from tagging data, numerous records are needed over a long time span, especially for slow growing, long-lived species such as poenskop, which may reach a maximum age of 45 years (Buxton and Clarke 1989). The majority of poenskop recaptured in this study were < 10 years old. Therefore, only limited inferences can be made about movement patterns, particularly for adult individuals, from such data. However, because the large majority of recaptures were made at the tagging location, at least some poenskop spend a lot of time in a relatively small area and should be considered a resident species. Familiarity with food resources, knowledge of refugia locations, and immunity against local diseases (Eristhee and Oxenford 2001), are all ecological advantages of resident behaviour. This would then ultimately enhance the success of the population (Harden Jones 1968).

No factor could be found that reliably differentiated those fish that had moved from those which displayed zero displacement. However, despite the possibility of an increased movement during the spawning season, there was no significant differentiation due to season (Figure 4.19). Only two adult male fish (> 700 mm FL) were recaptured (Buxton and Clarke 1989). One of these fish was caught at the tagging locality after only one day at liberty (in the Transkei), while the other moved 483 km eastward over a period of 1 034 days. As a result, it can be assumed that sex is not a differentiating factor. Similar results were found for galjoen

Dichistius capensis movements in the De Hoop Nature Reserve and Tsitsikamma National Park MPA (Attwood and Cowley 2005), and for adult carpenter *A. argyrozona* movements in the TNP (Brouwer et al. 2003).

Coastal region appeared to have no effect on fish size or the level of dispersal (Figure 4.13b and 4.17b). However, larger poenskop were recaptured in the Transkei and south-west coastal regions. High proportions of fish tagged in one coastal region were recaptured within the same coastal region, this providing strong evidence of regional residency (Figure 4.14). A similar observation was made for white steenbras *L. lithognathus* (Bennett 2012), with at least 85% of fish tagged in one coastal region being caught in the same region. Adult fish were found to undertake significantly greater movements than juveniles or sub-adults. A similar trend was evident for age, in that older fish moved greater distances. A number of other sparid species show greater movement amongst adults than juveniles or sub-adults. These include white musselcracker *S. durbanensis* (Watt-Pringle 2009), white steenbras *L. lithognathus* (Bennett 2012) and red steenbras *P. rupestris* (Brouwer 2002).

A number of studies have shown fish populations to include different movement strategies (Morrisey and Gruber 1993, Sheaves 1993, Holland et al. 1996, Lowry and Suthers 1998, Pellett et al. 1998, Beentjies and Francis 1999, Gillanders et al. 2001, Attwood and Cowley 2005). The New Zealand hapuku *Polyprion oxygeneios* is known to display station-keeping, ranging and spawning migrations (Beentjies and Francis 1999), where some fish moved great distances while others showed extreme residency, even over a period of five years. Lowry and Suthers (1998) on studying the home range of the red morwang *Cheilodactylus fuscus*, found that this fish displayed residency but undertook diel migrations, and displayed homing.

In South Africa, a number of sparid species with similar life histories to poenskop, display different movement behaviours. For example, red steenbras *P. rupestris* juveniles in inshore waters (10 to 30 m in depth) are highly resident, but adults then move offshore (20 to 160 m depth) and migrate up the coastline to Transkei waters, where it appears they remain for the rest of their lives (Smale 1988, Brouwer 2002). White musselcracker *S. durbanensis* juveniles, which live in shallow subtidal waters and intertidal pools, show strong site-fidelity and are extremely resident (Watt-Pringle 2009). Adults, known to occur in slightly deeper water over high relief inshore reefs, display both resident and dispersal behaviour (Buxton and Clarke

1991, Watt-Pringle 2009). Carpenter *A. argyrozona* juveniles and adults display residency with adults moving into deeper water (Brouwer et al. 2003). Roman *C. laticeps* juveniles and adults are extremely resident, although a small proportion of the adult population show movements that are one or two orders of magnitude greater than the average movement (Kerwath et al. 2007a). Red steenbras and white musselcracker adults are thought to undertake spawning migrations of the KwaZulu-Natal and Transkei coasts (Smale 1988, Buxton and Clarke 1991). These species have evolved life histories that utilise southward-moving inshore currents in these areas to transport eggs and larvae to nursery areas in the Eastern and Western Cape (Hutchings et al. 2002). The poenskop potentially shows similar movement strategies with juveniles, sub-adults and adults showing high levels of residency, while a small proportion of the population displays ranging movements (Dingle 1996). The possibility of the poenskop undertaking a similar spawning migration (Buxton and Clarke 1989) is high although more large adult fish would need to be tagged and recaptured in order to prove this.

As mentioned above, a number of sparid species display an ontogenic habitat shift with larger fish moving out onto deeper reefs (Smale 1988, Buxton and Clarke 1991, Brouwer 2002, Brouwer et al. 2003). The same situation probably applies to the poenskop. This is evident in the size of fish caught during the tagging projects in the TNP and PLD. Larger fish were tagged and recaptured offshore in the Pondoland MPA, while smaller juvenile poenskop were tagged and recaptured inshore in the Tsitsikamma National Park MPA. Due to the different size fish being tagged and recaptured in these two different regions and habitat types, one could infer that poenskop display a similar ontogenic habitat shift, moving offshore as they become adults.

Home-ranges have been found to be characteristic of many reef fish species, in both tropical (Sale 1971, Zeller 1997, Meyer et al. 2000) and temperate areas (Lowry and Suthers 1998, Lowe et al. 2003, March et al. 2010). Poenskop have been found to hold home-ranges (Maggs 2011a), with any other movement beyond these home-ranges being regarded as deviations from this behaviour (Attwood and Cowley 2002). The small-scale movements observed in the MPAs, being between 0 m and 250 m (TNP) and 0 m and 636 m (PLD) agree with the suggestion of poenskop holding a small home-range (Table 4.4). Additional information confirming this home-range behaviour is the patterns of recapture. The most common pattern still included two recaptures at the same site. Attwood and Cowley (2005) recorded similar movement patterns for galjoen *D. capensis* in that some fish kept a home-range, later abandoning it, while others moved from a site and established a home-range elsewhere. Poenskop in the TNP were found to hold smaller home ranges (based on the SLD and GLD estimates) than poenskop in PLD. Once again, this could be related to an ontogenic shift with an increase in the size of poenskop, with larger fish moving offshore. Because poenskop in the TNP were found to hold smaller home-ranges, home-ranges will most likely be directly related to the size of the fish, with larger fish holding larger home-ranges.

The topography of both the TNP and the PLD are fairly similar in that these coastlines are predominantly rural and rugged, with high rocky cliffs (Cowley et al. 2002, Maggs 2011a). The TNP has rocky ridges with interlaying gullies filled with either boulders or sand (Cowley et al. 2002), while PLD is predominantly rocky with small sandy bays and estuary mouths (Maggs 2011a). The TNP surface currents are strong but decrease with depth (Attwood et al. 2002, Roberts and van den Berg 2005), while a predominantly strong north-south current, influenced by the narrow continental shelf and close proximity to the powerful south-westerly flowing Agulhas Current, prevails along the PLD coastline (Maggs 2011a, Roberts et al. 2010) with relatively strong currents throughout the water column. As mentioned, the TNP poenskop home range is smaller than that of PLD poenskop. The average size of poenskop caught in PLD were 372 mm FL, with recaptures having an average length of 407 mm FL. Poenskop caught in the TNP were smaller, with an average length of 264 mm FL, and recaptures having an average length of 267 mm FL. Parsons et al. (2003) indicated that home range size can be related to feeding strategy, food density and resource demand. However, Savitz et al. (1983) on studying forage effects on home range size of largemouth bass *Micropterus salmoides*, found that when a constant supply of food was provided (fathead minnows), the bass established smaller home ranges as opposed to the controlled bass where no food was provided.

The TNP reefs are dominated by microalgae, being rich in ascidians (e.g. red bait *Pyura stolonifera*), porifera (sponges) and echinoderms (crinoids and brittle stars) (Buxton and Smale 1984). The shallow reefs in the northern parts of the Pondoland MPA are algal-dominated, being relatively low in benthic diversity; however, sponges and ascidians are also present (Celliers et al. 2007, Maggs 2011a). Poenskop (juveniles and adults) eat a range of prey items, the most important groups contributing to their diet include molluscs, crustaceans and echinoderms (Buxton and Clarke 1989, Heemstra and Heemstra 2004). Sander and Steven (1973) found that organic productivity increased as one moved from offshore towards inshore;

this perhaps also has an effect on the type of prey items available to the poenskop in the two different MPAs. The ontogenic habitat shift discussed earlier may also coincide with the type of prey items found in each MPA, as well as the differeing geographic locations and oceanography. However, even though the MPA habitat types differ, small poenskop are also found inshore in PLD (BQ Mann *pers comm.*). The difference in size could thus be a result of different habitats being sampled i.e. the surfzone in the TNP and subtidal reefs down to approximately 30 m in PLD.

When comparing the home-ranges of the TNP and PLD poenskop using the Kramer and Chapman (1999) equation, the values obtained were different (TNP: 492 m and PLD: 835 m). This is a direct result of the larger mean size of poenskop tagged in the PLD. These values are similar to a number of different South African fish species (Table 4.6). It could be possible that the predicted home-ranges for poenskop could be larger than the prediction by Kramer and Chapman (1999), such as that seen for scotsman *Polysteganus praeorbitalis* and slinger *Chrysoblephus puniceus* (Maggs 2011a). All poenskop caught in the TNP were caught within 250 m of the release site therefore comfortably falling within the predicted home-range, whereas 95% of PLD poenskop were caught within the predicted home-range. Distribution as well as the occurrence and scale of daily movements can be influenced by habitat structure (Nanami and Nishihira 2002, Pittman et al. 2007, Chateau and Wantiez 2008). Advantages of having smaller home-ranges include efficient refuge from predators, resting, retreat from strong currents and foraging (Watt-Pringle 2009).

Table 4.6: Home range sizes estimated for a number of South African linefish species. The examples are listed in descending order of linear home range size (length in metres). The following acronyms have been used: SLD – single linear distance (Maggs 2011a), GLD – greatest linear distance (Maggs 2011), DGD – difference of gamma deviates (Attwood and Cowley 2005).

