MOVEMENT PATTERNS, STOCK DELINEATION AND CONSERVATION OF AN OVEREXPLOITED FISHERY SPECIES, *LITHOGNATHUS LITHOGNATHUS* (PISCES: SPARIDAE)

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Abstract

White steenbras *Lithognathus lithognathus* (Pisces: Sparidae) has been a major target species of numerous fisheries in South Africa, since the late 19th century. Historically, it contributed substantially to annual catches in commercial net fisheries, and became dominant in recreational shore catches in the latter half of the 20th century. However, overexploitation in both sectors resulted in severe declines in abundance. The ultimate collapse of the stock by the end of the last century, and the failure of traditional management measures to protect the species indicate that a new management approach for this species is necessary.

The species was identified as a priority for research, management and conservation in a *National Linefish Status Report*. Despite knowledge on aspects of its biology and life history, little is known about juvenile habitat use patterns, home range dynamics and movement behaviour in estuaries. Similarly, the movement and migration of larger juveniles and adults in the marine environment are poorly understood. Furthermore, there is a complete lack of information on its genetic stock structure. Such information is essential for effective management of a fishery species. This thesis aimed to address the gaps in the understating of white steenbras movement patterns and genetic stock structure, and provide an assessment of its current conservation status. The study adopted a multidisciplinary approach, incorporating a range of methods and drawing on available information, including published literature, unpublished reports and data from long-term monitoring programmes.

Acoustic telemetry, conducted in a range of estuaries, showed high site fidelity, restricted area use, small home ranges relative to the size of the estuary, and a high level of residency within estuaries at the early juvenile life stage. Behaviour within estuaries was dominated by station-keeping, superimposed by a strong diel behaviour, presumably based on feeding and/or predator avoidance, with individuals entering the shallow littoral zone at night to feed, and seeking refuge in the deeper channel areas during the daytime. Conventional dart tagging and recapture data from four ongoing, long-term coastal fish tagging projects, spread throughout the distribution of this species, indicated high levels of residency in the surf zone at the late juvenile and sub-adult life stages. Consequently, juvenile and sub-adult white steenbras are vulnerable to localised depletion, although they can be effectively protected by suitably positioned estuarine protected areas (EPAs) and marine protected areas (MPAs), respectively.

It has been hypothesized that adult white steenbras undertake large-scale coastal migrations between summer aggregation areas and winter spawning grounds. The scale of observed coastal movements was correlated with fish size (and age), with larger fish undertaking considerably longer-distance coastal movements than smaller individuals, supporting this hypothesis. Given the migratory behaviour of adults, and indications that limited spawning habitat exists, MPAs designed to protect white steenbras during the adult life stage should encompass all known spawning aggregation sites. The fishery is plagued by problems such as low compliance and low enforcement capacity, and alternative management measures, such as seasonal closure, need to be evaluated.

Despite considerable conventional dart tagging effort around the coastline (5 782 fish tagged) with 292 recaptures there remains a lack of empirical evidence of fish migrating long distances (> 600 km) between aggregation and spawning areas. This uncertainty in the level of connectivity among coastal regions was addressed using mitochondrial DNA sequencing and genotyping of microsatellite repeat loci in the nuclear genome, which showed no evidence of major geographic barriers to gene flow in this species. Samples collected throughout the white steenbras core distribution showed high genetic diversity, low genetic differentiation and no evidence of isolation by distance or localised spawning.

Although historically dominant in several fisheries, analysis of long-term commercial and recreational catch data for white steenbras indicated considerable declines and ultimately stock collapse. Improved catch-per-unit-effort in two large MPAs subsequent to closure confirmed that MPAs can be effective for the protection of white steenbras. However, the current MPA network encompasses a low proportion of sandy shoreline, for which white steenbras exhibits an affinity. Many MPAs do not prohibit recreational shore angling, which currently accounts for the greatest proportion of the total annual catch. Furthermore, EPAs within the juvenile distribution protect a negligible proportion of the total available surface area of estuaries – habitat on which white steenbras is wholly dependent.

Despite some evidence of recent increases in abundance in estuaries and the surf zone in certain areas, white steenbras meets the criteria for “Endangered” on the *IUCN Red List of Threatened Species*, and for “Protected species” status on the National Environmental Management: Biodiversity Act of South Africa. The species requires improved management, with consideration for its life-history style, estuarine dependency, surf zone residency, predictable spawning migrations and its poor conservation status. The multidisciplinary approach provides valuable information towards an improved scientific basis for the management of white steenbras and a framework for research that can be adopted for other overexploited, estuarine-associated coastal fishery species.

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For Gambit.

Friend. Soldier. Teacher.

Chapter 1

General introduction

"The long, slender, well-proportioned and speedy steenbras appeals strongly to the tidal-river angler and fills the rock angler's imagination with envy of the unrivalled sport his comrade can enjoy. It is a firm-fleshed food fish as well as a splendid fighter, and with these attributes it is much sought for in localities where it abounds"

Biden (1948; 246)

1.1 The linefishery in South Africa

Increases in human population size, dependency on marine resources and technological advancements in fishing gear have resulted in steady increases in global fishing pressure over the last century. Consequently, more than half of the world's fish stocks are fully exploited and almost a third overexploited or depleted (FAO 2010). In South Africa, archaeological records provide evidence of a long history of the harvesting of marine fish by "line" and "spear". The first documenting of catch records started in the 17th century with the arrival of the Dutch seafarers at the Cape, and by the middle of the 20th century recreational and commercial fisheries had become increasingly important. The linefishery, defined by "the capture of fish with a hook and line" (Götz *et al*. 2008), and those species regarded as linefish (captured from shore or by boat, using rod or handline) are of considerable social, economic and recreational value. Despite the lack of more recent information, McGrath *et al*. (1997) indicated that by 1996 the South African linefishery provided employment for at least 131 500 people, had over 412 000 recreational and 3 100 commercial participants, and had an estimated annual value of ZAR 2 167 million.

The advent of trailable ski-boats in the 1940s and the construction of numerous small-boat harbours along the coast witnessed a rapid expansion in recreational and commercial fisheries (Penney 1991). This was followed by the development of the off-road vehicle in the 1960s, which facilitated beach driving and increased participation in coastal areas previously accessible only on foot. The consequent increase in fishing effort resulted in stock declines of numerous species, which called for stricter regulations, such as access, effort and catch restrictions (Hutton and Pitcher 1998). However, inefficient regulations coupled with increased fishing pressure resulted in overexploitation and the collapse of most linefish stocks. Consequently, in 2000, the South African linefishery was declared to be in a state of emergency (Government Gazette No. 21949, December 2000).

1.2 White steenbras *Lithognathus lithognathus*

The "steenbras" to which Biden (1948) referred was initially described as *Pagellus lithognathus* (Sparidae, Cuvier 1830), which was later split into two species, namely the white steenbras *Lithognathus lithognathus* and the west coast steenbras *Lithognathus aureti* (Smith and Smith 1986). The white steenbras *L. lithognathus* forms the subject of the current study, and is one of South Africa's most sought after and threatened coastal fishery species. The species is endemic to South African waters, with a narrow inshore distribution ranging from the Orange River (at the Namibian border) in the west to KwaZulu-Natal in the east (Smith and Smith 1986) (Figure 1.1).

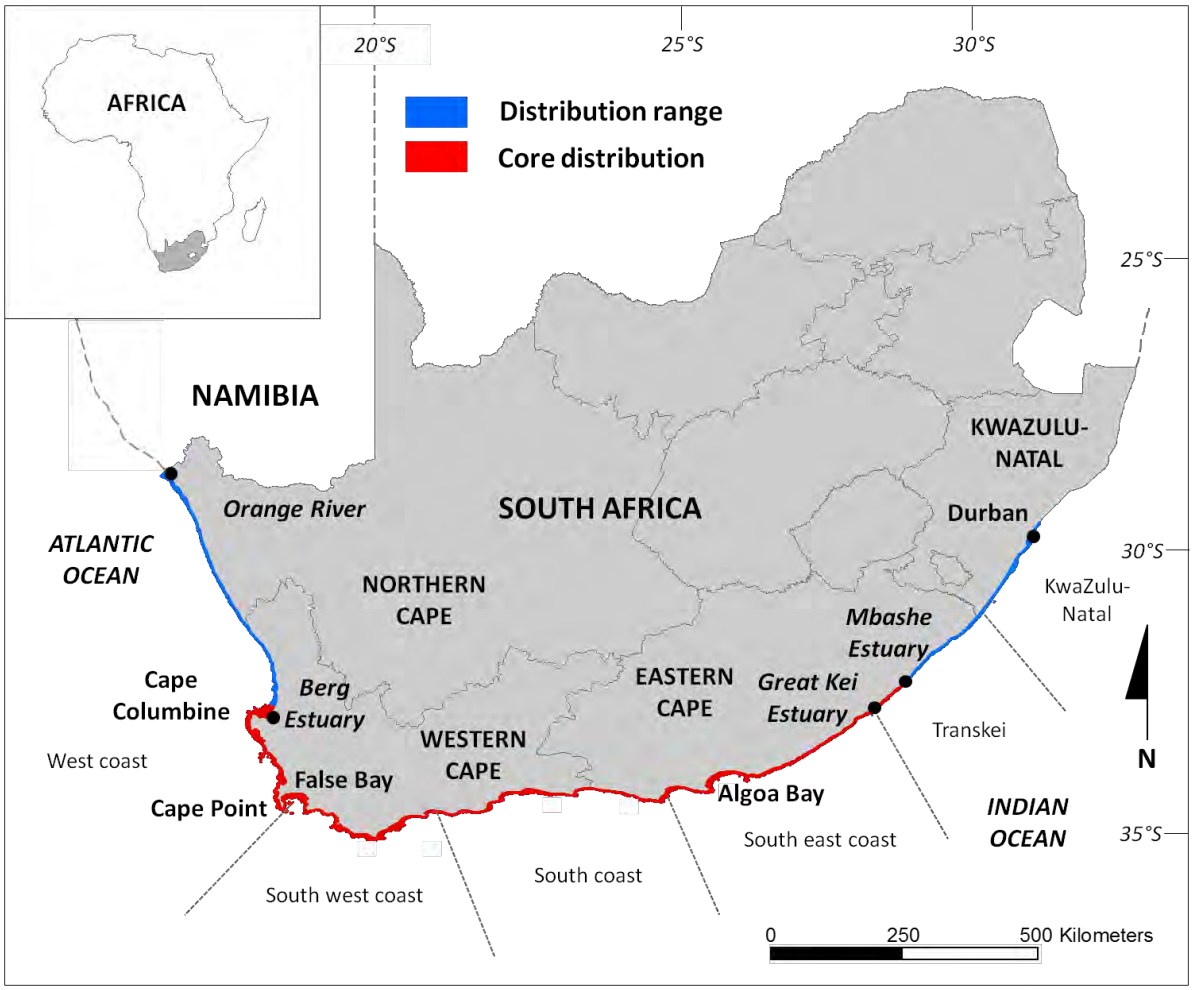

Figure 1.1: White steenbras distribution map, showing the narrow inshore distributional range (blue) from the Orange River in the west to KwaZulu-Natal in the east and the core distribution (red) from north of Cape Columbine in the west to the Mbashe Estuary in the east. Different coastal regions mentioned in the text are also presented

Bennett[1] (1993a) suggested that the white steenbras stock is distributed between the Orange River and the Mbashe Estuary (Eastern Cape Province), which represents approximately 2 200 km of coastline, and Lamberth and Mann (2000) suggested that the core distribution of the stock is from just north of Cape Columbine in the west, to the Mbashe Estuary in the east. Juvenile white steenbras have an obligatory estuarine-dependent nursery phase (Wallace *et al*. 1984a), although they are believed to use estuaries only between the Berg Estuary in the west and the Great Kei Estuary in the east (Bennett 1993b), and are rarely found in Transkei and KwaZulu-Natal estuaries (Begg 1984, Harrison and Whitfield 1995) (Figure 1.1).

1.2.1 White steenbras life-history based on available literature

1. White steenbras is a slow-growing and long-lived rudimentary hermaphrodite, reaching 50% sexual maturity at approximately 650 mm total length (TL) in both sexes, equating to roughly 600 mm fork length (FL) and an age of about 6 years (Bennett 1993b). This species attains an approximate maximum size and weight of 1.5 m and 30 kg, respectively, and lives for 25-30 years (van der Elst 1993, Bennett 1993b).
2. Early juvenile white steenbras recruit into estuaries between about 18 and 50 mm TL. The size at recruitment tends to increase and the timing of recruitment occurs later in the year in estuaries further west along the coastline (Beckley 1984, Bennett 1989, Whitfield and Kok 1992). Juveniles are dependent on estuaries for the first year after recruitment, until a size of about 150 mm TL, i.e. ± 130 mm FL (Beckley 1984, Bennett 1993b).
3. Fish larger than 130 mm FL are thought to leave estuarine nursery areas and move to subtidal marine habitats, where they inhabit shallow nearshore sandy and mixed sand and rock areas (Bennett 1993a). White steenbras larger than this size were common in commercial beach-seine catches in False Bay (Bennett 1993b) and fish between 160 and 240 mm FL were recorded in relatively high numbers in the surf zone of Algoa Bay, on the south east coast (Lasiak 1982).
4. Late juveniles (< 500 mm FL) show high levels of residency within the surf zone (Bennett 1993b, Attwood and Bennett 1995a, Cowley 1999), and exhibit a shallow inshore distribution (< 10m), with no fish under this size captured deeper than 10 m in the beach or purse seine fisheries in False Bay (Bennett 1993b), or in 10 to 50 m depths during a comprehensive inshore small-mesh trawl survey along the south and south east coasts (Wallace *et al*. 1984b).
5. Larger fish (500 – 600 mm FL) move to deeper areas (Bennett 1993b) and begin to undertake larger-scale coastal movements, although some individuals remain resident (Attwood and Bennett 1995a).

[1] The cited work was published by BA Bennett, who has no relation with this PhD candidate

6. There is circumstantial evidence of an annual adult (> 600 mm FL) spawning migration from the Western Cape Province to the Transkei in autumn (Bennett 1993a, b, Lamberth *et al*. 1994). Seine net catches from False Bay showed strong seasonal variation in the abundance of mature white steenbras; high from late spring to early autumn (October to April), peaking in summer (Bennett 1993a), with an almost complete absence during winter and early spring (June to September) (Lamberth *et al*. 1995). During the summer months, the gonads of mature individuals captured in False Bay are not well-developed (Penney 1991). Bennett (1993b) recorded gonads of white steenbras along the south west and south coasts in the early recovery stage from September to March, with active/ripe and ripe stages being the most common from April to July, while fish captured in the Transkei in August were all ripe-and-running, partially spawned or spent. This suggests that white steenbras aggregate in False Bay during the summer and autumn months, possibly using the area for feeding (Penney 1991), and migrate to the southern Transkei coast in winter, where spawning is believed to take place over marine fluvial mudbanks deposited off the estuaries in that region (Bennett 1993b, Hutchings *et al*. 2002a).
7. Eggs and larvae undergo a pelagic larval stage of up to three months, during which time they are passively transported in a south westerly direction along the coast, allowing dispersal to estuaries further west (Hutchings *et al*. 2002a).
8. Sub-adult and adult white steenbras appear to make use of permanently open estuaries (Marais 1983, Bennett *et al*. 1985, Bennett 1993b), although these visits are generally infrequent and the level of dependence on estuaries at these life stages remains unclear.

1.2.2 The fishery for white steenbras

White steenbras has been highly prized by shore-fishers since before the formal keeping of catch records, and is still heavily targeted in recreational shore- and spear-fisheries throughout its range (Brouwer *et al*. 1997). The species is also commonly caught in the recreational and subsistence fisheries in numerous south east, south and south west coast estuaries (Pradervand and Baird 2002; King 2005). Historically, white steenbras also formed an important component of the commercial beach-seine and purse seine fisheries in the Western Cape Province (Lamberth *et al*. 1994). Beach-seine nets are deployed from small rowing boats paddled from the shore, and hauled ashore by hand, while purse seine nets are deployed from larger, motorised vessels, which operate away from the shoreline. Until the mid 1990s, the commercial beach-seine fishery accounted for approximately 20 mt annually (reaching 100 mt in some years) and the recreational shore-fishery some 35 000 fish (accurate estimate of mass not available), while for a short period prior to 1982 the commercial purse seine fishery in False Bay caught up to 300 mt in some years (Bennett 1993a).

Overexploitation in the recreational and commercial sectors resulted in a steady population decline and reductions in catch-per-unit-effort (CPUE) over the past five decades (Bennett 1993a, b, Lamberth *et al*. 1994, Brouwer *et al*. 1997, Lamberth and Mann 2000, Pradervand and Baird 2002). Management interventions, including maximum daily bag and minimum size limits for recreational anglers and increasingly stringent catch and gear restrictions for commercial fishers (Penney 1991, Bennett 1993a) have failed to prevent overexploitation. Despite such interventions, the spawner biomass per recruit (SB/R) ratio of white steenbras was estimated at 6% of pristine (Bennett 1993a), with the stock considered collapsed (Griffiths *et al*. 1999). A commercial ban was imposed on white steenbras in 1995 although the commercial beach-seine fishery in False Bay was allowed an overall annual catch exemption of 20 mt. Abuse of this exemption resulted in its withdrawal and a complete ban from 2001 (SJ Lamberth, Department of Agriculture, Forestry and Fisheries, pers. comm.). Meanwhile, participation in the recreational sector remains uncapped.

A major contributing factor to the failure of historical management measures for white steenbras, and other linefish species, is a lack of empirical knowledge on their movement patterns, habitat use and genetic stock structure, which are essential for effective management of a fishery species. Aspects of the biology (Mehl 1973, Bennett 1993b), feeding (Wooldridge and Bailey 1982, Harris and Cook 1995), reproduction (Bennett 1993b), growth (Mehl 1973, Bennett 1993b), recruitment (Whitfield and Kok 1992, James *et al*. 2007a) and physiology (Mehl 1973, Whitfield *et al*. 1981, Du Preez *et al*. 1986, Harris and Probyn 1996) of white steenbras have been well-documented. However, despite being identified as a top priority in South Africa (van der Elst and Adkin 1991), research focussing on the movement and residency of this species was restricted to a preliminary assessment of coastal movement using conventional dart tagging (Cowley 1999), and no study has focussed on the movement patterns of white steenbras in estuarine environments.

1.3 Advancements in fisheries research and management in South Africa

As a result of increased fishing effort and the consequent declines in the stocks of white steenbras and numerous other South African linefish species in the latter part of the 20th century, it became obvious that improvements were required in fisheries management. Slowly fisheries research began to focus on those aspects of the biology and ecology of different species that were deemed (at that time) important for management. An extensive linefish research programme was launched, spanning roughly two decades (1970 to 1990), that included biological studies on many important linefish species. These studies focussed largely on age-based stock assessments to provide biological reference points for management, as well as reproductive and feeding ecology (Palmer *et al*. 2008).

In addition, a Linefish Management Protocol (LMP) was implemented in the South African linefishery in 1999 to provide a standardised method for assessing the status of linefish stocks, predominantly through the use of per-recruit analyses and age-structured production modelling. The LMP required that an operational management plan (OMP) be developed for each species, in which the species-specific type of data, type of stock assessment analysis, biological reference points and relevant management actions would all be specified *a priori* (Griffiths *et al*. 1999).

The second edition of the *Southern African Marine Linefish Status Reports* was published in 2000 (Mann 2000), and detailed the available ecological and fishery information obtained by the end of the last century for most of the important species, as well as stock assessment results for those species for which stock assessments had been conducted. While this period of research represents "one giant leap for man[agement]", what became apparent from this summary was that there were a number of gaps in the knowledge of the life-histories of many species. Common to most species was a lack of empirical data on their movement patterns. While biological and ecological studies on white steenbras had provided some evidence on which to base a proposed theory of migration, which Bennett (1993b) suggested was largely circumstantial, there is a lack of information on habitat use, residency, habitat connectivity, estuarine dependence and longshore dispersal. Secondly, there is a lack of understanding of spatial stock delineation, with no information on genetic stock structure. The paucity of this kind of information is common to most local fishery species, and information regarding stock structure has typically been based on morphological or other, similar, comparisons, for example the study on silver kob *Argyrosomus inodorus* by Griffiths (1997b).

It followed then, that the next phase of fisheries research in South Africa placed emphasis on movement studies, mainly through conventional dart tagging. A national marine linefish tagging project was initiated in 1984 and run by the Oceanographic Research Institute (ORI), which recruited the services of volunteer recreational anglers around the South African coastline to tag a range of species. There was also the establishment of the De Hoop and Tsitsikamma Marine Protected Area (MPA) inshore fish tagging programmes, and later the Greater Addo Elephant National Park proposed MPA coastal fish tagging programme, which were initiated, respectively, by BA Bennett (formerly University of Cape Town) in 1984, by the Rhodes University Department of Ichthyology and Fisheries Science in 1995, and by Dr PD Cowley (South African Institute for Aquatic Biodiversity) in 2005. Through these programmes, detailed studies on the coastal movements of a range of linefish species have been conducted, for example carpenter *Argyrozona argyrozona* (Brouwer *et al*. 2003) and galjoen *Dichistius capensis* (Attwood and Cowley 2005).

Later, technological advancements made available new tools to study fish movement patterns, including acoustic telemetry. This technique was quick to attract research interest, initiating a new phase of fisheries research in the country. Acoustic telemetry was successfully used in South Africa to determine movement patterns of spotted grunter *Pomadasys commersonnii* in the Great Fish (Næsje *et al*. 2007, Childs *et al.* 2008b) and East Kleinemonde (Kerwath *et al.* 2005) estuaries, dusky kob *Argyrosomus japonicus* in the Great Fish Estuary (Cowley *et al.* 2008) and white stumpnose *Rhabdosargus globiceps* (Attwood *et al.* 2007, Kerwath *et al.* 2008) and elf *Pomatomus saltatrix* in the Langebaan Lagoon (Hedger *et al.* 2010).

More recently, the genetic stock structure of fishery species in South Africa has also received considerable attention, and a number of important fishery species have been assessed, for example the shallow-water and deep-water hakes, *Merluccius capensis* and *M. paradoxus* (von der Heyden *et al*. 2007) and red roman *Chrysoblephus laticeps* (Teske *et al*. 2010).

1.3.1 Why study movement?

Overexploitation of fish stocks, particularly those of coastal and estuarine-dependent species, necessitates conservation actions, which require an understanding of the movement behaviour and area use patterns of the target species. However, at present, information on recruitment, movement patterns, residency and estuarine dependence for many species is lacking (Bellquist *et al*. 2008). This is particularly true in South Africa, as little is known about the movements and behavioural ecology of numerous important estuarine-dependent fishery species, including white steenbras (van der Elst and Adkin 1991).

Movement behaviour is dependent on how resources are utilised, and how the animal is affected by the environment and by inter- and intra-specific interactions (Anderson *et al*. 2008, Pépin *et al*. 2008). Movements of individuals can also affect community structure and population dynamics (Jones 2005) and facilitate genetic mixing (Turchin 1988). Therefore, understanding movement and area use patterns can improve our understanding of the species ecology (Meyer *et al*. 2000), as well as provide important information on the mechanisms responsible for observed coastal population structure and genetic stock structure (Able and Grothues 2007a).

Studies assessing home range and area use allow assessment of the value of different environments and habitat types to the population or species (Jones 2005), and provide insight into the ways in which the different resources are utilised (Hartill *et al*. 2003). In so doing, understanding area use

and home range dynamics can help to identify areas of high importance or habitats critical to particular life stages (Abecasis *et al*. 2009), which may contribute disproportionately to adult recruitment (Beck *et al*. 2001), such as the value of the estuarine environment as a nursery for estuarine-dependent species (Able and Grothues 2007a). This can also help to identify the characteristics that make the habitat or environment suitable (Vasconcelos *et al*. 2010), making it possible to quantify the contribution of such environments to the overall fitness of the population or species, as well as predict the potential effects of degradation to such habitats.

By analysing the relationships between environmental processes and both movement patterns and habitat utilisation, it is possible to understand the physical and biological factors that drive movement and determine habitat utilisation (Nathan *et al*. 2008, Sackett *et al*. 2008, Sakabe and Lyle 2010). It then becomes possible to predict the population's responses to changes in these factors (Ault *et al*. 2003, Meynecke *et al*. 2008), and the potential effects that environmental perturbations and changes in resource structure and ecosystem function may have on the population's movement, fitness and (ultimately) survival (Garshelis 2000 in Simcharoen *et al*. 2008, Hindell *et al*. 2008).

Understanding movement patterns and estuarine residency, and the effects of environmental factors and environmental changes on aspects such as area use patterns and habitat utilisation, is essential for developing appropriate management strategies, both for the species and its habitat (Hooge *et al*. 1999, Parsons *et al*. 2003, Taylor *et al*. 2006). The potential effectiveness of protected areas is often unknown, due to a lack of knowledge on species home range sizes and locations, movement patterns and habitat utilisation (Lembo *et al*. 2002, Attwood and Cowley 2005). Knowledge on the movement patterns of a population of individuals relative to protected area or reserve boundaries is, therefore, essential, to understand the potential effectiveness of such management measures (Attwood *et al*. 2007), and to assist with their design (Jones 2005). It is also important to determine movement patterns and spatial requirements at critical life stages, such as the juvenile nursery phase, to understand the importance of different areas, and the potential effectiveness of protective measures in these areas (Egli and Babcock 2004, Jones 2005). Successful fisheries management, therefore, requires empirical knowledge on fish movements and migrations (Kerwath *et al*. 2005), particularly of coastal migrant and estuarine-dependent species that are of social, ecological or economic value, or conservation concern (Able and Grothues 2007a).

It is believed that white steenbras is dependent on estuaries for at least the first year of its life (Wallace *et al*. 1984a, Bennett 1993b), but there has been little work in this regard and there is little

understanding of how they use estuaries, their home range dynamics within estuaries, and whether they move between estuaries and the marine environment, or between neighbouring estuaries. Such dependence on estuaries makes them vulnerable to overexploitation and habitat degradation; therefore, an understanding of spatial and temporal area use within estuaries, foraging areas and times and the factors affecting their distribution and area use within estuaries is essential for making management decisions to protect both the species and its environment. Understanding movement patterns in the marine coastal zone is equally important, as this will determine the potential effectiveness of marine reserves.

Information on movement needs to be qualified by being placed in a broader ecological context, which requires integration with abiotic and biotic environmental data, to understand the environmental factors influencing or driving movement, at the different spatial and temporal scales. This can be augmented with physiological and behavioural-state data (e.g. feeding, spawning migrations etc.), relative to the spatial scales under study, to provide a comprehensive understanding of the movement ecology of the species (Nathan *et al*. 2008). The terminology of different movement styles, station-keeping, foraging, ranging and migration, follows definitions proposed by Dingle (1996).

1.3.2 Why study genetic stock structure?

Conservation biology strives to ensure population viability and, in the face of overexploitation, this has become a priority also for fisheries management (Hallerman *et al*. 2003). Overexploitation is likely to affect geographically isolated populations in an inconsistent manner, and on different scales (Hauser and Ward 1998). Therefore, effective management of a fishery species such as white steenbras and maintenance of its genetic integrity require a comprehensive understanding of the genetic stock structure and stock delineation, to ensure the successful identification of discrete stocks within the population (Ward 2000), so that each distinct stock or population can be suitably managed (Teske *et al*. 2010). Ultimately, the evolutionary potential of a species is determined by its genetic variability (Lippe *et al*. 2006); therefore, the ability to detect reductions in genetic variability as a result of overexploitation is essential.

Genetic analysis of stock structure can provide useful information on reproductive isolation and the level of population mixing (Shaklee and Bentzen 1998). Understanding stock structure can provide insight into the mechanisms driving divergence among populations and the roles of migration (gene flow) and random genetic drift in this process (Arnaud *et al*. 2001, Wakeley 2005). Such information

can assist with the design of optimal management measures, for the conservation and protection of the species (Gold and Turner 2002). In South Africa, phylogeographic research has been used to evaluate the potential effectiveness of the current marine protected area (MPA) network; however, much additional work is still needed in this regard (von der Heyden 2009, Teske *et al*. 2011).

Population genetics studies can provide insight into reproductive patterns, historical population demography, dispersal patterns and connectivity of populations (Arnaud *et al*. 2001, Feral 2002, Gold and Turner 2002, Wakeley 2005). Such information is essential in order to understand and predict how habitat fragmentation and climate change might affect dispersal and gene flow (Nicastro *et al*. 2008). To this end, genetic studies can complement movement studies well, such as those based on conventional tagging or acoustic telemetry (Waples 1998).

Furthermore, movement patterns of a species, through larval dispersal, post-settlement movements and spawning migrations, can play a major role in defining the levels of stock mixing or isolation, which in turn define the genetic stock structure. Therefore, movement patterns and genetic stock structure should be assessed simultaneously, rather than in isolation. Understanding in one component could shed light on the other, thus together providing a more comprehensive interpretation of results (Waldman 1999).

In order to completely understand movement of a species, the lifetime track needs to be broken down into a series of functional units, representing different life-history stages. Each of these stages can then be assessed at a suitable spatial and temporal resolution (Nathan *et al*. 2008). Thus, the lifetime track can ultimately be described and analysed as a multi-tiered process, from small-scale movements at the early juvenile phase, to greater, exploratory movements as a late juvenile/sub-adult, and finally to large-scale adult spawning migrations (in species where this is the pattern). In a similar manner, the life-history of the species can be assessed in a three-tiered approach, looking first at the movement of individual fish, termed the 'Lagrangian' approach (Turchin 1998) within individual ecosystems, such as estuaries, then at dispersal patterns at the population level, termed the 'Eulerian' approach (Turchin 1998), such as small-scale coastal movements, and then finally at the species level by assessing the level of mixing among populations and geographical regions, which can be successfully achieved through analyses at the molecular level. This thesis adopted such an approach to assessing the movement patterns and genetic stock structure of the white steenbras (Figure 1.2).

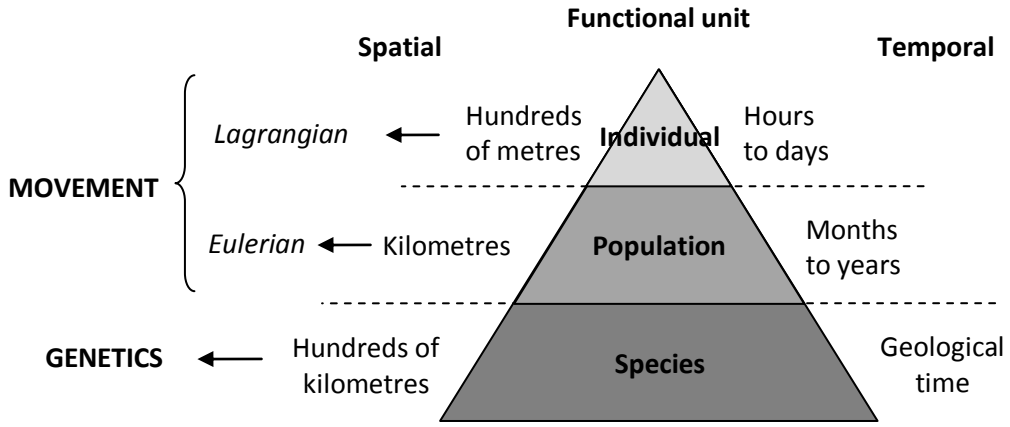

Figure 1.2: Schematic representation of analysis of the lifetime track, with appropriate scales at which analyses of the different functional units are addressed in this study

1.4 Coastal oceanography off South Africa

In order to fully understand the distribution, movement and stock structure of a species, it is important to understand the oceanographic processes operating in the region. Oceanographic features, such as current pathways, upwelling intensities and water temperatures, can play a major role in the distribution of both propagules (eggs, larvae, juveniles and adults) and genetic diversity (Grant and Bowen 1998). On the east and southeast coasts of South Africa, the primary oceanographic feature is the Agulhas Current, a typical well-defined south westerly flowing western boundary current. In this region, the Agulhas Current flows close inshore, with the inshore edge roughly following the 200-m isobath at the continental shelf break (Lutjeharms 1998) (Figure 1.3). Eggs and larvae of numerous marine organisms use this south westerly movement to assist dispersal, although it is suggested that most fish eggs and larvae remain inshore of the current core (Griffiths and Wilke 2002). Along the south east coast, the continental shelf diverges from the coastline, forcing the Agulhas Current further offshore. In the region of divergence, the oceanography can be quite complex, exhibiting cold-water eddies, intrusion onto the shelf (which may transport eggs and larvae onto the shelf at this point) or offshore meanders (which may transport eggs and larvae great distances offshore) (Hutchings *et al*. 2002a). West of this, the Agulhas Current continues to follow the continental shelf break, which begins to deepen, until it reaches the tip of the Agulhas Bank, at which point the current retroflects and moves offshore, where once again propagules may be transported further offshore (Hutchings *et al*. 2002a). Although the Agulhas Current has a strong influence on the continental shelf (Goschen and Schumann 1988), wind becomes the most dominant driving force in this area (McQuaid and Phillips 2000) and, as a result, water movement is bi-directional and strongly influenced by prevailing wind

direction (Attwood *et al*. 2002). While bottom waters on the Agulhas Bank tend to move in a net westerly direction (Hutchings *et al*. 2002a), surface waters tend to move in a net easterly direction, which may facilitate propagule transport in both directions.

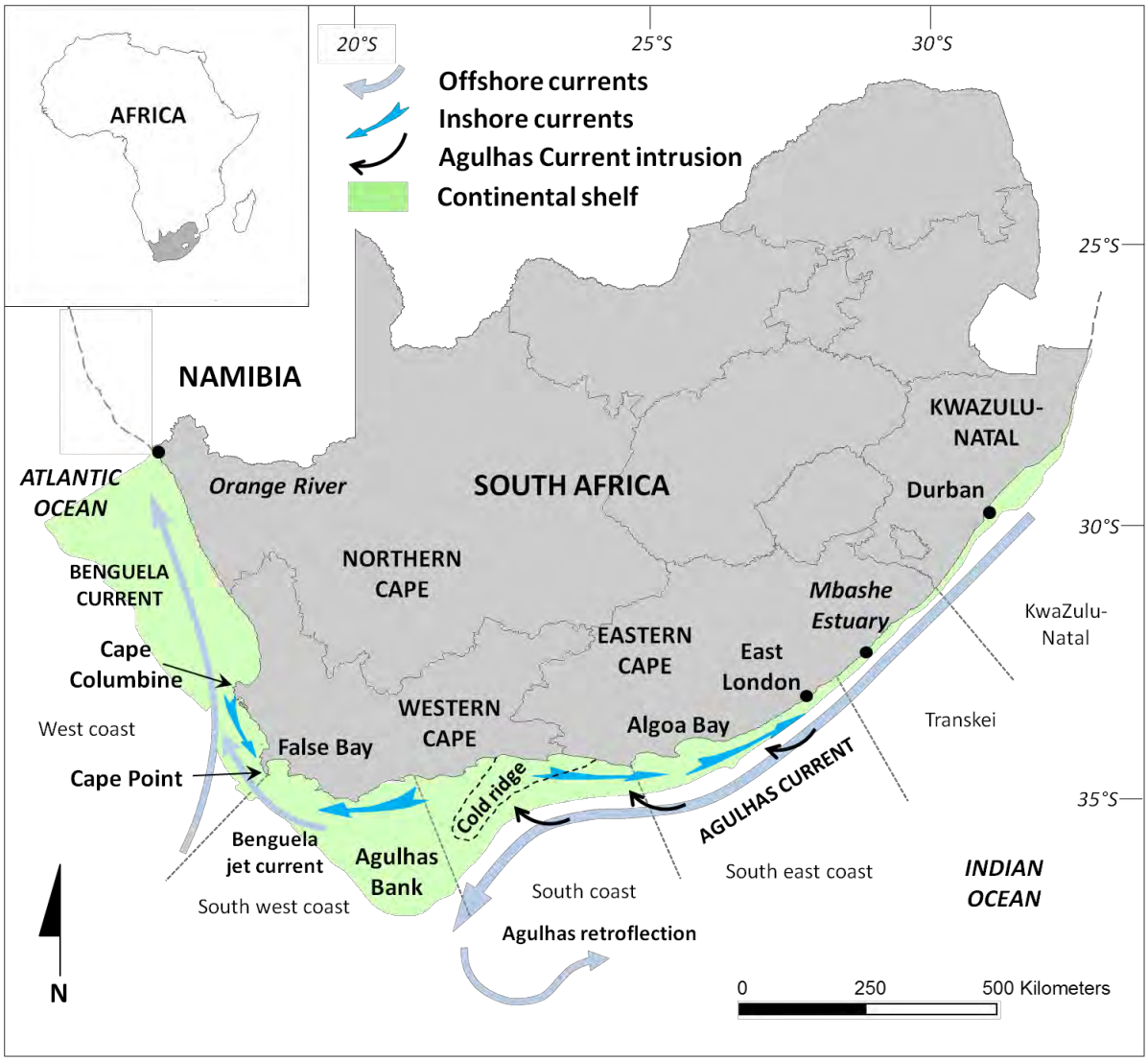

Figure 1.3: Schematic representation of the major oceanographic features along the east, south and west coasts of South Africa

Based on these features, it may be expected that eggs and larvae spawned along the South African east coast (KwaZulu-Natal or Transkei) would have high rates of dispersal south westwards along the coastline until the Agulhas Bank. However, these propagules may have considerably lower probability of being transported to inshore nursery areas and estuaries further west along the coastline. As such, lower genetic diversity may be expected in coastal localities further west.

The eastern part of the Agulhas Bank inshore is characterised by regular intrusions of a ridge of cold upwelled water, which moves close inshore during the summer months. Currents tend to circulate around this cold water ridge in a clockwise direction (Hutchings *et al*. 2002a), which may facilitate the transport of eggs and larvae in a westerly, then inshore direction, promoting retention on the Agulhas Bank and recruitment to nursery areas further west.