Species	Home range (m) *Kramer and Chapman (1999)*	Home range (m) *Other*	Source
Poenskop *Cymatoceps nasutus*	835	162 (GLD) 426 (SLD)	Maggs (2011a)
Scotsman *Polysteganus praeorbitalis*	742	642 (GLD) 748 (SLD)	Maggs (2011a)
Galjoen *Dichistius capensis*	400 (DH)	1380 (DGD)	Attwood and Cowley (2005)
Galjoen *Dichistius capensis*	373 (TNP)	340 (DGD)	Attwood and Cowley (2005)
Roman *Chrysoblephus laticeps*	282	N/A	Kerwath et al. (2007a)
Slinger *Chrysoblephus puniceus*	212	696 (SLD)	Maggs (2011a)
Blacktail *Diplodus capensis*	123	N/A	Watt-Pringle (2009)
White musselcracker (juvenile) *Sparodon durbanensis*	101	N/A	Watt-Pringle (2009)
Zebra *Diplodus hottentotus*	96	N/A	Watt-Pringle (2009)

Watt-Pringle (2009), on studying the movement behaviour of white musselcracker *S. durbanensis*, suggested that a number of spawning areas exist in different localities along the South African coastline. Algoa Bay individuals moved up the Transkei coast to KwaZulu-Natal, other Eastern Cape individuals moved towards Algoa Bay, and Western Cape fish moved towards the Tsitsikamma coastline. A similar situation may apply to the poenskop with all movements greater than 15 km being in a north-easterly direction. Most individuals moved from Port Alfred towards the Transkei coast and a large number of individuals also moved along the Tsitsikamma coastline (Figure 4.4). Of these large-scale movements, only four individuals were recorded moving out of spawning season, including the individual that moved the greatest distance (483 km). If these areas are potential spawning areas, the nearshore oceanography may support this idea. Off the Transkei coast, the Agulhas Current lies relatively close inshore. A number of other linefish species, making use of a spawning strategy utilizing the currents, include the white steenbras *L. lithognathus* (Bennett 1993b), red steenbras *P. rupestris* (Smale 1988) and geelbek *Atractoscion aequidens* (Griffiths and Hecht 1995). Eggs and larvae spawned off the KwaZulu-Natal and Transkei coast would then be transported along the coastline, eventually settlings in areas of suitable rocky habitat. The ability of small juveniles of marine fishes, to move deliberately towards a preferred habitat, is well established (Leis et al. 2002). Lutjeharms et al. (1986) and Hutchings et al. (2002) suggested that the Agulhas Current and its associated complex water circulation may displace eggs and larvae spawned along the central Eastern Cape coast (e.g. East London) further offshore. This may be further evidence as to why poenskop possibly undertake a spawning migration to Transkei waters (Buxton and Clarke 1989). Once the larvae have reached central Eastern Cape waters, they may be strong enough to avoid this offshore displacement. Many sparid eggs hatch within 48 hours e.g. santer *C. nufar* (33 hours), slinger *C. puniceus* (30 hours), seventyfour *Polysteganus undulosus* (48 hours) and strepie *Sarpa salpa* (40 hours) (Connell 2007), with settlement occurring within 2-3 weeks (Vigliola et al. 1998). Pattrick (2008) found that the swimming abilities of strepie *S. salpa* and blacktail *D. capensis* exceeded the average current velocities observed in the shallow nearshore of Algoa Bay. This would then enable the larvae to alter their passive dispersal trajectories, influencing their distribution in the nearshore (Pattrick 2008). If poenskop were to spawn in the Western Cape and Eastern Cape, southwest of Port Elizabeth and northeast of Cape Agulhas, eggs and larvae may be retained in these regions. Watt-Pringle (2009) suggested that this spawning strategy may be less physically-demanding for resident fish than to undertake a spawning migration to the Transkei.

Poenskop's distribution is thought to be temperature dependent, occupying deeper water in KZN, and being found at shallower depths as one moves westwards (Heemstra and Heemstra 2004). Garratt (1988) and Beckley and van der Lingen (1999) theorised that a seasonal extension of several coastal fish species' normal distributional range could occur. However, from the results of this study, it is unlikely that poenskop undertake seasonal migrations. Poenskop appear to have very similar movement patterns to red steenbras *P. rupestris* in that large adults move up the Transkei and KwaZulu-Natal coast, remaining there for the rest of their adult lives (Smale and Punt 1991, Brouwer 2002). Therefore, poenskop may gradually move in a north-easterly direction up the coastline of South Africa out to deeper reefs (adult poenskop are known to occur offshore) with increasing age and size. However, more research is needed to confirm this hypothesis. The use of acoustic telemetry along with the current development of the Ocean Tracking Network (OTN) could be used in the future. Long-life transmitters (and the associated receivers (OTN)) used for large adult poenskop along the Transkei coastline would be useful to confirm adult residency along this stretch of coastline or to detect continual movement along the South African coastline.

CHAPTER 5

GENETIC STOCK STRUCTURE

"Blue musselcrackers also migrate in shoals, but unlike most other species, big and small fish are frequently found together...these formidable fighters congregate in very large numbers among inshore reefs during the greater part of the year."

- Schoeman (1957: p 66) -

5.1. Introduction

Fish, amongst other animals, are characterised by discontinuous groups of individuals. Several studies have shown that the assumed high dispersal potential of many marine species, accompanied with a lack of physical barriers, does not necessarily result in large amounts of gene flow (Avise 1998, De Meester et al. 2002, Uthicke and Benzie 2003, Casteleyn et al. 2010). This could potentially mean that groups of individuals, known as "stocks" in fisheries, may have different genetic compositions (Shaklee and Bentzen 1998). However, accurate stock identification, as well as the estimation of exchange between such stocks, represents a major challenge for fisheries management.

The use of genetic technologies in fisheries biology has been increasing steadily over the past three decades (Ward 2000, Hauser and Carvalho 2008, Hauser and Seeb 2008). These methods have been recognised for their practicality in defining stock structures of fish (Ward 2000). The biological definition of a stock, according to Ihssen et al. (1981), is an intraspecific group of individuals which breed at random and show both spatial and temporal integrity. This stock may then be assessed and sustainable catch levels can be set (Ward 2000). The main applications of genetic data from fisheries include conservation of stocks present in low numbers, and contribute to the knowledge of the migratory behaviour of specific stocks (Shaklee et al. 1999).

The advances in molecular biology have allowed for a wide range of techniques to be developed for the examination of variation in DNA (Chauhan and Rajiv 2010). Most early studies have used restriction fragment length polymorphisms (RFLP) of the mitochondrial genome and allozymes, and more specifically, the use of the mtDNA control region has been successfully applied to many species of marine fish to detect the population structure (Gold and Richardson 1991, Smith 1994, Ovenden et al. 2004, Alvarado Bremer et al. 2005). Some authors have viewed their concerns about using this gene region, including Rocha-Olivares et al. (2000) and Lundy et al. (2000). They found that it may be of limited use in species where high levels of genetic diversity are recorded e.g. flathead mullet *Mugil cephalus* (Rocha-Olivares et al. 2000) or where analysis of the mtDNA control region may not be sensitive enough to reveal any genetic structure e.g. European hake *Merluccius merluccius* (Lundy et al. 2000). However, despite this concern by some, the control region has been found to be extremely useful for population studies due to its high substitution rate (Shalkee and Bentzen 1998). The haploid nature of mtDNA, maternal inheritance and the absence of recombination, means that the signal obtained from genetic drift, is stronger than that for nuclear loci (Hecht et al. 1984, Shaklee and Bentzen 1998). The variation expected for the mtDNA control region is also expected to be less within populations and greater between populations (Gold and Richardson 1991, Meyer 1993, Shaklee and Bentzen 1998, Waples 1998). The mtDNA control region has therefore been suggested as a means to evaluate genetic diversity and stock identification (Chauhan and Rajiv 2010).

Several genetic studies have investigated the stock structure of commercially important species in southern Africa, such as Cape hakes *Merluccius capensis* and *M. paradoxus* (von der Heyden et al. 2007), abalone *Haliotis midae* (Bester et al. 2004), pilchard *Sardinops sagax* and anchovy *Engraulis japonicus* (Grant 1985a, 1985b, 1985c). However, the inshore linefish species have received limited attention with the genetic stock structure having been investigated for only a few species; dusky kob *Arygrosomus japonicus* (Klopper 2005), roman *Chrysoblephus laticeps* (Forget 2007, Teske et al. 2010), white steenbras *Lithognathus lithognathus* (Bennett 2012), spotted grunter *Pomadasys commerssonii* (Klopper 2005) and Cape stumpnose *Rhabdosargus holubi* (Oosthuizen 2006). The outcome from each of these studies was extremely similar, with all species consisting of single, well-mixed stocks throughout their distributions. The roman has an extremely similar life-history to the poenskop (see Buxton 1989, Kerwath et al. 2007a, Teske et al. 2009a), and as a result, it was hypothesized that there would be a similar outcome for the genetic structure of the poenskop.

Making use of sequences for the mtDNA control region, this study aimed to identify potential discrete stocks by investigating the genetic structure of poenskop throughout its distribution range, and by comparing the levels of genetic diversity between sampling regions.

5.2. Materials and methods

5.2.1. Collection of material

Pectoral fin clips from a total of 371 fish were collected from 34 sites along the coastline of South Africa (spanning the core distribution of the species) between December 2009 and July 2011 (Figure 5.1). Sample sites were grouped into eight geographically separated regions, namely Western Cape, Tsitsikamma National Park MPA, Sardinia Bay MPA, Port Alfred and the surrounding area, East London and the surrounding area, southern Transkei, northern Transkei and KwaZulu-Natal (Figure 5.1). Two of the regions represented marine protected areas (MPAs) (Tsitsikamma National Park MPA and Sardinia Bay MPA), while two other regions included MPAs as collection sites. These were southern Transkei which included Dwesa-Cwebe and Hluleka MPAs, and northern Transkei which included Mtentu and Mnyameni (in the Pondoland MPA). Six of the regions included neighbouring sample sites that were combined in order to increase sample sizes. The geographic distances between these combined sites within each region, were relatively small. Figure 5.1 shows the number of fin clips obtained from each sample site in parentheses. The distance (taken from the mid-point of each region and measured as linear distance) separating each of the eight regions, ranged from 95 to 188 km with a mean of 136 km.

Fin clip samples were collected from fresh fish captured in the fishery. Information collected for each sample included capture locality, date and fish length (mm FL). Each fin clip was preserved in a labelled Eppendorf tube containing 96% absolute ethanol and stored at -20 °C until extractions were performed.

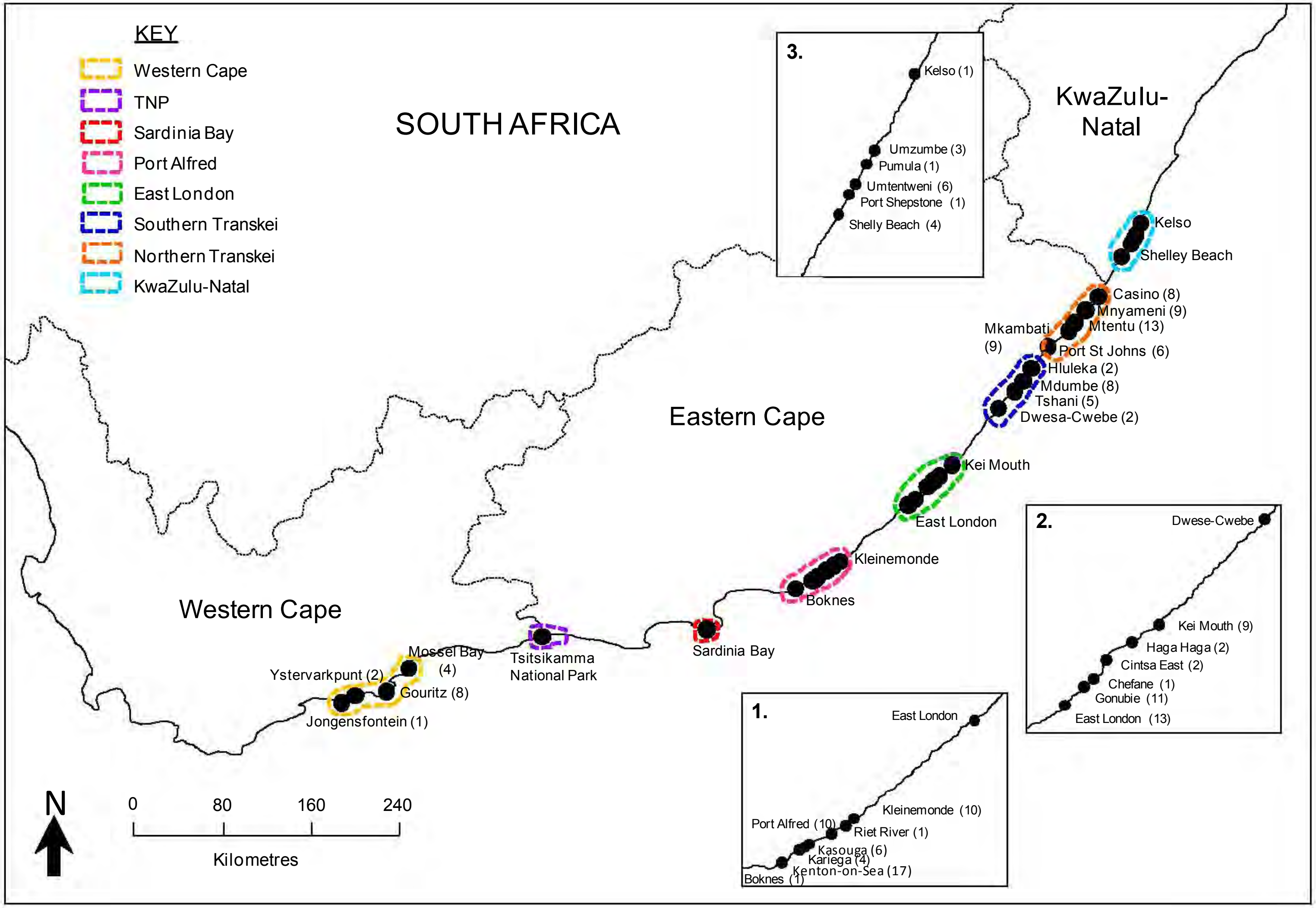

Figure 5.1: The coastline of South Africa showing the sampling sites within the eight study regions from where poenskop fin clips were collected between December 2009 and July 2011 (n = 217). The inserts show more detail of the Port Alfred (1), East London (2) and KwaZulu-Natal (3) regions. Numbers in brackets indicate the number of samples collected from each region.