The direction of water flow on the shelf is also largely influenced by south westerly swell (Martin and Flemming 1986) and coastal trapped waves (Tilney *et al*. 1996). As a result, there is often an inshore counter current moving eastward along the south east coast (Schumann *et al*. 1982). Counter currents running in a north easterly direction, occurring inshore of the Agulhas Current core (Lutjeharms 2004), can facilitate egg and larval dispersal in a north easterly direction (Schumann 1987). However, once these currents reach the area between East London and the Mbashe Estuary, the narrowing of the continental shelf and the proximity of the Agulhas Current close inshore (within 1 km at times) may act as a mechanical barrier to the further flow of these counter currents. Therefore, it is unlikely that propagules will be transported further up the coast in a north easterly direction, and eggs and larvae spawned along the Transkei or south east coasts are unlikely to recruit to nursery areas further east.

On the west coast of South Africa, the dominant oceanographic feature is the northerly-flowing Benguela Current. Here, wind can have a profound effect on water movement, generally driving the surface waters offshore, creating an extensive region of upwelling (Shillington 1986). At times, there can be a strong jet of water moving from the western Agulhas Bank to Cape Columbine, which can facilitate the transport of propagules westwards around Cape Point and up the west coast (Largier *et al*. 1992). There is also evidence of a counter-current flowing inshore along the west coast, which may facilitate the return movement of propagules (including sub-adults and adults of some species) from the west coast south eastwards and past Cape Point (Boyd *et al*. 1992). These oceanographic features along the east, south and west coasts of South Africa can have a major influence on the movement patterns, dispersal potential and genetic diversity of marine species.

1.5 Motivation and approach for the current study

White steenbras was identified as a top priority species for research, conservation and management in South Africa (Lamberth and Mann 2000). Stock assessments and the investigation of nursery areas, residency, movement patterns and stock distribution were identified as research priorities to ensure the development of an effective management plan for this species (van der Elst and Adkin

1991, Lamberth and Joubert 1999). White steenbras is an important recreational and subsistence species, and was (until 2001) an important commercial species. However, there are broad gaps in the information regarding movement, habitat use, estuarine dependency and genetic stock structure of the species.

1.5.1 Aim and objectives

The overall aim of this study was to determine and describe the area use, estuarine dependency, coastal movement behaviour, genetic diversity and stock status of the white steenbras, in South Africa. Specific objectives were to:

- *Determine habitat utilization, home range dynamics and movement patterns of juvenile white steenbras within temporarily open/closed and permanently open estuaries, and between the estuaries and the marine environment, using acoustic telemetry;*
- *Determine coastal residency, longshore movement patterns and dispersal of sub-adult and adult white steenbras in the marine environment, using conventional dart tagging and acoustic telemetry;*
- *Assess the spatial (population) genetic diversity of white steenbras across its distributional range, to provide information on genetic stock structure, using mitochondrial DNA and nuclear microsatellite DNA analyses;*
- *Assess the current status of the white steenbras stock from all available fishery and fishery-independent catch data to illustrate trends in catch, effort and catch-per-unit-effort (CPUE) over the past c50 years;*
- *Assess the current status of white steenbras protection and conservation.*

1.5.2 Thesis structure

Setting the scene

Chapter 1 – General introduction: This chapter provides background information on white steenbras, and fisheries management and research in South Africa, as well as the motivation for the study.

Chapter 2 – Research approach: This chapter assessed and explained the methods chosen to answer the key questions necessary to fill the gaps in the current knowledge of white steenbras life-history. The advantages and disadvantages of each of the chosen techniques were discussed, as well as their application to the current objectives.

The research chapters of this thesis are grouped into three research themes, focussing on *Movement*, *Genetic stock structure* and *Conservation*. The themes and the associated chapters are outlined in Figure 1.4, and will be described in the following chapter.

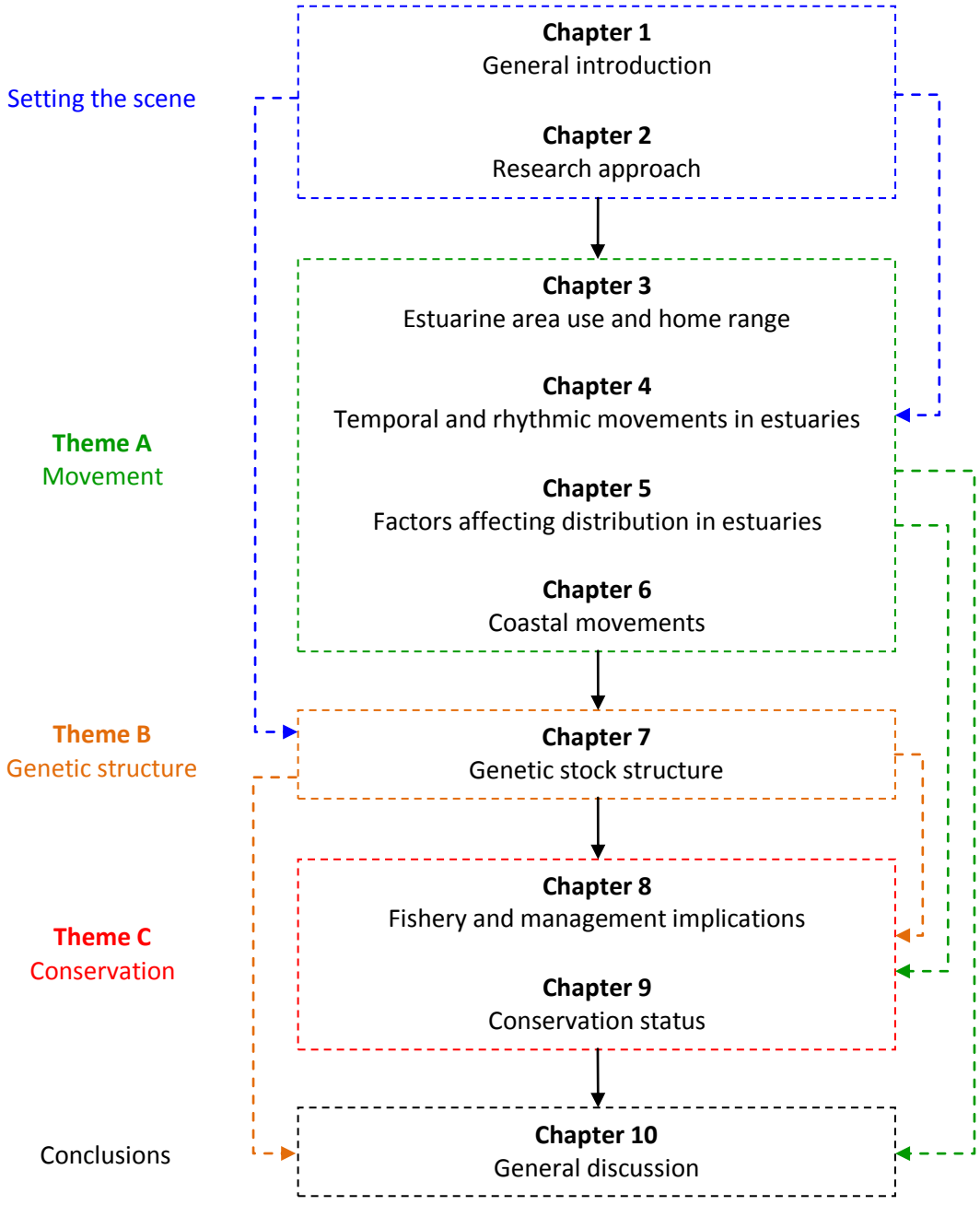

Figure 1.4: Flow diagram of thesis structure, defining the research themes and the thesis chapters

Theme A – MOVEMENT

Chapter 3 – Estuarine area use and home range: Movement patterns, area use patterns, home range dynamics and estuarine dependency were assessed and described, and critical habitats identified for juvenile white steenbras in a range of estuaries, through the use of acoustic telemetry.

Chapter 4 – Temporal and rhythmic movements in estuaries: This chapter identified the environmental rhythms underlying observed cyclical movement patterns of white steenbras in different estuaries, and explored the main environmental rhythms in detail.

Chapter 5 – Factors affecting distribution within estuaries: This chapter assessed the environmental variables that influence the movement of juvenile white steenbras in estuaries, as described in the previous two chapters.

Chapter 6 – Coastal movements: Surf zone residency and longshore movement patterns of late juvenile, sub-adult and adult white steenbras in the marine environment were described, using conventional dart tagging at a range of spatial scales, and acoustic telemetry conducted in the marine environment.

Theme B – GENETIC STRUCTURE

Chapter 7 – Genetic stock structure: This chapter assessed the genetic stock structure of white steenbras throughout its distribution, to support the findings of the movement studies, and provided information on the level of mixing between areas and movements at the coastal level, using mitochondrial and microsatellite genetic analyses.

Theme C – CONSERVATION

Chapter 8 – Fishery and management implications: This chapter assessed trends in catch, effort, targeting and CPUE of white steenbras, over the past *c*50 years, in relation to management interventions for the species.

Chapter 9 – Conservation status: The current status of white steenbras protection within estuarine and marine protected areas, and the availability of suitable habitat in estuaries and the inshore marine environment were assessed, as well as the status of white steenbras conservation, relative to national and international criteria.

Conclusions

Chapter 10 – General discussion: The thesis concludes with the key findings from the different chapters to describe movement patterns at different life stages, genetic stock structure and the conservation status of the white steenbras. By incorporating multiple techniques to answer the key ecological, conservation and management questions and thereby fill the gaps in the current knowledge of white steenbras, it is hoped that this project will provide an improved scientific basis for the management of this species.

Chapter 2

Research approach

2.1 Introduction

There are numerous methods and tools available to study the ecology of a species. Many of these are specific to terrestrial or aquatic environments, and generally each method is suitable for answering questions specific to certain aspects of a species' ecology or life-history. As this study focuses on providing information on the movement patterns, area utilisation, estuarine dependency, coastal dispersal patterns, genetic stock structure and stock status of a coastal fishery species, a suite of suitable methods was required.

The study adopted a multi-faceted approach, incorporating conventional dart tagging and acoustic telemetry to assess movement patterns, area utilisation and residency in estuaries and the marine environment, and genetic analyses to provide information on genetic stock structure, to fill the gaps in the knowledge of white steenbras life-history. The study also incorporated available fishery-dependent and fishery-independent catch data to determine the current stock, protection and conservation status and management needs for this overexploited fishery species.

The methods adopted in this study have been successfully applied to numerous coastal fishery species in South Africa, but mostly in isolation; for example, conventional dart tagging and recapture on *Dichistius capensis* (Attwood and Cowley 2005), acoustic telemetry on *Pomadasys commersonnii* (Childs *et al*. 2008b), mitochondrial and microsatellite DNA analyses on red roman *Chrysoblephus laticeps* (Teske *et al*. 2010), and an assimilation of catch data to identify trends in the catches of the soupfin shark *Galeorhinus galeus* (M^{c}Cord 2005). However, the employment of multiple complementary techniques in conjunction has been advocated by numerous fisheries researchers and ecologists (e.g. Lembo *et al*. 2002, Lyons and Lucas 2002, Jadot *et al*. 2006, Meynecke *et al*. 2008, Johnson *et al*. 2009, Simpfendorfer *et al*. 2010), to provide a more holistic view. Furthermore, geneticists advocate the incorporation of ecological information into population genetics studies to assist with the interpretation of molecular analysis results (Ovenden 1990, Waples 1998).

There are numerous examples in the literature of studies that have employed multiple techniques, commonly similar in principle, to answer ecological and conservation questions. Conventional external dart tagging has been used in conjunction with acoustic telemetry in a number of studies;

for example, external dart tagging and passive acoustic telemetry were used to determine home range and residency of *Diplodus sargus* and *Diplodus vulgaris* in the Ria Formosa Lagoon, Portugal (Abecasis *et al*. 2009). External dart tagging and manual acoustic tracking were used to assess habitat utilisation of the white goatfish *Mulloides flavolineatus* in Kaneohe Bay, Oahu, Hawaii (Holland *et al*. 1993). External dart tagging, passive acoustic telemetry and manual acoustic telemetry were used to determine movements and habitat use of white trevally *Pseudocaranx dentex* in the Faial Channel, Azores Islands, to assist with the design of marine reserves (Afonso *et al*. 2009). External dart tagging, internal PIT tagging and passive acoustic telemetry were employed to assess the fidelity of common snook *Centropomus undecimalis* to coastal spawning grounds in Charlotte Harbour, Florida, and the Gulf of Mexico (Adams *et al*. 2009). The use of complementary techniques has returned more robust results and increased the value of each of these studies.

Some studies, although considerably fewer, have employed techniques from across a range of research disciplines, for a more comprehensive understanding of a species' ecology. For example, manual acoustic telemetry was used in conjunction with mobile echosounding surveys to determine distribution and movements of common bream *Abramis brama* in the River Trent, England (Lyons and Lucas 2002). Manual acoustic telemetry and animal-borne videography were used to assess habitat usage of tiger sharks *Galeocerdo cuvier* in Shark Bay, Western Australia (Heithaus *et al*. 2002). Passive acoustic telemetry, manual acoustic telemetry and direct observation on SCUBA were used to determine activity patterns, home range sizes and habitat utilisation of salema *Sarpa salpa* in Calvi and Achiarina Bays, Corsica, Mediterranean Sea (Jadot *et al*. 2006). Internal PIT tagging, digital underwater videography and recreational angling catch data were integrated to determine movements of *Acanthopagrus australis*, *Lutjanus russelli*, *Pomadasys kaaken* and *Mugil cephalus* within an intertidal mangrove creek in Burrum River Estuary, Queensland, Australia (Meynecke *et al*. 2008). Manual acoustic telemetry and commercial fishery data were combined to determine nursery habitats of juvenile thresher sharks *Alopias vulpinus* in the Southern California Bight (Cartamil *et al*. 2010). Passive acoustic telemetry, satellite telemetry and stable isotope analysis were combined to assess movements, macro-scale habitat use and trophic ecology of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra Atoll, in the Central Pacific (Papastamatiou *et al*. 2010).

Depending on the species, geographic location and the selected methods, such multi-disciplinary studies are likely to incur considerable costs. However, the combined power of integrating results from numerous disciplines can contribute substantially to improved management (Waldman 1999), and considerably increase the value of the research, which has led to a move towards such studies.

2.2 Research methods

This thesis adopted a multidisciplinary approach by employing four broad complementary research techniques to address specific objectives:

i. Conventional dart tagging for the assessment of longshore coastal movements;
ii. Acoustic telemetry for the assessment of estuarine and marine residency and area use patterns;
iii. Genetic analyses for the assessment of genetic stock structure; and
iv. Assimilation of current and historical fishery-dependent and fishery-independent catch data for the assessment of the stock and conservation status of white steenbras.

The aim of this chapter is to provide an overview of these methods and show how they have been applied in the current study, to address specific key questions.

2.2.1 Conventional dart tagging

Until the early 1960s, information on the movement of fishes was obtained largely through plastic external dart- and anchor-type tagging studies, involving hook-and-line fishing. Dart and anchor tags are small, economical and easy to apply (Zeller and Russ 2000), making this a simple, cost-effective method to quantify residency, dispersal rates and migrations (Cartamil *et al*. 2003, Kerwath *et al*. 2005). The low cost of these tags and the simple equipment required for their application allows high numbers of individuals to be tagged, and has resulted in their widespread use in many studies, covering a range of species. For example, in South Africa, conventional dart tagging has been successfully used to determine the dispersal and residency of red roman (Kerwath *et al*. 2007a), galjoen *Dichistius capensis* (Attwood 2003, Attwood and Cowley 2005), adult carpenter *Argyrozona argyrozona* (Brouwer *et al*. 2003) and dusky kob *Argyrosomus japonicus* (Griffiths and Attwood 2005), and to assess the suitability of a marine protected area for the protection of blacktail *Diplodus sargus*, zebra *Diplodus cervinus hottentotus*, bronze bream *Pachymetopon grande* and galjoen (Cowley *et al*. 2002). Conventional dart tagging was also used in a preliminary investigation into the coastal dispersal of white steenbras (Cowley 1999). Globally, dart tagging has been applied to the study of a range of fish species, e.g. *Sebastes chrysomelas* (Hallacher 1984), *S. caurinus*, *S. maliger* and *S. auriculatus* (Matthews 1990a), *Acanthopagrus berda* (Sheaves *et al*. 1999) and *Epinephelus striatus* (Bolden 2000). The method provides valuable data on species range and dispersal patterns and is still widely used.

The disadvantage of this technique is that the information obtained is restricted to the locations of the fish at the times of capture and recapture. Little information can be gained regarding the actual distance or path travelled between the two positions, or the speed at which the fish moved (Matthews 1990a, Zeller 1997). The result is that the information is limited to one release location, and usually only a single recapture location (Zeller 1999), meaning that high numbers of recaptures are required to detect persistent trends (Attwood and Cowley 2005). Furthermore, although multiple recaptures are sometimes made, most tagged fish are never recaptured, as recapture rates are generally as low as 5 to 10% for many species, e.g. 5% for adult carpenter (Brouwer *et al*. 2003), 4.3 – 12% for galjoen (Attwood and Cowley 2005) and 7.1% for dusky kob (Griffiths and Attwood 2005). This means that high numbers of fish must be tagged before a useful number of recaptures can be expected. To compound this problem, certain species are prone to high rates of tag loss (Zeller and Russ 2000). While detailed information, such as fine-scale movements, habitat utilisation or activity patterns can only be speculated from external dart tagging (Cartamil *et al*. 2003, Egli and Babcock 2004), the technique is simple and cheap to apply and can provide useful information on dispersal and residency.

Application of conventional dart tagging in this study

In this study, conventional dart tagging data for white steenbras were extracted from four ongoing long-term coastal fish tagging programmes. Two of these are based on research angling conducted within well-established no-take MPAs, and one in a proposed MPA currently open to shore and boat angling. Their locations along the south west coast, south coast and south east coast are evenly distributed within the core distribution of white steenbras. The fourth programme operates at the National level, spanning the entire South African coastline. Tagging and recapture data obtained from these studies were used to determine the level of coastal residency and the scale of longshore movements, and to test the effects of geographic location, seasonality, fish size (age) and time at liberty on observed residency and movement patterns. The key research questions were:

1. *What are the longshore dispersal patterns of late juvenile, sub-adult and adult white steenbras in the marine environment, and do mature adults exhibit an annual spawning migration?*
2. *What is the level of residency of sub-adult and adult white steenbras within a large coastal embayment, and do sub-adult and adult white steenbras make use of estuaries?*

2.2.2 Acoustic telemetry

Over the past five decades, biotelemetry has been successfully used on a range of animals to provide information on spatial utilisation and movement patterns. This information is necessary for management and conservation purposes, particularly in the design and implementation of reserve areas (Meyer *et al*. 2000, Parsons *et al*. 2003, Attwood and Cowley 2005, Taylor *et al*. 2006). Technological advancements in telemetry equipment over the years have allowed the remote and accurate positioning of individual animals in real-time. Transmitters have become smaller and lighter, with longer battery lives, allowing researchers to study smaller animals, such as rodents, birds and juvenile fish.

There are three broad platforms for telemetry; radio, acoustic and satellite. Radio telemetry is based on the transmission of radio waves emitted by a radio transmitter, attached to the study animal, and the reception of these radio waves by a receiver operated by the researcher. Radio telemetry is useful for tracking terrestrial or avian animals, as well as freshwater aquatic animals. However, radio telemetry cannot be used in marine or estuarine aquatic environments, due to the high attenuation of radio waves caused by the high conductivity associated with the dissolved salts (ions) in seawater (Shroyer and Logsdon 2009), and was consequently not suitable for the current study.

Acoustic telemetry differs from radio telemetry, in that signals are transmitted through sound (acoustic) waves. Such sound energy relies on the dense medium of the aquatic environment for its transmission, and, unlike radio waves, is not subject to rapid signal attenuation in saline aquatic environments. Therefore, acoustic telemetry provides a useful means for tracking animals in both freshwater and saline environments.

Satellite telemetry provides a simple and useful, albeit more expensive, tool for tracking terrestrial animals and large marine vertebrates, such as cetaceans, and pelagic sharks (Zerbini *et al*. 2006). However, the transmitting unit is required to make regular direct contact with the satellite, which is not possible for aquatic species that do not break the surface of the water, such as many fishes. The larger size of satellite tags also increases the minimum size of fish that can be tagged. Studies on the movements of estuarine and coastal fishes are therefore more suited to using acoustic telemetry. For the remainder of the thesis, the term telemetry will refer to acoustic telemetry.

Acoustic telemetry has been used increasingly since the early 1960s, and can provide information on migration, movement, habitat utilization, activity patterns, home range use and homing ability of

fishes (Hart and Summerfelt 1975, Giacalone *et al*. 2005). Such information is essential for estuarine and marine management decisions, for understanding the effects of habitat alteration or degradation, habitat loss and environmental change on the species (Garshelis 2000, in Simcharoen *et al*. 2008), and for the effective design of any reserve where the protection of the species is envisaged (Spedicato *et al*. 2005).

By employing an array of automated stationary acoustic receivers in conjunction with active tracking of individual fish with a mobile receiver, acoustic telemetry can be implemented in such a way as to provide both continuous long-term data on area use and high resolution data on fine-scale movements of an individual (Hart and Summerfelt 1975, Giacalone *et al*. 2005, Heupel *et al*. 2006). Telemetry has been used to identify cyclic movement patterns in animals, which had previously been limited mainly to direct visual observation (Colton and Alevizon 1983). Telemetry can also be used to provide information over a range of temporal and spatial scales (Hartill *et al*. 2003), and results from telemetry studies conducted at different spatial and temporal scales can be combined to provide an understanding of the life-history of a species (Heupel and Simpfendorfer 2002). Telemetry, therefore, has the ability to provide complete information on the movement, home range and site fidelity of an individual fish, making it superior to conventional tag-recapture, as it can provide more data per individual (Brown and Orians 1970, Zeller and Russ 1998).

There are numerous advantages of acoustic telemetry over other methods of assessing movement of coastal fishery species. The technique is less labour-intensive than some other methods, such as large-scale netting programmes, and the non-destructive nature and complete lack of impact on the environment make the technique particularly useful in reserves and in areas of high conservation value, such as estuaries (Hartill *et al*. 2003). As the term describes, telemetry involves the remote study of animal movements, allowing animals to be studied in their natural environments (Lagardere *et al*. 1990, Arendt *et al*. 2001). The technique is, thus, free of the effects of observer presence.

Area use and movements can be overlaid onto habitat maps, to identify critical habitats and important areas, such as those used for feeding or shelter (Hartill *et al*. 2003). Telemetry also allows the remote recording of environmental and physiological variables, either through manual tracking and recording environmental variables *in situ*, or by equipping fish with transmitters that are able to record environmental or physiological data, such as water or fish temperature (Summerfelt and Smith 1990). By relating movement patterns to environmental data, the effects of different environmental variables on movement patterns and area use can be determined (Hartill *et al*. 2003).

Passive acoustic tracking

Passive acoustic tracking can be described as the remote monitoring of individuals through an array of stationary automated acoustic data-logging receivers. These receivers are programmed to receive and record the unique acoustic signals transmitted by individual transmitters, and record the date and time that each signal is received. This passive form of telemetry requires initial deployment of receivers and acoustic tagging and release of the study animals. Data collection is then automated, except for the planned retrieval and uploading of the data stored on each receiver, to a personal computer.

Due to the little field time required, the technique is not labour intensive. Data can thus be collected continuously, over long periods, and in unsafe or adverse environmental conditions, such as during rough seas or river flooding, as well as at night (Zeller and Russ 1998, Heupel *et al*. 2006). The permanent presence of the stationary receivers makes them particularly suited to determining site fidelity and long-term survivorship (Bellquist *et al*. 2008), as well as identifying cyclical movement patterns, such as tidal, diel or seasonal movement patterns (Heupel *et al*. 2006, Hedger *et al*. 2010b). Passive tracking has, therefore, been suggested to be more robust than the high-resolution data collected over short periods through manual tracking (Heupel *et al*. 2006). Passive telemetry can also be conducted in such a way as to determine movements among or between different environments, such as between a river and its estuary (Hindell *et al*. 2008), or between an estuary and the marine environment (Childs *et al*. 2008b), which can be used to determine proportions of time spent in different environments, as well as the timings of the onset and return of large-scale migrations.

Unlike manual tracking, the completely remote nature of passive telemetry means that the behaviour of the study animals is not affected by the presence of a tracking vessel, and passive receivers allow the tracking of multiple individuals simultaneously, allowing direct comparison and providing information on individual behaviour (Heupel *et al*. 2006, Hedger *et al*. 2010b).

The disadvantage of passive tracking is that stationary receivers have an omni-directional detection range, and provide no information on the distance of the transmitter-equipped fish from the receiver. This means that high-resolution positional information on an individual fish cannot be obtained using an array of independent stationary receivers. This can only be achieved through the employment of a linked array, in which the position of a fish can be triangulated based on the variable time taken for the signal to travel to receivers at variable distance from the fish, or through manual tracking with a mobile receiver (Heupel *et al*. 2006). Linked arrays require additional

technology and incur additional cost, and will not be discussed further in this thesis (see Heupel *et al*. 2006 for additional information). Furthermore, passive tracking relies on the fish remaining within the detection range of the receiver array (Simpfendorfer *et al*. 2002).

Manual acoustic tracking

Manual acoustic tracking differs from passive tracking in that it involves the active tracking of an individual, using a mobile receiver operated from a small vessel. The receiver hydrophone is able to determine the direction of a signal transmission, the strength of which (under adjustable reception gain) acts as an index of distance from the receiver. The tracker is thus able to actively follow and periodically locate an individual fish, at which time accurate positions can be recorded. From these positions, the home range size, shape and location of the animal can be estimated.

By tracking the fish closely from a vessel, the researcher can obtain accurate, high resolution positional information, and real-time, fine-scale temporal and spatial movement data on an individual fish, which cannot be achieved through passive tracking. This also allows *in situ* recording of environmental data, such as ambient water temperature, water depth and habitat type, which can provide insight into environmental factors affecting movements and assist with identification of critical habitats (Nathan *et al*. 2008, Abecasis *et al*. 2009). The fact that the researcher is able to follow the track of the fish means that the fish can be tracked beyond the boundaries of a stationary receiver array.

Manual tracking can provide information on behaviour, movement or displacement efficiency, inter- and intra-specific interactions and home range dynamics (Parsons *et al*. 2003), and provide an understanding of area and habitat use patterns, which is vital for informing management decisions for individual species and for conserving critical habitats (i.e. estuaries) in which they live (Hooge *et al*. 1999, Parsons *et al*. 2003, Humston *et al*. 2005, Taylor *et al*. 2006).

There are, however, a number of drawbacks to this technique. Manual tracking requires more resources than passive tracking, in the form of skilled personnel and some sort of vessel, and is highly labour-intensive. The technique requires long hours in the field, therefore limiting the feasible duration of data collection. Therefore, manual tracking cannot provide the long-term continuous data that can be obtained through passive tracking (Hedger *et al*. 2010a). Furthermore, the researcher and vessel cannot be in two places at once and, consequently, can only follow one individual, particularly if individual fish follow different trajectories.

There are multiple methods for estimating home range size, shape and location from manual tracking data, each of which has associated advantages and disadvantages, and specific applications (see Anderson 1982 and Boulanger and White 1990 for reviews), and "there is clearly no method that is universally acceptable" (Norton and Henley 1987). Furthermore, many of these estimators, such as the minimum convex polygon (Southwood 1966, in Anderson 1982), are designed for analyses of terrestrial animal home ranges (Brown *et al*. 2010), and are not suited to use in bounded aquatic or serpentine environments, such as many of the estuaries along the South African coast.

Complementary use of passive and manual tracking

The advantages and disadvantages of passive and manual tracking suggest that a combination of the two techniques should be used, to provide long-term, lower resolution area use and residency data, and short-term, high-resolution positional data (Lembo *et al*. 2002, Afonso *et al*. 2009). Examples of where passive telemetry has been used in conjunction with manual tracking, to assess movements in a range of environments, are common.

In the estuarine environment, passive and manual acoustic telemetry were used to assess estuarine space use of spotted grunter in the Great Fish Estuary, South Africa (Childs *et al*. 2008b), and to assess tidal and diel movements of leopard sharks *Triakis semifasciata* in Elkhorn Slough, California, USA (Carlisle and Starr 2010). The two techniques were used to assess diel and seasonal activity patterns of sixgill sharks *Hexanchus griseus* in Puget Sound and Elliot Bay, USA (Andrews *et al*. 2009), and to determine fine-scale movements and habitat use of smalltooth sawfish *Pristes pectinata* in south west Florida and the Florida Keys (Simpfendorfer *et al*. 2010). In the marine environment, passive and manual tracking were used to examine fine-scale movements of white sharks *Carcharodon carcharias* in Mossel Bay, South Africa (Johnson *et al*. 2009), to determine diel movement and habitat utilisation of salema *Sarpa salpa* in Calvi and Achiarina Bays in Corsica, Mediterranean Sea (Jadot *et al*. 2006), and to determine estuarine-marine movements of summer flounder *Paralichthys dentatus* on the continental shelf of the Mid-Atlantic Bight (Sackett *et al*. 2007).

Application of acoustic telemetry in this study

Acoustic telemetry was used to assess the movements of juvenile white steenbras in four estuaries differing in estuary type, size and flow regime. Passive tracking was conducted in all four estuaries to provide long-term, continuous high resolution data on area use, residency and site fidelity within the estuarine environment. Passive tracking was also used to determine the level of dependency of

juveniles on estuaries, by assessing the extent, timing and duration of movements between estuarine and marine environments. Manual tracking was conducted in three of the four estuaries, and was used to provide high-resolution data, to determine the home range sizes and locations of juveniles within these estuaries, and complement the data obtained through passive tracking. Data collected through passive and manual tracking were used to identify cyclical patterns in estuarine movements, as well as the environmental factors that affect movement and distribution. The key research questions were:

1. *What are the movement patterns, habitat use and home range sizes of white steenbras in a small temporarily open/closed estuary?*
2. *What are the movement patterns, habitat use and home range sizes of white steenbras in permanently open estuaries?*
3. *Are juvenile white steenbras entirely dependent on estuaries, according to Whitfield's (1994) IIa categorisation[2]?*
4. *What are the extent, timing and duration of juvenile white steenbras movements between the estuarine and marine environments, and between estuaries?*
5. *How do natural rhythmic cycles influence the estuarine movements of white steenbras?*
6. *How do cyclical movement patterns differ among estuaries of different type?*
7. *Which environmental variables affect the movement or position of white steenbras within estuaries?*

It has been suggested that researchers combine acoustic tracking, to provide detailed information on movement, and conventional dart tagging of a high number of individuals to supplement this with movement and dispersal information (Zeller and Russ 1998). The current study employed acoustic telemetry to assess the movement patterns of juvenile white steenbras within a range of estuaries. Conventional dart tagging was then used to assess residency and dispersal within the coastal zone in the post-estuarine life stages. Passive tracking was used to complement the conventional dart tagging in the marine environment, and provide higher resolution data on coastal residency and short-scale movements. The telemetry studies were also used to determine the level of connectivity between marine and estuarine environments, and thus provide information on the level of estuarine dependence at different life stages.

[2] Category IIa: euryhaline marine species which usually breed at sea, with juveniles dependent on estuaries as nursery areas (Whitfield 1994)

2.2.3 Genetic analysis

In the past, stock identification was largely achieved through comparisons of phenotypic characteristics, such as growth rate, maximum age, length-weight relationships, size at 50% sexual maturity and condition factor (Griffiths *et al*. 2002, Palma and Andrade 2002, Richardson *et al*. 2011). However, these markers are not genetic markers, and are not as sensitive in identifying discrete stocks as genetic markers that are used more commonly today.

Genetic markers are more sensitive for identifying stock structure than phenotypic characteristics, offering more suitable techniques for studying population genetics, to provide necessary information on long-term dispersal and reproductive patterns of populations (Arnaud *et al*. 2001, Feral 2002, Gold and Turner 2002, Wakeley 2005). Genetic markers can also provide information on evolutionary history of the population or species (Avise *et al*. 1987). Understanding genetic stock structure within and among populations can reveal current and historical population demography, and the factors (physical processes or individual behaviour) that influence the level of mixing, and thus help to identify the mechanisms driving and barriers preventing gene flow within or among populations (Avise 1998, Gold and Turner 2002). Frequently used genetic analysis techniques in stock determination studies are enzyme-based allozyme electrophoresis, mitochondrial DNA sequencing and analysis of microsatellite (nuclear) markers (Schlötterer 2004).

Allozyme electrophoresis is an analytical technique that examines variation among protein-coding genes that control much of cell metabolism. Allozymes are genetically different forms of an enzyme that are encoded at the same locus (May 2003). Allozymes are co-dominant Mendelian characters that have been proven to be informative nuclear genetic markers for monitoring the segregation or inheritance of a single gene (May 2003). They have simple and easy application, large quantities of data can be produced quickly and this technique is more cost-effective than other genetic markers (Begg and Waldman 1999, Carvalho and Hauser 1998, Park and Moran 1994, Shaklee and Bentzen 1998, Ward 2000). For these reasons, initially, the majority of genetic studies since the 1970s used allozyme electrophoresis (e.g. Arculeo *et al*. 2003, Bargelloni *et al*. 2003, 2005, Verspoor *et al*. 2005, González-Wangüemert *et al*. 2006).

There are, however, disadvantages to this technique. Only structural DNA is involved, representing less than 1% of the nuclear genome, and some allozymes may be under selection, making them unsuitable for the study of some of the fundamental processes in population genetics. The average heterozygosity for polymorphic loci and the number of variable loci are generally lower than for

other genetic markers (May 2003, Hauser and Seeb 2008). Furthermore, the process requires frozen or fresh sample material, which may be difficult or impossible to obtain.

While allozyme electrophoresis remains in use today and still provides useful information, it is used less frequently, with there being a present shift towards the use of mitochondrial and microsatellite markers (Liu and Cordes 2004). Mitochondrial markers are genes within the mitochondrial genome, while microsatellite markers are found within the nuclear genome. Owing to their different positions within the cell, the two genomes are inherited differently. As a result, the genetic markers based on the two genomes differ in their evolutionary process, and thus exhibit advantages and disadvantages for different applications.

Mitochondrial DNA sequencing

A powerful method of detecting genetic variability within or among populations is through the direct comparison of sequences of homologous DNA fragments obtained from individuals within each group. Mitochondrial DNA (mtDNA) is particularly suitable for such sequence comparison analyses because of the considerably higher rate of mutation of the mitochondrial genome compared to the nuclear genome (Campbell *et al*. 1999). Variations in the mitochondrial nucleotide sequence may be caused by nucleotide base substitutions (transitions or transversions), length variations (insertions or deletions of single or multiple nucleotides) or sequence rearrangement (chromosomal rearrangements that affect long sequences of DNA) (Moritz *et al*. 1987). Mitochondrial DNA evolves more simply than nuclear DNA, as there are fewer mechanisms of variation within mtDNA evolution (Moritz *et al*. 1987). It has rare or no recombination, rapid sequence evolution, high copy number, maternal inheritance, and is not inherited in a Mendelian way.

Due to strictly maternal inheritance, and under the assumptions of mutation-drift equilibrium and equal male and female dispersal, the effective mtDNA population size is expected to be one quarter that of nuclear DNA (Moritz *et al*. 1987), which would allow the detection of population subdivision more easily (Lee *et al*. 1995). The considerable variation among individuals within and between populations makes mtDNA an effective marker for studying population structure (Moritz *et al*. 1987).

Because allele frequencies of mtDNA are influenced by stochastic processes it is possible to track past population changes (Wilson *et al*. 1985, Moritz *et al*. 1987, Lee *et al*. 1995, Hare 2001). Mitochondrial markers are therefore used in molecular ecology, and the study of evolutionary and conservation genetics to determine population demography and evolutionary history (Avise *et al*.

1987). Analysing historical relationships of alleles in a geographic context (phylogeography) enables the inference of patterns of gene flow among geographically separated populations (Avise *et al*. 1987, Hare 2001). In most species, mtDNA has a higher mutation rate than single copy nuclear DNA, providing high-resolution analysis of recent evolutionary events (Ferris and Berg 1987, Birky *et al*. 1989, Wilson *et al*. 1985, Shaklee and Bentzen 1998, Waples 1998). The advantages of mtDNA have resulted in its widespread use, particularly within the Sparidae (e.g. Ostellari *et al*. 1996, Orrell *et al*. 2002, Orrell and Carpenter 2004, Domingues *et al*. 2007, Ponce *et al*. 2008). Most studies on South African marine organisms have used mtDNA sequence data (e.g. Matthee *et al*. 2007, Teske *et al*. 2007, von der Heyden *et al*. 2010, Zardi *et al*. 2011).

However, in some cases mtDNA may not be sufficiently sensitive to detect genetic structuring of populations, and in these circumstances microsatellites in the nuclear genome provide a better tool (Lundy *et al*. 2000). Furthermore, genetic analyses based on a single locus (i.e. the analysis of a single gene as is usually the case with mtDNA) are less informative than those based on multi-locus comparisons (Felsenstein 2006).

Microsatellite markers

The use of microsatellite genetic markers in population genetics (including fisheries research) is increasing rapidly (Hauser and Seeb 2008). Microsatellite markers are short tandem repeated genetic sequences, usually two to six base pairs in length and repeated 10 to 100 times (Campbell *et al*. 1999), and found throughout the nuclear genome (Goldstein and Pollock 1997). These genetic markers are co-dominant, inherited in a Mendelian way with biparental inheritance, and are normally selectively neutral (Moore *et al*. 1991, Garcia de Leon *et al*. 1997, Goldstein and Pollock 1997, Gold and Turner 2002). Genetic differentiation is determined by the variation in repeat unit length among locus-specific allele pairs within different individuals (Goldstein and Pollock 1997).