5.2.2. Preparation of material

DNA Extraction

Total DNA extraction was carried out using the Wizard® Genomic DNA purification kit (Promega, USA). The manufacturer's extraction protocol was followed and then samples were subsequently eluted in 100 µl DNA rehydration solution.

PCR Amplification

Polymerase chain reaction (PCR) amplifications on total genomic DNA were carried out using "universal" control region primers (L-Prof1 and H-DL1) (Ostellari et al. 1996), which yielded a visible product in poenskop. The thermal-cycling profile was: 30 s at 94 °C, 45 s at 52 °C, 1 min at 72 °C for 34 cycles, followed by 10 min at 72 °C. These primers yielded PCR products, which when sequenced, yielded usable sequences of varying lengths (between 180 and 320 bp). Based on the preliminary rounds of sequence information, primers specific to the control region of poenskop, were designed to try and increase the length of the sequences produced: forward primer (CNCR1-F): 5'-GCT CCC AAA GCT AAC GTT-3' and reverse primer (CNCR1-R): 5'-GAA GTA GGA ACC AGA TGC CAG-3'. Amplifications were performed in a 25 µl solution containing 5 µl DNA, 0.5 µl of each primer (10 pmol), 2.5 µl of 10X buffer PCR buffer (100 mM EDTA, 1 mM DTT, 20 mM Tris-HCL, pH 8), 3.0 µl 25 mM $MgCl_2$, 2.5 µl of dNTPs (8 mM), and 0.1 units of DNA Super-Therm Taq Polymerase (Southern Cross Biotechnologies, Cape Town, South Africa). The thermal-cycle profile involved an initial denaturaing step of 3 to 4 min at 94 °C, and then continued as follows: 30 s of denaturation at 94 °C, 35 cycles of 45 s of annealing at 56 °C, 1 min of extension at 72 °C and a final 35 cycles of 10 min extension at 72 °C. A 5 µl sample of each PCR product was subjected to (1%) agarose gel electrophoresis and stained with ethidium bromide for visualization using a UV transilluminator.

Sequencing

Of the 371 fin clips collected, only 217 samples yielded suitable PCR products. These PCR products were then sent to Macrogen Inc. (South Korea) for purification and sequencing. Sequencing was performed using either the forward or reverse primer. The individual sequences obtained were usable and of variable lengths (250 – 440 bp). Sequences were edited using Chromas Lite v2.01 (Technelysium Pty Ltd) and were edited and then aligned in SeqMan (DNASTAR, Madison, USA).

5.2.3. Data analysis

Genetic diversity

Genetic diversity within sampling regions was determined by estimating the nucleotide diversity (π) (Nei 1987), haplotype diversity (h) (Nei 1987), the number of polymorphic sites (S), and the average number of pairwise nucleotide differences (k) among sequences in each region (Tajima 1983). This was done using Arlequin v3.11 software (Excoffier et al. 2005). Nucleotide diversity represents the probability that two homologous nucleotides, drawn at random, will be different if the assumptions for no recombination and selective neutrality are met (Nei 1987). Haplotype diversity represents the probability that two haplotypes, drawn at random from a population, will be different (Nei 1987).

Genetic structure

MtDNA haplotypes may be spatially structured to comprise distinct geographical clusters. In order to determine whether there was such stock structure for poenskop, a median-joining haplotype network was constructed using Network v6.0 (Bandelt et al. 1999). This was done in order to gain an understanding of the spatial distribution and genealogical relationships of the haplotypes. All individuals (n = 217) were used during this analysis. Genetic structure (i.e. differentiation among the regional groups) was then analysed using two methods based on F-statistics in Arlequin v3.5.1.3. These methods included the calculation of pairwise ϕ_{ST}-values, and an Analyses of Molecular Variance (AMOVA) (Excoffier et al. 1992). These were calculated from the haplotypes of each region and considered genetic distances, corrected using the Tamura model. Modeltest v3.7 (Posada and Crandall 1998) was used to evaluate and select the most appropriate nucleotide sequence evolution model for the data set using the Akaike Information Criterion (AIC) to find the optimal combination of parameters (Akaike 1973). It was determined that the Tamura (1992) model of nucleotide substitution, available in Arlequin v3.5.1.3, would be used.

Groups for the AMOVA were defined according to geographic distance and included five main regions, namely (1) Western Cape, (2) Tsitsikamma National Park MPA, (3) Sardinia Bay MPA, (4) Port Alfred and East London regions, and (5) the southern Transkei, northern Transkei and KwaZulu-Natal combined. Significance was determined by 10 000 permutations, whereby haplotypes were randomly drawn from the sample to determine if the distribution and differentiation among regions was significantly different from those at random. In a separate AMOVA (Excoffier et al. 1992), samples were grouped as juveniles and adults. The AMOVA was used to determine the genetic variation between these two different life history stages. This was done in order to test whether differences between these life history stages were present, which may reflect different cohorts or sweepstake spawning events. This may then confound or complicate the examination of spatial structure. This analysis was also used to confirm the justification in grouping all poenskop samples together.

Isolation by distance and gene flow

Isolation by distance analysis was performed in order to determine whether geographic distance has a significant effect on the genetic variation between regions. Pairwise ϕ_{ST} values for the eight regions were plotted against geographical distance, with geographical distance being measured as the shortest continuous water-surface distance (between midpoints of regions). A Mantel (1967) test, using 10 000 random permutations, was used to determine the correlation between geographic distance and genetic variation between the sampling regions. This was calculated using Mantel Test for Windows v1.19 (Cavalcanti 2008).

Population history

In population studies, it is important to show that the evolution of a marker is a result of reproductive expectations and not selection. Because population differentiation is thought to be the result of reproductive isolation, this assumption becomes invalid in the presence of selection. In the absence of selection, a number of neutrality tests can also be used as indicators for population growth/decline in the evolutionary history of a taxa (Rand 1996). In order to test the neutrality of the locus, Tajima's (Tajima 1983) D and Fu's (Fu 1997) F_S tests were used. Tajima's test statistic, D, is the difference between the mean number of pairwise differences (π) between sequences drawn from random samples and the number of segregating sites (θ) (Rogers et al. 1996). The neutral model states that in a population at equilibrium, $\pi = \theta$. A negative D value may indicate a number of things, including: population expansion after a bottleneck event, a selective sweep or a small founder event (Rand 1996). A positive D value is consistent with balancing selection models, or a combination of distinct, isolated populations (Rand 1996). In population-growth studies using larger sample sizes, Fu's F_S test is preferred (Fu 1997, Ramos-Onsins and Rozas 2002). In cases of an excess of recent mutations, F_S tends to be negative i.e. with an excess of rare alleles. A large negative value is then seen as evidence against neutrality of mutations (Fu 1997).

Mismatch distribution (Harpending 1994, Schneider and Excoffier 1999) (for the entire dataset) was also used to examine the possibility of a historical demographic expansion. These distributions were calculated for all sample regions combined, as well as for each individual sample region, using the pairwise number of differences observed and comparing them to the expected values under a model for population growth and decline (Harpending 1994, Rogers 1995). A population at mutation-drift equilibrium shows a multimodal mismatch distribution, while a population which has undergone a recent population expansion is unimodal (Rogers and Harpending 1992, Excoffier 2004). A fit to a unimodal mismatch distribution was tested by using the Harpending (1994) raggedness index and the sum of squared deviations (S.S.D.) (Rogers and Harpending 1992) in order to evaluate the expansion model according to Rogers (1995). This was performed in Arlequin v3.5.1.3.

Approximate population expansion times were estimated using the formula $T = \tau/2u$ (Rogers and Harpending 1992) where T is the time since expansion, τ is the expansion time in scaled coalescent units and $2u = \mu$ (mutation rate) x number of bases sequenced x generation time. The universal mitochondrial control region mutation rate is estimated to be between 10% and 20% per million years (Myr) (Wilson et al. 1985), while that of teleosts is thought to be approximately 11% per Myr (McMillan and Palumbi 1997) and approximately 10% per Myr in sparids (Bargelloni et al. 2003). A generation time of 10.0 yrs was used for poenskop – this age corresponding to sexual maturity (for females) (Buxton and Clarke 1989). Estimated dates were rounded to the nearest 100 years.

5.3. Results

Sequence characteristics

PCR with the poenskop-specific primers yielded sequences of approximately 550 base pairs (bp) in length for 263 fish. Forty-six sequences were removed from the analysis due to them being too short. After removing the ambiguous ends during sequence editing, 334 base pairs (for 217 samples) of a portion of the control region were obtained. The mtDNA control region sequence followed an A-T-rich region, with a total of 74% A+T; this is in agreement with the results found in similar studies (McMillan and Palumbi 1997, Bargelloni et al. 2003). A total of 25 polymorphic sites containing 21 substitutions were observed, yielding a total of 29 haplotypes. Eight of these haplotypes were private (i.e. unique to a region), and 24% of individuals shared the most common haplotype.

Genetic diversity

Of the 29 haplotypes, only ten were found in a single region. The northern Transkei had the highest number of haplotypes (n = 16), while Port Alfred and East London regions had the highest number of private haplotypes (n = 2 per region). Haplotype diversity was high for all regions, ranging from 0.795 ±0.109 (Western Cape) to 0.903 ±0.031 (KwaZulu-Natal). The overall haplotype diversity for all samples was 0.878 ±0.013 (Table 5.1). Nucleotide diversity was fairly constant among each region, ranging from 0.0048 ±0.0034 (Western Cape) to 0.0075 ±0.0048 (KwaZulu-Natal). The overall nucleotide diversity for all samples was 0.0083 ±0.0049. In general, nucleotide diversity increased slightly from west to east (Table 5.1). However, no clear geographical trend presents itself in the diversity values for the poenskop (Figure 5.2).

Table 5.1: Genetic diversity indices (including standard deviations of the means) for poenskop at different sampling regions; sample size (n), number of haplotypes (N_H), number of private haplotypes (N_{PH}), haplotype diversity (*h*), nucleotide diversity (π), the average number of pairwise differences (*K*) and the number of polymorphic sites (PS).