Nuclear DNA may evolve through a number of mechanisms, such as polymerase slippage, where polymerase miscopies repeated units (Levinson and Gutman 1987), and slipped-strand mispairing during replication (Hancock *et al*. 1999). As a result, the rates of mutation of the nuclear genome and microsatellite repeat sequences within the genome are relatively high, which allows for a high level of variation among alleles at a given locus (Teske *et al*. 2011). Furthermore, the abundance of microsatellites in living organisms is high (Bhargava and Fuentes 2010), allowing comparisons of genetic variability at multiple discrete loci. Microsatellites have high reproducibility, amplification requires little genetic material and the allele scoring process is simple (Moore *et al*. 1991, Garcia de

Leon *et al*. 1997, Goldstein and Pollock 1997). These characteristics make microsatellites an ideal marker for fine-scale stock structure investigations in population genetics studies (O'Connell and Wright 1997, Carvalho and Hauser 1998, Shaklee and Bentzen 1998, Ward 2000).

Microsatellite markers are more sensitive, and thus more suitable for detecting subtle population structure than mtDNA and protein polymorphisms (allozymes), particularly in high gene flow species (Waples 1998). Due to the high mutation rate of microsatellite markers, they allow the study of recent genetic patterns, e.g. those driven by fishing pressure or climate change, and provide more information on gene flow (Teske *et al*. 2011). Microsatellite markers are thus useful for studying closely related populations (Takezaki and Nei 1996), and have been used for population studies on numerous fish species, for example to investigate genetic variability and population genetics of gilthead seabream *Sparus auratus* from the Atlantic Ocean and Mediterranean Sea (De Innocentiis *et al*. 2004), to identify population structure of turbot *Scophthalmus maximus* between the Baltic Sea and the North Sea (Nielsen *et al*. 2004), to identify existence of isolation-by-distance in pike *Esox lucius* (Laikre *et al*. 2005), and to identify spatial and temporal population structure in European flounder *Platichthys flesus* (Hemmer-Hansen *et al*. 2007). However, despite their obvious suitability, microsatellites have been used little in South African marine phylogeography (Teske *et al*. 2011).

The disadvantage of microsatellite markers is the expense and time required to isolate the repeat units and design primers for the amplification of these regions (Mueller and Wolfenbarger 1999), although once developed they are easily maintained and cost-effective (Bhargava and Fuentes 2010).

Mitochondrial DNA sequencing and microsatellite analysis in conjunction

While mitochondrial and microsatellite markers are the most suitable for population genetic studies, there are nonetheless disadvantages to each of these techniques. Populations in mutation-drift equilibrium with equal male and female dispersal are expected to have four times the degree of divergence in mtDNA than nuclear DNA, because of maternal inheritance (Hare 2001, Gold and Turner 2002). Thus, genetic drift in the mitochondrial genome may produce higher genetic differentiation (Birky *et al*. 1989), making mtDNA markers more sensitive for detecting large-scale geographic differences, genetic bottlenecks and phylogeographic breaks (Wilson *et al*. 1985, Teske *et al*. 2011). Conversely, microsatellite markers have been successful in the identification of subtle population structure, when mtDNA has failed (Waples 1998, Gold and Turner 2002, Stockley *et al*. 2005). Mitochondrial and nuclear genomes are not physically connected, meaning that they may

evolve differently and may be subject to influence by different processes (Lemaire *et al*. 2005). Therefore, the employment of mitochondrial and microsatellite markers in conjunction, to provide information on past genetic structure and current population structure (Wilson *et al*. 1985, Gold and Turner 2002), may be the most informative approach to assessing intraspecific genetic variability (Lemaire *et al*. 2005), particularly where weak genetic structure is suspected (Machado-Schiaffino *et al*. 2009).

Population genetics studies utilising a mitochondrial gene marker in conjunction with microsatellite markers have been conducted on numerous fish species, for example the silverside fish *Odontesthes argentinensis* in the south west Atlantic (Beheregaray and Sunnucks 2001), the striped sea bream *Lithognathus mormyrus* in the Mediterranean Sea and eastern Atlantic Ocean (Sala-Bozano *et al*. 2009), and red roman in South Africa (Teske *et al*. 2010).

Application of genetic analyses in this study

Molecular analyses were conducted on juvenile and adult samples collected from eight different coastal localities, to assess the spatial genetic stock structure of white steenbras throughout its distribution, and provide information on the level of genetic mixing between areas to support the findings of the movement studies. Mitochondrial DNA and microsatellite analyses were used in conjunction, in a phylogeographic approach to infer demographic history and contemporary population genetic structure over the species' distribution range, and assess whether population declines are reflected by reductions in genetic diversity. The key research questions were:

1. *What is the spatial genetic variability of white steenbras?*
2. *Does white steenbras exist as a single stock, or is there evidence of multiple genetic stocks?*

2.2.4 Assimilation of catch and other fishery-related data

There are numerous methods available for assessing the status of fish stocks and determining the effects of fishing on fishery resources. Data for such assessments are usually collected from the fishery (fishery-dependent data) or through controlled research surveys (fishery-independent data) (Samoilys and Gribble 1997).

Fishery-dependent data

Fishery-dependent data are related directly to the fishery, and may be collected for recreational, commercial or subsistence sectors. These data can be collected by the fishery, and are therefore

cheap and can be collected for a long time-series (Penney *et al*. 1999). Such surveys provide information on catch, effort, gear types, fishing patterns and locations of fishing grounds, which are important for understanding the impacts of fishing on the stocks (Die 1997). The National Marine Linefish System (NMLS) was developed in South Africa from 1983 to 1985, by the Oceanographic Research Institute and the former Sea Fisheries Research Institute, to provide a database of catch and effort data from the fisheries (commercial and recreational) that target linefish (van der Elst and Penney 1995). The NMLS, regarded as the largest geo-referenced species database globally (McIntyre 2010), contains data resulting from voluntary recreational catch card returns, compulsory commercial catch returns, and competition angling data as well as from access point and roving creel surveys (Mann *et al*. 1997).

Commercial fishery data can be obtained from catch returns (Crawford and Crous 1982, Penney *et al*. 1999), which have been a compulsory requirement in most commercial fisheries in South Africa since 1976 (Lamberth 1996). However, such fishery-dependent data are limited to certain times and areas of operation, and many fisheries target specific groups of species (Penney *et al*. 1999) or areas of higher density (Saville 1977) and may, therefore, provide data that are not representative of a population or a species as a whole (Die 1997). Due to the nature of the fish processing onboard fishing vessels, catch data are commonly pooled by genus or family, or other groupings, such as the grouping of certain species of the family Sparidae into "redfishes" (Crawford and Crous 1982), making individual species assessments difficult or impossible. Furthermore, catch data are based on that recorded by the industry and may be inaccurate or untrustworthy (Lamberth *et al*. 1994).

Recreational fishery data can be collected through roving creel surveys (e.g. Brouwer *et al*. 1997, Mann *et al.* 2003), access point surveys (Brouwer and Buxton 2002, Fennessy *et al*. 2003), daily catch cards (Hanekom *et al*. 1997, Penney *et al*. 1999), and telephonic or postal surveys (Mann *et al*. 1997, McGrath *et al*. 1997). Roving creel surveys are suitable for collection of shore-based catch and effort data, and allow high numbers of respondents to be intercepted, but rely on reports of individual anglers (Brouwer *et al*. 1997). Access point surveys, suitable for assessment of skiboat catches, are inexpensive and allow measuring and accurate species identification, but provide no record of discarded catch (Brouwer and Buxton 2002). Catch cards are inexpensive and can provide large datasets, but are often inadequately completed and the accuracy of the catch data and species identification are unknown (Hanekom *et al*. 1997). Fishery-dependent data are also not available for protected areas, therefore preventing the possibility of comparison between protected and exploited areas (La Mesa and Vacchi 1999).

Despite the disadvantages described, the low cost and ease of collection, the possibility of collecting long series of data and the high number of participants involved make fishery-dependent data a valuable tool for the assessment of fish stock status. However, to overcome these drawbacks, and to provide some form of calibration of catch rates, fishery-dependent data can be complemented with fishery-independent data, recorded during research or long-term monitoring programmes.

Fishery-independent data

Fishery-independent surveys are more accurate, more representative and more reliable, as the data are recorded by researchers or rangers, and fish that are caught can be accurately identified and measured (Attwood 2002). Furthermore, research sampling can be conducted in protected areas. A review of methods is beyond the scope of the current thesis, and this section will be restricted to research angling, as applied to the current study.

Research angling is commonly used in recreational and commercial fishery assessments to provide an index of abundance (Bannerot and Austin 1983), and is effective for use in long-term monitoring (Millar and Willis 1999, Attwood 2003). Research-based catch-per-unit-effort (CPUE) data provide an empirical means for monitoring temporal variability, particularly for assessment of the effects of fishing on fish populations, and assessment of the effectiveness of marine reserves, and have therefore been used in numerous such programmes (Bennett and Attwood 1993, Underwood 1991, Edgar and Barrett 1997, Zeller and Russ 1998, Millar and Willis 1999, Cowley *et al*. 2002). As hook-and-line angling is both species and size selective, fishing surveys are suggested to provide non-representative estimates of species composition and length-frequency distributions (Perrow *et al*. 1996, Willis *et al*. 2000). However, fishing can provide a good representation of the species and length-frequency distributions of fishes available to the fishery, i.e. “fish of harvestable size” (Zeller and Russ 2000).

As an index, CPUE assumes constant catchability of individuals (Arreguin-Sanchez 1996). Buxton and Allen (1989) caution researchers that line fishing fails the assumption of equal catchability, as this may vary according to the level of fishing pressure or because of density-dependent competition for food, particularly in areas of high fish density (Millar and Willis 1999). When captured, fish are subjected to stress and possible injury or incidental mortality as a result of barotrauma injuries or damage to the gills or viscera that may be caused by complete hook ingestion (Willis *et al*. 2000). However, hook-and-line fishing is relatively inexpensive, requires simple equipment and less skilled

personnel, and a large sample size can be easily achieved. Importantly, the method allows comparisons among studies that have used this technique (Perrow *et al*. 1996).

Fishery-independent and fishery-dependent data in conjunction

Numerous studies have employed either fishery-independent or fishery-dependent catch data for assessing a fish stock, or trends in its abundance. Bennett (1993a) presented recreational and commercial fishery-dependent catch data for white steenbras, up to 1992. Attwood (2003) adopted a novel approach to assess the impacts of fishing on the stock of galjoen, in South Africa, based on relatively long-term (13-year) fishery-independent CPUE and conventional tag-recovery data. However, a combination of the two data sources would provide a more robust assessment, although few such studies have been conducted and these are mainly focussed on offshore species. M^{c}Cord (2005) assessed trends in the catch and CPUE of soupfin sharks *Galeorhinus galeus* in South Africa, from fishery-dependent and -independent longline and handline data, although this assessment was based largely on short-term datasets (3 to 5 years). An assessment of longer-term (16 years) data was conducted by Pecquerie *et al*. (2004) on 15 pelagic and demersal fishery species off the South African south and west coasts, based on commercial trawls, research trawls and hydroacoustic surveys, aimed at providing spatial density classification for each species, for incorporation into stock assessment models.

Stock assessment methods

The Linefish Management Protocol in South Africa requires that linefish stocks be assessed using conventional stock production or age-structured models (Griffiths *et al*. 1999), based largely on fishery-dependent data. Such analyses have been applied to a number of species; for example, red roman and dageraad *Chrysoblephus cristiceps* (Buxton 1992), white steenbras (Bennett 1993a), panga *Pterogymnus laniarius* (Booth 2000) and stonebream *Neoscorpis lithophilus* (Mann *et al*. 2002). However, in many cases, suitable data are not available on which to base such models (Potts *et al*. 2008), the growth rate of the species has not yet been determined or validated, or the mortality rate has not been determined. Spatial variation in population structure and abundance within the stock range may also complicate such modelling procedures or bias results (Attwood 2003). In such cases, the stock status can be assessed by elucidating trends in catch and CPUE (Honey *et al*. 2010). Analysis of trends in fishery-dependent and -independent catch data is simpler and more cost effective than obtaining the required data for stock assessment based on production models (Attwood 2003).

Application of historical catch and fishery-related data in this study

Available commercial and recreational fishery catch data were analysed, to identify trends in catch, effort, targeting and CPUE of white steenbras, over the past *c*50 years, in relation to historical management regulations for the species. These data were obtained from published roving creel and access point surveys, commercial catch returns, private catch logs and the NMLS, and supplemented by fishery-independent data collected through long-term ecological research programmes, both in estuaries and the marine environment. The key research questions were:

1. *What is the current status of the white steenbras stock?*
2. *What are the trends in catch, effort and CPUE in the recreational and commercial fisheries?*
3. *Have historical and current management regulations been effective in protecting white steenbras during different stages of its life history?*

Furthermore, by drawing from the movement, genetics and stock status components of this study, and from the literature, the current status of white steenbras conservation along the South African coastline was assessed. The current level of protection offered to white steenbras within estuarine and marine protected areas, and the availability of suitable habitat in estuaries and the inshore marine environment were also assessed, to assist in the identification of suitable management measures, for corrective management of the species. The key research questions were:

1. *Are white steenbras and its critical habitats suitably protected?*
2. *What is the current status of white steenbras conservation, relative to national and international criteria?*
3. *What future management measures would be most suitable for the white steenbras?*

Chapter 3

Estuarine area use and home range

3.1 Introduction

Understanding movement behaviour of a fish species is central to understanding its ecology. This requires information on movement patterns within key habitats and during different life stages throughout the animal's life history. Estuaries provide essential nursery habitats for numerous fish species, by offering shelter, protection from marine predators and a rich supply of food during the juvenile life stage (Bennett and Branch 1990). In so doing, estuaries form important components in the life-histories of many estuarine-dependent coastal fish species, and contribute substantially to coastal fish populations (Baird *et al*. 1996, Lamberth and Turpie 2003).

In South Africa, many of the species that depend on estuaries, such as dusky kob *Argyrosomus japonicus*, leervis *Lichia amia* and white steenbras *Lithognathus lithognathus* (Whitfield 1983), are fishery species of commercial or recreational value. A comprehensive understanding of the movement patterns, home range dynamics and habitat use of estuarine-dependent fish species within the estuarine environment is essential for effective conservation and the formulation of management decisions regarding such species (Egli and Babcock 2004, Whitfield and Cowley 2010). Despite this need, information pertaining to estuarine movement patterns, habitat use and dependency of many estuarine-associated fishery species is lacking (Cowley and Whitfield 2001). In recent years, however, the movement patterns of fishes in South African estuaries have received some attention, through the use of acoustic telemetry, for example spotted grunter *Pomadasys commersonnii* in the Great Fish (Næsje *et al*. 2007, Childs *et al*. 2008b) and East Kleinemonde (Kerwath *et al*. 2005) estuaries, and dusky kob in the Great Fish Estuary (Cowley *et al*. 2008). However, movement behaviour of one of South Africa's most threatened coastal fishery species, white steenbras, has been the focus of little attention.

White steenbras is classified as a category IIa[3] species (Whitfield 1994), meaning that the species has an obligatory estuarine-dependent juvenile phase. It has even been suggested that if denied access to estuaries as juveniles, the species may become extinct (Wallace *et al*. 1984a). The range of estuaries within which juvenile white steenbras are found is also limited, as a result of the restricted

[3] Euryhaline marine species which usually breed at sea: juveniles dependent on estuaries as nursery areas (Whitfield 1994)

geographical range of the stock, from the Orange River mouth in the west to the Mbashe Estuary in the east (Bennett 1993a). Juveniles use estuaries predominantly from the Berg Estuary in the west to the Great Kei Estuary in the east (Bennett 1993b), and are found in low numbers in estuaries further west (Lamberth *et al*. 2008) or further east (Begg 1984, Harrison and Whitfield 1995).

According to Day's (1980) definition, there are 259 systems along the South African coastline that function as estuaries. However, only 117 occur approximately within the distributional range of juvenile white steenbras. According to Whitfield's (1992) classification, the majority (70%, n = 82) of these 117 estuaries are classified as temporarily open/closed estuaries (Reddering and Rust 1990), although other estuary types, such as freshwater-deprived and freshwater-dominated permanently open estuaries are also present (Whitfield 2000). These different estuary types differ widely in physico-chemical and biological characteristics. Therefore, to fully understand the movement patterns of an estuarine species and the implications of estuarine dependency it is important to understand how movements and area use patterns change from one estuary type to another.

Research investigations are therefore essential, to provide information on movement patterns, distribution and habitat use (Able and Hales 1997). Movement studies can also assist in elucidating the role of different habitats in the life history of a species (Egli and Babcock 2004), thereby helping to identify ecologically important areas (Able and Grothues 2007a). Such information enhances the understanding of the species' ecology, and is essential for identifying suitable management measures for species of fishery importance, such as determining the potential effectiveness of estuarine or marine protected areas (Jones 2005).

3.1.1 Aims and objectives

The aims of this chapter were to determine and compare home range characteristics and area use patterns of juvenile white steenbras in a range of estuary types. Specific objectives were as follows:

i. Conduct a preliminary assessment of estuarine movement patterns of juvenile white steenbras;
ii. Determine distribution, area use and home range size and location in a temporarily open/closed estuary;
iii. Determine distribution, area use and home range size and location in two permanently open estuaries; and
iv. Compare area use and home ranges among the different estuaries.

3.2 Methods and materials

3.2.1 Telemetry study design

Acoustic telemetry studies were conducted in four warm-temperate estuaries along the Eastern Cape coastline of South Africa, including the medium-sized permanently open freshwater-dominated Great Fish Estuary, the small temporarily open/closed East Kleinemonde Estuary, the large permanently open freshwater-deprived Kariega Estuary and the large permanently open freshwater-dominated Sundays Estuary (Figure 3.1).

Figure 3.1: Map of the general study area showing the locations of the four estuaries in which the white steenbras acoustic telemetry studies were conducted, and the nearby estuaries. The inset shows the Eastern Cape Province and the position of the general study area along the coastline

The scientific approach adopted during the telemetry study in each estuary differed, according to the specific objectives being addressed. Consequently, the acoustic transmitters implanted into fish during each estuary also differed in size, battery life and pulse frequency (Table 3.1).

The first study was conducted in the permanently open Great Fish Estuary (Figure 3.1), from September to October 2003. This estuary is a medium-sized, channel-like system with uniform bathymetry, providing a simple estuary in which to conduct a preliminary acoustic telemetry study. This preliminary study provided the first assessment of juvenile white steenbras area use, residency and home range size and location within in an estuary, and the results assisted in the design of the subsequent studies in the other estuaries. This study focussed on assessing area use of small individuals, so small transmitters with short battery lives were used. Furthermore, the random nominal delay between transmitter signals was short (5 to 15 s), to allow for manual tracking.

The second study was conducted in the small, temporarily open/closed East Kleinemonde Estuary (Figure 3.1), from February to September 2008. Biological and physiological components of this estuary have been well documented (*inter alia* Badenhorst 1988, Cowley and Whitfield 2001, Teske and Wooldridge 2001, Smakhtin 2004, Whitfield *et al*. 2008). This estuary is predominantly closed to the sea, which provided the opportunity to assess home range dynamics and area use, whilst excluding the tidal influence and the associated fluctuations in salinity and temperature. The closed mouth also provided a safe environment in which to undertake night-time, boat-based manual tracking. This study was aimed at assessing long term area use patterns as well as home range dynamics. As such, two groups of fish were equipped with transmitters of different specifications, each to meet different objectives. The assessment of long-term area use required transmitters with a longer battery life. Ten individuals were equipped with "long-period" transmitters, with a nominal delay of 60 to 180 s. The assessment of home range dynamics required manual tracking and, thus, transmitters with a shorter nominal delay. It was felt that a nominal delay of 20 to 60 s was suitable for manual tracking in this system, due to the closed mouth, lack of current, and weak thermocline and halocline, but would still provide sufficient battery life for assessing area use. Six individuals were tagged with these "short-period" transmitters (Table 3.1). This represented the first long-term (eight months) telemetry study on white steenbras, and used both manual and passive acoustic telemetry.

The third and fourth studies were conducted in the freshwater-deprived Kariega Estuary from March 2009 to February 2010, and the freshwater-dominated Sundays Estuary from March to November 2010, respectively (Figure 3.1). Both estuaries are permanently open to the sea, but differ considerably in their freshwater input. The aims of these two studies were to assess distribution and area use within permanently open estuaries, and provide insight into the environmental variables influencing white steenbras movement within estuaries, which will be addressed in Chapter 5. These two studies were aimed at collecting long-term data; therefore transmitter size had to be increased, to allow for greater battery life. The Kariega Estuary is characterised by large shallow sandbanks near the mouth and above the road bridge (Figure 3.2), where it was not possible to position acoustic receivers, as they would have been exposed during the low tide. As such, it would be possible for fish to enter these shallow areas on the high tide, without being detected.

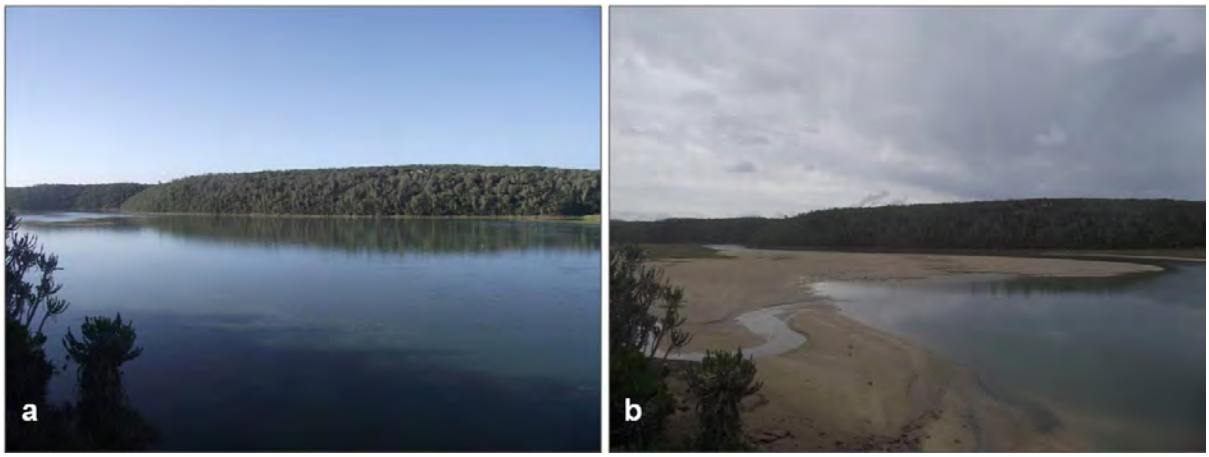

Figure 3.2: Kariega Estuary main sandbank at a) high and b) low spring tides

Therefore, manual tracking was conducted to confirm whether fish absent from the moored receiver array at high tide had moved onto the shallow sandbanks. As the main aim of this study was to assess area use and tidal influence on movement, the transmitters had to be suitable for both manual tracking and long-term area use assessment by means of stationary receivers. Coded transmitters with a nominal delay of 15 to 30 s were thus selected for this study. The study conducted in the Sundays Estuary aimed to assess long-term area use and temporal movement patterns. As manual tracking was not required, a nominal signal delay of 20 to 60 s was selected, to allow for a longer battery life. The specifications of the acoustic transmitters used in each estuary are presented in Table 3.1.

Table 3.1: Specifications of coded transmitters surgically implanted into white steenbras in the Great Fish, East Kleinemonde, Kariega and Sundays estuaries. Battery life (days) was that expected by the manufacturer (THELMA BIOTEL, Trondheim, Norway or VEMCO, Halifax, Canada). The delay was the random nominal delay between signal transmissions. All transmitters emitted signals on a frequency of 69 kHz

Estuary	n	Model	Make	Length (mm)	Diameter (mm)	Weight in water (g)	Battery life (d)	Delay (s)
Great Fish	10	MP-7	THELMA	18.0	7.3	1.2	14	5 - 15
East Kleinemonde	10	V7-4L-R64K	VEMCO	20.5	7.0	0.8	230	60 - 180
East Kleinemonde	6	V7-4L-R04K	VEMCO	20.5	7.0	0.8	100	20 - 60
Kariega	10	MP-9-SHORT	THELMA	23.0	9.0	2.2	140	15 - 30
Sundays	15	V9-2L- R04K	VEMCO	29.0	9.0	2.9	206	20 - 60

3.2.2 Study areas

Each of the study estuaries was divided into mouth region and lower, middle and upper reaches, based on current speed, sediment and salinity divisions as suggested by McLusky (1989) and Cowley and Whitfield (2001). Salinity was classified in each region according to the Venice system: oligohaline (0.5 – 4.9), mesohaline (5.0 – 17.9), polyhaline (18.0 – 29.9) or euhaline (30.0 – 39.9).

Great Fish Estuary

The Great Fish (Figure 3.3) is a permanently open, freshwater-dominated estuary with a mean annual runoff (MAR) of approximately 479 x 10^6 m^3 (Grange and Allanson 1995), fed by a catchment of 29 937 km^2 (Grange *et al*. 2000). The narrow channel-like estuary is approximately 12 km long, 30 to 100 m wide, has a mean depth of 1.9 m (Harrison 2004) and approximate surface area of 1 360 000 m^2.

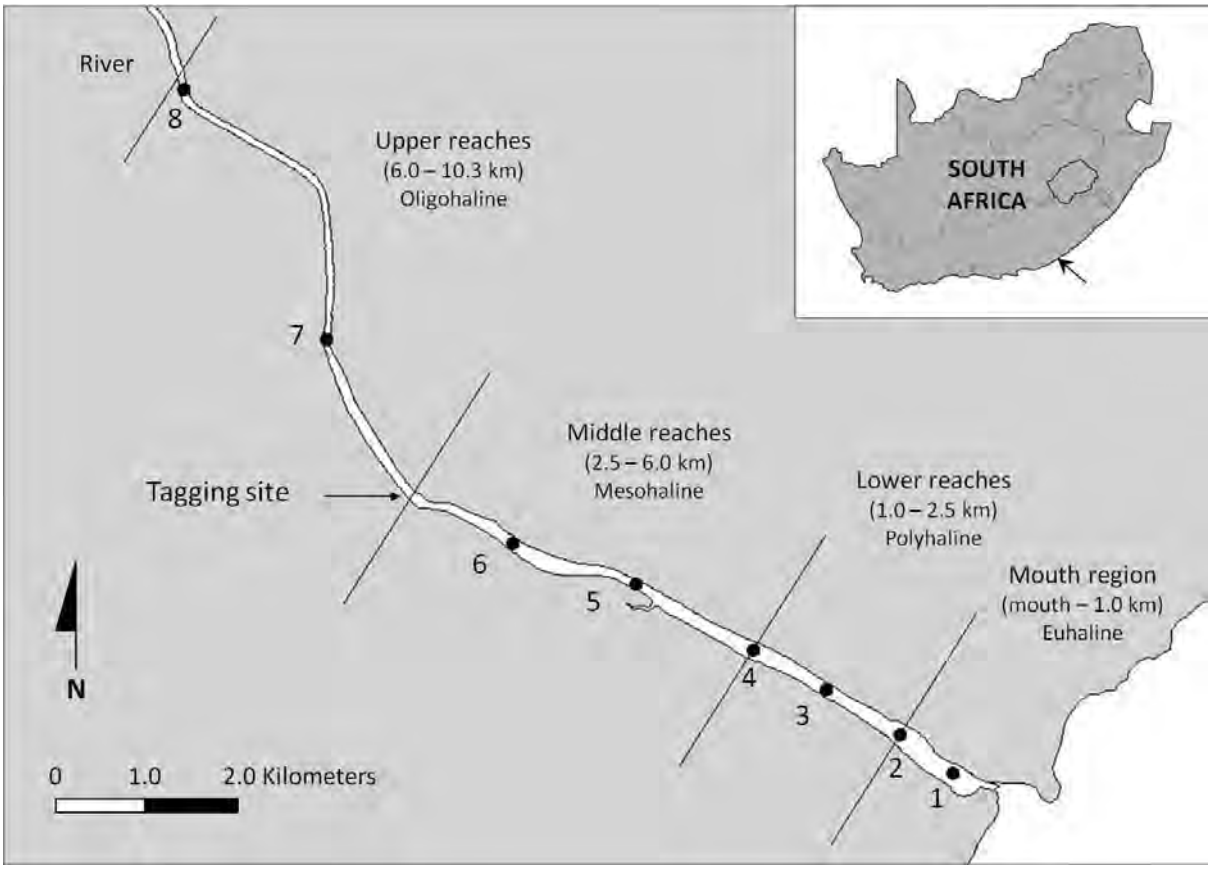

Figure 3.3: Map of the Great Fish Estuary study area, showing the positions of the eight stationary acoustic receivers (numbered black dots) and approximate boundaries and salinity categories of the different estuary reaches

The estuary receives water from the Orange River, through the Orange-Fish River inter-basin transfer (IBT) scheme and, as a result, exhibits high nutrient and phytoplankton production levels

(Whitfield *et al*. 1994). The estuary is highly turbid (Whitfield 1994, Grange *et al*. 2000), exceeding 200 FTU during the current study. There is a moderate axial and strong vertical salinity gradient (Table 3.2) and values recorded during this study were similar to those reported by Whitfield (1994). The temperature range, 13 to 21°C in the lower reaches (Allanson and Read 1987) and 11 to 26°C in the upper reaches (Whitfield 1994), reflects the warm-temperate biogeographical region of the South African coastline within which the estuary enters the sea, at 33°30'S; 27°08'E (Whitfield *et al*. 1994). Environmental variables were recorded daily from 29 September to 17 October 2003, at eight fixed stations that corresponded with the location of each stationary data-logging acoustic receiver (Table 3.2).

Table 3.2: Summary of mean (± SD) surface (S) and bottom (B) environmental variables recorded daily at each stationary acoustic receiver in the Great Fish Estuary (29 September to 17 October 2003)

Station		Salinity	Water temp (°C)	Turbidity (FTU)	Current speed ($m.s^{-1}$)	Depth (m)
1	S	20.8 (± 8.8)	18.0 (± 1.0)	17.6 (± 6.5)	0.38 (± 0.18)	1.28 (± 0.28)
	B	29.2 (± 6.3)	17.1 (± 0.7)	19.3 (± 10.3)	0.14 (± 0.09)	
2	S	14.1 (± 4.6)	18.8 (± 1.1)	26.5 (± 9.1)	0.33 (± 0.18)	2.75 (± 0.32)
	B	31.4 (± 2.9)	17.1 (± 0.6)	61.8 (± 43.1)	0.10 (± 0.18)	
3	S	10.4 (± 4.9)	19.7 (± 0.8)	33.3 (± 15.2)	0.28 (± 0.17)	1.49 (± 0.26)
	B	27.8 (± 4.5)	17.9 (± 0.7)	50.5 (± 27.4)	0.10 (± 0.10)	
4	S	7.6 (± 4.3)	20.3 (± 0.9)	48.7 (± 29.4)	0.30 (± 0.17)	0.90 (± 0.20)
	B	16.0 (± 11.5)	19.1 (± 1.3)	56.2 (± 27.2)	0.10 (± 0.11)	
5	S	4.6 (± 3.2)	20.5 (± 1.0)	68.1 (± 48.2)	0.35 (± 0.18)	2.38 (± 0.23)
	B	26.8 (± 7.0)	18.1 (± 0.8)	80.3 (± 59.6)	0.04 (± 0.04)	
6	S	2.7 (± 2.5)	21.1 (± 0.7)	82.6 (± 47.6)	0.35 (± 0.15)	1.89 (± 0.31)
	B	13.7 (± 12.5)	19.8 (± 1.5)	94.6 (± 65.2)	0.12 (± 0.09)	
7	S	2.8 (± 3.7)	21.6 (± 0.9)	114.6 (± 48.2)	0.24 (± 0.13)	4.78 (± 0.70)
	B	7.0 (± 6.6)	20.7 (± 0.9)	167.8 (± 67.5)	0.06 (± 0.12)	
8	S	0.0 (± 0.0)	21.8 (± 0.8)	121.8 (± 38.4)	0.13 (± 0.07)	4.43 (± 0.70)
	B	0.4 (± 0.9)	21.4 (± 1.0)	154.9 (± 42.9)	0.10 (± 0.09)	

Variables recorded included surface and bottom salinity (Atago handheld refractometer), temperature (°C, digital thermometer), turbidity (FTU, Hanna 93703 turbidity meter) and current speed ($m.s^{-1}$, Höntzsch Flowtherm current meter), as well as depth (m, graduated weighted rope). Bottom water was sampled using a Van Dorn-type water sampler, from approximately 0.3 m above the substrate to avoid disturbing the sediment.

East Kleinemonde Estuary

The East Kleinemonde (Figure 3.4) is a small temporarily open/closed estuary fed by a catchment of 46.3 km^2 with an estimated MAR of 2 x 10^6 m^3 (Badenhorst 1988), and enters the sea at 33°32′S; 27°03′E. The estuary is approximately 3.5 km in length, with a surface area of approximately 307 600 m^2 when at maximum capacity and 205 000 m^2 at its lowest state (Whitfield *et al*. 2008).

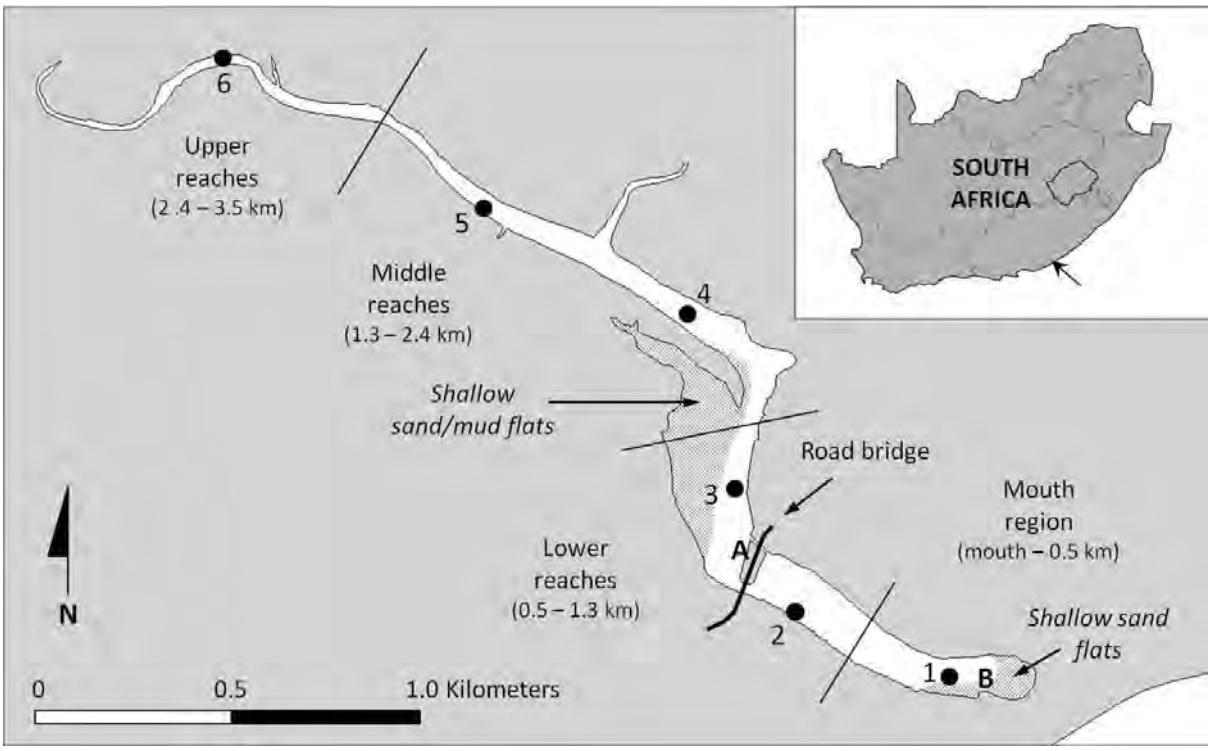

Figure 3.4: The East Kleinemonde Estuary showing the different estuarine reaches, locations of shallow sand and sand/mud flats, tagging localities for fish tagged with long-period (A) and short-period (B) transmitters, and positions of the six stationary acoustic receivers (numbered black dots)

The estuary is relatively narrow, with a maximum width of approximately 220 m, occurring above the road bridge. Due to regular long periods of mouth closure, the estuary has been referred to as an intermittently open system (Bell *et al.* 2001, Cowley *et al*. 2001). During this study, the estuary mouth remained closed for most of the eight-month period (12 February to 18 September 2008). However, a single open mouth phase, lasting only one day, occurred at the beginning of September 2008 as a result of overwash associated with an exceptionally rough sea event. Temperature loggers (VEMCO, Halifax, Canada, model Minilog8-TR) were attached to the moorings of two data-logging acoustic receivers, receiver 1 (2.5 m deep) and receiver 6 (0.5 m deep), to record the axial temperature gradient between the mouth and upper reaches, respectively. Two additional temperature loggers, one attached to a buoy at the surface near receiver 2 and one at the base of

the bridge pylon (Figure 3.4), in the deepest part of the estuary (4.5 m deep), were positioned to record temperature trends in the potentially warmest and coolest depth strata of the estuary, respectively, throughout the study period (Figure 3.5).