Region	**n**	**N_H**	**N_{PH}**	***H***	**π**	***K***	**PS**
Western Cape	13	7	0	0.795 ±0.109	0.0048 ±0.0037	1.588 ±1.007	7
Tsitsikamma	31	12	1	0.903 ±0.031	0.0056 ±0.0037	1.868 ±1.099	13
Sardinia Bay	36	13	0	0.876 ±0.034	0.0058 ±0.0037	1.911 ±1.114	13
Port Alfred	39	14	2	0.862 ±0.034	0.0051 ±0.0034	1.690 ±1.011	14
East London	22	12	2	0.900 ±0.045	0.0063 ±0.0041	2.100 ±1.218	13
Southern TKI	17	8	1	0.816 ±0.071	0.0056 ±0.0037	1.827 ±1.104	10
Northern TKI	43	16	1	0.875 ±0.034	0.0061 ±0.0039	2.023 ±1.160	15
KwaZulu-Natal	16	8	1	0.892 ±0.048	0.0075 ±0.0048	2.491 ±1.418	14
SOUTH AFRICA	*217*	*29*	*8*	0.878 ±0.013	*0.0083 ±0.0049*	*2.734 ±1.456*	*25*

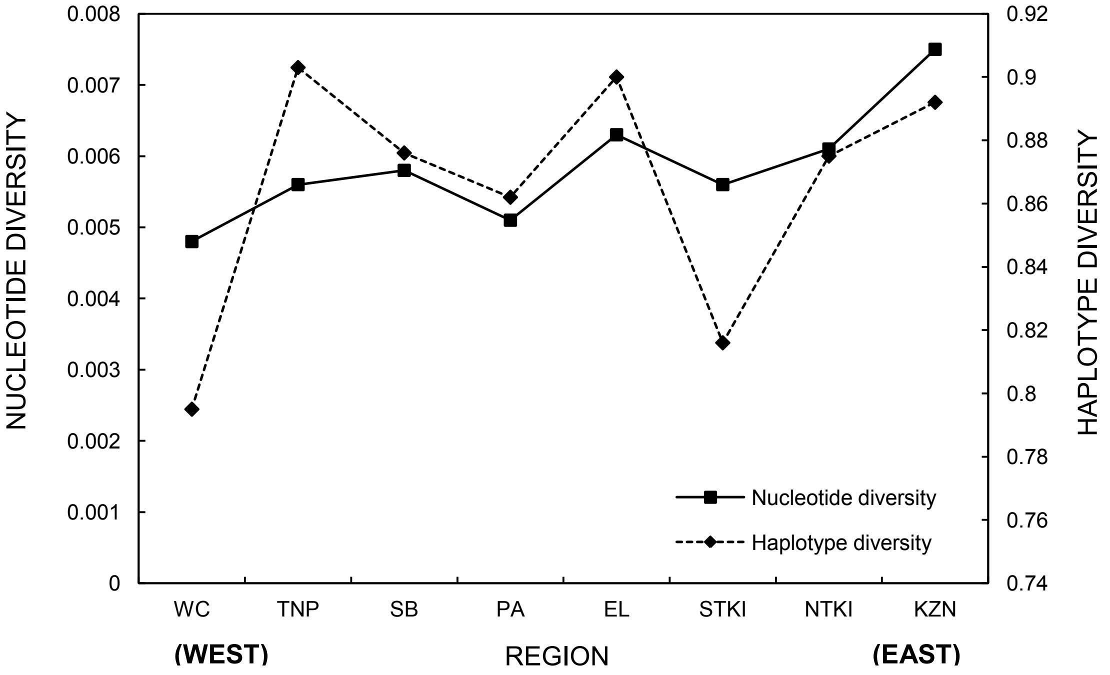

Figure 5.2: Nucleotide and haplotype diversities for the poenskop for each study region, from west (Western Cape) to east (KwaZulu-Natal).

Genetic structure

The haplotype network shows mtDNA heterogeneity. A total of 34 mutations were observed for all samples. It should be noted that most of the haplotypes within this network differed by no more than three mutation steps. MtDNA haplotype frequencies among the eight regions was tested for spatial heterogeneity and was found to be non-significant (χ^2 = 218.56, p = 0.13), indicating that no significant structure exists between the eight sampling regions. No population genetic subdivision was observed. A haplotype network for all samples (n = 217) revealed no relationship between haplotype genealogy and geographic location (Figure 5.3). A small number of low-frequency haplotypes surround three dominant haplotypes. Haplotype 1 was most common, shared by 52 individuals (23.96%). This was followed by haplotype 5, shared by 44 individuals (20.28%), and haplotype 3, shared by 26 individuals (11.98%). Haplotype 1 and 5 were shared by individuals, representative of all sampling regions. This suggests that poenskop have a lack of structure or population subdivision. Poenskop also underwent recent population expansion with the more dominant haplotypes being ancestral (Templeton 1998), although there is no clear evidence of this. Eight (27.6%) haplotypes were found to be private. The Port Alfred and East London regions had two region-specific

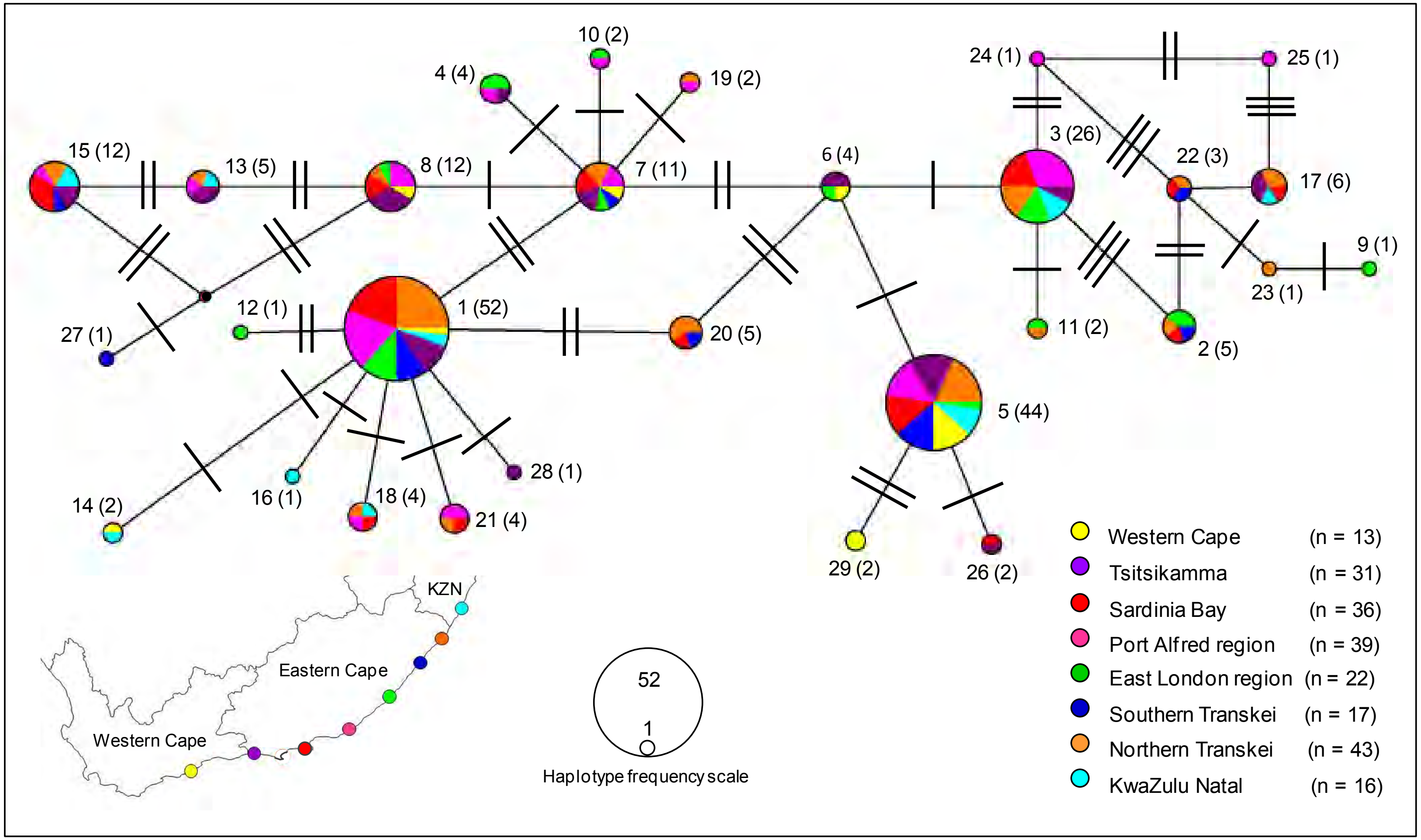

Figure 5.3: A median-joining haplotype network showing genealogical relationships among the mitochondrial DNA control region haplotypes for the overall sample of poenskop. Pie charts indicate the relative occurrence of each haplotype among the regions, and the numbers indicate the haplotype number with the total number of samples sharing that specific haplotype given in parentheses. The size of the circles is proportional to haplotype frequency. All haplotypes are separated by at least one mutational step – indicated by hatch marks across the connecting lines. The small black node represents a missing haplotype needed to obtain the resulting connection.

haplotypes, followed by one haplotype each for Tsitsikamma National Park MPA, southern Transkei, northern Transkei and KwaZulu-Natal.

Table 5.2: Aligned nucleotide sequences showing the variable nucleotide positions among the 334 sites of the mitochondrial DNA control region for poenskop *Cymatoceps nasutus*. The top row of the table indicates the dominant haplotypes; only nucleotides which differ from this row as given for the different haplotypes. Nucleotides identical to the top row are represented by a dot (.). Note that gaps are indicated by an asterisk (*).

Haplo-type	Nucleotide position																					
	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3
	3	3	7	9	3	3	4	5	5	5	6	7	7	8	1	5	6	7	8	9	9	0	2
	4	8	0	5	3	6	8	1	2	7	8	3	4	9	8	6	6	6	4	7	8	3	8
	A	T	T	G	C	A	A	*	T	T	A	T	C	*	G	T	A	C	T	C	G	T	A
1	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.
2	.	.	.	.	.	.	.	.	.	.	G	.	T	.	.	.	.	.	.	.	A	.	.
3	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	A	.	.
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.
5	.	.	.	.	.	.	G	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.
6	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.
7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9	.	.	.	A	.	.	.	.	.	.	G	.	T	.	A	.	G	.	.	.	A	.	.
10	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	C	.	A	.	.
12	.	.	.	.	.	.	.	.	A	.	.	.	.	A	.	.	.	.	.	.	.	.	.
13	.	*	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.
15	.	*	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G
16	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	T	.	.	.
17	.	.	.	A	.	.	.	.	.	C	G	.	T	.	.	.	.	.	.	.	A	.	.
18	.	.	.	.	.	G	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.
19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.
20	.	.	.	.	.	.	.	.	.	.	.	.	T	A	.	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	C	.	.	.	.	.	.	.
22	.	.	.	A	.	.	.	.	.	.	G	.	T	.	.	.	.	.	.	.	A	.	.
23	.	.	.	A	.	.	.	.	.	.	G	.	T	.	A	.	.	.	.	.	A	.	.
24	.	.	.	A	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	A	.	.
25	.	.	.	A	.	.	.	.	.	C	.	.	T	.	.	.	.	.	.	.	A	.	.
26	.	.	.	.	T	.	G	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.
27	*	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G
28	.	.	.	.	.	.	.	.	.	.	.	C	.	A	.	.	.	.	.	.	.	.	.
29	.	.	.	.	.	.	G	.	A	.	.	.	T	.	.	.	.	.	.	.	.	.	.