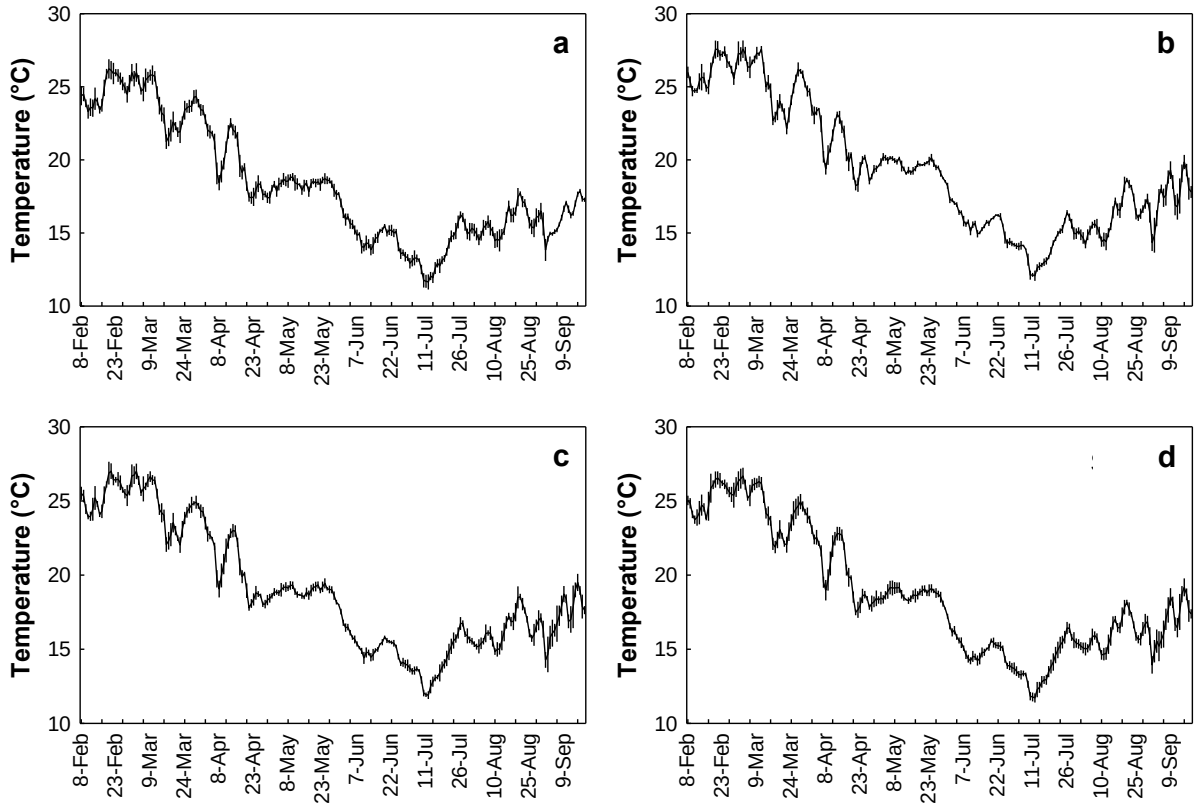

Figure 3.5: Mean daily temperatures (± SD) recorded at the temperature loggers positioned a) in the mouth region, b) in the upper reaches, c) at the substrate and d) at the surface, in the East Kleinemonde Estuary

There was little vertical or horizontal temperature stratification during the study period, with similar trends (based on hourly recordings) recorded at all four loggers (Figure 3.5). However, a distinct seasonal variation in temperature was observed during the study period with a maximum temperature of 29.9°C recorded during summer (January) at the upper temperature logger and a minimum of 10.9°C recorded in winter (July) at the mouth temperature logger (Figure 3.5). Salinity could not be recorded on an hourly basis, as was done for temperature; however, surface and bottom salinity recordings taken at each positional fix (n = 153 fixes) during manual tracking differed by only 0.5 (±1.0), indicating a weak or often absent halocline.

Kariega Estuary

The Kariega Estuary (Figure 3.6) is a medium-sized, permanently open estuary that is tidal to approximately 17 km from the mouth and enters the sea at 33°41' S; 26°44' E (Grange *et al*. 2000). The estuary is supplied by a small catchment (688 km^2), has a low MAR (15 x 10^6 m^3) and is characterised by a series of impoundments and excessive water abstraction, resulting in severe freshwater deprivation (Grange and Allanson 1995). Mean annual flow from 1985 to 2010 was 4.75 x 10^6 m^3 (± 8.48 x 10^6 m^3) (DWAF 2011). As a result, the estuary is marine-dominated, with deposition of marine sand up to 3.5 km from the mouth. The ratio of tidal prism volume to river volume is 106:1, further highlighting the low freshwater inflow.

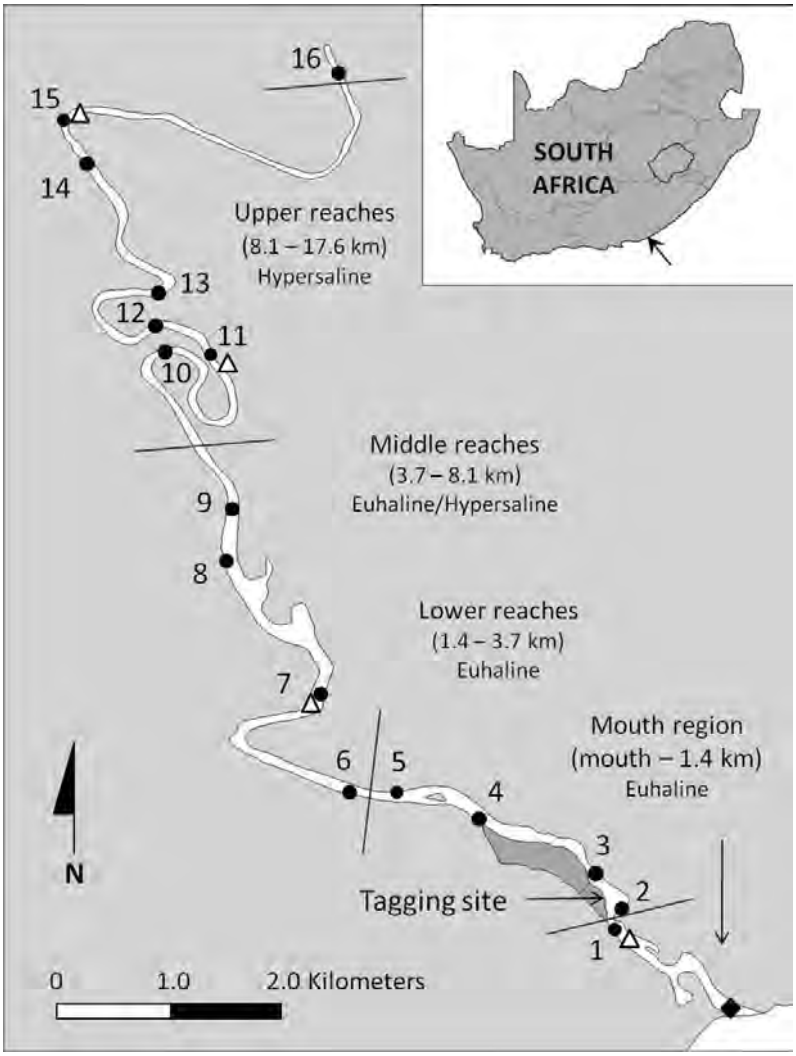

Figure 3.6: The Kariega Estuary showing positions of the stationary acoustic receivers (numbered black dots), temperature/pressure data loggers (white triangles), the tagging site and the different estuarine reaches. The dark grey section represents the large intertidal sandbank, and the diamond in the mouth represents station 1 for recording of environmental data

As a result of this low inflow, turbidity throughout the system seldom exceeds 10 NTU. The most striking feature is the presence of a reverse salinity gradient, with salinity values in the upper reaches remaining as high as 45. Environmental data were recorded every third day from 26 March to 5 June 2009 (every manual tracking day), at five locations within the Kariega Estuary; at the mouth and at receivers 1, 7, 11 and 15 (Figure 3.6). Environmental variables recorded included surface and bottom recordings for salinity (Extech RF20 refractometer), water temperature and turbidity, as well as surface current speed (rate of movement of a neutrally buoyant object to drift 2 m) and direction, water depth and secchi depth (Table 3.3). Four temperature/pressure data loggers (VEMCO, model Minilog8-TDR) were positioned at the same receivers (1, 7, 11 and 15), to record hourly temperatures and water depths.

Table 3.3: Summary of mean (± SD) surface (S) and bottom (B) environmental variables recorded daily at each station in the Kariega Estuary, during the study period (26 March to 5 June 2009)

Station (Receiver)		Salinity	Water temp (°C)	Turbidity (FTU)	Current speed ($m.s^{-1}$)	Depth (m)
1 (Mouth)	S	37.8 (± 0.8)	16.7 (± 1.5)	4.0 (± 1.2)	0.48 (± 0.24)	2.22 (± 0.37)
	B	38.1 (± 0.8)	16.7 (± 1.5)	4.5 (± 1.7)		
2 (Rec 1)	S	37.9 (± 0.6)	17.0 (± 1.6)	4.5 (± 1.4)	0.38 (± 0.16)	2.24 (± 0.34)
	B	38.2 (± 0.4)	17.1 (± 1.6)	4.7 (± 1.6)		
3 (Rec 7)	S	38.1 (± 0.9)	18.5 (± 2.3)	4.4 (± 1.0)	0.13 (± 0.09)	2.71 (± 0.38)
	B	38.3 (± 0.8)	18.4 (± 2.5)	6.2 (± 1.7)		
4 (Rec 11)	S	40.9 (± 1.4)	19.7 (± 3.2)	4.9 (± 1.9)	0.12 (± 0.07)	2.52 (± 0.34)
	B	41.8 (± 1.1)	19.5 (± 3.0)	8.4 (± 3.1)		
5 (Rec 15)	S	43.5 (± 1.5)	19.7 (± 3.4)	5.3 (± 1.8)	0.08 (± 0.05)	2.3 (± 0.28)
	B	44.3 (± 0.8)	19.7 (± 3.2)	8.1 (± 2.4)		

Sundays Estuary

The Sundays Estuary (Figure 3.7) is a channel-like system, approximately 21 km in length, which enters Algoa Bay at 33°43' S; 25°51' E (Beckley 1984). The system is characterised by a lack of sandflats, mudflats and salt marches, and has few submerged aquatic macrophytes. The estuary is supplied by a large catchment (20 729 km^2) with a mean annual rainfall of 323 mm (Harrison and Whitfield 1990), has a high MAR of 200 x 10^6 m^3 (Perry 1983 in MacKay and Schumann 1990) and is subject to periodic flooding and high levels of freshwater inflow (Wooldridge and Bailey 1982). Mean annual flow volume from 1985 to 2010 was 107.87 x 10^6 m^3 (± 22.40 10^6 m^3) (DWAF 2011). A horizontal salinity gradient is present, with salinity increasing from the upper reaches to the mouth

(Harrison and Whitfield 1990), and a strong vertical salinity gradient is present as a result of saltwater intrusion (Wooldridge and Bailey 1982).

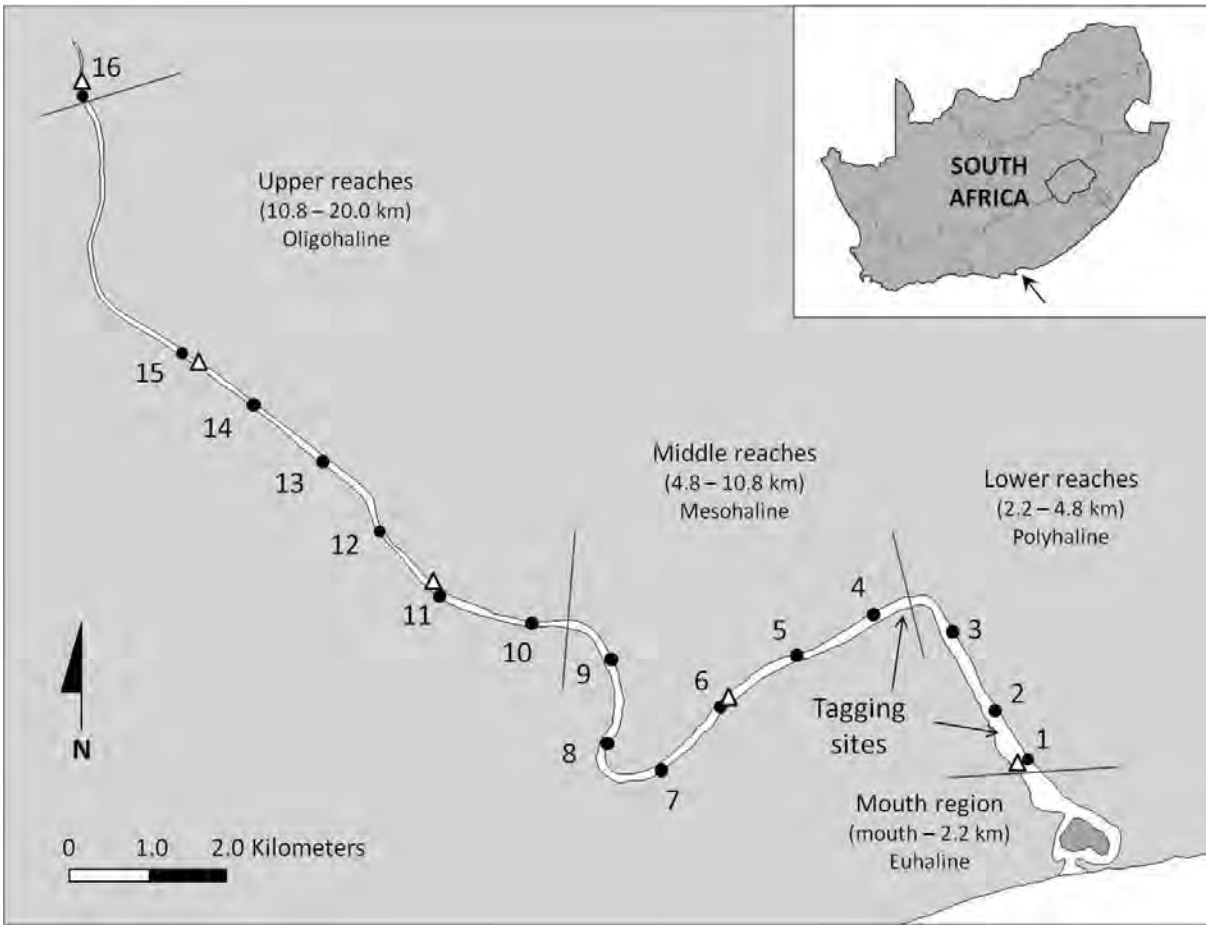

Figure 3.7: The Sundays Estuary showing positions of the stationary acoustic receivers (numbered black dots), temperature/pressure data loggers (white triangles), tagging sites and the different estuarine reaches

Environmental data in the Sundays Estuary were collected on an *ad hoc* basis from March 2008 to November 2010 (Table 3.4). Five temperature/pressure data loggers (VEMCO), positioned on receivers 1, 6, 12, 15 and 16, recorded hourly water temperatures and water depths.

Table 3.4: Summary of mean (± SD) surface (S) and bottom (B) environmental variables recorded at fixed stations in the Sundays Estuary, over an extended period (March 2008 to November 2010)

Station (Receiver)		Salinity	Water temp (°C)	Turbidity (FTU)	Current speed ($m.s^{-1}$)	Depth (m)
1 (Rec 1)	S	31.2 (± 7.0)	19.4 (± 3.4)	9.8 (± 7.9)	0.27 (± 0.15)	1.76 (± 0.27)
	B	34.2 (± 4.6)	19.3 (± 3.1)	9.0 (± 9.0)		
2 (Rec 3)	S	26.3 (± 9.2)	19.9 (± 4.0)	11.4 (± 9.6)	0.31 (± 0.11)	4.18 (± 0.70)
	B	34.3 (± 3.7)	19.4 (± 3.6)	19.0 (± 10.7)		
3 (Rec 5)	S	18.5 (± 8.6)	20.8 (± 4.3)	10.5 (± 7.5)	0.23 (± 0.08)	2.32 (± 0.38)
	B	28.8 (± 6.4)	20.1 (± 3.6)	47.3 (± 39.4)		
4 (Rec 7)	S	17.4 (± 5.7)	20.9 (± 4.3)	9.5 (± 6.4)	0.22 (± 0.11)	2.43 (± 0.50)
	B	29.8 (± 1.5)	20.1 (± 3.2)	36.7 (± 32.3)		
5 (Rec 9)	S	13.9 (± 9.4)	20.9 (± 4.4)	12.8 (± 11.2)	0.14 (± 0.11)	2.11 (± 0.37)
	B	24.7 (± 5.4)	20.1 (± 4.1)	29.1 (± 28.2)		
6 (Rec 11)	S	11.8 (± 6.9)	20.3 (± 4.3)	12.7 (± 11.4)	0.19 (± 0.17)	2.20 (± 0.44)
	B	22.0 (± 3.6)	20.2 (± 3.6)	20.6 (± 13.5)		
7 (Rec 13)	S	6.8 (± 4.9)	20.3 (± 4.4)	14.1 (± 14.0)	0.17 (± 0.11)	1.54 (± 0.30)
	B	13.4 (± 8.8)	20.3 (± 3.7)	25.5 (± 19.6)		
8 (Rec 15)	S	9.0 (± 12.9)	20.0 (± 4.5)	13.0 (± 11.3)	0.16 (± 0.11)	1.88 (± 0.36)
	B	9.7 (± 9.2)	20.2 (± 3.7)	26.7 (± 23.3)		
9 (Rec 16)	S	1.8 (± 1.0)	19.7 (± 4.5)	21.2 (± 24.4)	0.14 (± 0.06)	1.71 (± 0.27)
	B	2.2 (± 1.2)	19.7 (± 4.2)	33.0 (± 27.2)		

3.2.3 Fish capture and transmitter implantation

White steenbras in the Great Fish Estuary were captured opportunistically while sampling for a different species during a separate study. The presence of these individuals, associated with a small patch of sand deposited in the upper reaches after a flood event in May 2003 (Childs *et al*. 2008a), provided an opportunity to investigate home range size and area use patterns of juvenile white steenbras in an estuary, for the first time. However, to prevent possible bias associated with sampling highly resident individuals in one section of an estuary, in the subsequent studies in the East Kleinemonde, Kariega and Sundays estuaries, attempts were made to capture and tag white steenbras throughout each system, by netting from the upper reaches to the mouth, However, in all three estuaries, white steenbras could only be captured in the lower reaches. All fish were captured using a seine net (50 m × 2 m, 15-mm bar mesh), deployed from a small boat, and held *in situ* in a 75-L perforated container until surgery.

Fish were anaesthetised in a 25-L container, filled with estuary water containing 2-phenoxyethanol at a concentration of 0.3 ml/L. Once anaesthetized, each fish was measured to the nearest millimetre fork length (FL) and total length (TL), and placed ventral side up in a V-shaped wooden trough, lined with foam and a wet, super-absorbent cloth (Cowley *et al*. 2008). An incision of approximately 12 to 15 mm in length (minimum required for the transmitter) was made slightly lateral of the ventral midline of the fish, approximately 20 mm anterior to the anus (Kerwath 2005). Each transmitter was sterilised in alcohol and allowed to air dry before insertion into the peritoneal cavity, after which the incision was closed with two independent sutures (3/0 PermaHand suede, Johnson and Johnson). Opposing tissue layers were aligned, and held together by hand while the suture was tied. The fish was then placed in a 75-L 'recovery' bath filled with fresh estuary water and allowed to recover. After resuming an upright swimming position, it was released. During the surgery process the gills were continuously flushed with fresh estuary water to supply dissolved oxygen, maintain body temperature and remove metabolic waste (Johnson 2000). To prevent contamination of the open wound, all surgical tools were cleaned in alcohol prior to surgery. Fish in an excited state were not tagged, as oxygen debt can increase during surgery, which may result in post-surgery mortality from lactic acidosis (Summerfelt and Smith 1990). All fish were released at their site of capture.

Ten white steenbras (± 1.5 years old), ranging from 154 to 184 mm FL (mean = 170 ± 8 mm), (Table 3.5) were captured in the Great Fish Estuary, on 29 and 30 September 2003, and equipped with individually coded MP-7 acoustic transmitters. Mean surgery duration (time out of anaesthetic until time into recovery) was 3 min 22 s (± 16 s). Ten white steenbras (± 2.5 years old), ranging from 238 to 302 mm FL (mean = 262 ± 21 mm), were captured in the lower reaches of the East Kleinemonde Estuary (Figure 3.4) on 12 February 2008, approximately 30 m above the road bridge, and tagged with long-period V7 transmitters, and six fish (± 2.5 years old), ranging from 235 to 266 mm FL (mean = 253 ± 14 mm), were captured in the mouth region and tagged with short-period V7 transmitters. Mean surgery duration was 3 min 44 s (± 55 s). Ten white steenbras (± 2.5 – 3.5 years old), ranging from 215 to 379 mm FL (mean = 278 ± 51 mm) were captured in the Kariega Estuary on 5 March 2009, approximately 1.5 km from the mouth (Figure 3.6). Fish were surgically equipped with MP-9 transmitters. Mean surgery duration was 2 min 57 s (± 21 s). Fifteen juvenile white steenbras (± 2.5 - 3 years old), ranging from 208 - 315 mm FL (mean = 238 ± 28 mm), were captured in the Sundays Estuary from 7 to 9 March 2010, between 2 km and 5 km from the mouth (Figure 3.7). These fish were tagged with V9 acoustic transmitters. Mean surgery duration was 3 min 1 s (± 21 s). Details of transmitter implantation for all fish are presented in Table 3.5.

Table 3.5: Capture and transmitter implantation details for white steenbras tagged in the Great Fish (GFR), East Kleinemonde (EKM), Kariega (KAR) and Sundays (SUN) estuaries

Estuary	Fish ID	Capture date	FL (mm)	TL (mm)	Surgery duration (mm:ss)	Transmitter type
GFR	73	29-09-2003	174	184	02:30	MP-7 (5 – 15)
GFR	77	29-09-2003	178	197	04:34	MP-7 (5 – 15)
GFR	79	30-09-2003	171	199	02:51	MP-7 (5 – 15)
GFR	82	30-09-2003	154	192	03:34	MP-7 (5 – 15)
GFR	83	29-09-2003	168	186	03:22	MP-7 (5 – 15)
GFR	84	29-09-2003	167	181	03:05	MP-7 (5 – 15)
GFR	86	30-09-2003	171	186	03:50	MP-7 (5 – 15)
GFR	87	30-09-2003	170	187	03:06	MP-7 (5 – 15)
GFR	88	29-09-2003	166	190	03:01	MP-7 (5 – 15)
GFR	92	29-09-2003	184	172	03:48	MP-7 (5 – 15)
EKM	3759	12-02-2008	291	325	05:15	V7 (60 – 180)
EKM	3760	12-02-2008	302	341	05:22	V7 (60 – 180)
EKM	3761	12-02-2008	274	309	03:57	V7 (60 – 180)
EKM	3762	12-02-2008	267	300	05:06	V7 (60 – 180)
EKM	3764	12-02-2008	254	284	03:28	V7 (60 – 180)
EKM	3765	12-02-2008	247	276	04:06	V7 (60 – 180)
EKM	3766	12-02-2008	238	266	04:15	V7 (60 – 180)
EKM	3768	12-02-2008	247	280	03:25	V7 (60 – 180)
EKM	3769	12-02-2008	255	288	03:21	V7 (60 – 180)
EKM	3770	12-02-2008	247	278	03:00	V7 (60 – 180)
EKM	2001	12-02-2008	247	278	02:25	V7 (20 – 60)
EKM	2002	12-02-2008	235	267	02:56	V7 (20 – 60)
EKM	2003	12-02-2008	266	300	03:05	V7 (20 – 60)
EKM	2004	12-02-2008	265	299	02:57	V7 (20 – 60)
EKM	2005	12-02-2008	240	272	04:12	V7 (20 – 60)
EKM	2006	12-02-2008	262	293	02:51	V7 (20 – 60)
KAR	2036	05-03-2009	379	428	02:40	MP-9 (15 – 30)
KAR	2037	05-03-2009	307	337	02:44	MP-9 (15 – 30)
KAR	2038	05-03-2009	268	304	03:11	MP-9 (15 – 30)
KAR	2039	05-03-2009	244	273	03:17	MP-9 (15 – 30)
KAR	2040	05-03-2009	215	242	03:40	MP-9 (15 – 30)
KAR	2041	05-03-2009	227	256	02:30	MP-9 (15 – 30)
KAR	2042	05-03-2009	318	363	03:04	MP-9 (15 – 30)
KAR	2043	05-03-2009	234	262	02:44	MP-9 (15 – 30)
KAR	2044	05-03-2009	302	351	02:56	MP-9 (15 – 30)
KAR	2045	05-03-2009	284	319	02:43	MP-9 (15 – 30)
SUN	64989	07-03-2010	236	267	03:20	V9 (20 – 60)
SUN	64990	08-03-2010	224	253	02:30	V9 (20 – 60)
SUN	64991	08-03-2010	208	233	03:00	V9 (20 – 60)
SUN	64992	08-03-2010	208	233	03:12	V9 (20 – 60)
SUN	64993	08-03-2010	315	356	02:55	V9 (20 – 60)
SUN	64994	08-03-2010	256	278	03:17	V9 (20 – 60)
SUN	64995	08-03-2010	236	264	02:54	V9 (20 – 60)
SUN	64996	08-03-2010	277	310	03:30	V9 (20 – 60)
SUN	64997	08-03-2010	208	233	03:07	V9 (20 – 60)
SUN	64998	08-03-2010	223	248	03:21	V9 (20 – 60)
SUN	64999	08-03-2010	235	260	03:03	V9 (20 – 60)
SUN	65000	08-03-2010	235	262	03:24	V9 (20 – 60)
SUN	65001	09-03-2010	235	266	02:44	V9 (20 – 60)
SUN	65002	09-03-2010	232	262	02:33	V9 (20 – 60)
SUN	65003	09-03-2010	245	274	02:23	V9 (20 – 60)

3.2.4 Acoustic telemetry

Passive tracking

To provide information on long-term area use, the positions of the tagged fish were passively monitored by an array of stationary automated data-logging acoustic receivers (models VR2 and VR2W, VEMCO, Nova Scotia, Canada) positioned throughout each estuary, spanning the mouth region and lower, middle and upper reaches (Figures 3.3, 3.4, 3.6, 3.7). When a fish entered the detection range of a receiver, the signal of the transmitter was detected by the receiver, and the unique transmitter code and the time and date were recorded. Each receiver was secured in a PVC pipe embedded in a 40-kg concrete mooring block (Figure 3.8). Receivers and PVC housings were coated with anti-fouling paint and deployed prior to capture of the fish. The receivers were strategically positioned, in areas of non-complex topography to avoid reduction of signal range due to 'shadowing' by solid obstacles (Egli and Babcock 2004, Kerwath 2005). Arrays of eight and six receivers were used in the Great Fish and East Kleinemonde estuaries, respectively, while 16 receivers were used in each of the Kariega and Sundays estuaries.

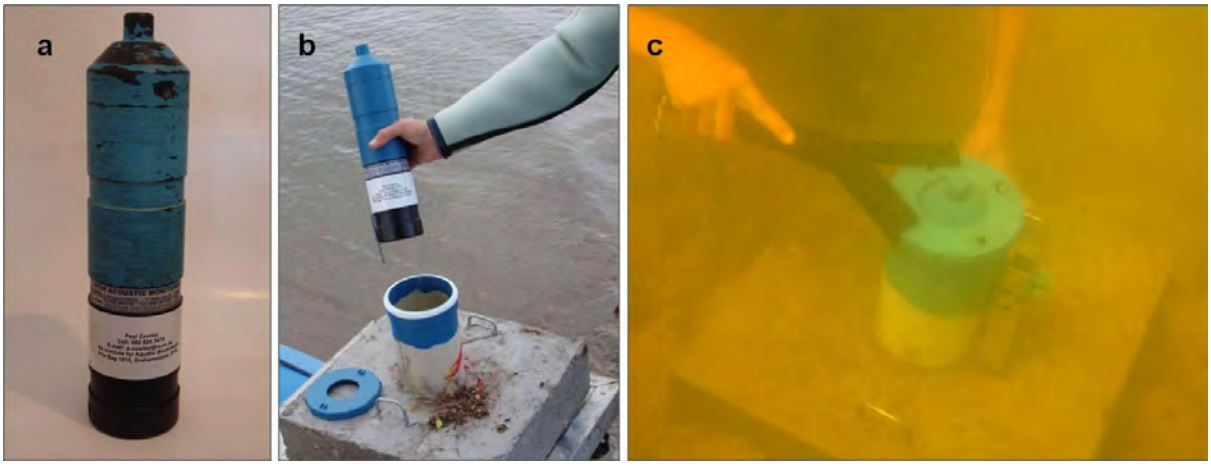

Figure 3.8: Mooring system used to secure stationary receivers in the study areas showing a) VR2W data-logging acoustic receiver, b) receiver and mooring block before deployment and c) diver retrieving receiver from mooring block

The range over which transmitter signals are detected can be affected by submerged vegetation, bottom topography, water flow (Giacalone *et al*. 2005), propagation effects, ambient noise, temperature and salinity discontinuities, and suspended particulate matter (Stasko and Pincock 1977, Lepage *et al*. 2005). Detection range decreases with increased ambient noise produced by heavy rains, breaking waves and strong wind, and the associated entrapment of air bubbles in the water (Lembo *et al*. 2002). As a result of the variability in detection ranges in different environments, each telemetry study was preceded by *in situ* range testing trials (Giacalone *et al*. 2005). An acoustic

transmitter, attached to a weighted line, was deployed at a range of distances from each receiver, to determine the maximum detection range. Detection ranges varied among and within estuaries, depending on the environmental conditions, such as tidal phase and wind speed (Childs *et al*. 2008b). Maximum detection ranges of 110 to 610 m, 50 to 340 m, 110 to 350 m and 250 to 500 m, were observed at individual receivers in the Great Fish, East Kleinemonde, Kariega and Sundays estuaries, respectively.

Passive tracking was continuous throughout each study period: September to October 2003 in the Great Fish Estuary, February to September 2008 in the East Kleinemonde Estuary, March 2009 to February 2010 in the Kariega Estuary and March to November 2010 in the Sundays Estuary.

Manual tracking

Manual tracking was used to assess home range sizes and locations in the Great Fish, East Kleinemonde and Kariega estuaries. Tagged fish were manually tracked from a small boat, using a directional hydrophone (VH110, VEMCO), connected to a portable receiver (VR60 or VR100, VEMCO). Tracking during each session was conducted systematically, starting at the mouth of each estuary and ending once all active transmitters had been located. When a transmitter signal was detected, the hydrophone gain was reduced and the boat was manoeuvred in the direction of maximum signal strength, until equal in all directions at the lowest gain (i.e. 0 db), at which time a GPS positional fix (Garmin GPS12, ± 5 m accuracy) was recorded for that fish. The boat was then anchored over the recorded position, and environmental variables (air and water temperatures, salinity, turbidity, current speed, secchi depth and water depth) were measured.

Manual tracking was conducted daily in the Great Fish Estuary, from 30 September to 12 October 2003, during daylight hours (07:00 – 18:00). In the East Kleinemonde Estuary, the aim of the manual tracking was to identify whether home range location was affected by time of day. As such, three tracking sessions, night-time (after 20:00), dawn (05:00 – 09:00, to record crepuscular activity) and midday (12:00 – 15:00), were conducted on each tracking day, during which all fish with active transmitters were detected. Manual tracking in this estuary was conducted every third day, from 28 February to 30 April 2008. Manual tracking was conducted in the Kariega Estuary to provide information on home range sizes and locations, and to confirm whether fish used the shallow sandbank area outside the range of the receiver array. Manual tracking was conducted every third day from 26 March to 5 June 2009, during daylight hours (07:00 – 18:00).

Manual tracking accuracy can be affected by the swimming speed and depth of the fish, pulse-repetition rate of the transmitter and the experience of the tracker (Stasko and Pincock 1977). Therefore, prior to the initiation of this study, the precision and accuracy with which fish positions could be detected during manual tracking were assessed. A transmitter, attached to a weighted line, was deployed by an assistant at a number of positions throughout an estuary, and the location of each deployment was withheld from the manual tracker, to test the accuracy with which the position of the transmitter could be detected. The error in position estimation was less than 2 m on each occasion.

3.2.5 Data Analysis

Fish require up to 24 hours to overcome the imbalance in blood concentrations of calcium, magnesium, sodium and other electrolytes caused by a change in gill permeability as a result of adrenalin and cortisol, released as a response to the stress of handling and surgery (Kreiberg 2000). Mulcahy (2003) suggests that after release (post surgery) fish often remain at the release site, reluctant to leave. Lower *et al*. (2005) agree that behaviour after release may be affected by the surgery or capture process, and that behaviour recorded within 12 to 24 hours post-surgery should not be included in the results. Pickering *et al*. (1982) reported recovery times of brown trout in excess of a week, and suggested that results obtained within the first two weeks should be interpreted with caution. Robichaud and Rose (2002) delayed tracking of Atlantic cod for 15 days after release to avoid inclusion of "potentially abnormal behaviour after surgery". Similarly, Masters *et al*. (2005) allowed 10 days before tracking pike, to avoid distortion of results, as a result of the tagging process. Zeller (1997) commenced manual tracking immediately after release, but the first 24 hours were not included in his analysis. In the current study, data for the first 24 hours were excluded from analyses, to avoid irregular behaviour that may result as a response to the stress of handling and surgery (Kreiberg 2000).

Area use

The length of estuary used by each individual was determined as the distance between the upper- and lower-most stationary receivers on which it was detected. While this is a conservative estimate, as a fish may have moved slightly beyond the upper- or lower-most receiver on which it was detected, the short distances between reception ranges of adjacent receivers and the low variability in estimates suggest that the method provides a suitable estimate of the length of the estuary used by each individual. Lengths of estuary used in each of the study estuaries were compared using a Kruskal-Wallis ANOVA (after a Shapiro-Wilk test showed that data were not normally distributed;

$p < 0.001$). Mean length of estuary used was then plotted against estuary length using linear regression, to determine whether the length of estuary used was related to estuary size. Statistical analyses were conducted in Statistica 10.0 (StatSoft. Inc., USA).

Area use was quantified by the proportion of time each fish spent in the vicinity of each receiver (Cowley *et al.* 2008). All time spent between consecutive detections at each receiver was summed, and allocated to that receiver. Similarly, time spent between consecutive detections at neighbouring receivers was divided, and half the time allocated to each of the respective receivers. The total time spent by each individual within the vicinity of each receiver was thus determined as the sum of a) the time between consecutive detections at a single receiver, and b) half the time between consecutive detections at neighbouring receivers.

Absence periods

Stationary receiver data from the Great Fish, Kariega and Sundays estuaries showed that some fish were absent from the array (undetected) for extended periods, being last recorded and again first recorded on receiver 1, in the mouth region of each system. Such absence periods, depending on duration, have been treated in previous studies as representing "sea trips", where the fish was assumed to have left the estuary if absent from the array for a certain minimum period e.g. 24 h. However, the position of the lower-most receiver in each estuary in the current study differed, due to the physical differences among estuaries. Therefore, assumptions of these periods representing time out of the estuary (i.e. the duration of a sea trip) varied among systems. Consequently, for the estuarine area use analysis, such absence times were neither allocated to a sea trip, as this could not be confirmed, nor to receiver 1, as presence within the estuary could not be confirmed. Absence periods in excess of 24 hours were, therefore, allocated simply to "absence" time, presented in the relevant figures as receiver '0'.

To provide an assessment of these absence periods, or sea trips, considering the varying distances between the mouth and lower-most receiver within each system, two different minimum absence period durations were defined. Childs *et al*. (2008b), working in the Great Fish Estuary, South Africa, considered a fish to have undertaken a sea trip, if it was not detected on the receiver closest to the mouth (receiver 1) for a duration of at least 6 h (approximating one tidal phase), during which time it was not detected on any other receiver in the system. Alternatively, Cowley *et al*. (2008), working in the same estuary, considered such absence periods as representing sea trips only if they exceeded 24 h (representing one diel cycle). In this estuary, in the current study and those of Childs *et al*.

(2008) and Cowley *et al*. (2008), receiver 1 was approximately 0.4 km from the open mouth. However, in the Sundays Estuary, receiver 1 was 2.3 km from the mouth. This meant that fish could have left the detection range of receiver 1 by moving towards the mouth, but not necessarily have left the estuary. Two minimum absence durations, 6 h and 24 h, were thus used as criteria.

Home range analysis

Home range sizes and locations were determined using a geographic information system (GIS) in ArcView 3.3 (Environmental Systems Research Institute) with the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997). Core (50% utilisation distribution, UD) and home range (95% UD) areas were calculated from manual tracking positional fixes, using the fixed kernel home range utilisation distribution method (Worton 1989). The core areas and home ranges of each fish in the East Kleinemonde Estuary were calculated using all positional fixes, as well as separately for each time-of-day category (i.e. dawn, midday and night-time). The view projection parameters for the analyses were set according to those required for the geographical location of the general study area, as follows:

Projection: Transverse Mercator (projection to retain accurate size and shape of study area)
Spheroid: WGS84 (standard spheroid for GIS analyses of the South African context)
Central meridian: 26 or 27 (based on the study area, 26 to 27° E)
Scale factor: 0.9996 (precision of area estimates within 180 km east and west of central meridian)
False Easting: 500 000 (the value added to the easting value, i.e. distance east of the centre of the zone of study from a central meridian, to ensure a positive easting value)
False Northing: 10 000 000 (value added to northing value, i.e. distance north of a reference latitude, based on the study area being in the Southern Hemisphere)

Depth during manual tracking

Depth data recorded during tracking sessions conducted in the East Kleinemonde Estuary at the three different times throughout each tracking day (dawn, midday, night-time) were compared for Fish 2002, 2003 and 2004, for each of which 42 positional fixes were made (three positions per day for 14 days). These comparisons were made using the Kruskal-Wallis ANOVA (as the Shapiro-Wilk test for normality showed that variables differed significantly from the normal distribution, $p < 0.01$ in most cases).