The low, non-significant ϕ_{ST} value (0.012, $p = 0.208$) also suggested homogeneity among the sample regions and is consistent with the assumption of high female gene flow among populations. Pairwise ϕ_{ST} analysis also indicated low differentiation between sample regions

(Table 5.3). Interestingly, five pairwise ϕ_{ST} values were found to be significantly different. These were between the Western Cape and TNP (0.084), Western Cape and Sardinia Bay (0.124), Western Cape and Port Alfred region (0.163), Western Cape and East London region (0.196), and Western Cape and northern Transkei (0.117). Results from the AMOVA with regions grouped into five larger areas (based on geographic distance), revealed that most of the variation (98.84%) was found within populations for all samples, while little (2.58%) could be attributed to variation among sample regions.

Table 5.3: Pairwise ϕ_{ST}-values among regions for all poenskop (n = 217) using the Tamura model (values in bold are significant: $p < 0.05$).

	WC	**TNP**	**SB**	**PA**	**EL**	**STKI**	**NTKI**	**KZN**
Western Cape	0.000							
Tsitsikamma	**0.084**	0.000						
Sardinia Bay	**0.124**	0.000	0.000					
Port Alfred	**0.163**	0.000	0.000	0.000				
East London	**0.196**	0.028	0.004	0.000	0.000			
Southern TKI	0.035	0.000	0.000	0.017	0.045	0.000		
Northern TKI	**0.117**	0.000	0.000	0.000	0.000	0.000	0.000	
KwaZulu-Natal	0.068	0.000	0.000	0.000	0.000	0.000	0.000	0.000

AMOVA results also revealed that most of the variation, comparing the adult and juvenile samples, was within populations (98.26%) (Table 5.4).

Table 5.4: Analyses of molecular variance (AMOVA) results of a comparison of areas between adult and juvenile poenskop ($\phi_{ST} = 0.055$, $p > 0.05$)

Regions	**Source of variation**	**d.f**	**Sum of squares**	**Variance components**	**Percentage of variation**
WC vs. TNP vs. SB vs. PA & EL vs. STKI, NTKI & KZN	Among groups	4	6.472	0.014	1.43
	Among populations within groups	10	10.074	0.003	0.30
	Within populations	202	197.046	0.975	98.26
	TOTAL	**216**	**213.592**	**0.993**	

Isolation by distance and gene flow

The Mantel test was used to determine isolation-by-distance by examining the correlation among pairwise ϕ_{ST} values for all samples against geographic distances (Figure 5.4).

Although a weak positive correlation was found between these two variables, suggesting that there may be some isolation-by-distance, it was not significant (r = 0.230, *p* = 0.877).

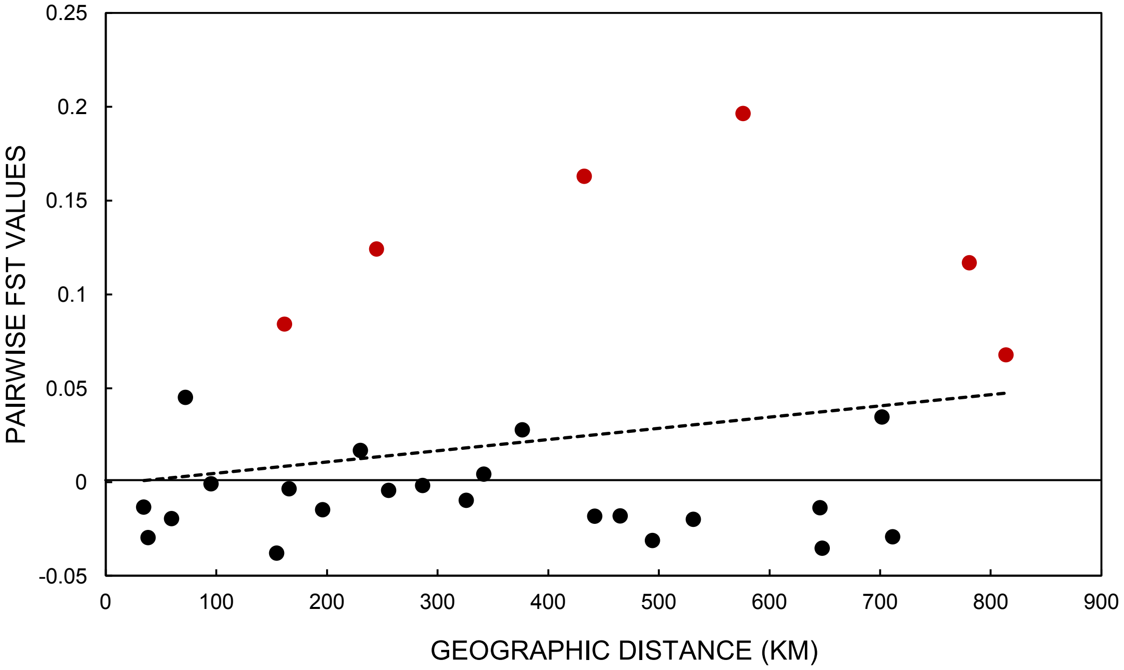

Figure 5.4: Pairwise ϕ_{ST} values plotted against geographical distance (km) between the eight South African regions for poenskop. Mantel correlation value r = 0.229, *p* = 0.877. The red dots indicate Western Cape ϕ_{ST} values plotted against geographical distance (km).

Population history

Tajima's D-values for each region were negative, except for southern Transkei (D = 0.037). A negative value was also obtained for the pooled sample regions (Table 5.6). However, there was no significant departure from neutrality, as indicated by the non-significant values for all estimates of D (Table 5.5). Most of Fu's (1997) F_S values were highly significant and negative. These results indicate deviations from neutrality in all the samples i.e. a departure from the mutation-drift equilibrium (Díaz-Jaimes et al. 2006, von der Hyden et al. 2007). The Fu's F_S value for the pooled sample regions was also negative and highly significant (F_S = -12.908, *p* = 0.003). These neutrality tests therefore support the unimodal mismatch distribution for poenskop (Figure 5.5), indicating a recent demographic expansion of the population.

Table 5.5: Neutrality and demographic history test results for poenskop mitochondrial DNA control region, analysed per sampling region and the overall South African population (n = 217).

Sampling region	**Tajima D**	***P***	**Fu's F_S**	***P***
Western Cape	-0.10429	0.481	-2.29520	0.052
Tsitsikamma	-0.84272	0.219	-3.47255	0.048
Sardinia Bay	-0.67623	0.262	-3.78930	0.042
Port Alfred	-1.10071	0.156	-5.47683	0.007
East London	-1.09734	0.143	-5.45274	0.004
Southern TKI	0.03657	0.563	-1.59334	0.175
Northern TKI	-0.86438	0.214	-6.39721	0.001
KwaZulu Natal	-0.99535	0.179	-1.94711	0.160
SOUTH AFRICA	*-1.23244*	*0.089*	*-12.90769*	*0.003*

The mismatch distributions for the overall South African population (Figure 5.5), as well as the eight regions (Appendix I), were unimodal and generally comparable. Those obtained from the Western Cape, southern Transkei and KwaZulu-Natal, differed the most to the overall distribution. The frequency of pairwise differences for these regions was low; probably due to low sample sizes. The raggedness index (Harpending 1994) overall, which measures the smoothness of the mismatch distribution, was low (r = 0.046), and although it was not significant (*p* = 0.146), it indicated a decent fit to a population growth model.

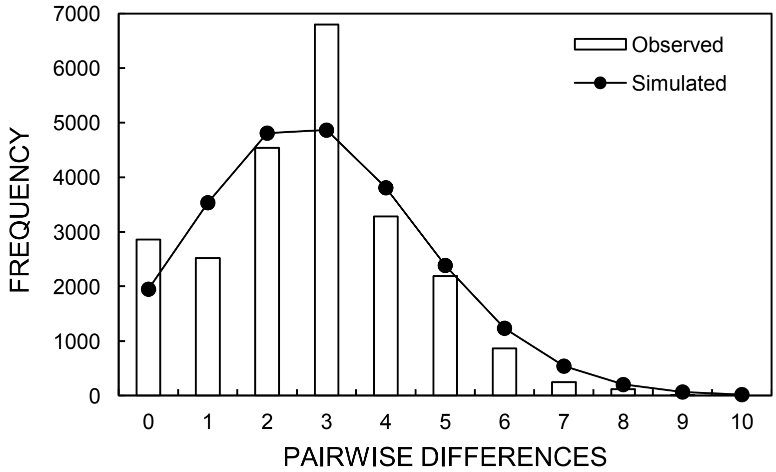

Figure 5.5: Mismatch distribution of pairwise differences between 217 poenskop samples based on 334 bp of the mtDNA control region. The expected frequency is based on a population growth-decline model determined using Arlequin v3.11 (S.S.D. = 0.001 *p* = 0.078, r = 0.046 *p* = 0.154, θ_0 = 0.000 and θ_1 = 18.623).

The location of the mismatch distribution peak is reflected in the τ value, and provides an approximate estimation of when the population expansion took place. The observed value of

τ was 3.176 (95% CI: 1.426 - 4.639). Using this τ value and a mutation rate of 10% (mutation rate for sparids, Bargelloni et al. 2003), the estimated population expansion for poenskop occurred approximately 95 100 years ago. Even though the estimated time of population expansion can be calculated, this is speculative at best. As a result, in this study, it is interpreted as an approximation of geological time. Using the universal mitochondrial control region mutation rates (10% and 20%) (Wilson et al. 1985), the population expansion is thought to have occurred between approximately 47 500 and 95 100 years ago.

5.4. Discussion

Poenskop have been extensively studied, with most aspects of this species' biology being researched. These include feeding, reproduction, age and growth (Buxton and Clarke 1989), as well as validation of growth rings (Potts and Cowley 2005) and estimation of important fishery and population parameters (Götz et al. 2008). Such information is necessary for the management of fishery species, but without knowledge of the genetic stock structure throughout its distributional range, this could lead to inappropriate management actions e.g. managing multiple stocks as a single stock. This study provides the first assessment of the genetic stock structure of the poenskop.

The results from mtDNA analysis suggest that poenskop has no significant population genetic structure over much of its distribution. This is further supported by the lack of isolation-by-distance (along the South Africa coastline). These results are very similar to other local sparid species with similar life history traits, such as the Cape stumpnose *R. holubi* (Oosthuisen 2006), roman *C. laticeps* (Forget 2007, Teske et al. 2010), bronze bream *Pachymetopon grande* (M Mwale, South African Institute for Aquatic Biodiversity, *pers comm.*), white steenbras *L. lithognathus* (Bennett 2012) and hottentot *Pachymetopon blochii* (Reid, unpublished) (Table 5.6). Almost all the molecular variation was found within poenskop sampling localities. There was generally no evidence of spatial heterogeneity as indicated by the low, non-significant ϕ_{ST} value. Similarly, Teske et al. (2010) found no genetic structure in roman (also a protogynous hermaphrodite). However, samples from the Western Cape were significantly different from other sample regions (indicated by the ϕ_{ST} comparisons seen in Table 5.3).

Furthermore, Western Cape samples are only shared amongst a few haplotypes, being entirely absent in the top right hand part of the haplotype network (Figure 5.3).

Table 5.6: Comparisons of genetic diversity of a number of different sparid species, with similar life history characteristics, found along the coastline of South Africa. All studies analysed the mitochondrial DNA control region. Percent (%) variation refers to variation within populations.