3.3 Results

In the Great Fish Estuary, numbers of positional fixes made during manual tracking (range 1 – 13) and detections logged on the stationary receivers (range 1 – 9 491) varied considerably among individuals (Table 3.6). Three fish (ID codes 73, 77 and 79) were detected infrequently during manual tracking and also produced few receiver detections, and were, therefore, excluded from all analyses. While Fish 87 was detected only seven times by the stationary receivers, it was located on 11 manual tracking days, possibly because it spent most of its time between receivers (i.e. outside of their detection ranges). This fish was included in the manual tracking analysis but was excluded from the passive tracking analysis due to the low number of detections.

In the East Kleinemonde Estuary, the total numbers of stationary receiver detections also varied among individuals (range 1 261 – 95 853), for fish tagged with both long- and short-period transmitters (Table 3.6). The number of positional fixes obtained for the six individuals manually tracked also varied. Transmitter 2006 remained in the same location throughout the study period and the use of an underwater receiver (VEMCO, model VUR), confirmed that the transmitter had been expelled and covered by sediment. This fish was excluded from all analyses. Data for home range analyses were obtained from the remaining five fish. Fish 2001 and Fish 2005 were last detected 20 and 37 days after tagging, respectively. Their absence from the estuary after these dates was confirmed by the subsequent data upload from the stationary receivers, which showed that neither fish had passed the uppermost receiver into the riverine environment. As the estuary mouth was closed during this period, these fish were assumed to have been removed from the system by avian predation or capture by anglers. Consequently, 12 and 15 positional fixes were made for Fish 2001 and 2005, respectively, while 42 were made for each of Fish 2002, 2003 and 2004. For each of these three fish, 14 detections were made during morning, midday and night-time tracking sessions.

In the Kariega Estuary, nine of the ten individuals were present in the system until at least 92 days post-tagging, representing the end of the manual tracking period, with up to 685 025 stationary receiver detections for a single fish (Table 3.6). Fish 2044 left the estuary through the open mouth, prior to manual tracking. However, this individual was detected 3 526 times on the stationary receivers, and was therefore included in the area use analyses.

In the Sundays Estuary, the number of receiver detections was again highly variable (range 1 305 – 178 813) (Table 3.6). Although Fish 64989 was only detected 1 305 times on the stationary receivers, it was present in the estuary for 103 days post-tagging, and was thus included in the analyses.

Table 3.6: Stationary receiver detections, manual tracking positional fixes and home range (95% UD) and core area (50% UD) sizes for white steenbras tracked in the Great Fish (GFR), East Kleinemonde (EKM, L/S = long-/short-period), Kariega (KAR) and Sundays (SUN) estuaries (*individuals excluded from passive tracking analyses, $^{+}$ individuals excluded from manual tracking analyses)

Estuary	Fish ID	FL (mm)	Receiver detections	Days passively monitored	Length of estuary used	Positional fixes	Home range size (m^2)	Core area size (m^2)
GFR	73	174	1 *	-	-	1 $^{+}$	-	-
GFR	77	178	3 *	-	-	6 $^{+}$	-	-
GFR	79	171	9 *	-	-	1 $^{+}$	-	-
GFR	82	154	2 790	14	1 200	13	118 518	23 839
GFR	83	168	556	13	-	13	119 876	36 065
GFR	84	167	2 858	15	3 800	13	122 992	23 374
GFR	86	171	629	12	3 200	10	69 772	14 042
GFR	87	170	7 *	-	-	11	81 357	8 152
GFR	88	166	355	5	-	11	91 729	19 256
GFR	92	184	9 491	13	4 600	13	77 551	9 028
EKM	3759 *L*	291	8 231	202	1 400	-	-	-
EKM	3760 *L*	302	31 345	269	2 800	-	-	-
EKM	3761 *L*	274	12 573	270	1 980	-	-	-
EKM	3762 *L*	267	70 274	232	1 980	-	-	-
EKM	3764 *L*	254	30 408	270	1 980	-	-	-
EKM	3765 *L*	247	11 825	262	1 980	-	-	-
EKM	3766 *L*	238	1 261	9	850	-	-	-
EKM	3768 *L*	247	69 293	175	2 800	-	-	-
EKM	3769 *L*	255	48 938	262	1 980	-	-	-
EKM	3770 *L*	247	59 867	247	2 800	-	-	-
EKM	2001 *S*	247	28 736	29	1 980	12	48 142	10 670
EKM	2002 *S*	235	95 853	122	1 980	42	47 282	9 286
EKM	2003 *S*	266	41 443	84	1 980	42	70 711	8 693
EKM	2004 *S*	265	32 957	96	1 400	42	83 870	6 684
EKM	2005 *S*	240	30 836	42	440	15	26 917	10 311
EKM	2006 *S*	262	-	-	-	-	-	-
KAR	2036	379	82 388	120	4 440	15	44 964	8 496
KAR	2037	307	404 174	351	11 290	15	115 748	18 759
KAR	2038	268	440 089	331	5 900	14	66 110	8 163
KAR	2039	244	45 938	132	520	14	70 853	10 251
KAR	2040	215	161 961	187	2 330	15	80 194	9 407
KAR	2041	227	685 025	342	2 330	15	62 551	13 423
KAR	2042	318	422 721	355	4 440	15	136 457	25 771
KAR	2043	234	320 220	191	520	14	81 738	11 883
KAR	2044	302	3 526	6	4 440	-	-	-
KAR	2045	284	275 138	319	7 950	15	77 393	16 687
SUN	64989	236	1 305	103	12 070	-	-	-
SUN	64990	224	76 334	204	9 900	-	-	-
SUN	64991	208	44 269	175	15 911	-	-	-
SUN	64992	208	70 106	187	9 900	-	-	-
SUN	64993	315	103 576	204	2 830	-	-	-
SUN	64994	256	57 982	204	4 820	-	-	-
SUN	64995	236	94 846	167	630	-	-	-
SUN	64996	277	35 569	202	1 710	-	-	-
SUN	64997	208	33 326	204	4 820	-	-	-
SUN	64998	223	83 838	203	630	-	-	-
SUN	64999	235	178 813	256	1 710	-	-	-
SUN	65000	235	103 001	204	630	-	-	-
SUN	65001	235	70 013	203	9 900	-	-	-
SUN	65002	232	22 958	202	-	-	-	-
SUN	65003	245	154 947	203	3 780	-	-	-

3.3.1 Estuarine distribution and area use

Length of estuary used

Fish tagged in the Great Fish Estuary were detected on stationary receivers 1 to 7, located 0.4 km and 7.6 km from the mouth, respectively (Figure 3.3). Similarly, fish were manually located from 0.4 km to 8.1 km from the mouth, providing agreement of results between methods. The length of estuary used by each individual in this estuary, recorded as the distance between lower- and uppermost positional fixes, ranged from 1 200 to 4 600 m (mean = 3 200 ± 1 451 m; n = 4), representing 10 to 38% of the estuary length. Fish 83 and 88 were excluded from this analysis, due to being detected on a single receiver. If Fish 92 (i.e. the only fish to undertake a large-scale excursion in this estuary) is excluded, mean length of estuary used decreases to 2 700 m (± 1 361 m), highlighting the restricted area use of the remaining individuals. Overall, 76% (n = 64) of all positional fixes were made within a 700-m stretch of the estuary, while 85% (n = 72) were made within a 2-km stretch, between 5.3 and 7.3 km from the mouth. The mean of individual proportions of positional fixes within this stretch of the estuary was equally high (mean = 85 ± 25%; n = 7).

The lengths of estuary used by each individual in the East Kleinemonde Estuary ranged from 440 to 2 800 m (mean = 1 888 ± 666 m, n = 15), representing 13 to 80% of estuary length. The individual mean distance between each positional fix and the capture location for the five fish manually tracked was 511 m (± 344 m) (range: 96 - 887 m), indicating fidelity to their capture locations. Ninety-five percent of detections for each fish were made within a mean distance of 1 100 m (± 690 m), and 50 % within 530 m (± 350 m) of the closed mouth. The greatest distance a fish was detected from the mouth was 1 600 m, in the vicinity of receiver 4. Overall, less than 1% of time (determined from the passive tracking) was spent beyond this receiver. No fish were recorded in the upper reaches during the manual tracking sessions.

The lengths of estuary used in the Kariega and Sundays estuaries ranged from 520 to 11 290 m (mean = 4 416 ± 3 350 m, n = 9) and 630 to 15 911 m (mean = 5 660 ± 4 993 m, n = 14), representing 3 to 66% and 3 to 77% of estuary length, respectively. Fish 65002 in the Sundays Estuary was excluded from this analysis, as it was detected on a single receiver. Lengths of estuary used did not differ significantly between these two estuaries (t-test, p = 0.50). In the Kariega Estuary, fish were manually tracked from approximately 1 400 to 3 300 m from the mouth, between receivers 1 and 5.

The minimum lengths of estuary used were similar, ranging from 440 to 1 200 m in the East Kleinemonde and Great Fish estuaries, respectively, and the median length of estuary used did not

differ significantly among estuaries (Kruskal-Wallis ANOVA, p = 0.091). However, mean length of estuary used increased with increasing estuary length, and a regression analysis showed a strong significant correlation between the two variables (p = 0.015, R^2 = 0.970) (Figure 3.9).

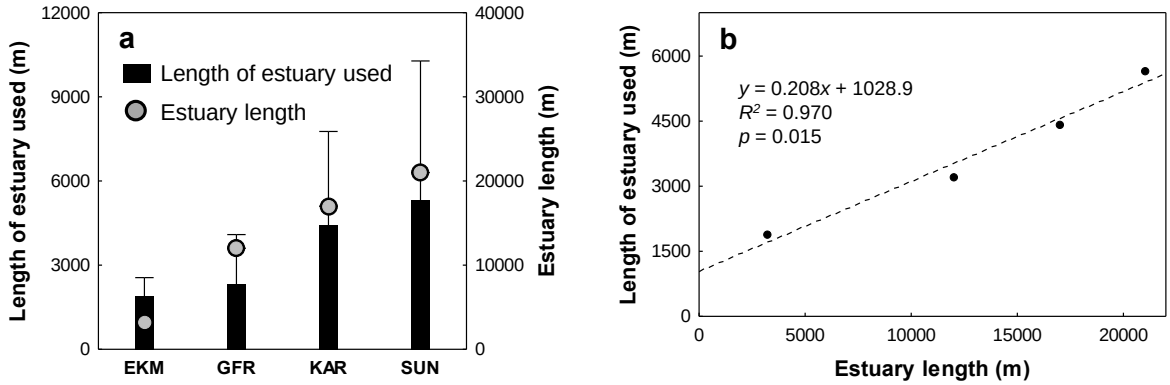

Figure 3.9: (a) Mean (±SD) length of estuary used (m, bars, left y-axis) plotted with estuary length (m, solid circles, right y-axis) in East Kleinemonde (EKM), Great Fish (GFR), Kariega (KAR) and Sundays (SUN) estuaries, and (b) regression plot of the two variables (p = 0.015, R^2 = 0.970),

Area use

In the Great Fish Estuary, the fish exhibited high levels of site fidelity and occupied small areas within their estuarine nursery habitat throughout the study period (14 days). On average, fish spent the majority of their time in the vicinity of receiver 6 (Figure 3.10), which was closest to the tagging site. Two fish spent 100% and three fish at least 90% of their time in this area. The mean of 4.5% spent in the vicinity of receiver 1 was a result of Fish 92 spending more than 25% of its time in this area. Data from the stationary receivers indicated a rapid downstream movement of this fish nine days after tagging, after which it was regularly located within a new, similarly small area in the mouth region.

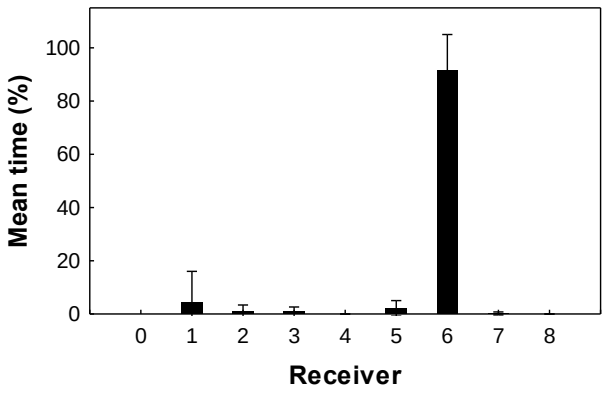

Figure 3.10: Mean (± S.D.) time (%) spent in the vicinity of each receiver for all fish included in the passive tracking analyses (n = 6) for the Great Fish Estuary (receiver 0 represents absence time)

In the East Kleinemonde Estuary, mean time spent by all fish tagged with long-period transmitters was highest in the vicinities of receivers 3 and 4, in the lower to middle reaches, near the capture site (Figure 3.11 a). Similarly, mean time spent for all short-period transmitter fish was highest in the vicinity of their capture site, at Receiver 1 nearest the mouth, with a secondary peak at Receiver 3 in the lower reaches (Figure 3.11 b).

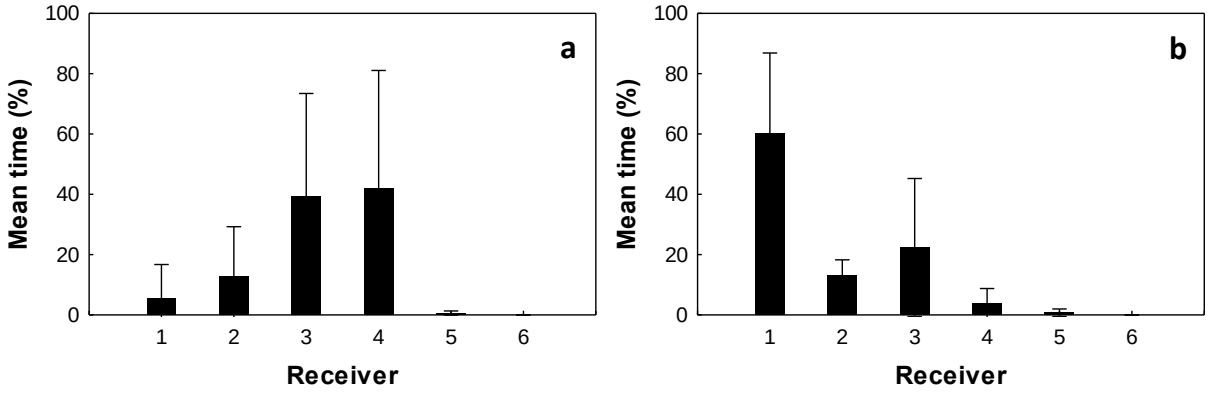

Figure 3.11: Mean time (% ± SD) spent in the vicinity of each receiver for a) the ten long-period transmitter fish, and b) the five short-period transmitter fish

In the Kariega and Sundays estuaries, the majority of time was spent in the lower reaches, with some activity in the mouth region and middle reaches. In the Kariega Estuary, the fish spent the majority of their time, on average, in the vicinity of receiver 3, approximately 1.9 km from the open mouth (Figure 3.12 a). In the Sundays Estuary, two peaks were observed, in the vicinities of receivers 2 and 4, approximately 2.9 and 5.1 km from the mouth, respectively (Figure 3.12 b). Each peak, representative of a centre of activity, was frequented by different individuals (i.e. no fish exhibited peaks at both receivers). Small peaks at receivers 10 and 15 in the Sundays Estuary were the result of three individuals making use of the upper reaches of this system. Fish 64992 and 65001, spent 18 and 58%, respectively, of their time between approximately 10 and 12.5 km from the mouth, while Fish 64991 extended its distribution beyond this area, where it spent more than 30% of its time in the vicinity of receiver 15 (roughly 16 km from the mouth). It also undertook numerous excursions to receiver 16, at the river-estuary interface. Two other individuals (Fish 64989 and 64990) made excursions as far as receiver 12, but spent very little time further than 7 km from the mouth. In contrast, only one individual (Fish 2037) was detected beyond receiver 7 in the Kariega Estuary (5.8 km from the mouth), where it spent less than 1% of its time. In the Kariega Estuary, the combined time spent by all individuals beyond approximately 4 km from the mouth, was only 3% of the total time tracked.

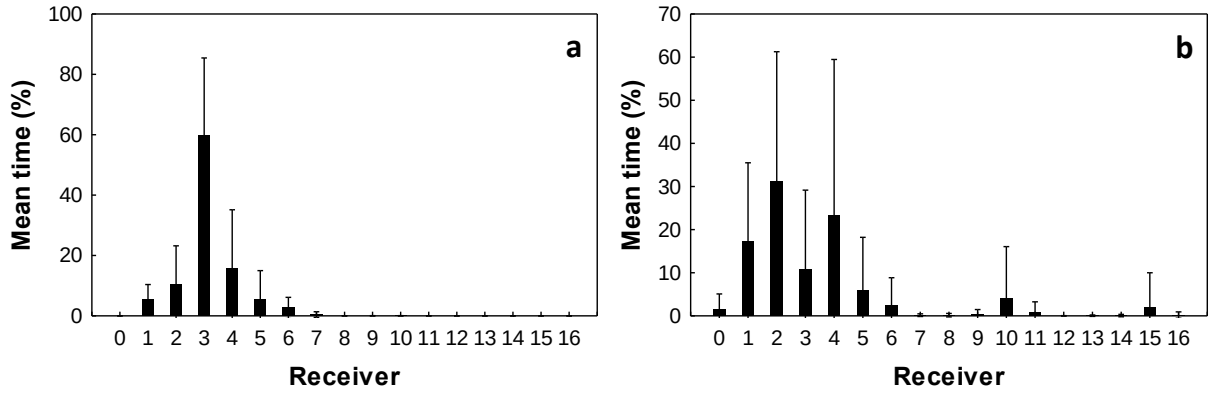

Figure 3.12: Mean times (%) spent in the vicinities of each receiver, for white steenbras tagged in the a) Kariega (n = 10) and b) Sundays (n = 15) estuaries (receiver 0 represents absence time)

Absence periods

The numbers of absence periods, and the numbers of individuals undertaking such absence periods (long-term excursions from receiver 1) varied considerably among estuaries, and were dependent on whether the 6-h or 24-h minimum absence period duration was used (Tables 3.7 and 3.8)

Table 3.7: Minimum, maximum, mean and total duration (d hh:mm:ss) of absence periods in excess of 6 h from receiver 1, for white steenbras from the Great Fish, Kariega and Sundays estuaries

Estuary	Fish ID	No. trips	Min duration	Max duration	Mean duration	SD duration	Total duration	% of total time
GFR	92	3	0 08:20:54	0 10:32:06	0 09:32:28	0 01:06:24	1 04:37:23	9.69
KAR	2038	1	0 13:20:03	0 13:20:03	0 13:20:03	-	0 13:20:03	0.17
KAR	2041	3	0 12:23:02	0 16:03:51	0 13:50:55	0 01:57:06	1 17:32:44	0.51
KAR	2042	5	0 06:06:00	0 07:17:23	0 06:41:35	0 00:33:22	1 09:27:57	0.39
KAR	2043	2	0 09:10:15	0 10:14:58	0 09:42:36	0 00:45:46	0 19:25:13	0.43
SUN	64990	3	0 06:56:19	0 08:45:30	0 07:35:31	0 01:00:45	0 22:46:32	0.47
SUN	64992	93	2 03:03:24	5 11:24:51	3 04:19:57	1 08:16:33	65 06:57:16	31.05
SUN	64993	5	0 06:26:17	1 12:05:34	0 15:46:54	0 12:14:14	3 06:54:29	1.62
SUN	64994	1	0 06:26:53	0 06:26:53	0 06:26:53	-	0 06:26:53	0.13
SUN	64995	5	0 06:02:20	3 20:20:51	1 00:33:54	1 13:57:02	5 02:49:32	3.03
SUN	64996	1	0 07:05:47	0 07:05:47	0 07:05:47	-	0 07:05:47	0.15
SUN	64997	2	0 06:11:30	0 06:32:12	0 06:21:51	0 00:14:38	0 12:43:42	0.26
SUN	64998	22	0 12:47:36	1 12:08:00	0 23:56:47	0 08:24:12	10 14:31:59	5.48
SUN	64999	15	0 10:14:21	1 00:48:34	0 14:17:22	0 06:04:56	6 04:11:50	2.41
SUN	65000	21	0 10:40:11	1 10:35:52	0 19:55:37	0 09:58:29	9 05:13:14	4.54
SUN	65001	4	0 06:23:12	0 09:47:01	0 07:47:05	0 01:30:42	1 07:08:21	0.64
SUN	65003	2	0 06:34:46	0 06:57:36	0 06:46:11	0 00:16:09	0 13:32:22	0.28

Using the 6-h minimum duration, 17 white steenbras undertook a total of 188 excursions, although 50% of these (n = 93) were undertaken by a single individual. In total, Fish 92 was the only fish from the Great Fish Estuary to undertake such excursions, and the total time spent absent from receiver 1 (for all excursions > 6 h) for this fish was almost 10% of the total time it was monitored. For fish 64992, 64998 and 65000 in the Sundays Estuary, 31.0, 5.5 and 4.5%, respectively, of their total time tracked was allocated to absence time. For the remaining 13 fish undertaking such absence periods, the total absence time was considerably less (Table 3.7). There were considerably fewer absence periods exceeding 24 h (Table 3.8). These periods were limited to six individuals from the Sundays Estuary. The cumulative duration of all 14 such excursions of fish 64992 was over 29 days, almost 15% of its total time tracked, although the proportions of absence time for the remaining fish were low.

Table 3.8: Minimum, maximum, mean and total duration (d hh:mm:ss) of absence periods in excess of 24 h from receiver 1 (only observed in the Sundays Estuary)

Fish ID	No. trips	Min duration	Max duration	Mean duration	SD duration	Total duration	% of total time
64992	14	1 00:26:40	5 11:24:51	2 01:54:06	1 03:45:52	29 02:37:20	14.37
64993	1	1 12:05:34	1 12:05:34	1 12:05:34	-	1 12:05:34	0.74
64995	1	3 20:20:51	3 20:20:51	3 20:20:51	-	3 20:20:51	2.28
64998	4	1 00:18:18	1 12:08:00	1 03:31:37	0 05:44:42	4 14:06:28	2.26
64999	1	1 00:48:34	1 00:48:34	1 00:48:34	-	1 00:48:34	0.40
65000	2	1 00:26:41	1 10:35:52	1 05:31:17	0 07:10:45	2 11:02:33	1.21

3.3.2 Home range size and location

Mean home range size (95% UD) of the seven white steenbras tracked in the Great Fish Estuary was 97 399 m^2 (± 22 557 m^2; range 69 772 – 122 992 m^2; n = 7), while mean core area size (50% UD) was 19 108 m^2 (± 9 794 m^2; range 8 151 – 36 065 m^2; n = 7) (Table 3.6). Mean home range size was small relative to the size of the estuary (approx. 1 360 000 m^2), and all home ranges were in close proximity to the capture/release site. Despite individual variability in home range size, home ranges of all individuals overlapped in a small section of the mesohaline to oligohaline region of the estuary, between approximately 5 and 7 km from the mouth (Figure 3.13).

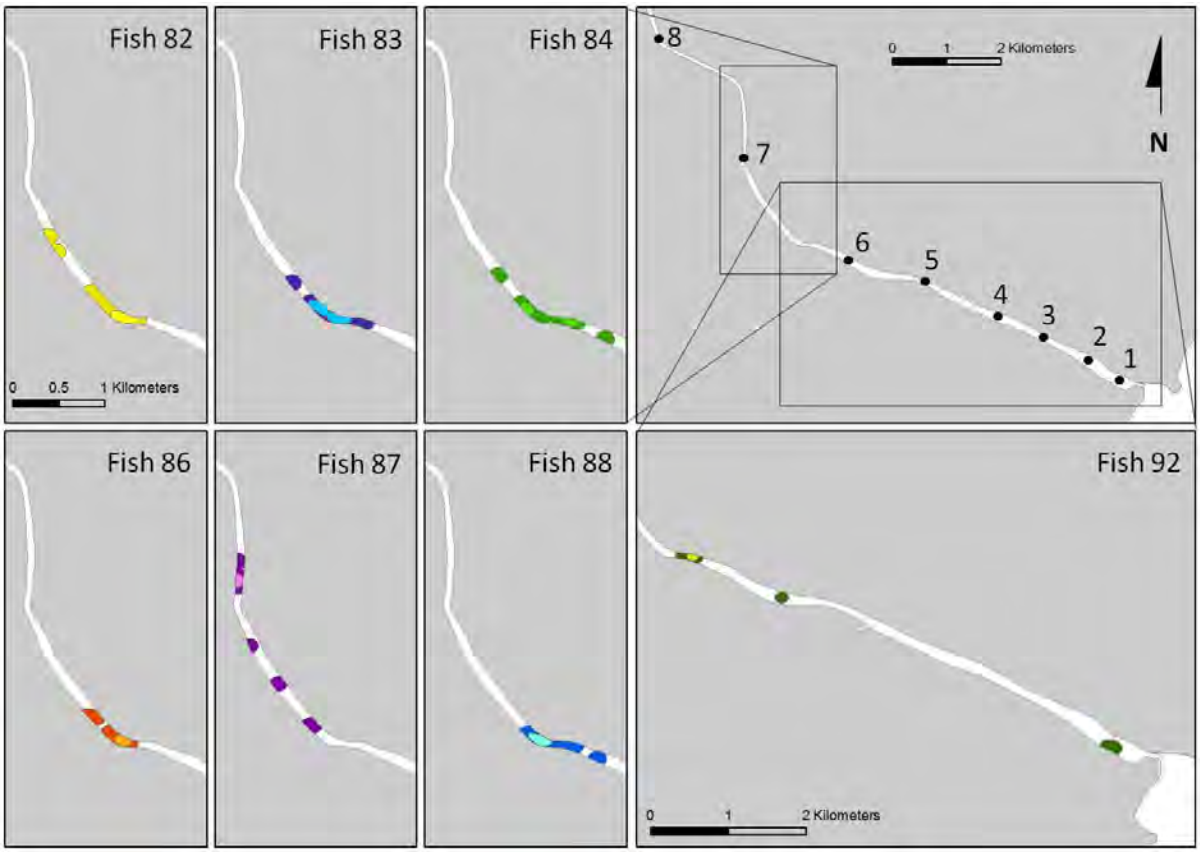

Figure 3.13: Core areas (50% UD) and home ranges (95% UD) of seven white steenbras manually tracked in the Great Fish Estuary (black dots represent receivers, lighter coloured polygons in each figure represent 50% UD)

Home ranges of the five white steenbras manually tracked in the East Kleinemonde Estuary ranged from 26 917 m^2 to 83 870 m^2 (mean = 55 385 ± 22 220 m^2, while core areas ranged from 6 684 m^2 to 10 670 m^2 (mean = 9 129 ± 1 578 m^2) (Table 3.6). The home ranges of most fish extended from the mouth region to the lower or middle reaches. The home range of one fish (Fish 2005) was restricted to the mouth region. The location of core areas differed among individuals, but all five fish had at least one core area within the mouth region (Figure 3.14).

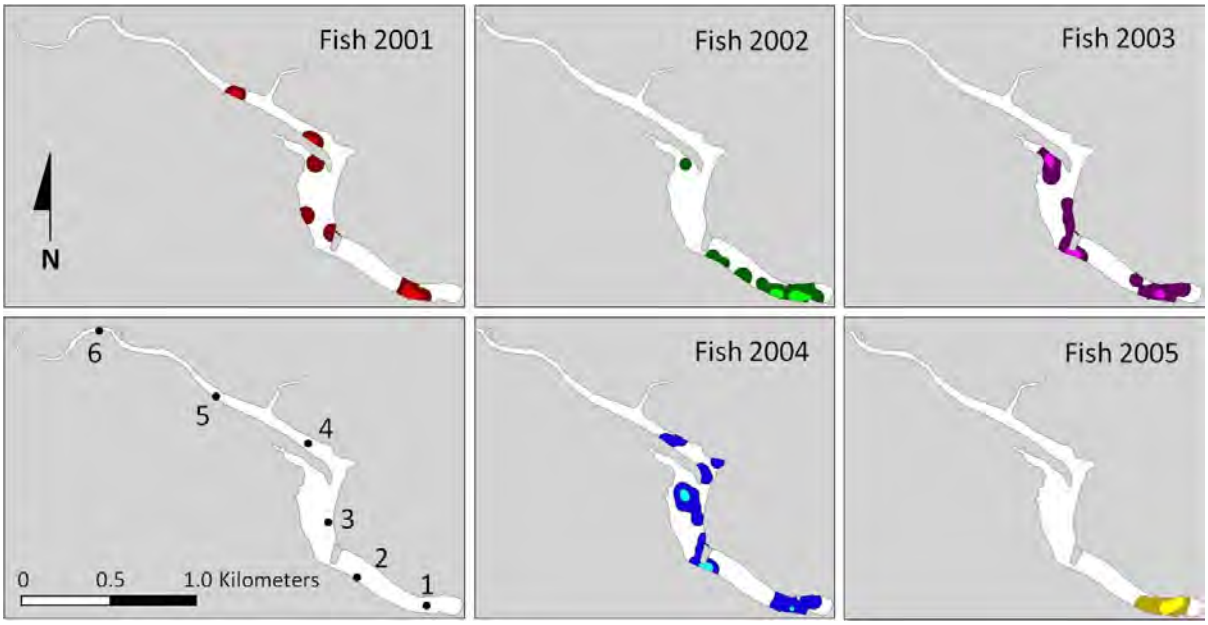

Figure 3.14: Core areas (50% UD) and home ranges (95% UD) of five white steenbras manually tracked in the East Kleinemonde Estuary (numbered black dots represent receivers, lighter coloured polygons in each figure represent 50% UD)

Home ranges and core areas calculated separately for day, night and dawn (crepuscular) positional fixes, for each of the three fish with 42 positional fixes (Fish 2002, 2003 and 2004), provided evidence of diel variability in home range and core area locations (Table 3.9).

Table 3.9: Core area (50% UD) and home range (95% UD) sizes (m^2) for the five white steenbras tagged with short-period transmitters in the East Kleinemonde Estuary, based on manual tracking positional fixes. Separate 50% and 95% UDs for different times of day were not calculated for Fish 2001 and 2005, due to the low numbers of positional fixes made for these two fish

Fish ID	Total fixes	50% UD (m^2)				95% UD (m^2)			
		All	Daytime	Night-time	Dawn	All	Daytime	Night-time	Dawn
2001	12	10 670	...	...	...	48 142	...	...	...
2002	42	9 286	5 499	8 500	8 099	47 282	36 883	30 872	30 052
2003	42	8 693	2 770	8 181	14 173	70 711	31 656	36 783	57 044
2004	42	6 684	3 060	6 599	8 240	83 870	33 494	43 175	71 426
2005	15	10 311	...	...	...	26 917	...	...	...
Mean		9 129	3 776	7 760	10 171	55 384	34 011	36 943	52 841
SD		1 578	1 499	1 018	3 467	22 220	2 652	6 153	21 005

Daytime home ranges for all three fish were fragmented. Daytime core areas were less fragmented and situated in the deeper channel area against the west bank, with at least one core area of each fish coinciding with a deep hole (± 4 to 5 m deep) under the road bridge (Figure 3.4). Night-time home ranges of the three fish were also all fragmented. Night-time core areas were almost exclusively located over the shallow sand area in the mouth region or the shallow sand/mud flats above the road bridge. Dawn home ranges were greater, and appeared more protracted, than day and night-time home ranges. For all fish, dawn home ranges were geographically located between night and day home range locations, providing the possible route between night and day areas (Figure 3.15).

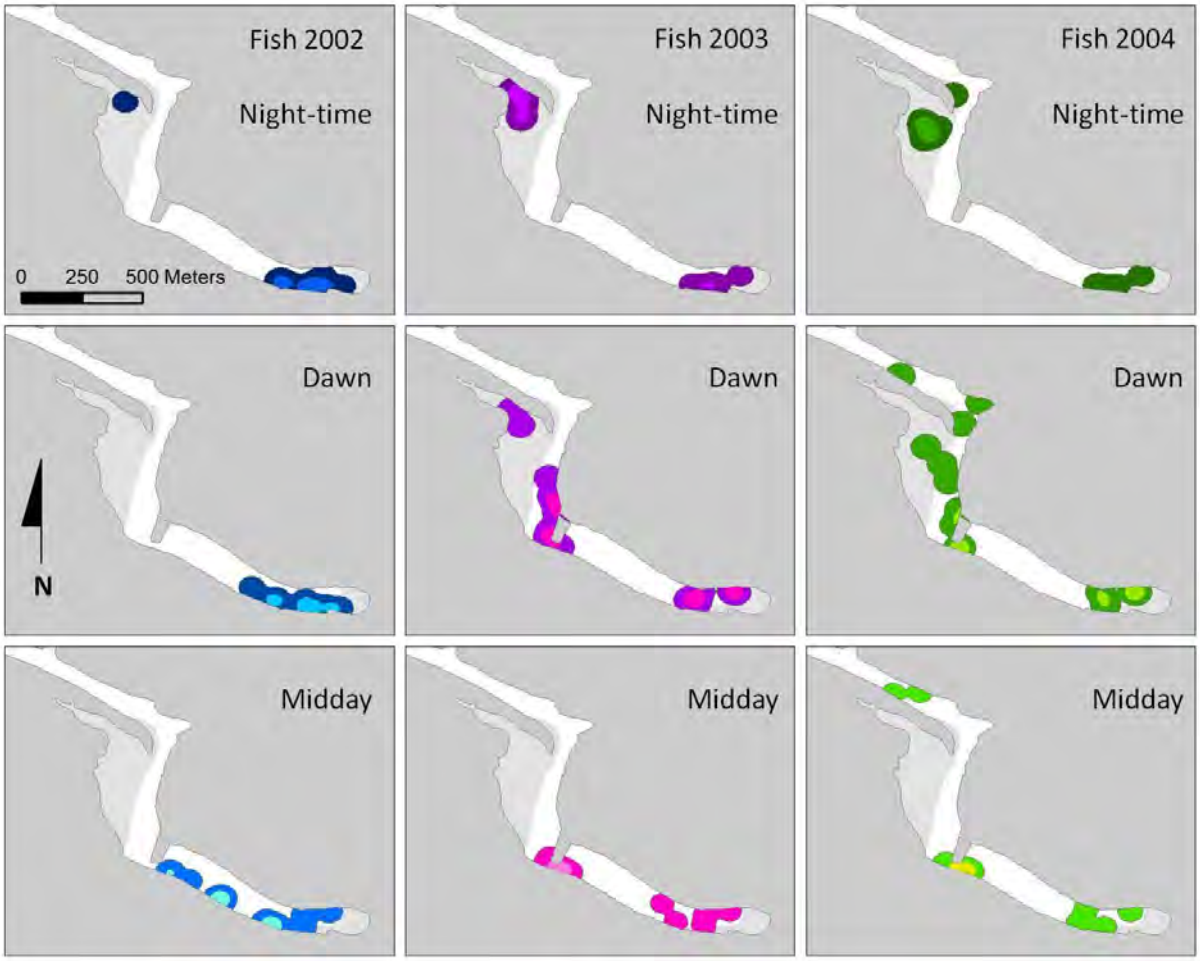

Figure 3.15: Night-time, dawn and midday home ranges (95% UD) and core areas (50% UD) for three fish (Fish 2002, Fish 2003 and Fish 2004, n = 14 positional fixes per fish per time period) manually tracked in the East Kleinemonde Estuary (lighter coloured polygons in each figure represent 50% UD). The lighter grey shaded areas indicates the shallow sand/mud area above the road bridge near receiver 3 and the shallow sand area at the closed mouth

Depths recorded at positional fixes made during different tracking sessions throughout the day in the East Kleinemonde Estuary were significantly different for two of the three individuals with 42 positional fixes (Figure 3.16). For these two individuals, Fish 2003 and 2004, depths recorded during midday sessions were significantly greater than those recorded during dawn or night-time sessions ($p < 0.001$ in both cases). Dawn and night-time depths did not differ significantly for these two individuals. When positional fixes of all fish were grouped, daytime, dawn and night-time depths all differed significantly ($p < 0.001$) (Figure 3.16 d).

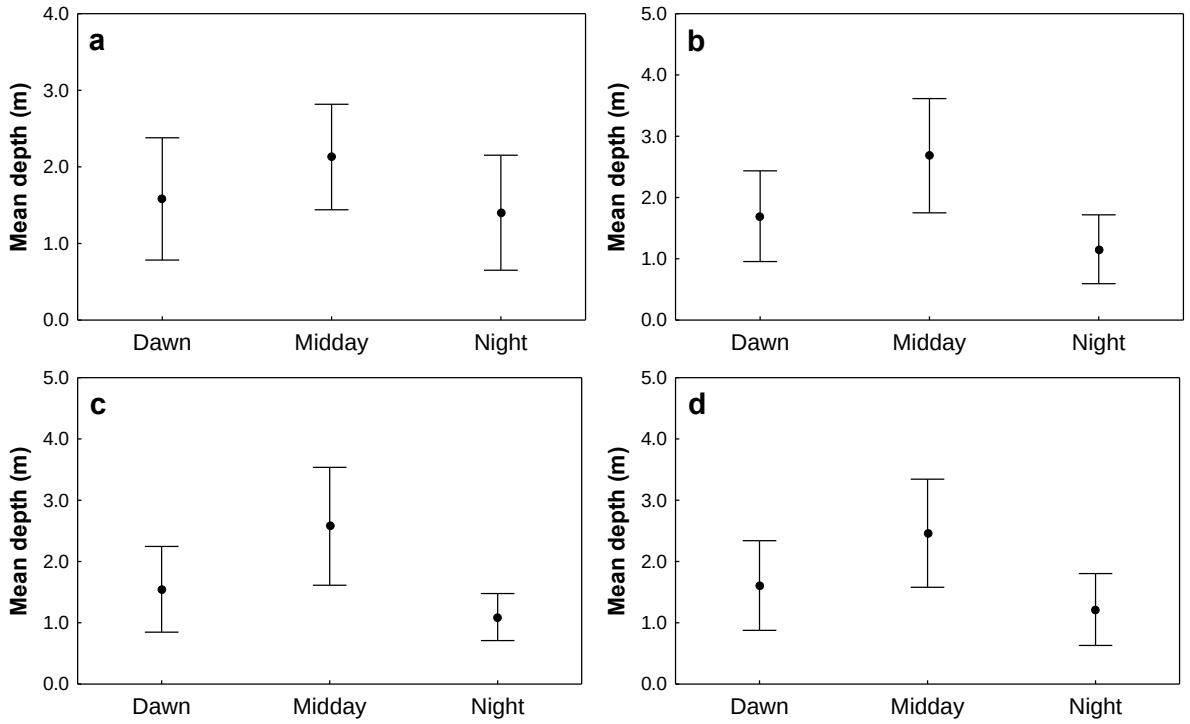

Figure 3.16: Mean (±SD) depths (m) recorded during different tracking sessions throughout the day, for a) Fish 2002, b) Fish 2003, c) Fish 2004, and d) for all fish as a group (Kruskal-Wallis ANOVA $p = 0.546$ (a), $p < 0.001$ (b – d))

Home ranges of the nine fish manually tracked in the Kariega Estuary were situated exclusively in the lower reaches, in close proximity to the capture location (Figure 3.17). Home ranges ranged in size from 44 964 m^2 to 136 457 m^2 (mean = 81 780 ± 27 960 m^2), while core areas ranged from 8 160 m^2 to 25 770 m^2 (mean = 13 649 ± 5 827 m^2) (Table 3.6). Seven of these individuals were detected on at least one day on the large sandbank adjacent to receiver 3, when the water level allowed boat access, providing evidence that the shallow banks are utilised when they become inundated.

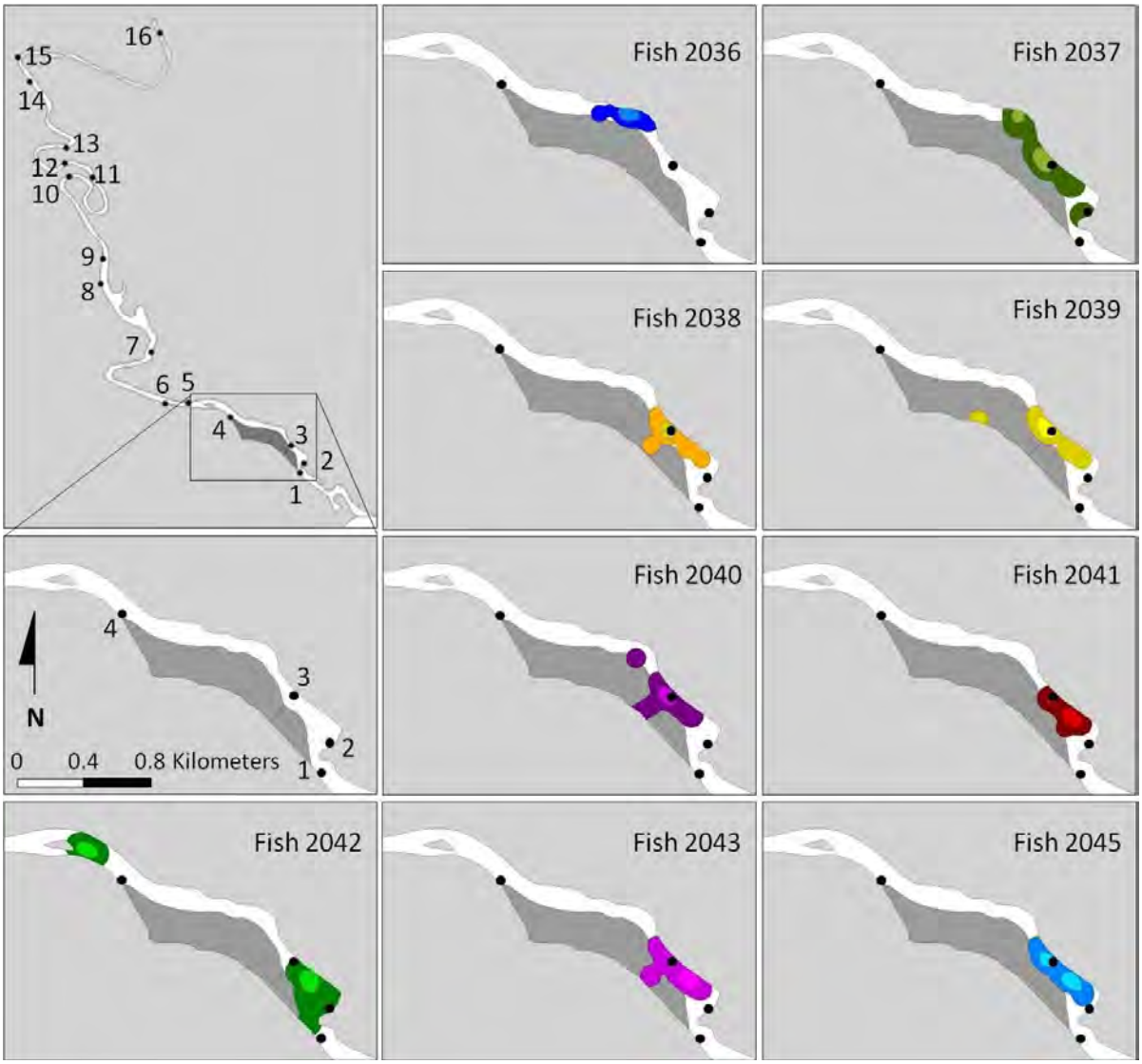

Figure 3.17: Core areas (50% UD) and home ranges (95% UD) of the nine white steenbras manually tracked in the Kariega Estuary (numbered black dots represent stationary receivers, lighter coloured polygons in each figure represent 50% UD, the dark grey shaded area represents the large intertidal sandbank near the mouth)

3.4 Discussion

The aim of this chapter was to describe area use patterns and home range characteristics of white steenbras, in a range of Eastern Cape estuaries, using acoustic telemetry. Both area use and home range were assessed in three estuaries; the medium-sized permanently open freshwater-dominated Great Fish, the small temporarily open/closed East Kleinemonde and the large permanently open freshwater-deprived Kariega Estuary. Area use patterns were also assessed in the large, permanently open freshwater-dominated Sundays Estuary. Fish tagged in each estuary showed similar distributional and area use patterns, with an apparent affinity for the sandy lower reaches.

As the study focused on juvenile white steenbras, (less than 380 mm FL), the maximum size of the acoustic transmitters used was constrained by the sizes of the fish monitored, and thus restricted the duration of the different study periods. The study in the Great Fish Estuary was a preliminary study, aimed at providing a first assessment of juvenile area use and home range characteristics in an estuary, and the fish monitored were small (154 – 184 mm FL), which limited the size of the transmitters used, and consequently the battery life. The results of this study were thus not intended to be nor are interpreted as a reflection of long-term area use or home range. The results did, however, provide evidence of capture site fidelity, which was taken into account in the sampling designs of the three subsequent studies. The fish monitored in the subsequent studies were larger (208 – 379 mm FL), allowing the use of larger transmitters, with longer battery lives.

3.4.1 Estuarine distribution and area use

Length of estuary used

The lengths of estuary used by tagged individuals were fairly consistent in each estuary, with means of 3 200 (± 1 451 m), 1 888 (± 666 m), 4 416 (± 3 350 m) and 5 660 (± 4 993 m), in the Great Fish, East Kleinemonde, Kariega and Sundays estuaries, respectively. Most fish in each system utilised only a portion of each estuary; however, the mean length of estuary used was significantly correlated to the estuary length. Therefore, although the lengths of estuary used are small, relative to the lengths of each estuary available to the fish, the length of estuary used appears to increase as a function of estuary length, and there is evidence that they explore parts of the estuary outside of their home ranges. In the Kariega Estuary the result was slightly different, where it appeared that the upper limit of the white steenbras distribution was restricted, possibly by the physical conditions further from the mouth. Environmental factors affecting the observed movement and area use in these estuaries are addressed in Chapter 5.

Although the lengths of estuary used did not differ significantly between the Kariega and Sundays estuaries, the maximum length of estuary used by an individual was considerably greater in the Sundays Estuary, and only a single individual ventured outside of the first third of the freshwater-deprived Kariega Estuary. Five individuals ventured up the Sundays Estuary as far as 12 km from the mouth, further than any recorded movements in the Kariega Estuary, and one individual spent at least one third of its time (68 days) between 16 and 20 km from the mouth, where the salinity ranges between approximately 0 and 3, suggesting that there are few or no obstructions to the movement of white steenbras into the upper reaches of the Sundays Estuary. Considering that the substrate in the Sundays Estuary becomes predominantly mud about 4 km from the mouth,

substrate is unlikely a factor limiting up-estuary movement in the Kariega Estuary, indicating that the uppermost limit of white steenbras movement in this estuary is likely governed by another factor, such as salinity. It is also interesting to note that all the time spent by Fish 64991 between 15 and 20 km from the mouth in the Sundays Estuary was from July to September, during which the water temperature in the upper reaches decreased to a minimum of 10.8°C, with a mean of 13.3 (± 0.8°C). Whitfield (1995) identified that most mass mortalities of fish in South African estuaries occurred with a combination of low salinity (< 3) and low temperatures (< 14°C). Bennett (1985) recorded white steenbras mortalities in the Bot Estuary, after prolonged periods of unusually low salinity (3), during which the temperature was approximately 16°C. Therefore, the excursions in the Sundays Estuary into conditions of potentially low suitability are unlikely to be random exploratory movements. Hindell *et al*. (2008) speculated that the use of riverine or low-salinity environments by estuarine fishes may be for parasite removal, or for feeding. Similarly, Cowley *et al*. (2008) suggested that dusky kob excursions into the freshwater region of the Great Fish Estuary may have been associated with attempts to rid the fish of parasites. This may also have been the case with the white steenbras in the Sundays Estuary. The fact that only one individual exhibited this behaviour suggests that such excursions are uncommon in white steenbras behaviour.

Area use

Fish tagged in the Great Fish Estuary spent the majority of their time in the mesohaline middle to oligohaline upper reaches of the estuary in the vicinity of receiver 6, which was closest to the tagging site. Netting for these fish was, however, not conducted elsewhere in this estuary; therefore, the observed area used by these fish may be biased by the distribution of the sampling effort. Consequently, the observed distribution in the middle to upper reaches may not reflect the general pattern for white steenbras within this system. The results were, however, suitable to provide evidence of high site fidelity and restricted area use. This high fidelity prompted a change in the sampling in the subsequent studies, to be designed in such a way as to avoid this bias.

Despite sampling to catch white steenbras throughout each of the East Kleinemonde, Kariega and Sundays estuaries, the fish equipped with acoustic transmitters could only be caught (by seine net) in the lower reaches and mouth regions of each estuary. This result was reflected in the stationary receiver data from each estuary. In the East Kleinemonde Estuary, the majority of time was spent in the mouth region and lower reaches, with some time spent in the middle reaches, but very little in the upper reaches. The result was similar in the Sundays Estuary, although it was not possible to record the time spent in the mouth region due to the dynamic nature of the substrate preventing

the permanent mooring of acoustic receivers in this area. In the Kariega Estuary, most fish remained within the lower reaches, with very little time spent in the mouth region or middle reaches, and negligible time in the upper reaches. The fact that most of the tagged fish in all three estuaries spent the majority of their time in the lower reaches, suggests that juvenile white steenbras in estuaries have an affinity for the lower reaches of estuaries, usually dominated by sandy substrates.

These results are confirmed by seine net catches made over a 15-year period (1996 to 2010) in the East Kleinemonde Estuary, which indicated a predominantly lower reaches/mouth region distribution of juvenile white steenbras (mean 165 mm FL) in this system (Whitfield AK, Cowley PD and James NC, unpublished data). A similar result was obtained by Marais (1981), for 2- to 3-year old fish in a gill-net survey of the Sundays Estuary, while Whitfield *et al.* (1994) found white steenbras to be most abundant in the middle to lower reaches of the Great Fish Estuary. This suggests that the observed behaviour and distributional patterns of the fish tagged in the current study were not biased by the sampling procedure, and that the results of the telemetry studies are representative of the populations within each estuary (Aebischer *et al*. 1993). Overall, juvenile white steenbras activity was predominantly in the lower reaches of these estuaries, associated with the sandy substrates, which signifies ecological importance of the resources within this area (Block and Brennan 1999 in Simcharoen *et al*. 2008). Thus, spatially, the lower reaches of these (and other) estuaries represent critical habitat for juvenile white steenbras utilising estuaries, during their nursery phase. A similar result was obtained by Kerwath *et al*. (2005), for spotted grunter acoustically tagged in the East Kleinemonde Estuary. These authors ascribed the observed result to the higher availability of prey in the lower reaches of this system.

Similarly, Cowley and Whitfield (2001) attributed distribution of white steenbras in the lower reaches of the East Kleinemonde Estuary to the dominance of sand prawn *Callianassa krausii* (an important component in the diet of juvenile white steenbras between 150 and 400 mm, Mehl 1973), in the lower reaches. Forbes (1974) asserted that sand prawns are predominantly found in the sandy lower reaches of estuaries. This suggests that the distribution of white steenbras within this estuary may be driven indirectly by substrate type. The observed distribution of tagged white steenbras in the middle to upper reaches of the Great Fish Estuary may also be a response to substrate type, with these individuals opportunistically using a sandbank deposited in that area after a flood event (Childs *et al*. 2008a), which may have influenced the distribution of macroinvertebrate fauna in the area. However, it is likely that the general pattern of juvenile white steenbras distribution in the Great Fish Estuary is similar to that of the other three estuaries studied, with white steenbras more common

closer to the mouth and in the lower reaches, where sandy sediments persist, and sand prawns are likely to be more common. The movement of a single fish from the upper reaches to the mouth region may, therefore, represent the return of this fish to its long-term home range, after an opportunistic exploratory excursion to the upper reaches, where it became temporarily associated with the flood-deposited sandbank.

Whitfield and Kok (1992) found highest numbers of white steenbras (1- to 2-year olds) in the middle to upper reaches of the Swartvlei and Knysna estuaries, while Harrison and Whitfield (1990) sampled 0+ juveniles in plankton nets exclusively in the middle to upper reaches of the Sundays Estuary. The fact that these studies provide varying results suggests that distribution in estuaries may be driven by specific environmental characteristics within each system. It is also possible that the longitudinal distribution of juvenile white steenbras in estuaries may be influenced by fish size (or age), with a possible seaward ontogenetic shift in estuarine distribution from an early juvenile upper- to middle-reaches phase to a juvenile lower-reaches phase. This notion is supported by the fact that fish tagged in the East Kleinemonde, Kariega and Sundays estuaries were larger (208 to 379 mm FL, i.e. 2- to 3-year old fish) than those tagged in the Great Fish Estuary (154 to 184 mm FL).

Although area use in the Kariega and Sundays estuaries was predominantly in the lower reaches of both systems, the actual distributions of area use differed noticeably between the two. In the Kariega Estuary, the fish centred their activity in a short stretch of estuary encompassing receiver 3, about 1.9 km from the mouth. This area consists of a deep channel of uniform depth, adjacent to a large intertidal sandbank, providing shallow feeding areas and deeper refugia. The only other large sandbank is closer to the sea, which is possibly less suitable for white steenbras. This sand bank remains shallow when inundated, and is subject to stronger currents, which keep marine sediments in suspension, contributing to the dynamic nature of the substrate in that area. Upstream of receiver 3, a number of smaller sandbanks and mudbanks are present. However, the limited use of the middle reaches suggests that these areas are also not suitable for white steenbras. Noticeably, there was very little time spent up-estuary of receiver 7, about 5 km from the mouth, beyond which the salinity exceeds 40 and the substrate is comprised largely of mud. This is despite the successful colonisation by a potential prey species of the white steenbras, the bivalve *Solen cylindraceus*, in the middle reaches of the estuary, where densities can exceed 400.m^{-2} (Hodgson 1987).

In the Sundays Estuary, there were two centres of activity, at receivers 2 and 4. The area around receiver 2 is characterised by extensive shallow banks, which are permanently submerged, and the

area around receiver 4 is characterised by an extensive shallow mudbank. The area between these two receivers, encompassing receiver 3, is characterised by steep banks and a deep channel (> 5 m depth), with an uneven substrate. This area is also a popular angling spot for dusky kob, a large predatory fish (personal observation). The relatively low proportion of activity here is therefore likely a result of the habitat and/or predator avoidance in an area less suitable for white steenbras.

The resident nature of juvenile white steenbras within estuaries was confirmed at all four study sites. Most individuals in each estuary showed long-term residency within a particular area. The fact that these high use areas coincided with the respective sites of capture provides evidence of fidelity towards their capture site. This suggests that most fish were captured within their high use area, not during exploratory movements away from this area. Such residency has been observed in other sparids; for example, gilthead seabream *Sparus aurata* and two-banded and white seabreams *Diplodus vulgaris and D. sargus* (Abecasis and Erzini 2008, Abecasis *et al.* 2009) in the Formosa Coastal Lagoon, Portugal; and snapper *Pagrus auratus* in the Mahurangi Harbour Estuary, New Zealand (Hartill *et al.* 2003). The observation of resident behaviour across a range of species and aquatic habitat types, for example yellowbelly rockcod (*Epinephelus marginatus*) in the Ustica Island Marine Reserve, Italy (Lembo *et al*. 2002) and tigerfish (*Hydrocynus brevis*) in the River Niger, Mali, emphasizes the ecological advantage of such behaviour (Baras *et al*. 2002). Familiarity with a particular area could result in reduced predation risk and improved feeding efficiency (Eristhee and Oxenford 2001). Residency within estuarine environments highlights the ecological importance of these systems (Abecasis *et al.* 2009).

3.4.2 Estuarine residency and sea trips

The low number and generally short durations of absence periods for most individuals, in all three open estuaries, provide strong evidence of residency within and dependence on the estuarine environment, highlighting the importance of estuaries as nurseries during the juvenile life stage. No fish from the Great Fish or Kariega Estuaries exhibited absence periods exceeding a full 24-h cycle.

The higher incidence of absence periods from receiver 1 in the Sundays Estuary was due to this receiver being further from the mouth than in the Great Fish or Kariega estuaries. Therefore fish in the Sundays Estuary were able to move further from receiver 1 (i.e. longer duration absence periods, which consequently increased the numbers of excursions exceeding 6 and 24 h), while still remaining within the estuary. In contrast, fish in the Great Fish and Kariega estuaries were not able to venture too far from receiver 1 towards the mouth without exiting the estuary. Therefore, absence periods

from receiver 1 in each estuary appear not to represent sea trips, but rather short-term excursions away from individual home ranges towards the open mouth. The results indicate a reluctance of white steenbras to leave the estuarine environment, at the sizes (ages) monitored in this study.

Evidence to support this notion was provided by opportunistic manual tracking in the Sundays Estuary, between receiver 1 and the mouth. This was aimed at determining whether the tagged white steenbras were still present in the estuary (albeit below the receiver array) during what appeared to be absence periods from the array. On numerous occasions, individuals were shown from the receiver data to have been absent from the receiver array (from receiver 1) for periods exceeding 24 h, but were manually located in a false keel of the estuary close to receiver 1, which is partially separated from the main channel by a subtidal sand bank. As a result of the bathymetry in the area, fish within this arm of estuary were not detectable by the stationary receivers. This result showed that absence periods in the Sundays Estuary, of any duration, could not confidently be allocated to time at sea. Furthermore, even if all absence periods were treated as sea trips, the low proportion of time spent absent, by most individuals, suggests that sea trips are of little importance for juvenile white steenbras.

Previous studies on white steenbras have indicated dependence on estuaries for the first year, up to ± 130 mm FL (Beckley 1984, Bennett 1993b), after which individuals enter the marine environment (Lasiak 1982). However, the findings of the telemetry studies presented here, particularly in the Kariega and Sundays estuaries, revealed that white steenbras are dependent on estuaries for considerably longer periods, possibly even three or four years. Long-term residency within the estuarine environment, of similar duration, was also reported for red drum *Sciaenops ocellatus* and black drum *Pogonias chromis* (Sciaenidae) in eastern United States estuaries, with few fish undertaking marine excursions (Gold and Richardson 1998). In contrast, snapper were shown to undertake regular emigrations from the Mahurangi Harbour Estuary, New Zealand, into the marine environment, which the authors suggested was possibly attributable to foraging or spawning behaviour (Hartill *et al*. 2003). Spotted grunter, tagged in the Great Fish Estuary, South Africa, undertook frequent and long-duration excursions into the marine environment, which the authors attributed to a response to the onset of sexual maturity (Childs *et al*. 2008a). Similarly, certain juvenile dusky kob tagged in the Great Fish Estuary made frequent and long duration sea trips, with fish spending on average 13% of their time at sea (Cowley *et al*. 2008).

3.4.3 Home range size and location

Home range parameters were quantified using manual tracking data obtained in three of the four study estuaries. In the East Kleinemonde Estuary, core areas (50% UD) were located predominantly in the mouth region and lower reaches, and in the Kariega Estuary all core areas were located in the lower reaches, highlighting the importance of the habitat in the lower reaches and mouth region of each estuary. This distribution is likely associated with the suitable habitat and distribution of prey items in the lower reaches (Cowley and Whitfield 2001).

As with the lengths of estuary used, mean home range sizes were small relative to the respective surface area of each estuary, but increased in larger estuaries. Mean home range size (81 780 ± 27 960 m^2) observed in the Kariega Estuary was greater than that observed in the East Kleinemonde Estuary (55 385 ± 22 220 m^2), but comparable to that in the permanently open Great Fish Estuary (97 399 ± 22 557 m^2). Such a result was expected, as the absolute area of suitable habitat is likely to be greater in the larger estuaries than the small intermittently open East Kleinemonde Estuary.

In all three systems, there was a considerable amount of overlap among individual home ranges, which were confined to small areas within each system. Similarly, overlapping of home ranges within a confined area was observed for spotted grunter in the Great Fish (Childs *et al.* 2008a) and East Kleinemonde (O' Connell 2008) estuaries. Utilisation of an established home range facilitates the learning of feeding and shelter locations (Chapman and Kramer 2000), thereby improving efficiency of feeding and reducing predation risk. The overlapping of home ranges of different individuals also provides evidence of a lack of territoriality (Parsons *et al*. 2003, Taylor *et al*. 2006).

Manual tracking in the Kariega Estuary confirmed that most fish made use of the shallow sandbank adjacent to receivers 2 and 3, when submerged. Shallow sand and mud areas were also utilised extensively by juvenile white steenbras in the East Kleinemonde Estuary, potentially providing a rich source of burrowing macroinvertebrates (Whitfield 1998) and protection from predatory fishes (Vinagre *et al*. 2006).

Diel shift in home range position

Variability in the locations of daytime, dawn and night-time home ranges of those individuals manually tracked in the East Kleinemonde Estuary indicated a diel movement pattern. Manual tracking confirmed the night-time use of the shallow sand flats near the mouth and the mudflats adjacent to receiver 3, as well as the use of significantly deeper areas during the day. Dawn home

ranges were more protracted, possibly indicating more directed movement at this time of day (Kelly *et al*. 2007), as opposed to more spherical home ranges where an animal may be feeding or seeking shelter. Furthermore, for each of the three fish, the dawn home ranges were geographically located between night and day home ranges. Thus, observed dawn home ranges may represent transition areas, through which the fish follow a regular diel pattern of movement between night-time areas positioned almost exclusively within the shallow sand and mud areas, and daytime areas in the deeper channel. It is possible that these white steenbras were feeding in the shallow sand and mud areas at night, and utilising the deeper channel areas during the day, representing a shift between feeding and shelter areas (Taylor *et al.* 2006). The observed activity pattern is likely a trade-off between foraging behaviour and predator avoidance, to allow them to utilise the space and food resources most efficiently (McArthur and Pianka 1966, Andrews *et al*. 2009). Similarly, Holland *et al*. (1993) recorded crepuscular movements of white goatfish *Mulloides flavolineatus* along consistent routes between daytime schooling areas and night-time feeding grounds on shallow sand flats in Kaneohe Bay, Oahu, Hawaii. Such diel shifts in home range location are common among the Sparidae, for example snapper tracked in Mahurangi Harbour Estuary, New Zealand, were also shown to move from the main channel onto shallow banks at night (Hartill *et al.* 2003), and black bream *Acanthopagrus butcheri* in the Gippsland Lakes estuary network, Australia, moved from night-time foraging areas to shelter in areas of woody debris during the day (Hindell *et al*. 2008).

Entering the shallow areas at night may reduce the risk of predation by larger fishes, such as the dusky kob, which exhibits higher nocturnal and crepuscular activity levels than during the day (Taylor *et al.* 2006). Use of the shallow areas may not be possible during the day, as avian predation in the shallow areas may be too great a threat (Vinagre *et al*. 2006), particularly in the low turbidity conditions recorded during this study, with piscivorous birds contributing 70% of all bird numbers in the East Kleinemonde Estuary (Whitfield *et al.* 2008). Evidence to support this theory is provided by the considerably shallower mean depths (0.9 ± 0.5 m) at positional fixes made during daytime manual tracking in the Great Fish Estuary than the East Kleinemonde (2.3 ± 0.9 m) and Kariega (2.8 ± 1.1) estuaries, where the extreme turbidity in the Great Fish Estuary may facilitate avoidance of piscivorous avian predation.

3.4.4 Practical considerations

Sampling within the Great Fish Estuary was conducted only in the middle to upper reaches in the vicinity of a sand bank deposited after a flood event. While exhibiting similar behaviour to the white steenbras in the other three estuaries monitored, these fish were predominantly found in the

middle to upper reaches, whereas fish from the other estuaries were found predominantly in the lower reaches and mouth region. It is possible that there were white steenbras resident within the lower reaches of the Great Fish Estuary at the time of the current study; however, the sampling design was not able to determine this. In the East Kleinemonde and Sundays estuaries, where not all fish were tagged at the same locality, fish showed fidelity to their respective capture sites. Sampling, for telemetry studies aimed at determining the general movement patterns representative of a species within an estuary, should thus be designed in such a way as to avoid this type of bias (Aebischer *et al*. 1993), by attempting to sample fish throughout the particular estuary (Sackett *et al*. 2008).

The evidence of diel behaviour and differences in the locations of night-time and daytime home ranges highlights the importance of tracking throughout the 24-hour cycle. Assessments of home range based solely on daytime manual tracking would have provided skewed and non-representative estimates of home range location (Lowry and Suthers 1998), suggesting dominance of deeper channel areas in the distribution of the species. Concluding that juvenile white steenbras make no use of the shallow mud and sand banks and that inundation of these areas with estuarine water may not be important to this species would be erroneous. Tracking during different periods of the day provided a different result, with individuals utilising shallow areas at night, possibly for foraging, and moving through dawn transition areas to deeper daytime home ranges. As such, it may be concluded that these shallow areas represent critical habitats for this species within intermittently open estuaries.

Manual and passive acoustic telemetry techniques provided complementary results. Manual tracking provided high resolution positional data on home ranges showing distinct diel differences therein, while the stationary receivers provided continuous area use data and actual times of departure from and return to the receiver array. Similarly, the observed area use pattern determined by passive tracking closely reflects the spatial distribution of white steenbras as determined by regular netting over a 15-year period (Whitfield AK, Cowley PD and James NC, unpublished data). The distribution data obtained from the historical netting dataset, the detailed high-resolution home range data from manual tracking and the continuous long-term spatial use data provided by passive tracking highlight the complementary value of employing multiple techniques to answer key questions. Such an approach has been advocated by numerous authors (e.g. Lembo *et al*. 2002, Lyons and Lucas 2002, Jadot *et al.* 2006, Simpfendorfer *et al.* 2010).

3.5 Conclusions

Previous studies have suggested that juvenile white steenbras are dependent on estuaries for the first year after recruitment, until a size of about 130 mm FL (Wallace *et al*. 1984a, Beckley 1984, Bennett 1993b), after which they move to the marine environment (Lasiak 1982). This means that successful recruitment into the spawning population requires each individual to spend at least the first year of its life within an estuary. However, Lamberth and Mann (2000) suggested that white steenbras may remain within the estuarine environment up to three years old, and James *et al*. (2007a) showed that white steenbras juveniles were resident in the intermittently open East Kleinemonde Estuary for up to 38 months after recruitment, despite the mouth opening on multiple occasions during this period. After this, they move to the marine environment, as food resources for fish of this size class become limiting in estuaries (Bennett 1993b). The results of this chapter have confirmed this dependence on estuaries, and suggest that certain individuals may remain within an estuary for up to three or four years. Thus, the juvenile estuarine nursery phase represents a bottleneck in the life history of white steenbras, during which time the species is highly vulnerable to threats associated with estuaries.

Area use differed between the freshwater-deprived Kariega and freshwater-dominated Sundays estuaries. Environmental conditions differ considerably between the two systems, most notably as the Kariega exhibits a reverse salinity gradient, caused by a combination of a small catchment, low MAR and excessive water abstraction (Grange *et al*. 2000), which created a limit to the upper distribution of white steenbras within this estuary. Excessive water abstraction can lead to a reduction in the available habitat for fishes and invertebrates, thereby reducing available food and space resources (Grange *et al*. 2000). Effective conservation of estuarine species and habitats, therefore, requires suitable catchment management and water abstraction practices, without which estuaries may become sub-optimal habitats for these species.

The results of this study showed that juvenile white steenbras use limited portions of each estuary, within which they showed high levels of long-term residency. High use areas were found predominantly in the lower reaches of each estuary, extending into the mouth region as well as the middle reaches. The diel home range shift in the East Kleinemonde Estuary highlighted the importance of the shallow littoral areas to juvenile white steenbras, most likely for feeding, while results from the permanently open estuaries identified the intertidal sand and mud banks as important areas. These shallow intertidal and littoral areas, as well as the lower reaches of estuaries should, therefore, be considered as critical habitats for juvenile white steenbras in estuaries, and

thus essential to the maintenance of coastal populations. Dependence on these critical habitats within estuaries further restricts the resources available to juvenile white steenbras. These critical habitats are subjected to severe threats, such as estuarine habitat degradation, excessive water abstraction, resource overexploitation and infrastructural development (Whitfield and Cowley 2010). The lower reaches of estuaries also represent areas of intense human impacts (e.g. infrastructure, boating activity). High levels of residency, dependence on estuaries and occupation of small areas within the estuaries makes juvenile white steenbras vulnerable to localised depletion within estuaries, which could lead to growth overfishing if poorly managed, ultimately nullifying the effectiveness of estuaries as nursery areas (Cowley *et al*. 2008). Consequently, management or conservation intervention in estuaries should focus not only on the species, but also on protection of these critical habitats (Beck *et al*. 2001). As estuaries are already amongst the most threatened and degraded aquatic environments globally (Vasconcelos *et al*. 2007, Whitfield and Cowley 2010), their effective management is of critical importance to the biota dependent on them.

Chapter 4

Temporal and rhythmic movements in estuaries

4.1 Introduction

The position of an animal at any point in time is dependent on its movement trajectory. Such movements may be influenced by environmental factors, biotic interactions and the animal's behaviour (e.g. feeding, spawning or refuge-seeking) (Nathan *et al*. 2008). These factors, as well as anthropogenic disturbances, change over time; thus, the area used by an animal in space is also likely to vary over time (Sackett *et al*. 2008). Consequently, it is insufficient to simply assess distribution, area utilisation or home range with a snapshot, as snapshots neglect any component of temporal variability (Turchin 1998). Studies aimed at determining area use patterns, movement patterns or home range dynamics of a species must, therefore, be conducted over temporal scales and resolutions that are suitable for that species and life stage, to allow detection of short- and long-term patterns in the animal's movements. Studies of insufficient duration may fail to detect movements over periods as long as seasons or may underestimate the spatial extent of movements (Parsons *et al*. 2003), while studies of low temporal resolution may sample at a frequency too low to detect short-period cycles, such as movements with diel periodicity (Taylor *et al*. 2006).

Geophysical cycles are caused by the movement of the earth relative to the position of the sun, as well as the movement of the moon through its orbit of the earth (Morgan 2001, Chabot and Watson 2010). The most prominent of these geophysical cycles are those associated with annual, synodic-month (29.5 d), lunar-month (28.4 d), lunar-day (24.8 h), solar-day (24.0 h) and tidal-cycle (12.4 h) periodicities. These cycles can individually or collectively influence or even drive the movement and behaviour of terrestrial and aquatic organisms (Palmer 1973). The corollary to this is that the effects of the stronger environmental phenomena influencing the movement of an organism may be manifest as observable patterns in the organism's behaviour, synchronised to the respective environmental cycle (Boehlert and Mundy 1988). These movement patterns occurring over periodicities associated with geophysical cycles may be endogenously controlled, by an internal biological clock, or may be exogenously controlled by direct response to the physical changes in the environment (Vinagre *et al*. 2006).

The most studied of these cycles is undoubtedly the 24-h period of the light/dark solar-day cycle (Palmer 1973). Movements over circadian cycles have been well-documented for terrestrial animals

(e.g. Kreeger *et al*. 1996, Brillinger *et al*. 2004, Wittemyer *et al*. 2008, Polansky *et al*. 2010) and, to a lesser extent, in aquatic organisms mainly in the marine environment, for example American horseshoe crab *Limulus polyphemus* (Chabot and Watson 2010) and Hawaiian stingray *Dasyatis lata* (Cartamil *et al*. 2003). In addition to the diel cycle, coastal habitats (including estuaries that are predominantly open to the sea) are subjected to regular patterns of tidal inundation, which in turn cause measurable physical changes in estuarine conditions, e.g. water depth, temperature, salinity and turbidity. As a result of such physicochemical fluctuation, the biological rhythms underlying the behavioural patterns of organisms within estuaries are commonly influenced or driven by their environment (Wilcockson and Zhang 2008). Cyclical behavioural rhythms in estuarine invertebrates have received considerable research attention (e.g. Natarajan 1989, Holsman *et al*. 2006), while movements at periodicities associated with diel (Hartill *et al*. 2003), tidal (Næsje *et al*. in press), lunar-day (Morgan 2001), spring/neap (Vinagre *et al*. 2006), lunar (Gibson 1978), seasonal (Heupel and Simpfendorfer 2005) and annual (Reyier *et al*. 2010) cycles have also been reported for estuarine-associated fishes. By identifying the cyclical patterns in an animal's behaviour it is possible to determine the environmental phenomena that drive, or at least influence, the animal's movements.

This chapter makes use of the passive acoustic receiver detection data that were presented in the previous chapter, to investigate trends in temporal and cyclical movement patterns of juvenile white steenbras in estuaries. The long-term nature of the studies conducted in the East Kleinemonde, Kariega and Sundays estuaries renders them suitable for the analysis of long-term temporal movement patterns, and investigation of the cyclical phenomena that influence both short- and long-term spatio-temporal movements. Data collected from the Great Fish Estuary were not considered due to the short and preliminary nature of that study.

4.1.1 Aims and objectives

The chapter aimed to assess the temporal and rhythmic movement patterns of white steenbras in the East Kleinemonde, Kariega and Sundays estuaries. The specific objectives were to:

i. Determine whether area use patterns change seasonally;
ii. Identify the periodicity of natural rhythms underlying cyclical movement patterns;
iii. Further explore and describe the dominant cyclical patterns in detail; and
iv. Identify and explain the variability in cyclical movement patterns in different estuaries.

4.2 Methods and materials

4.2.1. Long-term area use patterns in estuaries

Stationary receiver data for individual acoustic transmitters deployed in each of the four estuaries were used to estimate the mean monthly time spent by fish in the vicinity of each receiver, and the monthly proportions of fish with active transmitters that were detected on each receiver, to provide information on the seasonal changes in the ranges of estuarine movements. In the East Kleinemonde Estuary, the short-period transmitters (100-day battery life) were not active for sufficient duration to assess long-term area use. Thus, analysis in this estuary was limited to the fish equipped with long-period transmitters, which were active for up to eight months. Fish 3766 was excluded from this analysis as it was detected for only 10 days before detections ceased. In the Kariega Estuary, Fish 2044 was excluded from the analysis, as it left the system soon after tagging, while the transmitters in the remaining nine fish were active for up to 12 months. In the Sundays Estuary, all 15 fish were included in the analyses, with most transmitters active for up to seven months.

4.2.2. Identification of cyclical rhythms

Temporal movement patterns within the East Kleinemonde, Kariega and Sundays estuaries were identified using single series spectral (Fourier) analysis of the receiver data. Fourier analysis involves the decomposition of a time series of data (from the time domain), to produce a finite sum of cosine and sine (cyclical) functions of variable frequencies (i.e. a data series in the frequency domain). In the frequency data series, comprised of these cosine and sine functions, the period (time taken to complete one cycle) of each cosine and sine function is equal to the inverse of the frequency with which the cycle takes place (i.e. doubling the time required to complete a cycle will halve the frequency at which the cycles take place) (Heupel and Simpfendorfer 2005). The squares of the cosine and sine coefficients for each frequency are summed and fitted to the data based on least squares, providing a Fourier amplitude for each respective Fourier frequency (Diggle 1990). Peaks in Fourier amplitudes, presented in a periodogram of sums of squares of cosine and sine coefficients, indicate the frequencies most correlated with the data (Polansky *et al*. 2010), thereby identifying periods over which underlying cycles take place. For example, a peak in the periodogram value indicating a cycle period of 24 hours would represent movement over a diel cycle.