Common name	Species	n	No. bp sequenced	# haplotypes	H_D	Π	% variation
Poenskop This study	*Cymatoceps nasutus*	217	550	28	0.87	0.013	99.16
Cape stumpnose Oosthuizen (2006)	*Rhabdosargus holubi*	214	500	36	0.91	0.590	99.84
Roman Forget (2007) & Teske et al. (2010)	*Chrysoblephus laticeps*	96	541	71	0.91	0.018	99.42
White steenbras Bennett (2012)	*Lithognathus lithognathus*	307	720	174	0.985	0.011	100.69

High levels of genetic diversity (h = 0.878, π = 0.008) were found in poenskop, these comparing well with that observed in other studies on marine species (Gold and Richardson 1991, Rocha-Olivares et al. 2000, Bargelloni et al. 2003). Grant and Bowen (1998) suggested that either a long evolutionary history in a stable population or secondary contact of previously differentiated lineages, could result in species typically exhibiting both high haplotype (h) and nucleotide (π) diversities. However, no evidence of a secondary contact was evident for poenskop. Grant and Bowen (1998) also proposed that species with high h and low π, such as the poenskop, most likely underwent population expansion after a period of low effective population size and that this rapid expansion enhances the retention of new mutations (Avise et al. 1984, Ramos-Onsins and Rozas 2002). This signature was also observed in the minimum spanning network (Figure 5.3). Even though the minimum spanning network is not the typical star-like shape, it does represent a relatively stable population. Only one to three mutational steps separated all other alleles from the three main alleles (haplotype 1, 3 and 5). If the genetic marker is selectively neutral, mutations can only be removed through genetic drift. In large populations, this process would require many generations to remove such mutations (Hauser and Ward 1998, Waples 1998).

Little genetic differentiation existed among seven of the South African sample regions (Western Cape is significantly different from the other sample regions). Samples were obtained throughout the poenskop's distribution range, including both inshore and offshore sites, as well as from juveniles and adults, yet there remained little genetic variation. Both genetic diversity indices from the individual localities are comparable with the indices obtained for all the samples. The exception could be the slightly lower h and π seen in the Western Cape ($h = 0.795$, $\pi = 0.0048$). Originally thought to be a result of low sample size ($n = 13$), indices were lower than the other regions, even compared to KZN ($n = 16$) and southern Transkei ($n = 17$) which also had low samples sizes. Nucleotide diversities for all sample regions were near identical (except for KwaZulu-Natal). This indicates that any two individuals being drawn at random from one region will be as different as any two individuals drawn from different regions (regarding their mtDNA haplotypes). Similar patterns were observed in the dusky kob *A. japonicus* (Klopper 2005) and the Cape hakes *M. capensis and M. paradoxus* (von der Heyden et al. 2007).

According to Ward et al. (1994), the mean ϕ_{ST} value for marine fish, is similar to the value estimated for other groups of animals with no limits to movement, for example birds (0.076) and insects (0.097). However, Waples (1998) found that the mean ϕ_{ST} for marine fish was only 0.020. Ward et al.'s (1992) findings were in agreement with the significant ϕ_{ST} values obtained in this study. However, poenskop show high degrees of residency (Chapter 4) and the non-significant ϕ_{ST} values were more in line with Waples (1998).

The spatial homogeneity test, to test for homogeneity of the haplotype frequencies, proved to be non-significant. This, combined with a low non-significant overall ϕ_{ST} value obtained for this study ($\phi_{ST} = 0.0116$, $p = 0.208$), indicates no existing population structure amongst poenskop at the eight sampling regions. The results of the AMOVA analyses also showed no population structuring for poenskop; all variation was seen within sampling localities (98.84%) and minimal variation was seen between areas. This evidence strongly suggests a panmictic gene pool. It is important to note that even though the values were significant, ϕ_{ST} values between the Western Cape and all other regions, bar the southern Transkei and KwaZulu-Natal, were eight – ten times greater than that of the overall ϕ_{ST} value. This, along with the weak positive correlation found between geographic distances and pairwise ϕ_{ST} values ($r = 0.230$, $p = 0.877$), suggests that there may be some isolation-by-distance.

The long-held assumption of a lack of dispersal barriers in the marine environment is generally thought to result in homogeneity between populations. The results of this study were expected to follow this trend due to the complexity of the ocean currents along the South African coastline. Numerous studies have been conducted on the ocean currents surrounding South Africa, in an attempt to understand their movement and the related movement of larvae and eggs. These include studies by Tilney et al. (1996) that found that larvae within the Tsitsikamma National Park (TNP) can be transported 250 km westwards of the TNP; Attwood et al. (2002), who suggested that egg and larval dispersal can occur both east- and westwards with a maximum dispersal potential of 580 km in 30 days; Brouwer et al. (2003), that measured water movement throughout the water column during spawning events of the carpenter *Argyrozona argyrozona*; and Hutchings et al. (2002), which considered various mechanisms such as eddies, retroflections and filaments which may pose problems for retention of eggs and larvae along the coastline of South Africa. These authors suggested that the mean dispersal distance from spawning grounds in the TNP was 299 km eastwards. Attwood and Cowley (2005) estimated galjoen *Dichistius capensis* larvae have the potential to disperse up to 240 km within one week after spawning, by making use of inshore currents. All these studies suggest that the longshore hydrology along the south coast of South Africa could promote extensive egg and larval dispersal, resulting in connectivity in all directions. The primary methods used to transport these eggs and larvae, are passive transport and active behaviour (Norcross and Shaw 1984). The above-mentioned studies largely deal with passive transport, regarding larval dispersal as a process of modulated drift (Power 1984). Many species within the sparids produce small pelagic eggs containing an oil droplet, such as roman *C. laticeps* (Forget 2007), slinger *Chrysoblephus puniceus* (Connell et al. 1999) and santer *Cheimerius nufar* (Connell et al. 1999). This provides the eggs with extra buoyancy and increased dispersal potential. Certain species even adopt life histories that include tactics for minimising larval drift (Parrish et al. 1981), while others make use of drift in their migrations (Power 1984). Even after extensive larvae surveys along the coastline of South African, poenskop larvae have never been documented (see Beckley and van Ballegooyen 1992, Tilney et al. 1996, Wood et al. 2000, Roberts and van der Berg 2005, Connell 2010). Therefore it is not known whether poenskop employ these same mechanisms.

Poenskop is a resident reef fish species, showing high degrees of residency during all life-history stages (Chapter 4). However, adults have been recorded moving larger distances. Numerous studies on other sparid species with similar life histories as the poenskop, suggest that gene flow occurs primarily by the transport of eggs and early stage larvae (Brouwer et al. 2003, Teske et al. 2010, Pattrick 2008). This transport takes place via variable oceanic currents and could be responsible for the homogeneity observed in this study. This life history strategy has been found in several other reef-associated species with sedentary adult phases (Shaklee and Samollow 1984, Johnson et al. 1993, Gold and Richardson 1998), including the resident poenskop. Adult poenskop have, however, been recorded moving larger distances, moving to a variety of locations along the coastline. Therefore, this would allow for eggs and larvae to be dispersed from a number of locations along the South African coast. However, this homogeneity may reflect historical rather than current patterns of gene-flow (Gold and Richardson 1998). The effect of high-levels of gene flow can result in a pattern of homogeneity, not only between different regions that are close to each other, but also in regions that are geographically separated, as seen in this study.

The final destinations of larvae are determined by interactions between the physical properties of the water (velocity and turbulence), as well as the biological properties of the larvae (buoyancy and active swimming) (Tilney et al. 1996). Understanding the movement and dispersal of these fish larvae requires knowledge of active swimming abilities (Pattrick 2008). Mora and Sale (2002) found that a number of coral reef fish larvae are capable behaviourally of participating actively in their own dispersal. Pattrick (2008) recorded that the swimming abilities of certain sparid larvae from South African temperate waters, are known to exceed ocean current velocities in the nearshore environment. Some larvae of local sparids (e.g. blacktail *Diplodus capensis* and strepie *Sarpa salpa*) were also found to be strong swimmers (Pattrick 2008). This suggests that fish larvae may be capable of playing an active role in their own movement and dispersal.

This is in contrast to many invertebrates along the South African coastline. McQuaid and Phillips (2000) found that the Mediterranean mussel *Mytilus galloprovincialis* relied on wind as a process of dispersal and as a result only dispersed under 100 km, with most recruits appearing within 5 km of the parent population. Robinson et al. (2005) reported limited movement by a number of marine alien species, including an ascidian *Ciona intestinalis*, the European shore crab *Carcinus maenas*, an oyster *Crassostrea gigas*, a periwinkle *Littorina saxatilis*, and two anemones *Metridium senile* and *Sagartia ornata*. Teske et al. (2009b) reported a phylogeographic break associated with the tropical/sub-tropical transition zone in the sandprawn *Callianassa kraussi*. This dispersal barrier resulted in allopatric fragmentation.

Temperature further exerted a measure of diversifying selection, which may have inadvertently resulted in speciation (Teske et al. 2009b). Teske et al. (2011) documented this and other important phylogeographic breaks for marine intertidal invertebrates along the South African coast. The distribution and population of poenskop appears to be unaffected by these breaks and transition zones. This could be attributed to their strong swimming capabilities (Pattrick 2008), as well as passive transport via oceanic currents. Spawning events may also take place offshore, with larval transport relying more on oceanic rather than non-coastal currents.

The lack of population differentiation seen in poenskop could also be explained by the presence of discrete spawning populations (Waples 1998). Poenskop are a resident fish species (Chapter 4) and due to this movement behaviour, it may be possible that there are several discrete spawning populations. Different discrete breeding groups might exist at a particular locality at the same time. Such groups may not necessarily be stable or completely isolated (Scribner and Chesser 2001). Therefore, the observed results for poenskop could be a result of mixing of discrete stocks during the adult stage and during larval stages (Oosthuisen 2006). Buxton and Clarke (1989) suggest that poenskop migrate up the east coast to spawn during the breeding season, and reject the idea of the fish on the east coast forming a resident breeding stock. In this study, large sexually mature individuals were sampled from as far west as Stilbaai and as far up the east coast as Kelso. While these large adults may be resident, the possibility of them undertaking a spawning migration cannot be excluded. Since more juvenile poenskop samples were obtained along the northern Transkei coastline, as well as in the TNP, Sardinia Bay MPA and Port Alfred region, this may be an indication of transport of the larvae by the Agulhas Current to the southern coast. The majority of the Western Cape fish were mature adults, which may account for the high number of juveniles in the TNP being dispersed from the Western Cape eastwards (Brouwer et al. 2003). A large number of mature adult fish were also sampled from the East London region, but few juveniles. This could be due to counter currents existing off Port Alfred and East London, which may assist the northwards movement of larvae and juveniles (Roberts et al. 2010). A similar larval dispersal situation exists with *C. cottoides* (von der Heyden et al. 2008), where the Indian Ocean Agulhas counter-current plays an important role in facilitating dispersal. A large number of adult fish were also sampled in both the southern and northern Transkei. This is in agreement with good poenskop catches being made in these waters (Chapter 3). However, it was found that poenskop do not undertake spawning migrations (Chapter 4). The more likely situation is that larger poenskop move up the coastline into deeper Transkei waters where they remain for the duration of their lives. Therefore, the possibility of small resident breeding populations should be taken into consideration.