Receiver detections for each individual made within the first 24 hours post surgery were excluded, as in the data analyses in the previous chapter, and data series were discontinued once the number of detections per day had decreased below 200 as this was assumed indicative of battery failure (Hartill *et al*. 2003). For the fish tagged with long-period transmitters in the East Kleinemonde

Estuary, this cut-off was made at 100 receiver detections per day, due to the comparatively longer nominal delay between signal transmissions (60 – 180 s). The receiver data for each fish were then binned into 15-minute bins, from which two metrics were calculated. The first metric was a measure of presence/absence within the receiver array, during each 15-minute period. This provided information on the probability of detecting the fish within each period, which was expected to decrease when the fish entered shallow sand or mudbank areas, such as the shallow littoral area above the road bridge in the East Kleinemonde Estuary, or over the shallow sandbank area adjacent to receivers 2 and 3 in the Kariega Estuary. Consequently, this metric could be used as a measure of a fish's movement, between deep and shallow areas within the estuary (i.e. transverse movements, as opposed to axial movements). The second was a measure of the average receiver visited within each 15-minute period, where the receiver number acted as a proxy for its position along the axis of the estuary (i.e. if a fish visited receivers 2 and 3 within the 15 minutes, the average receiver location was 2.5) (Hartill *et al*. 2003). This provided two time series of data (one for each metric) for each fish, suitable for spectral (Fourier) analysis.

Fourier transformation for spectral analysis is based on the Fast Fourier Transform described by Cooley and Tukey (1965). This analysis requires that each series has a sample size (i.e. the number of 15-minute bins) equal to a power of 2 (e.g. 512, 1024 . . . 8 192, 16 384). Therefore, data series were truncated at the maximum number of bins that equalled a power of 2, and data bins in each series occurring beyond the last full power of 2 were excluded from the analyses. Two fish (Fish 2003 in the East Kleinemonde Estuary and Fish 64995 in the Sundays Estuary), however, had only slightly fewer data bins than the closest power of 2. Therefore, to avoid the loss of almost half of each of these data series through truncation to the next highest power of 2, these two data series were increased to the closest power of 2 through the process of zero-padding (Fish 2003 had 7 410 data bins padded to 8 192, Fish 64995 had 16 205 data bins padded to 16 384). Zero-padding refers to the addition of a number of data points (all of value zero) to the data series, to increase the sample size, effectively allowing an increase to the next greatest power of 2, to avoid data loss associated with data series truncation. This resulted in cleaner periodogram peaks than the truncated series in both cases, but had no effect on the result for either fish. A Hamming weighted moving average window (width m = 5, Hamming weights: 0.036, 0.24, 0.45, 0.24, 0.036) was applied during spectral analyses, to smooth periodogram values, to decrease the effects of random fluctuations or spurious scatter therein, which often occur with Fast Fourier Transform (Chatfield 1980). All analyses were conducted in Statistica 10.0, using the *single series spectral (Fourier) analysis* function. Prior to analysis, all data series were transformed by subtraction of the mean, and each data series was reviewed, and those

exhibiting non-stationarity of the mean (i.e. long-term trends greater than the duration of the time series) were detrended prior to analyses.

Fish for which there were fewer than 5 000 detections, or that were detected for fewer than 56 days (two full lunar cycles) were excluded from the Fourier analysis. These included three fish from the East Kleinemonde Estuary and one each from the Kariega and Sundays estuaries. For the presence/absence data series for Fish 64998, 64999 and 65000 from the Sundays Estuary, results of the Fourier analyses on the first 8 192 data bins are presented, as these produced considerably cleaner periodogram peaks than the truncated data series of 16 384 bins (used for average receiver location data series for these three fish), with no observable differences in the results. This was based on the suggestion of Shepard *et al*. (2006) that analysis of subsets of the data can help to distinguish shorter period frequencies from background (white) noise.

Fourier analysis periodogram interpretation

Periodograms are presented in the frequency domain, with x-axes expressed on a decreasing exponential scale, with the origin representing the number of bins in the data series. Peaks occurring at a frequency of zero, i.e. the origin of the x-axis, are likely caused by long-term cycles at periods greater than the duration of the data series (Heupel and Simpfendorfer 2005). These peaks were, therefore, ignored. In certain periodograms presented, the y-axes were re-scaled by decreasing the height of these excessively large zero-frequency peaks to that of the next highest (non-zero frequency) peak.

The occurrence of multiple smaller peaks adjacent to a significant peak in a periodogram is termed spectral leakage. Spectral leakage refers to the phenomenon in which the variation (periodogram amplitude) at a single frequency is divided and split across multiple adjacent discrete frequencies, appearing as multiple lower amplitude peaks instead of a single large sharp peak (Diggle 1990), which commonly occurs when a strongly correlated frequency component is not an integer multiple of the sampling period (e.g. a frequency of 0.0104, representing a period of approximately 24.0 h). Such spectral leakage peaks are ignored. Similarly, in the frequency domain (i.e. a time series presented as a data series at different frequencies), each successive frequency in the series is a multiple of the sampling frequency being approximated. For example, if a spectral peak occurs at a frequency of x, representing 24.0 h, then it is possible that peaks may occur at frequencies that are integer multiples of x (i.e. $2x$, $3x$, $4x$, representing 12.0, 8.0 and 6.0 h, respectively). Such peaks, known as spectral harmonics, as commonly observed in the periodograms of white steenbras

monitored in this study, should not be interpreted as indicative of the presence of distinct cyclical mechanisms at those frequencies (Diggle 1990); as such, these were ignored. Numerous peaks also occurred at periods associated with 2^n 15-minute intervals, particularly 2 048, 4 096 or 8 192 intervals, representing cycles of 512 h (21.3 d), 1 024 h (42.7 d) and 2 048 h (85.3 d), respectively, which have no geophysical or biological relevance. These peaks are likely harmonics of the zero-frequency peak, or an artefact of the 2^n power-scale of the frequency domain.

4.2.3 Further exploration of observed rhythms

Results from the Fourier analysis indicated that the two dominant rhythmic movements of white steenbras in the East Kleinemonde, Kariega and Sundays estuaries were diel and tidal cycles. These two rhythms were, therefore, further investigated to provide an understanding of how the movements of the tagged fish were related to each of these cycles. Owing to the absence of tidal influence, only diel movements were assessed for fish in the temporarily open/closed East Kleinemonde Estuary. Rhythmic tidal movements were assessed for fish tracked in the permanently open Kariega and Sundays estuaries, although diel movements were not assessed for these fish, as night-time positions of the fish in these estuaries was not determined using manual tracking.

Diel movement patterns

The manual tracking data from fish tagged in the East Kleinemonde Estuary (presented in Chapter 3) indicated that certain individuals made extensive use of the shallow sand/mudflats to the north west of receiver 3 at night. Although this area was outside of the detection range of the receiver array, the receiver presence/absence data were used to provide insight into the timing of these movements. The receiver detection data for each individual were scrutinised, to identify periods representing forays away from the receiver array, onto the shallow sand/mudflats. To be classified as a movement away from the array and onto the sand/mudflats, the duration of the absence period had to exceed six hours. Absence periods associated with departure from or return to receivers other than receivers 2 and 3 were not included and the fish had to leave the array and/or return to the array at receiver 3, to ensure that its movement had been onto the shallow flats. The mean times of departure from and return to the receiver array in this area (receivers 2 and 3) were determined for each individual, using circular statistics (Batschelet 1981).

Because time data are of a cyclical nature, it was first necessary to convert times of departure from and arrival at the receiver array to degrees, with a 24-hour cycle being represented as a full circle (360°), and times being presented as angles (i.e. 15° representing 1 hour). Mean angles ($\bar{\phi}$), angular

deviations (*s*) and confidence limits were then calculated (see Appendix I for calculations) and converted from degrees back to time. The Rayleigh test for significance was used to test the null hypothesis that mean angles ($\bar{\phi}$), and thus mean times of departure from and arrival at the array, were not significantly different from random (significance criterion $\alpha = 0.05$). Mean times of departure and arrival were calculated separately for each individual. Mean departure and arrival times were also calculated for all excursions undertaken by all individuals combined. Of the 16 fish tagged, 14 provided results suitable for such analysis of diel movement patterns. Fish 2006 expelled its transmitter soon after release, while Fish 2005 undertook no excursions from the receiver array.

Tidal movement patterns

Stationary receiver data were analysed to determine whether white steenbras in the permanently open Kariega and Sundays estuaries made movements synchronous with tidal water movements. Detection data for each individual white steenbras tagged in the two estuaries were scrutinised to identify any up-estuary or down-estuary movements that could be considered as 'significant' movements. These 'significant' movements were defined by the following criteria:

i. The movement was unidirectional (i.e. either up-estuary or down-estuary, because when a fish changed direction, the movement was considered to have ended);
ii. The duration of the movement did not exceed 6.2 hours (approximately one tidal phase, i.e. half the 12.4-h duration of one tidal cycle) (Note: unidirectional movements exceeding 6.2 h were also considered, but only when a period of stationary behaviour in the vicinity of a single receiver was evident. These movements were split into two or more periods not exceeding 6.2 h);
iii. The movement covered a minimum distance of 1 km between the detection range of the receivers where the movement was initiated and where it ended.

In the Sundays Estuary, a movement was deemed 'significant' if the fish was detected on at least three sequential receivers within a 6.2-hour period. This required an up-estuary or down-estuary movement of at least 1 km, starting within the detection range of one receiver, moving through the detection range of an adjacent receiver and into that of a third receiver in sequence. The exception to this was movements between receivers 15 and 16, which were spaced approximately 5 km apart; as such, movements between these two receivers were considered 'significant'. In the Kariega Estuary, 'significant' movements were not simple to define, as the receivers were not evenly spaced along the estuary. Movements among the first three receivers were not considered 'significant' due

to their close proximity. In contrast, movements between certain adjacent receivers spaced considerably further apart (receivers 6 – 7, 7 – 8, 9 – 10, 10 – 11, 12 – 13, 13 – 14, 15 – 16) were considered 'significant'. All 'significant' movements were then compared to the tidal direction over the duration of the movement, to determine the proportions of movements made with or against the tide, or that spanned two tidal phases.

4.3 Results

4.3.1 Long-term patterns in area use

In the East Kleinemonde Estuary, three of the nine fish analysed exhibited long-term station-keeping behaviour with little change in the proportions of time spent at each receiver over the eight-month study period. Two fish showed no clear pattern in their monthly area use. However, four individuals changed their movement patterns, exhibiting up-estuary shifts in their spatial extents of area used, with the onset of autumn (March to May). These fish also moved to and from the upper reaches of the estuary, while this behaviour had not previously been observed, and was not observed with the onset of spring (August and September). These movements were reflected in the mean monthly proportions of time spent at receivers further from the mouth, and the proportions of fish with active transmitters that were detected in the vicinities of these receivers (Figure 4.1).

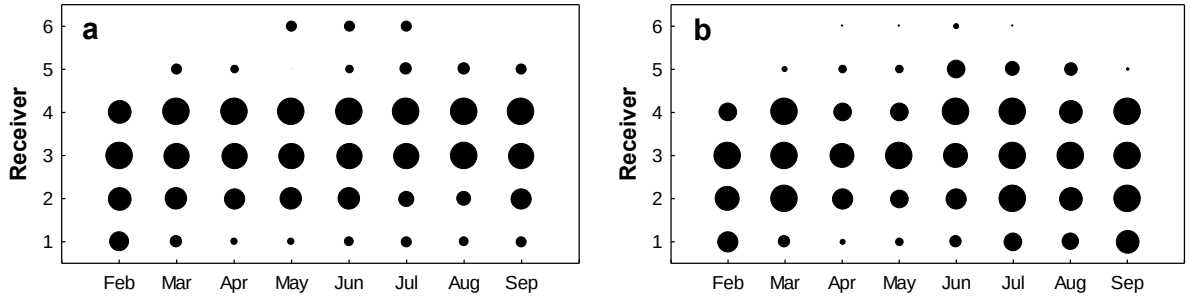

Figure 4.1: Bubble plot representation of a) the mean monthly proportions of time (%) spent and b) monthly proportions of individuals detected in the vicinity of each of the six stationary receivers from February to September in the East Kleinemonde Estuary, for all fish tagged with long-period transmitters (n = 9). The sizes of the circles are proportional to the magnitude in each case

In the Kariega Estuary, four individuals exhibited station-keeping behaviour over the twelve-month study period, while four individuals exhibited up-estuary shifts in area use during the winter and spring months (July to November), which ceased with the onset of summer (December). The remaining individual showed no observable pattern. These movements were again reflected in the

mean monthly proportions of time spent at receivers further from the mouth, and the proportions of fish with active transmitters that were detected in the vicinities of these receivers (Figure 4.2).

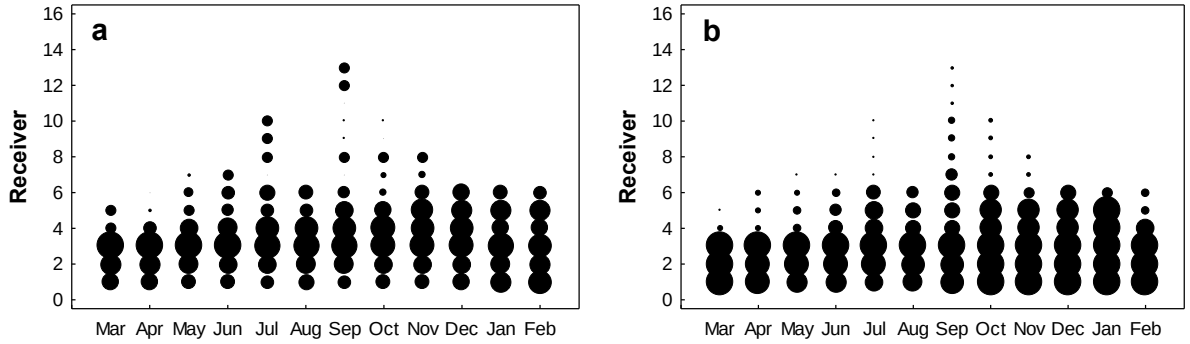

Figure 4.2: Bubble plot representation of a) the mean monthly proportions of time (%) spent and b) monthly proportions of individuals detected in the vicinity of each of the 16 stationary receivers from March to February in the Kariega Estuary (n = 9 fish). Receiver '0' refers to absence time (periods absent from receiver 1 in excess of 24 h), and the sizes of the circles are proportional to the magnitude in each case

Eight of the fifteen fish tagged in the Sundays Estuary exhibited station-keeping behaviour, while six exhibited up-estuary shifts in area use over the winter months (July to August) (Figure 4.3). One fish showed no observable pattern.

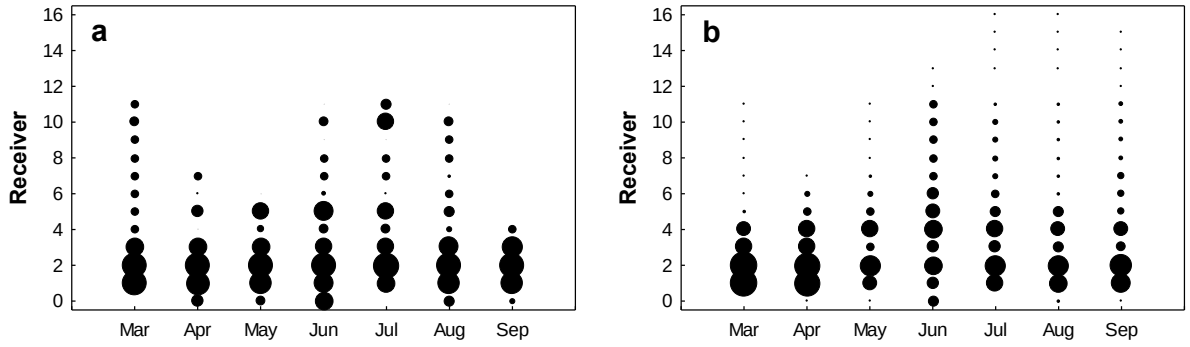

Figure 4.3: Bubble plot representation of a) the mean monthly proportions of time (%) spent and b) monthly proportions of individuals detected, in the vicinity of each of the 16 stationary receivers from March to September in the Sundays Estuary (n = 15 fish). Receiver '0' refers to absence time (periods absent from receiver 1 in excess of 24 h), and the sizes of the circles are proportional to the magnitude in each case

As the fish tagged in the Sundays Estuary were captured at two different locations (see Figure 3.7, Chapter 3), with fish exhibiting site fidelity, pooling individuals from the two groups may mask behavioural differences between them. As such, the results are presented separately for those fish captured in the vicinity of receiver 4 (upper group), and those captured in the vicinity of receiver 2 (lower group) (Figure 4.4). Although the trends observed in both groups reflected those in the overall dataset (Figure 4.3), the gradual up-estuary shift from summer to winter was more apparent in the upper group (Figure 4.4 a, b).

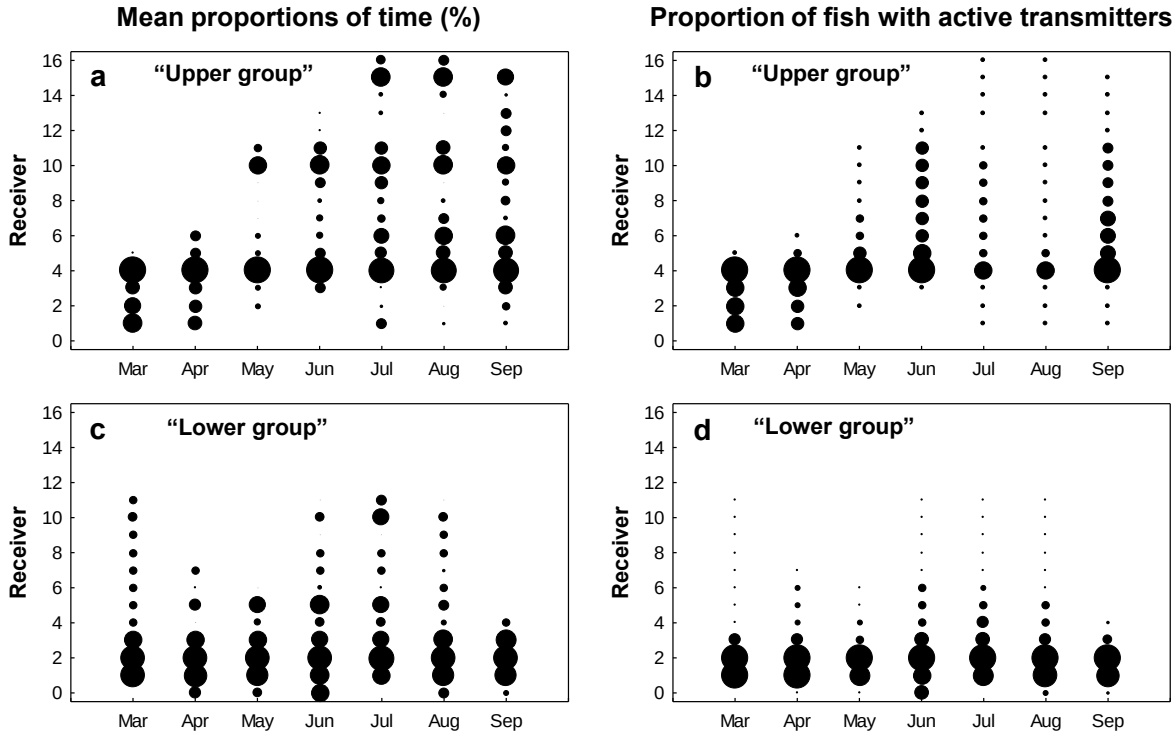

Figure 4.4: Bubble plot representation of a, c) the mean monthly proportions of time (%) spent and b, d) monthly proportions of individuals detected, in the vicinity of each of the sixteen stationary receivers in the Sundays Estuary, for the "upper group" of fish tagged in the vicinity of receiver 4 (n = 6), and the "lower group" tagged in the vicinity of receiver 2 (n = 9). Receiver '0' refers to absence time (periods absent from receiver 1 in excess of 24 h), and the sizes of the circles are proportional to the magnitude in each case

4.3.2 Cyclical movement patterns

Of the 41 fish monitored in the three estuaries, 35 provided data suitable for Fourier analysis. Of these 35 fish, five (Fish 3765 in the East Kleinemonde Estuary, Fish 2039 in the Kariega Estuary and Fish 64991, 64992, and 65002 in the Sundays Estuary) showed no trend in their average receiver location data series. The Fourier analyses yielded variable results among estuaries and individuals, as well as between the presence/absence and average receiver location metrics (Table 4.1).

Table 4.1: Results for spectral (Fourier) analysis of stationary receiver data, for white steenbras monitored in the East Kleinemonde (EKM; *n* = 12), Kariega (KAR; *n* = 9) and Sundays (SUN; *n* = 14) estuaries. The five different cycles observed in the data (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month) are presented, showing the rank (1 – 5) of each cycle within the presence/absence and average receiver location data series of each fish. Dashes indicate cycles not detected in that data series

Estuary	Fish ID	No. 15-min bins	Presence/Absence					Average Receiver				
			D	T	LD	S/N	L	D	T	LD	S/N	L
EKM	2002	8 192	1	-	-	2	-	2	-	-	3	1
EKM	2003	8 192	1	-	-	-	-	1	-	-	-	-
EKM	2004	8 192	2	-	-	-	1	2	-	-	-	1
EKM	3759	16 384	1	-	-	-	-	1	-	-	-	-
EKM	3760	16 384	1	-	-	-	-	1	-	-	-	-
EKM	3761	16 384	1	-	-	-	-	1	-	-	-	-
EKM	3762	16 384	1	-	-	-	-	1	-	-	-	-
EKM	3764	16 384	1	-	-	-	-	1	-	-	-	-
EKM	3765	16 384	1	-	2	-	-	-	-	-	-	-
EKM	3768	16 384	1	-	2	-	-	1	-	-	2	-
EKM	3769	16 384	1	-	-	-	-	1	-	-	-	-
EKM	3770	16 384	1	-	-	-	-	1	-	2	-	-
KAR	2036	8 192	1	-	-	-	-	3	4	2	1	-
KAR	2037	32 768	1	2	-	-	3	3	4	-	1	2
KAR	2038	16 384	1	2	-	3	-	1	3	2	-	-
KAR	2039	8 192	1	2	-	-	-	-	-	-	-	-
KAR	2040	16 384	2	1	-	-	-	1	-	-	-	2
KAR	2041	16 384	3	4	-	2	1	1	2	3	-	-
KAR	2042	32 768	2	1	-	-	-	1	2	-	-	-
KAR	2043	8192	3	1	-	2	-	1	2	3	-	-
KAR	2045	16 384	1	-	-	-	-	3	4	2	1	-
SUN	64990	16 384	1	-	3	2	-	3	-	2	1	-
SUN	64991	16 384	1	-	-	-	-	-	-	-	-	-
SUN	64992	16 384	1	3	-	2	-	-	-	-	-	-
SUN	64993	16 384	1	-	-	-	-	1	2	-	-	-
SUN	64994	16 384	1	4	5	2	3	1	-	-	-	2
SUN	64995	16 384	2	3	-	1	-	1	-	-	-	-
SUN	64996	8 192	1	4	2	3	-	1	3	-	2	-
SUN	64997	16 384	1	2	-	-	-	3	-	-	2	1
SUN	64998	16 384	1	4	3	2	-	1	-	-	-	-
SUN	64999	16 384	1	4	2	3	-	1	2	-	-	-
SUN	65000	16 384	1	5	2	3	4	1	-	-	-	2
SUN	65001	16 384	1	2	-	-	-	2	-	-	1	-
SUN	65002	16 384	1	2	-	-	-	-	-	-	-	-
SUN	65003	16 384	1	3	2	-	-	1	-	-	-	-

Cycles were observed, in both the presence/absence and average receiver location metrics, at periods of approximately 24.0 hours (diel cycle), 12.4 hours (tidal cycle), 24.8 hours (lunar day), 14.2 days (spring/neap cycle) and 28.4 days (lunar cycle). The overriding period, observed in all 65 data series (presence/absence in 35 fish plus average receiver location in 30 fish), was ± 24.0 h (range 23.7 to 24.3 h), representing the diel cycle. In 29 of the 35 presence/absence data series and 22 of the 30 average receiver time series, the diel peak was dominant.

East Kleinemonde Estuary

In the temporarily open/closed East Kleinemonde Estuary, there was an overwhelming dominance of the diel rhythm, being dominant in 20 of the 23 data series (Figures 4.5 and 4.6). Five individuals exhibited movement associated with lunar or spring/neap cycles, but none with the tidal cycle (Table 4.1). Three fish (Fish 3765, 3768, 3770) showed secondary peaks related to the lunar day (± 24.8 h).

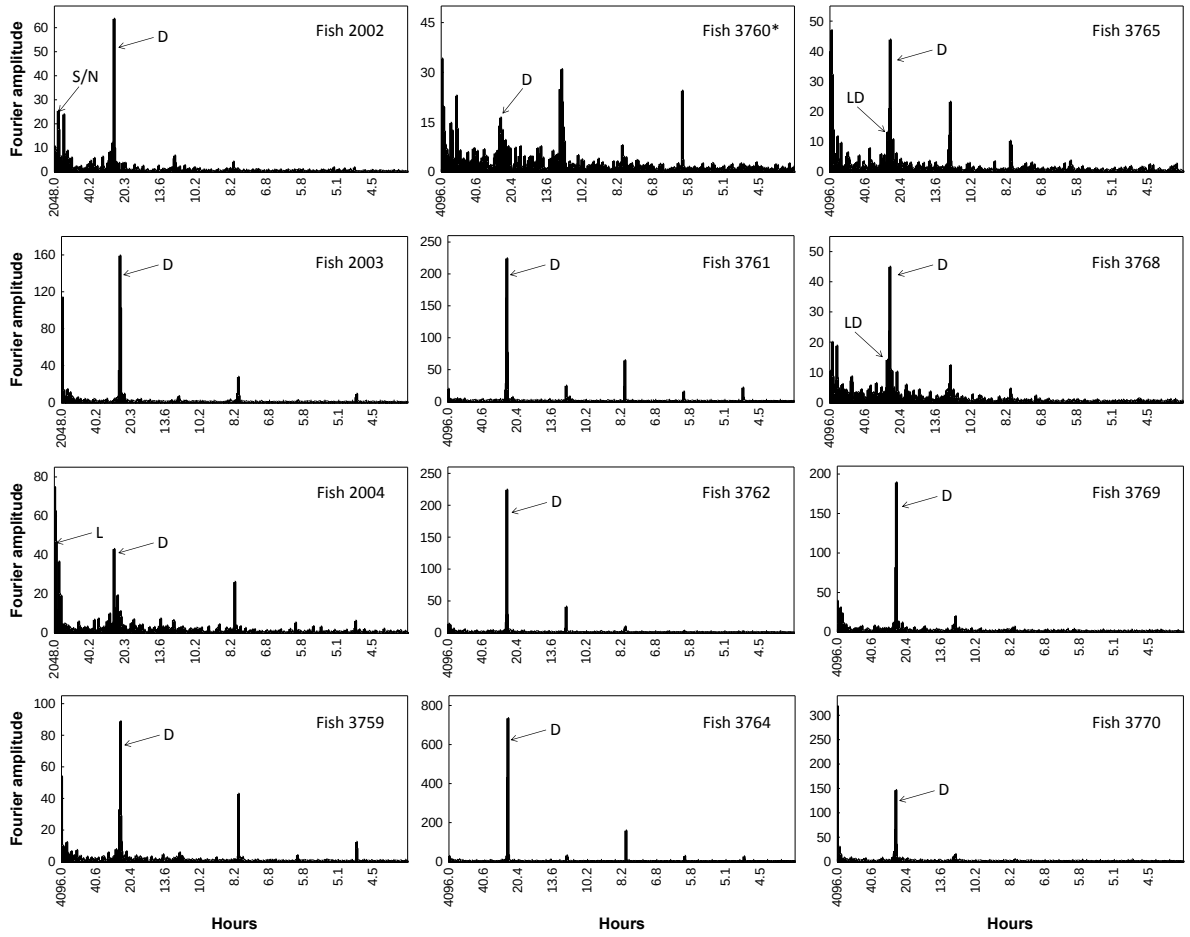

Figure 4.5: Periodograms of the spectral (Fourier) analyses of the presence/absence data series for white steenbras from the East Kleinemonde Estuary (n = 12). Letters indicate cycles with which the respective peaks are associated (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month). Fish ID codes presented with * indicate periodograms with re-scaled y-axes

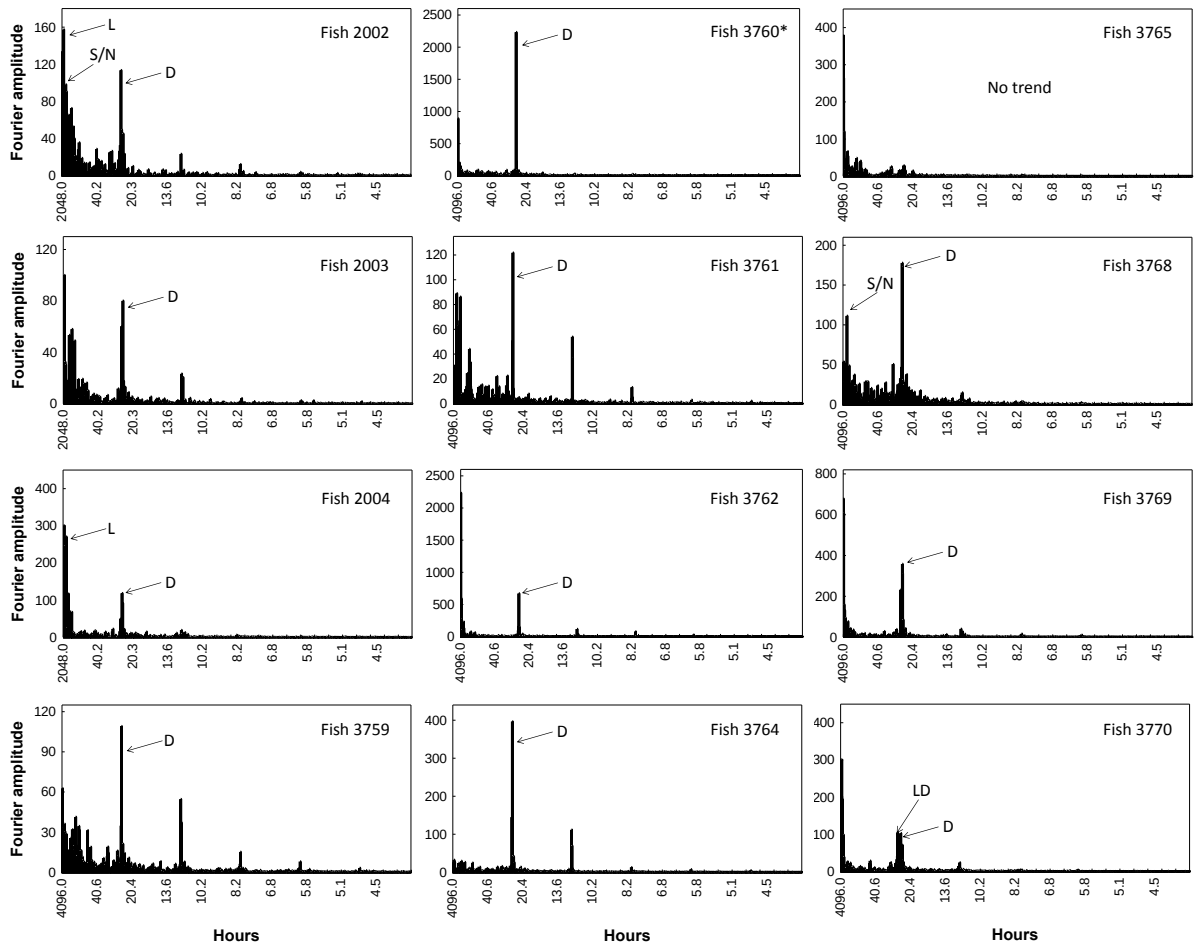

Figure 4.6: Periodograms of the spectral (Fourier) analyses of the average receiver location data series for white steenbras from the East Kleinemonde Estuary (n = 12). Letters indicate cycles with which the respective peaks are associated (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month). Fish ID codes presented with * indicate periodograms with re-scaled y-axes

Kariega Estuary

As the average receiver location metric assessed axial estuarine movements, it was expected that tidal-associated cycles would be more prevalent in average receiver location data series than in the presence/absence data series; however this did not occur in the Kariega or Sundays estuaries. In the Kariega Estuary, peaks at the tidal cycle (12.4 h) were observed; occurring in either one or both data series for most fish, and in some fish this was the dominant peak. However, the diel cycle remained the most prevalent rhythm (Figures 4.7 and 4.8). Interestingly, peaks associated with the lunar day (24.8 h) were common in the average receiver location data series of the Kariega Estuary fish, but were not observed in their presence/absence data series. Peaks occurring at lunar or spring/neap cycles were less common among the Kariega Estuary fish than diel or tidal peaks, although when they were present they were generally the dominant or secondary peak.

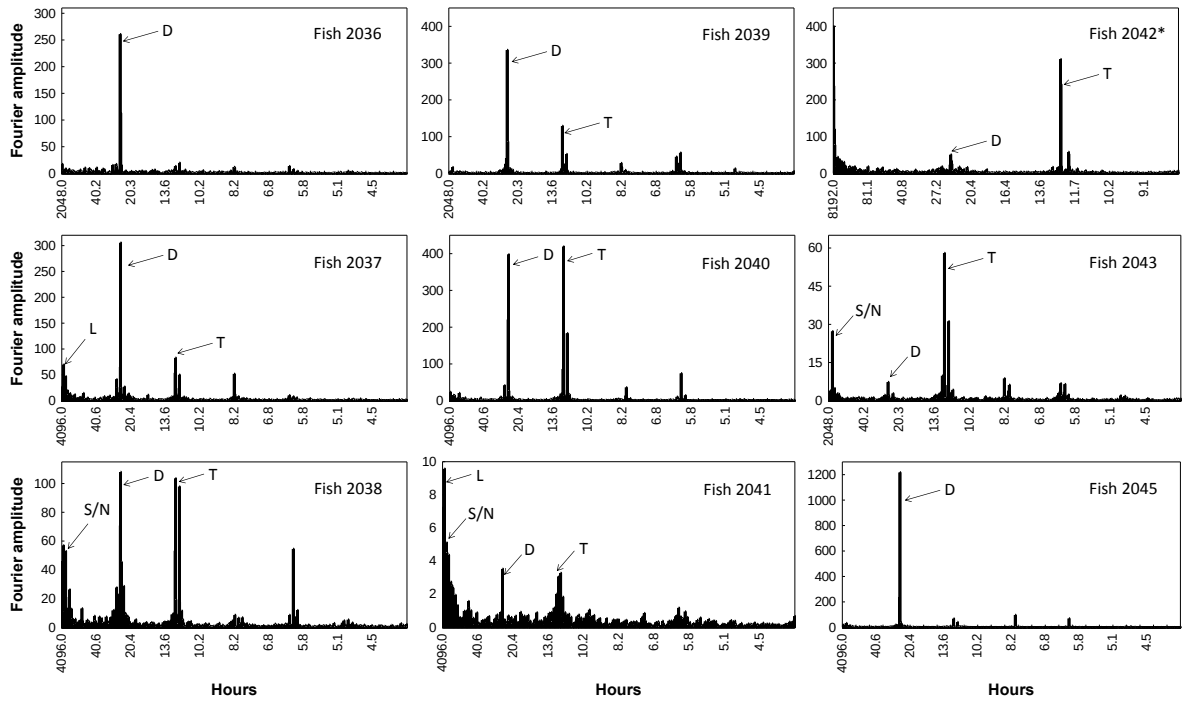

Figure 4.7: Periodograms of the spectral (Fourier) analyses of the presence/absence data series for white steenbras from the Kariega Estuary (n = 9). Letters indicate cycles with which the respective peaks are associated (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month). Fish ID codes presented with * indicate periodograms with re-scaled y-axes

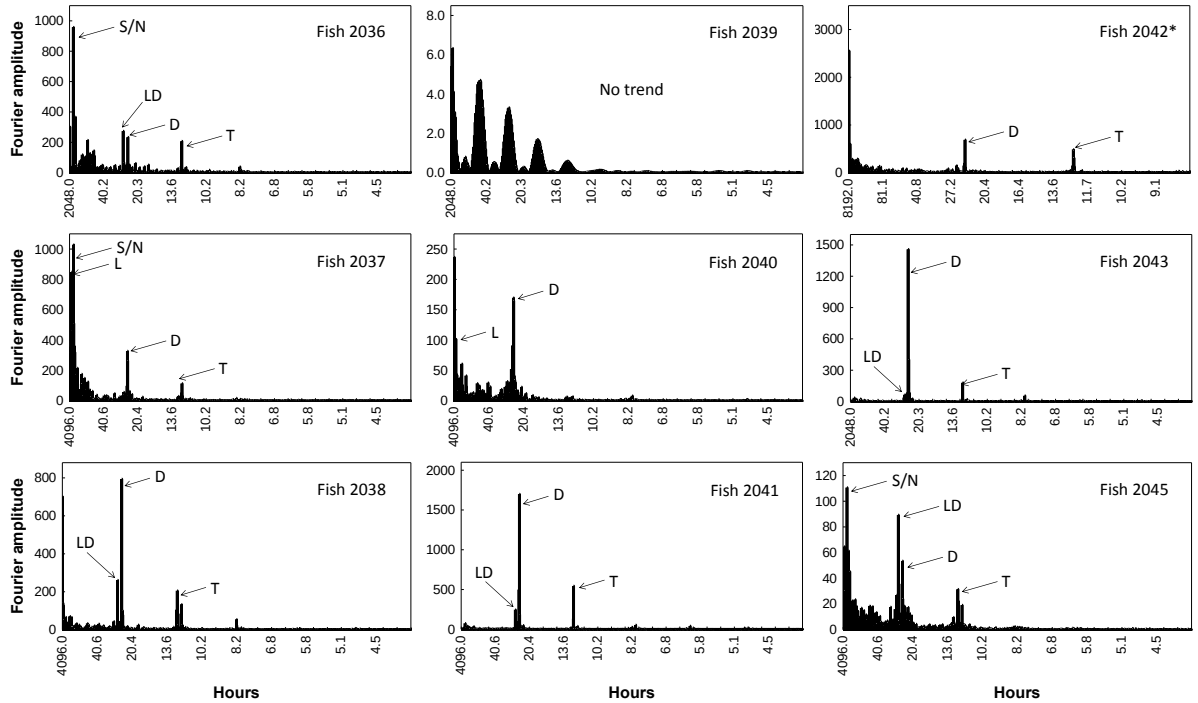

Figure 4.8: Periodograms of the spectral (Fourier) analyses of the average receiver location data series (Figure 4.8) for white steenbras from the Kariega Estuary (n = 9). Letters indicate cycles with which the respective peaks are associated (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month). Fish ID codes presented with * indicate periodograms with re-scaled y-axes

Sundays Estuary

In the Sundays Estuary, the diel cycle was most prevalent and dominated 21 of the 25 data series. Although tidal cycle peaks (12.4 h) were common, they were always superseded by diel peaks, and were uncommon in the average receiver location time series. Movements associated with the lunar day (24.8 h) were also common in the presence/absence data series, but almost completely absent from the average receiver location data series (Figures 4.9 and 4.10).