Mismatch distributions and the neutrality tests, all suggest that poenskop has undergone population expansion. The negative and highly significant Fu's F_S value could be interpreted as either a historical bottleneck or selective sweep, followed by population expansion. This population expansion could have occurred with sufficient intensity or duration to leave detectable traces in present day levels of mtDNA polymorphism (see Bargelloni et al. 2003). The population expansion signal is supported by the slightly star-shaped haplotype network, where low-frequency sequences stem out from a dominant haplotype, being removed by one or a few mutational steps (Bargelloni et al. 2005). Similar results were obtained for the white seabream *Diplodus sargus* (Bargelloni et al. 2005, González-Wangüemert et al. 2010), which showed high genetic variation and low to moderate nucleotide diversity, giving rise to a starlike haplotype network (Grant and Bowen 1998, González-Wangüemert et al. 2010). The black-spot seabream *Pagellus bogaraveo* (Stockley et al. 2005), red porgy *P. pagrus* (Bargelloni et al. 2003) and South African shallow water hake *M. capensis* (von der Heyden et al. 2007) also show similar trends.

Based on calculations, the population expansion of poenskop is approximated to have taken place 95 000 years ago. Between 130 000 – 35 000 before present, the earth was not continuously warm. The Cenozoic era saw global aridification and cooling trends (Roberts et al. 2006). This was supplemented with sea level rises and regressions along the South African coastline, occurring approximately every 1 200 years during the late Pleistocene and early Holocene (Ramsay 1994). The last interglacial period ended approximately 125 000 years ago, and as a result of melting sea ice, the sea-level rose to 5 m higher than present (Ramsay and Cooper 2002, Botha et al. 2008). Approximately 116 000 – 110 000 years before present, rapid lowering of the sea-level took place, only to rise again approximately 100 000 years ago (Botha et al. 2008). Botha et al. (2008) also recorded a rapid sea-level change occurring 90 000 years ago, resulting in a warming period that coincided with a 5 °C rise in sea-surface temperature (Shackleton et al. 2003). This rise in sea-level, combined with an increase in sea-surface temperature, may have opened up the shallow inshore shelf environment (previously restricted to a narrow range on the continental slope), increasing suitable habitat for poenskop, thus allowing expansion of the population. Cold intervals were evident, such as the interval approximately 75 000 years ago. This cooler period was most likely the result of the Toba volcanic eruption which took place during the late Pleistocene (Ambrose 2003) and resulted in a large temperature drop. But, since the initial population expansion of poenskop took place prior to this cooling period, as well as before the sea-level fluctuations experienced off the coastline of South Africa, the population may not have been greatly influenced by these events, moving accordingly and allowing for continual expansion.

A single stock can be identified if a population shows genetic homogeneity and an absence of spatial patterns in the distribution of alleles. However, a number of authors (Gold and Richardson 1998, Hauser and Ward 1998) recognise the limitations of mtDNA markers, pointing out that observed homogeneity may be the result of historical dispersal rather than representing present-day gene flow (Forget 2007). The use of mtDNA markers to distinguish stock structure within species has been found to be limited. Therefore, it is advisable to additionally use a different marker set, such as microsatellite markers, that are generally assumed to be more suited to detecting fine-scale genetic population differentiation (e.g. Ward 2000). Microsatellite DNA markers have been found to be successful in detecting subtle genetic heterogeneity among geographic localities, due to its higher level of variation (Gold and Turner 2002). Microsatellite analysis may also indicate current gene flow rather than historical genetic information (Hauser and Ward 1998).

These results suggest that a single-stock model can be adopted for appropriate management of poenskop along the coastline of South Africa. This suggestion is in agreement with results from other studies on similar species (see Ooshuizen 2006, Bennett 2012). This trend was identified by making use of mitochondrial DNA. In future, it may be highly informative to include both mitochondrial and nuclear markers to assess intraspecific genetic variability (Wilson et al. 1985, Gold and Turner 2002, Lemaire et al. 2005).

CHAPTER 6

GENERAL DISCUSSION

"Even if the steenbras is small, perhaps a fish of 10 lb., the angler will need both his own ability and all the luck ever granted to any fishermen if he is to merge victorious from the contest, for he has hooked a strong fish from among many powerful bottom feeders."

- Horne (1955: p 120) -

Poenskop is one of South Africa's iconic recreational angling species. Even though aspects of this species' life history have been studied (Buxton and Clarke 1989), the movement behaviour and genetic stock structure of poenskop, prior to this study, had not been addressed. The movement behaviour of several of other South African sparid species has been documented (see Brouwer 2002, Griffiths and Wilke 2002, Brouwer et al. 2003, Kerwath et al. 2007a, Watt-Pringle 2009, Bennett 2012). Similarly, some studies have investigated the genetic diversity of South African sparids (see Oosthuizen 2006, Teske et al. 2010, Bennett 2012). With the exception of Bennett's (2012) study, which examined various aspects of movement behaviour, habitat use and genetic stock structure of white steenbras *Lithognathus lithognathus*, poenskop is the first species to have both of these aspects studied. Therefore, the primary aim of this study was to address the gaps in the current understanding of poenskop life history in terms of movement behaviour and genetic structure, and supplement the knowledge on its ecology.

The study incorporated conventional dart tagging to assess movement in the marine environment, and molecular techniques to assess the genetic stock structure. An additional component of the study was to assimilate all available catch data (both fishery-dependent and fishery-independent data). Each method employed had strengths and weaknesses associated with it.

Fishery data

CPUE estimates and information on numerical and gravimetrical percentage contribution of poenskop to total catch were obtained from available literature (Chapter 3). This was supplemented by catch information recorded in the National Marine Linefish System (NMLS), *Stywe Lyne/Tight Lines*, personal angling records, Robberg Diaries and marine protected areas (MPAs). A number of inherent biases are associated with the NMLS data and the coverage and quality of the information has been questioned (Sauer et al. 1997). Therefore, the NMLS is characterized by considerable flexibility with regards to data sources (Penney 1993). For these reasons, only catch data from the south-east coast and KwaZulu-Natal were analysed. Analysis of the catch data showed that the number of poenskop caught (predominantly by recreational shore and commercial and recreational skiboat anglers) has been declining steadily since the 1980s. The size of fish being caught has also decreased, current catches being dominated by fish less than 5 kg (i.e. sub-adult). This trend is also evident in a number of other sparid species, for example red steenbras *Petrus rupestris* (Smale 1988), seventyfour *Polysteganus undulosus* (Chale-Matsau et al. 2001) and white steenbras *L. lithognathus* (Bennett 2012). Red steenbras and seventyfour are now considered to be economically extinct.

Movement behaviour

Inshore (shore-based) and offshore (boat-based) information obtained from the ORI Tagging Project provided good coastal coverage of tagged and recaptured fish across South Africa (Chapter 4). However, resolution was low, and accuracy was between 0 and 5 km. Therefore, this tagging data was supplemented by research-based tagging projects within MPAs, providing fine-scale, high-resolution information from the shore (TNP) and offshore (Pondoland) zones, with precision ranging from 15 to 100 m. Despite the good coverage, very few adult fish were tagged. This can be attributed to stock depletion (Chapter 3). From the tagging information, it was inferred that juvenile and sub-adult poenskop are highly resident, with the vast majority of fish being recaptured at the tagging location. Home-range size estimations revealed smaller poenskop to hold small home-ranges (as seen in the TNP). Even though poenskop displayed a high level of residency, a number of large-scale movements, between coastal regions, were evident. Despite few adult poenskop being tagged and recaptured, these larger fish were found to move greater distances. One individual moved 483 km in a north-easterly direction up the Transkei coastline confirming that poenskop are capable of moving vast distances. Because such extensive movements can take place, one would therefore expect the population to be well mixed as these individuals contribute to the genetic homogeneity seen (Chapter 5). Poenskop may also undertake these movements if conditions became unfavourable. Other South African sparids that are resident as juveniles, but move larger distances as sub-adults to adults, are the white steenbras *Lithognathus lithognathus* (Bennett 1993b), red steenbras *P. rupestris* (Smale and Punt 1991, Brouwer 2002), and white musselcracker *Sparodon durbanensis* (Watt-Pringle 2009).

Genetic stock structure

Genetic structure and connectivity of poenskop among different regions along the South African coastline was explored (Chapter 5). Samples were collected across the core distributional range of poenskop, and included samples from inshore and offshore reefs within five marine protected areas (TNP, Sardinia Bay, Dwesa-Cwebe, Hluleka and Pondoland). The distribution of sampling localities/regions was also evenly spaced along the coastline. Evidence for the strength of using the mtDNA control region was provided by a number of studies, which addressed similar questions, having successfully used this technique. It was also chosen because the markers are more variable than nuclear markers. This is due to the fixation of mutations through genetic drift due to its haploid nature and smaller effective population size. Samples collected throughout the core distribution of poenskop showed the species to have high genetic diversity, generally little genetic differentiation among regions, limited spatial structure and no evidence of isolation by distance.

Panmixia is not limited to poenskop. Many other South African sparids show similar genetic structure (Table 6.1). One of the biggest challenges to population biologists is incorporating molecular genetics into species biology, identifying non-biological factors that influence species demography (DeSalle and Amanto 2004). Analyses of the mitochondrial DNA control region revealed that this species has a high level of haplotype- and nucleotide diversity, and generally exists as a single, well-mixed population (with the possible differentiation of the Western Cape, Chapter 5). The observed pattern of genetic variation with no geographical differentiation can be explained by either (a) more than one genetically-isolated population of poenskop, with extensive mixing between these groups during the larval phase; or (b) only one spawning stock exists with migration along the coastline. With regards to poenskop, and a single stock, the latter is most applicable. The movement component of the study (Chapter 4) revealed that poenskop show high degrees of residency in both juvenile and adult life history stages. Results also suggested that large adult poenskop progressively migrate up the coastline of South Africa to KwaZulu-Natal and Transkei waters (being found in the highest numbers, and of a larger size, in these regions, Chapter 3). Chapter 5 revealed the single stock status of poenskop and therefore, extensive mixing of the population may result from the transport of eggs and larvae from KZN and Transkei waters to other reaches of the coastline. The presence of large adult poenskop in the Western Cape (along the south-western coast of South Africa, Chapter 3 and 5) could also suggest the possibility of different spawning areas along the coast (even though the majority of poenskop move up the coastline to KZN and Transkei). The location of these areas will most likely take advantage of the prevailing oceanographic currents, maximising transport of eggs and larvae to areas of the coast with suitable rocky intertidal nursery habitat. While poenskop larvae have never been documented, even after extensive ichthyoplankton studies (see Buxton and Smale 1984, Beckley and van Ballegooyen 1992, Tilney et al. 1996, Wood et al. 2000, Roberts and van der Berg 2005, Connell 2010), it is assumed that a larval phase does exist that is similar to other sparid species such as red steenbras and white musselcracker. Until fish larvae are able to play an active role in their dispersal, their movement is dictated by prevailing ocean currents. However, Beckley and van Ballegooyen (1992) listed a number of additional mechanisms likely to aid entrainment and retention of larvae close to the KZN shelf, including minor upwellings, cyclonic eddies, and changes in wind direction or current reversals (Hutchings et al. 2002). Beckley and van Ballegooyen (1992) and Beckley (1993) also dispelled the myth that the Agulhas Current was the main vector for transport of shelf-zone fish to the south along the east coast (Heydorn et al. 1978). Westward-flowing bottom currents assist with egg and larval dispersal along the Agulhas Bank (situated along the southern/south-western stretch of the South African coastline) (Boyd and Shillington 1994), while shear-edge eddies, resulting in counter-flow, enable eggs and larvae to be retained on shallower parts of the Bank (Hutchings et al. 2002). Most fish species spawn downstream from upwelling centres, where wind mixing and offshore advection are minimised.

Management recommendations

Management strategies for conservation and sustainable utilisation of exploited marine species need to recognise, amongst other aspects, dynamics of their movement behaviour and genetic diversity (Attwood and Cowley 2005). The effectiveness of particular management measures is dependent on patterns of exploitation of individuals or populations. Poenskop is exploited in the recreational and commercial linefisheries and potentially vulnerable to over-exploitation. Therefore, management measures need to be developed in order to afford this species maximum protection.

Conventional fisheries management tools

The conventional tools available for fishery management include size limits, bag limits, gear restrictions, closed seasons and restricted access (introduced at the beginning of 1985 under the Sea Fisheries Act No. 58 of 1973, revised in October 1992 under Act No. 12 of 1988) (McClanahan and Castilla 2007). Even though these tools are widely used, there is growing concern over their efficacy in achieving management goals such as resource sustainability and the preservation of biodiversity (Bohnsack 1993, Ludwig et al. 1993, Bohnsack and Ault 1996). Reasons include high mortality of released fish, enforcement problems, and conflict between regulations and traditional systems of management (Bohnsack and Ault 1996).

Size limits are typically set to a length at which the fish matures in order to allow individuals the chance to reproduce at least once before becoming vulnerable to capture (Richardson 2010). Currently, the size limit for poenskop equates to a length of approximately 445 mm FL (Buxton and Clarke 1989). However, Buxton and Clarke (1989) recorded the smallest reproductively active female as being 530 mm FL. Poenskop are also protogynous hermaphrodites, becoming males at approximately 700 mm FL (Buxton and Clarke 1989). Therefore, the current size limit only protects female juveniles and sub-adults, allowing for the exploitation of all adult fish, including all males. Roberts and Polunin (1991) found that fecundity generally increased with the size of the fish and, therefore, the large females and subsequent males need alternative means of protection. If a gear restriction was imposed it would involve setting a maximum hook size that fishers are allowed to use. Poenskop have strong robust jaws and therefore, if smaller hooks were used by anglers, the probability of hooking a poenskop would be greatly reduced. However, the poenskop is one of South Africa’s sought after trophy species and, as a result, restrictions on hook size would probably not be supported.

Daily bag limits (DBLs) are set in order to allow adequate protection to the parent stock and therefore reduce the risk of recruitment overfishing (Richardson 2010). Decisions on whether to alter a bag limit or not is often related to information on catch rate and CPUE (Attwood and Bennett 1995). The current bag limit for poenskop is one per licensed fisher per day; a decrease from the previous limit of two following the development of the new Linefish Management Protocol (Griffiths et al. 1999).

The national ban on off-road vehicles on South African beaches may also play an important role in the continued protection of a number of fish species. This ban has resulted in the creation of a number of inaccessible areas, thereby reducing fishing pressure on resident populations. These areas would then act as harvest refugia and provide a buffer against exploitation in other areas, for example, supplying recruits in larval dispersal as well as spillover of adults.

As poenskop form an important part of the recreational shore-angling and skiboat fishery, and due to their relatively low abundance, size and bag limits should be adhered to. However, these conventional management measures will be biased, favouring the protection of small poenskop. Larger individuals of this fish species are also still targeted and caught in the commercial linefishery. A suggestion to protect poenskop from this fishing sector could include the decommercialisation of the species, thereby allowing poenskop to be managed as a prime recreational trophy fish. Another sparid, seventy-four *Polysteganus undulosus*, was decommercialised in 1998 (seventy-four were placed on the specially protected species list under the new South African Marine Living Resources Act) due to its dwindling stocks (Chale-Matsau et al. 2001). This move to protect the seventy-four has been highly successful. As poenskop have life-history characteristics which make them vulnerable to overexploitation (including residency), MPAs are undoubtedly one of the most useful management tools for the conservation of this species. MPAs have been found to effectively protect a number of different reef species, including blacktail *D. capensis*, zebra *D. hottentotus*, Cape stumpnose *Rhabdosargus holubi*, white musselcracker *Sparodon durbanensis* (Bennett and Attwood 1991) and roman *Chrysoblephus laticeps*, dageraad *C. cristiceps* and red steenbras *Petrus rupestris* (Buxton and Smale 1989), all of which were more abundant and larger within MPAs than in adjacent exploited areas.

Marine protected areas as a management tool for poenskop

MPAs are gaining widespread attention as tools for conserving biodiversity while maintaining healthy sustainable fisheries (Bohnsack 1993, Bohnsack and Ault 1996, Roberts and Hawkins 2000, Roberts et al. 2001). One of the objectives of establishing MPAs is to create undisturbed populations and ecosystems against which the ecosystem effects of fishing can be measured (Griffiths and Wilke 2002). In order to establish undisturbed populations, species need to be protected. A number of studies have attempted to assess protection offered by MPAs by determining (a) comparison of abundance and size structure inside and outside no-take MPAs (Buxton and Smale 1989, Bennett and Attwood 1993, Cowley et al. 2002, Maggs 2011a, 2011b), (b) movement of adults with mark and recapture studies (Attwood and Bennett 1994, Munro 2000, Kerwath et al. 2008); and (c) genetic stock structure (Trexler and Travis 2000, von der Heyden 2009). MPAs are now regarded as the foundation of marine conservation in South Africa, being essential for fisheries management (Attwood et al. 1997, Tunley 2009). Currently, there are 22 MPAs Gazetted in South Africa, covering approximately 21% of the coastline length, incorporating a range of management areas consisting of, amongst others, multi-purpose MPAs and no-take zones (Tunley 2009, von der Heyden 2009).

Given the life history characteristics of poenskop, the reef-like physical environment of large portions of the South African coastline and the lack of compliance of many fishers with regards to conventional management measures, MPAs are considered to be the most applicable management tool for this species. MPAs will especially warrant the protection of resident juveniles and sub-adults, allowing these fish to reach sexual maturity. The MPA network in South Africa is already well-established and because MPAs are not single species management tools, other reef species would also be afforded protection through inshore MPAs. These include species such as roman *C. laticeps* (Kerwath et al. 2008), bronze bream *Pachymetopon grande* (PD Cowley, South African Institute for Aquatic Biodiversity, *pers comm.*), white stumpnose *Rhabdosargus globiceps* (Attwood et al. 2007), white musselcracker *S. durbanensis* (Bennett and Attwood 1991), etc. Not only could these MPAs protect resident species but they could also provide temporary refuge for migratory species in transit (Richardson 2010). However, for an MPA network to be effective, various reserves need to be connected, either by adult or larval movement (Planes et al. 2009, von der Heyden 2009). Although movement is generally limited (Chapter 4), poenskop are capable of moving great distances and may potentially find refuge in MPAs, as well as being capable of moving between MPAs. Poenskop larvae have never been studied but, assuming poenskop do have a dispersive larval stage (discussed in Chapter 5), and taking South Africa's oceanography into account (Chapter 2), the MPAs are probably well connected, affording protection to all of the life history stages of poenskop.

Enforcement issues as well as poaching within MPAs are major concerns in South Africa's linefishery and could deter the effectiveness of additional MPAs along South Africa's coastline (Cockcroft et al. 1999, Griffiths et al. 1999, Mann et al. 2002). However, with increased surveillance and monitoring of these MPAs, this should remain under control. Effective public education programmes should be implemented in order to instil a more sustainable attitude towards the use of coastal resources. Reopening sections of existing MPAs for "restricted access" fishing (Sunde and Isaacs 2008) should also not be considered.

Closed seasons

Closed seasons are normally implemented in order to protect a species over a particularly vulnerable period of the life cycle. This period frequently coincides with the breeding season (Clarke 1988). If the catch rate of a species declines below a pre-determined level, then management strategies may have to be reassessed and implemented, and in extreme cases, the fishery should be closed. Such temporal catch restrictions have been used with success in the management of species such as shad *Pomatomus saltatrix* (van der Elst 1988b) and galjoen *Dichistius capensis* (Clarke and Buxton 1989). A three-month closed season for poenskop could be implemented between 1 July and 30 September each year. Poenskop are often caught during the winter months and the proposed closed season coincides with the known breeding season for this species (Buxton and Clarke 1989).

Recommendations for future research

Although this study has contributed to the understanding of the movement behaviour and genetic stock structure of poenskop along the coastline of South Africa, more information is still required to fully understand its life history. Based on the results of this study, the following recommendations for future research are identified:

1. *Fishery data*

- Data from the National Marine Linefish System are highly variable and inconsistent in terms of the types of data collected. Length or weight measurements are seldom collected and data is generally of a low resolution. If efficient management of poenskop and other endemic reef species is to take place, then good quality catch and effort data needs to be reliably and consistently collected.
- The number of anglers fishing and hours fished is critical for estimates of effort and for further quantifying the status of different reef fish species. A public participation campaign could assist in the appropriate collection of catch and effort details, possibly by a revamped system of submitting voluntary catch cards. In addition, all competition data from the various recreational linefishery sectors should be submitted for capture onto a system such as the NMLS.
- Furthermore, boat-based angling effort and catches should be documented at all launch sites along the South African coastline, not only along the KZN coast.

Training inspectors, as they do for Ezemvelo KwaZulu-Natal Wildlife, along the entire coastline to collect this information would also assist in job creation.

2. *Movement behaviour*

- The vast majority of tagging data excludes fish smaller than 200 mm FL (i.e. juveniles). An additional dart tag could be manufactured to enable tagging of these smaller fish living in rock pools and gullies. It is assumed that the juveniles of most reef-associated species are resident. However, by tagging the juveniles, one could obtain a full understanding of all movement behaviours of a species.
- Buxton and Clarke (1989) suggested that poenskop undertake coastal displacements similar to red steenbras *P. rupestris* (Brouwer 2002) and white musselcracker *S. durbanensis* (Watt-Pringle 2009). However, the use of tag and recapture studies does not allow for investigation of small-scale localised movements as no information on the fish position between release and recapture dates is available. Therefore the use of acoustic telemetry or the newly established Ocean Tracking Network (OTN) could provide more insight into these movements. Such studies are necessary to understand long-term movement patterns.

3. *Genetic stock structure*

- Additional gene regions could be amplified, sequenced and analysed in order to confirm and make the current findings (using mtDNA control region) more robust. Additionally, an effort to collect more samples from the extremities of the poenskop's distribution could be made. Some variation within the Western Cape samples was noticed and with the collection of more samples from this region, this could be confirmed.
- In future, a nuclear DNA assessment could prove helpful. This could be done using microsatellite analyses. Microsatellites are highly variable and sensitive, are better to detect fine-scale structure and subdivision, as well as detecting contemporary patterns of gene flow and connectivity.

Forty-one species of sparid fish are found in South African waters. Twenty-nine of these are endemic and approximately 30 are important components of the linefishery (Smith and Heemstra 1986, Griffiths and Wilke 2002). The large majority of the warm-temperate representatives of this family have been heavily exploited since the mid 1900s, including the poenskop (Penney et al. 1999, Griffiths 2000). By combining all components of this study, appropriate management recommendations for poenskop can be developed which would work towards the conservation of this species for fishery purposes as well as the preservation of its genetic integrity. Target reference points from past or recent studies involving reef fish species with similar life histories may be used as indicator of the health of the stock. MPAs, concentrating on protecting early life history stages of poenskop as well as resident adults, will be the most efficient management tool. Combining the movement and genetic aspects (as done in this study), as well as the biological, oceanographical and socio-economic aspects, will provide a basis for improved management of this, and possibly other large, slow-growing, resident, reef-associated fishery species.

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APPENDIX I

Mismatch distributions of poenskop at the eight South African regions, moving from West to East. Bars represent observed values, and lines represent simulated values.