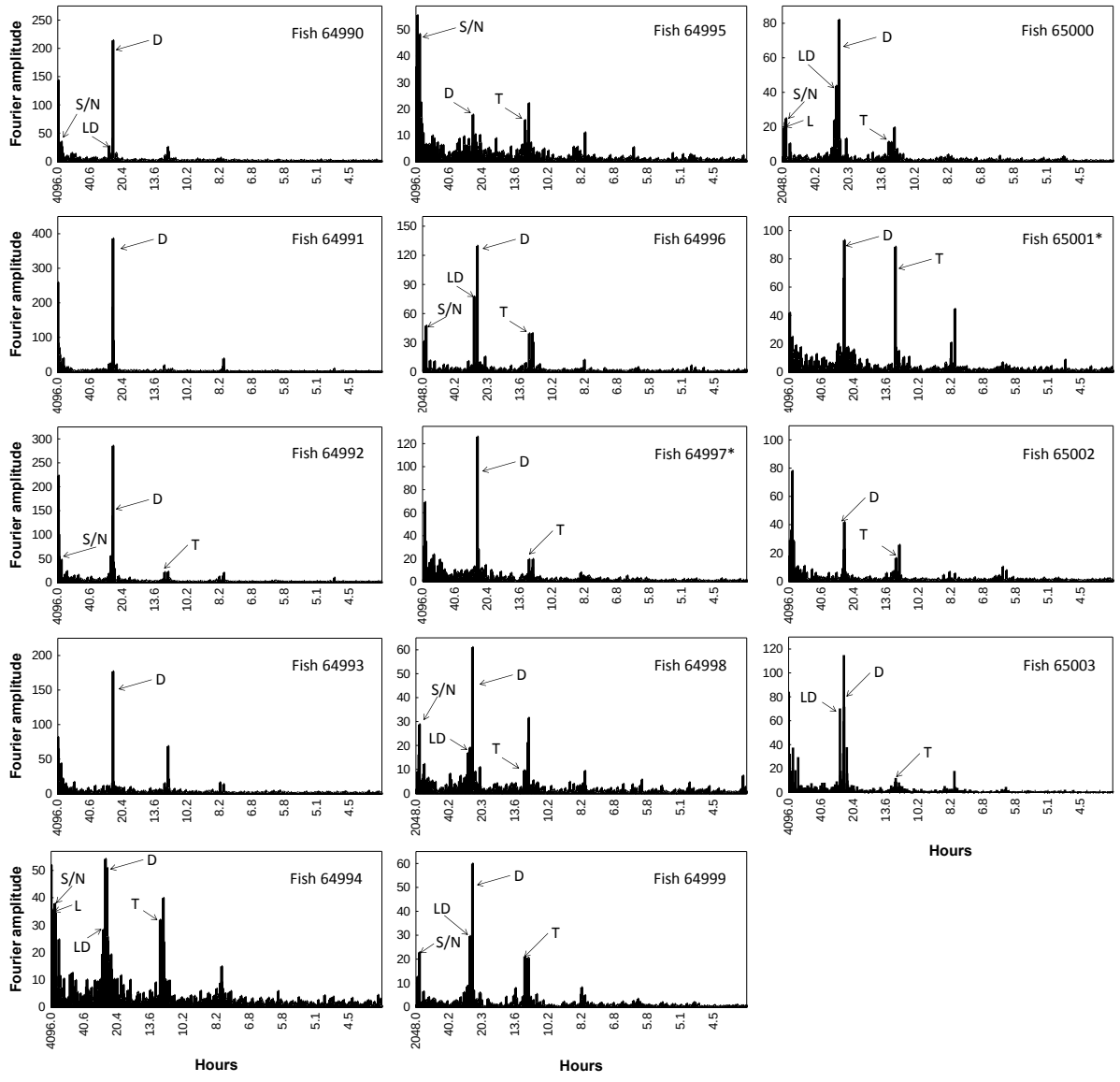

Figure 4.9: Periodograms of the spectral (Fourier) analyses of the presence/absence data series for white steenbras from the Sundays Estuary (n = 14). Letters indicate cycles with which the respective peaks are associated (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month). Fish ID codes presented with * indicate periodograms with re-scaled y-axes

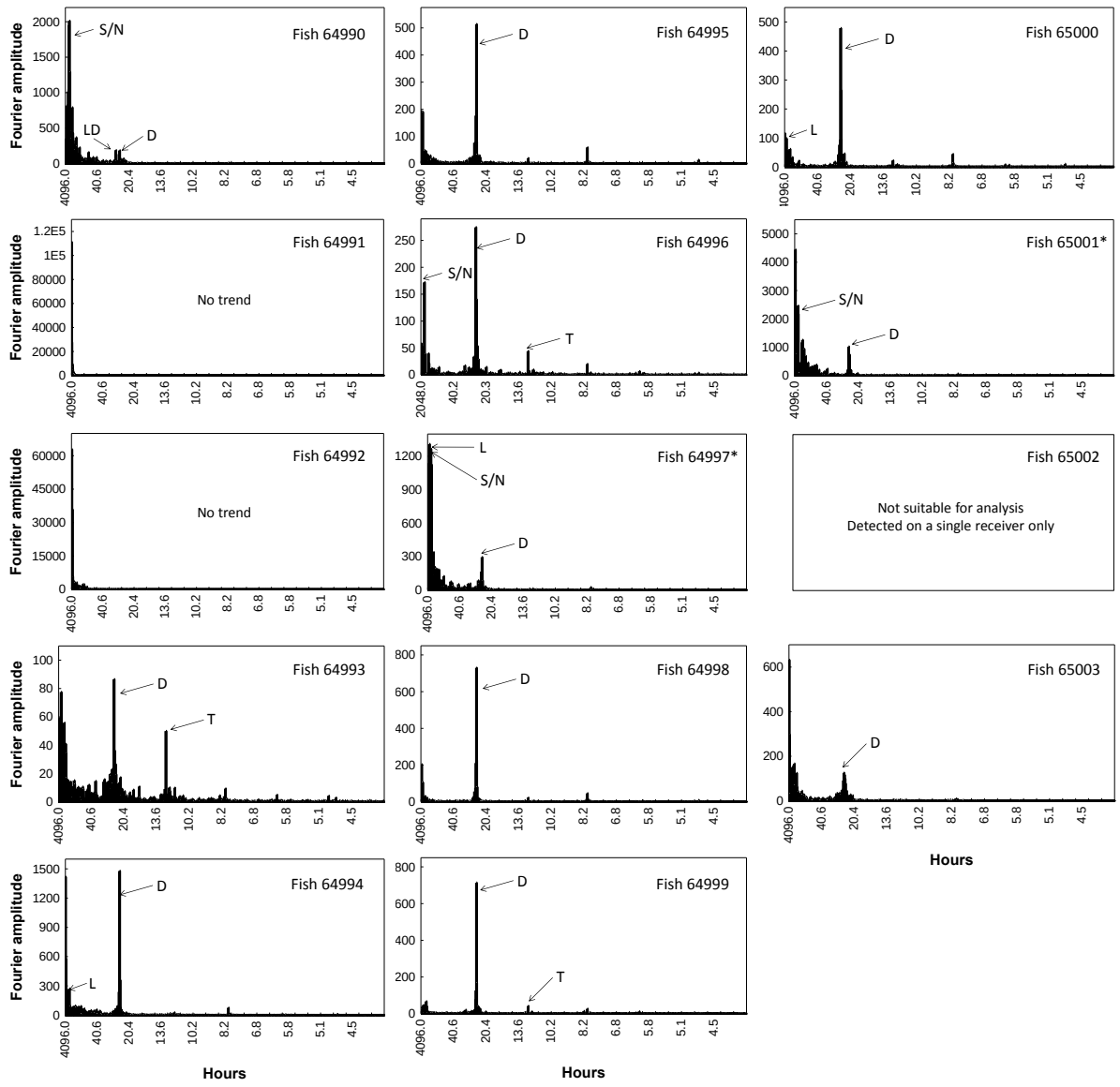

Figure 4.10: Periodograms of the spectral (Fourier) analyses of the average receiver location data series for white steenbras from the Sundays Estuary (n = 13). Letters indicate cycles with which the respective peaks are associated (D – diel, T – tidal, LD – lunar day, S/N – spring/neap, L – lunar month). Fish ID codes presented with * indicate periodograms with re-scaled y-axes

4.3.3 Further exploration of rhythmic movement patterns

Diel movement patterns in the East Kleinemonde Estuary

Mean times of departure and arrival associated with excursions (> 6 h) from the receiver array, in the vicinity of receivers 2 and 3 in the East Kleinemonde Estuary, varied among individuals. Three individuals tagged with long-period transmitters (Fish 3759, 3761, 3764) and one fish tagged with a short-period transmitter (Fish 2003) exhibited mean departure and arrival times significantly different from random (Figures 4.11 and 4.12, respectively).

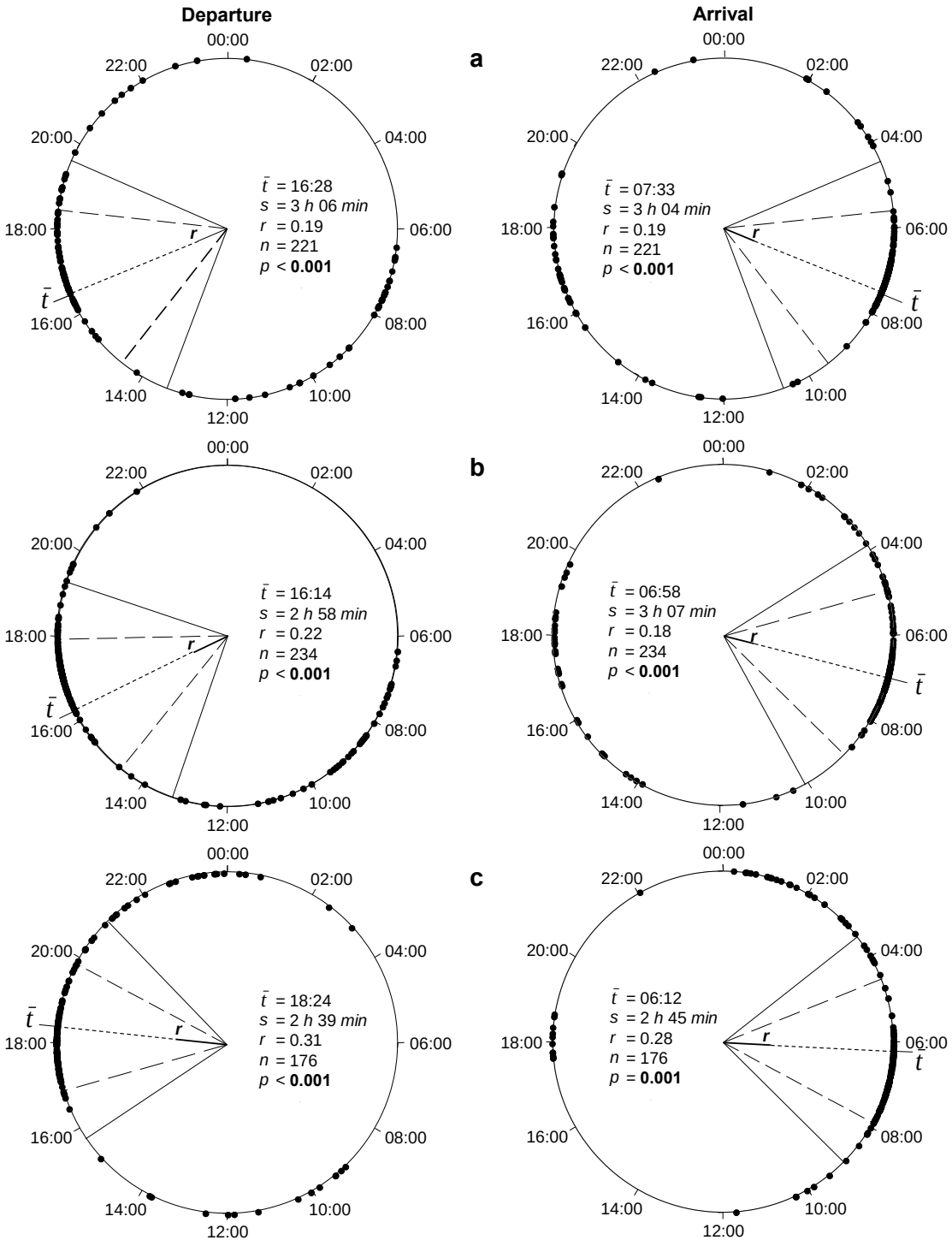

Figure 4.11: Mean times of departure from and arrival at the receiver array, associated with excursions from the array (> 6 h), for a) Fish 3759, b) Fish 3761 and c) Fish 3764 in the East Kleinemonde Estuary. Dotted lines represent mean times ($\bar{t}$), solid radials represent angular deviation (s), dashed radials represent upper and lower confidence limits and the solid line indicated by *r* is the mean vector length, representing an index of concentration of data points

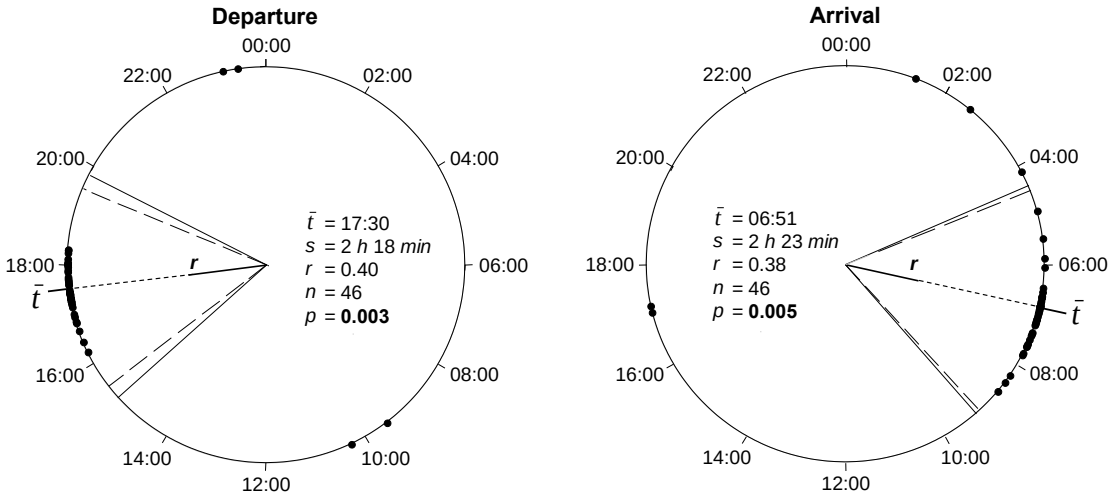

Figure 4.12: Mean time of departure from and arrival at the receiver array, associated with excursions from the array (> 6 h), for Fish 2003 in the East Kleinemonde Estuary. Dotted lines represent mean times ($\bar{t}$), solid radials represent angular deviation (s), dashed radials represent upper and lower confidence limits and the solid line indicated by *r* is the mean vector length, representing an index of concentration of data points

One individual (Fish 3769) tagged with a long period transmitter, exhibited a mean departure time significantly different, but a mean arrival time not significantly different from random (Figure 4.13).

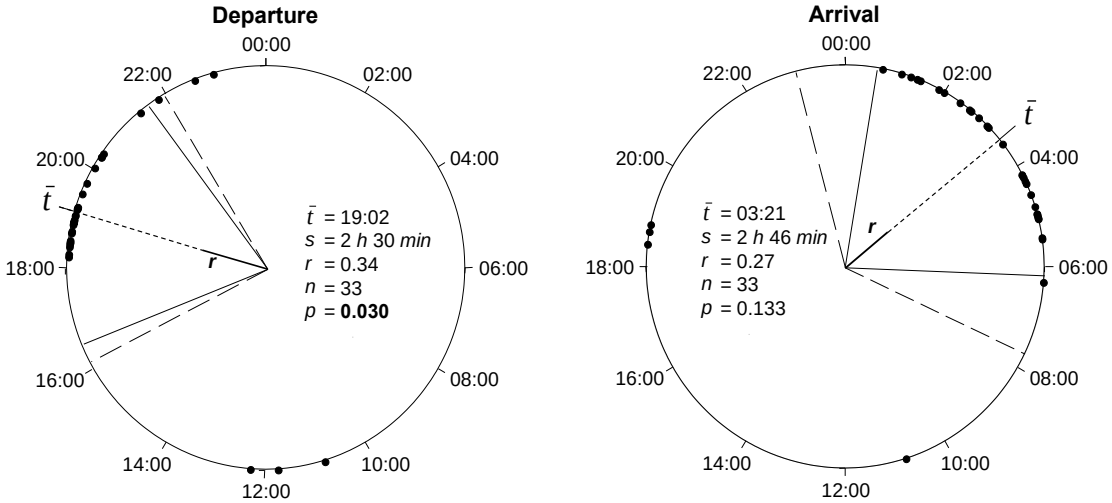

Figure 4.13: Mean time of departure from and arrival at the receiver array, associated with excursions from the array (> 6 h), for Fish 3769 in the East Kleinemonde Estuary. Dotted lines represent mean times ($\bar{t}$), solid radials represent angular deviation (s), dashed radials represent upper and lower confidence limits and the solid line indicated by *r* is the mean vector length, representing an index of concentration of data points

For these five individuals, mean times of departure and arrival were closely associated with daily times of sunset and sunrise, and showed little variability, ranging from 16:14 to 19:02 and 03:21 to 07:33, respectively (Table 4.2), providing further evidence of the distinct diel movement pattern.

Table 4.2: Mean departure and arrival times and associated angular deviations (hh:mm) for fish showing departure or arrival times significantly different from random (* refers to the number of observed excursions from the array exceeding 6 h)

Fish	* No. of excursions	Departure mean time	Angular deviation	Departure p-value	Arrival mean time	Angular deviation	Arrival p-value
2003	46	17:30	02:18	**0.003**	06:51	02:23	**0.005**
3759	221	16:28	03:06	**<0.001**	07:33	03:04	**<0.001**
3761	234	16:14	02:58	**<0.001**	06:58	03:07	**<0.001**
3764	176	18:24	02:39	**<0.001**	06:12	02:45	**0.001**
3769	33	19:02	02:30	**0.030**	03:21	02:46	0.132
Overall	805	17:09	03:00	**<0.001**	06:35	03:08	**<0.001**

When excursions undertaken by all individuals were analysed, the overall mean departure and arrival times were found to be significantly different from random (Figure 4.14). Furthermore, these overall mean departure (17:09) and arrival (06:35) times for all excursions by all fish fell within the ranges of the five individuals exhibiting mean times significantly different from random.

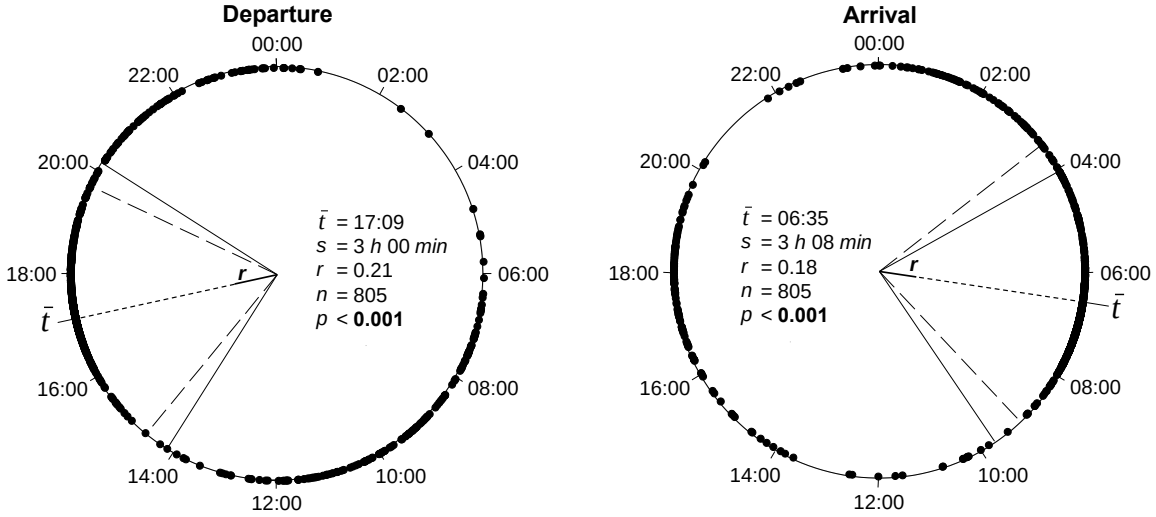

Figure 4.14: Mean time of departure from and arrival at the receiver array, associated with all excursions from the array (> 6 h), by all fish tagged in the East Kleinemonde Estuary combined. Dotted lines represent mean times ($\bar{t}$), solid radials represent angular deviation (s), dashed radials represent upper and lower confidence limits and the solid line indicated by *r* is the mean vector length, representing an index of concentration of data points

Tidal movements in the Kariega and Sundays estuaries

Fish tagged in the Kariega and Sundays estuaries displayed two types of behaviour; (i) six fish exhibited station-keeping behaviour throughout the period during which they were detected on the stationary receivers, and (ii) nineteen fish undertook varying numbers of 'significant' movements (i.e. 'significant' unidirectional movements between stationary receivers) during the period of a single tidal phase (i.e. < 6.2 h). In the Kariega Estuary, two of the ten fish made no significant movements, and a further two fish made only two significant movements each. The remaining fish all made numerous movements (Table 4.3). In the Sundays Estuary, a similar pattern was observed, with four of the 15 fish making no significant movements, two making only one such movement, and the rest undertaking multiple significant movements (Table 4.4). Individual fish in the Kariega Estuary made considerably more movements than those in the Sundays Estuary, with individual maxima of 232 and 146 movements by fish in the Kariega and Sundays estuaries, respectively.

Table 4.3: Summary of 'significant' estuarine movements made by the ten white steenbras tagged in the Kariega Estuary. The mean number of movements is based on all fish (n = 10), all other means are based only on fish that made significant movements (n = 8)

Movements		Up-estuary		Down-estuary		Mean duration	Spanning two tides		With tide		Against tide	
Fish ID	n	n	%	n	%	(h:min)	n	%	n	%	n	%
2036	103	52	50.5	51	49.5	01:42	23	22.3	66	64.1	14	13.6
2037	219	110	50.2	109	49.8	02:45	38	22.2	116	67.8	5	2.9
2038	122	59	48.4	63	51.6	01:31	22	18.6	74	62.7	21	17.8
2039	0	-	-	-	-	-	-	-	-	-	-	-
2040	2	1	50.0	1	50.0	02:19	0	0.0	1	50.0	1	50.0
2041	2	1	50.0	1	50.0	02:00	0	0.0	1	50.0	1	50.0
2042	232	116	50.0	116	50.0	02:10	38	19.4	151	77.0	6	3.1
2043	0	-	-	-	-	-	-	-	-	-	-	-
2044	14	7	50.0	7	50.0	02:43	4	28.6	10	71.4	0	0.0
2045	102	50	49.0	52	51.0	02:36	29	28.4	59	57.8	14	13.7
Mean	*80*	*50*	*49.8*	*50*	*50.2*	*02:13*	*19*	*17.4*	*60*	*62.6*	*8*	*18.9*
SD	*91*	*46*	*0.7*	*46*	*0.7*	*00:27*	*16*	*11.4*	*55*	*9.7*	*8*	*20.2*

Table 4.4: Summary of 'significant' estuarine movements made by the 15 white steenbras tagged in the Sundays Estuary. The mean number of movements is based on all fish (n = 15), all other means are based only on fish that made significant movements (n = 11)

Movements		Up-estuary		Down-estuary		Mean duration	Spanning two tides		With tide		Against tide	
Fish ID	n	n	%	n	%	(h:min)	n	%	n	%	n	%
64989	1	1	100.0	0	0.0	05:53	1	100.0	0	0.0	0	0.0
64990	76	33	43.4	43	56.6	03:31	37	48.7	15	19.7	24	31.6
64991	14	7	50.0	7	50.0	03:41	7	50.0	4	28.6	3	21.4
64992	43	20	46.5	23	53.5	03:48	23	53.5	13	30.2	7	16.3
64993	4	3	75.0	1	25.0	02:11	0	0.0	3	75.0	1	25.0
64994	79	44	55.7	35	44.3	02:49	38	48.1	27	34.2	14	17.7
64995	0	-	-	-	-	-	-	-	-	-	-	-
64996	20	13	65.0	7	35.0	02:47	8	40.0	9	45.0	3	15.0
64997	41	23	56.1	18	43.9	03:10	23	56.1	9	22.0	9	22.0
64998	0	-	-	-	-	-	-	-	-	-	-	-
64999	1	0	0.0	1	100.0	02:24	0	0.0	0	0.0	1	100.0
65000	0	-	-	-	-	-	-	-	-	-	-	-
65001	146	77	52.7	69	47.3	02:50	50	41.0	46	37.7	20	16.4
65002	0	-	-	-	-	-	-	-	-	-	-	-
65003	33	20	60.6	13	39.4	01:48	6	18.2	17	51.5	10	30.3
Mean	*31*	*22*	*55.0*	*20*	*45.0*	*03:10*	*18*	*41.4*	*13*	*31.3*	*8*	*26.9*
SD	*42*	*23*	*24.1*	*22*	*24.1*	*01:05*	*18*	*28.2*	*14*	*21.8*	*8*	*25.7*

The total numbers of 'significant' movements made by each individual were averaged over the number of months for which each individual was detected. This provided a measure of the frequency with which each fish undertook 'significant' movements, to i) allow direct comparison among individuals and between estuaries, while removing any bias associated with individual tracking duration, and ii) determine whether such movements constituted an important contribution to behaviour at the individual level. In the Kariega Estuary, the individual average number of movements per month ranged from 0 to 84, with a mean of 16.8 (± 25.5), which equates to one significant movement approximately every two days, or every eight tidal phases. In the Sundays Estuary, the range was 0 to 22, with a mean of only 4.5 (± 6.2) movements per month.

The directions of movements were classified as being made with the tide (i.e. up-estuary or down-estuary on the incoming and outgoing tides, respectively), against the tide (up-estuary or down-estuary on the outgoing and incoming tides, respectively) or as spanning two tides (i.e. had started

during one tidal phase and ended during the next tidal phase; by definition having moved with the tide and against the tide for some part of its movement). On average, the fish in the Kariega Estuary undertook 62.6% (± 9.7%) of their movements with the tide, with less than 20% of movements made either against the tide (18.9 ± 20.2%) or spanning two tidal phases (17.4 ± 11.4%). In contrast, the majority of movements in the Sundays Estuary spanned two tidal phases (41.4 ± 28.2%), while 31.3 % (± 21.8%) were made with the tide, and 26.9% (± 25.7%) against the tide. Some fish in the Sundays Estuary undertook long unidirectional movements. Some of these movements spanned great distances, for example fish 65001 undertook multiple movements between receivers 1 and 11, spanning a distance of approximately 10 km, and fish 64991 made multiple movements between receivers 3 and 16, spanning a distance of approximately 18 km. The durations of most of these long-distance movements exceeded 6.2 h, and spanned multiple changing tidal phases. In the Kariega Estuary, such long-duration movements were considerably less frequent. Here, the fish mainly utilised the area from receiver 1 to receiver 7, with few movements spanning distances of more than 5 km.

4.4 Discussion

Snapshots of animals' whereabouts are insufficient to fully understand their movement patterns, and how movement, distribution and area use change over time. This study assessed area use, movements and distribution of juvenile white steenbras over a range of temporal scales in a range of estuaries, and has provided a more comprehensive understanding of this species' ecology.

4.4.1 Long-term patterns in area use

Analyses of mean monthly time spent in the vicinity of each receiver, and the monthly proportions of individuals with active transmitters that were detected on each, indicated an up-estuary shift in the area of utilisation for some individuals, with the onset of the winter months. These shifts were characterised by visits to parts of the estuary further from the mouth, and in many cases decreased time spent in areas closer to the mouth; although the winter and summer areas for individuals were rarely completely discrete. This behaviour was not observed for all individuals, with roughly equal proportions exhibiting the behavioural shift and long-term station-keeping behaviour. This trend was consistent among estuaries. The seasonal shift in area utilisation may be a result of seasonal changes in the physical environmental conditions, or may reflect a form of resource partitioning (Akin *et al*. 2003). White steenbras cannot be sexed macroscopically, negating the possibility of assessing the effects of sex on long-term movements, and there appeared to be no relationship between fish size and whether they undertook such seasonal shifts in area use.

The observed result is in contrast to that reported by Lamberth *et al*. (2008), who showed that white steenbras distribution in the permanently open Breede and Olifants estuaries along the South African south west and west coasts, respectively, was closer to the mouths of these estuaries in winter. However, these authors speculated that prior to the current high levels of water abstraction from these two estuaries, the increased levels of freshwater inflow would have resulted in lower salinities within the upper and middle reaches, which would have restricted benthic macroinvertebrates, such as sand prawn *Callianassa krausii* and mud prawn *Upogebia africana*, to the lower reaches. As a result, benthic macroinvertebrate feeders, such as white steenbras, would have been present closer to the mouth of each estuary, under higher freshwater inflow conditions (Lamberth *et al*. 2008). The winter down-estuary shift in these two estuaries may, therefore, have been in response to the winter rainfall climate in the Western Cape Province (Lamberth *et al*. 2008).

Harrison (2003) reported a positive correlation between white steenbras abundance in estuaries and salinity. The Eastern Cape Province experiences summer rainfall, which is likely to reduce salinity in the upper reaches of the estuaries within this Province, in the summer months, which in turn could restrict white steenbras to the lower or lower-to-middle reaches at this time of year. However, during the study periods in the Kariega Estuary (March 2009 to February 2010) and Sundays Estuary (March 2010 to November 2011), the volume of freshwater discharge into each estuary was elevated over the winter months, suggesting that freshwater inflow is not the driving factor of the up-estuary shifts observed in this study.

Estuaries are characterised by seasonal changes in environmental conditions (Marshall and Elliot 1998), the most obvious of which is temperature (e.g. see Figure 3.5, Chapter 3). Harrison (2003) reported a negative correlation between white steenbras abundance and estuarine water temperature, as well as dissolved oxygen concentration. Russell (1994) recorded mass mortalities of white steenbras in the Swartvlei and Wilderness Lakes system, along the South African south coast, as a result of excessively low concentrations of dissolved oxygen. The higher summer temperatures in the upper reaches of the three estuaries, which regularly exceed 20°C, and by inference the associated decreased dissolved oxygen levels, may act as a physiological obstruction to the upper limit of white steenbras movement during the summer months. Akin *et al*. (2003) reported a similar finding, showing strong spatial variation in fish and macrocrustacean species composition in the Mad Island Marsh Estuary, Texas, USA, during the summer months, as a result of combined high temperature and low dissolved oxygen, with particular influence on the estuarine-dependent species, which were found closer to the mouth during these conditions.

An environmentally-driven change could be expected to affect all or most individuals in the same way. The fact that roughly equal proportions of fish exhibited the seasonal shift in area use and the long-term station-keeping behaviours, despite seasonal changes in environmental conditions, suggests that environmental conditions are not the only factor influencing the seasonal behavioural change. Alternatively, the fact that the two behaviours were exhibited by roughly equal proportions of individuals, and that the behaviour in some of the "movers" was an up-estuary shift, rather than expansion of area used, suggests that the split in seasonal behaviours may be a form of resource partitioning among juvenile white steenbras, to decrease intraspecific competition (Matthews 1990b, Akin *et al*. 2003).

A home range contains a finite amount of energy as a resource, proportional to its area, with habitats of greater productivity resulting in smaller home ranges for a given species (Avenant and Nel 1998). Decreased solar energy is likely to cause lower primary productivity during winter, which may be detectable at lower trophic levels. Therefore, animals may be required to expand their home ranges during periods or seasons of lower productivity. The observed behaviour in white steenbras may, therefore, reflect seasonal variability in prey availability (Simcharoen *et al*. 2008). This could be tested by simultaneous examination of the distributions, home range sizes and condition factors of white steenbras and their predominant prey items, as well primary productivity levels at different depths in the water column, at regular intervals over a one-year period.

4.4.2 Rhythmic movement patterns

Results of the Fourier analyses indicated movement rhythms over diel (24.0 h), tidal (12.4), lunar-day (24.8 hours), spring-neap (14.2 days) and lunar month (28.4 days) cycles, associated with abiotic environmental cycles at their respective periodicities (Boehlert and Mundy 1988). However, the dominant rhythm underlying the observed periodicities in the movements of white steenbras from the East Kleinemonde, Kariega and Sundays estuaries was the diel cycle (i.e. circadian), with secondary 12.4-h tidal cycles (i.e. circatidal) in the permanently open Kariega and Sundays estuaries. A similar result was obtained by Hartill *et al*. (2003) for snapper *Pagrus auratus*, in the Mahurangi Harbour Estuary, New Zealand, in which the dominant rhythm was diel, followed by a secondary tidal peak occurring in fewer individuals. This may be a result of the presence of separate circadian and circatidal rhythms within individual fish (Wilcockson and Zhang 2008). Individual circadian and circatidal rhythms were further explored.

Diel movement

A diel behavioural rhythm was observed for every fish, in all three estuaries studied. This agrees with the diel movement pattern identified through the use of circular statistics in the East Kleinemonde Estuary, where individual movements away from the stationary receiver array were associated with the daily sunset time and return to the array associated with sunrise. The results of the Fourier analyses and the circular statistics, from the stationary receiver data, also confirmed the cyclic variation in the locations of daytime and night-time home ranges observed in the East Kleinemonde Estuary through manual tracking (see Chapter 3), reinforcing that time of day plays a significant role in the distribution of individual juvenile white steenbras within estuaries. The fact that in all three estuaries the diel pattern in the Fourier analyses was the most dominant suggests that time of day is one of the most important factors influencing their movements.

The strictly nocturnal presence of 1- to 2-year old white steenbras in the shallow littoral sand/mudflats in the East Kleinemonde Estuary above the road bridge was confirmed by Becker *et al*. (2011), using dual frequency identification sonar imagery. Juvenile snapper in the Mahurangi Harbour Estuary, New Zealand, followed a very similar pattern to that exhibited for white steenbras during the current study, with most individuals exhibiting a diel pattern of movement from the main channel areas where they spent the daylight hours, onto the surrounding shallow banks at night. These snapper were also resident in small areas, making diel movements over small spatial scales (Hartill *et al*. 2003). Diel changes in activity have also been observed in numerous other sparid species. White stumpnose *Rhabdosargus globiceps* in the Langebaan Lagoon, South Africa, were observed to be more active at dusk and at night-time than during the day (Attwood *et al.* 2007). Black bream *Acanthopagrus butcheri* in the Gippsland Lakes estuary network, Australia, were more active in foraging areas at night, and took shelter during the day (Hindell *et al*. 2008), while salema *Sarpa salpa* tracked in Calvi and Achiarina Bays in Corsica, in the Mediterranean Sea, were shown to be inactive at night, and became more mobile during the day (Jadot *et al.* 2006). Jadot *et al.* (2002) suggested that nocturnal and crepuscular activity is a mechanism for optimising foraging and reducing predation risk. Gilthead seabream *Sparus aurata* in the Ria Formosa Coastal Lagoon, Portugal, also showed diel movement behaviour, although some individuals exhibited nocturnal activity and others diurnal activity (Abecasis and Erzini 2008).

The observed diel movement pattern for white steenbras in the East Kleinemonde Estuary was closely associated with sunset and sunrise times, suggesting that the behaviour was driven by light intensity. The change in light intensity during the crepuscular periods has been suggested to be the

cue to initiate foraging behaviour in certain pelagic fishes Andrews *et al*. (2009). Similarly, Jadot *et al*. (2002, 2006) recorded increased crepuscular activity of salema, in Calvi and Achiarina Bays in the Mediterranean Sea, during movements between daytime feeding and night-time resting home ranges. Light intensity-associated movements have been observed for numerous fish species, e.g. juvenile Atlantic cod *Gadus morhus* in Conception Bay, Newfoundland, USA (Clark and Green 1990), whitesaddle goatfish *Parupeneus porphyreus* in Kaneohe Bay, Hawaii (Meyer *et al*. 2000), California sheephead *Semicossyphus pulcher* around Santa Catalina Island, California, USA (Topping *et al.* 2005), Hawaiian stingray *Dasyatis lata*, in Kanoehe Bay, Hawaii (Cartamil *et al*. 2003), and a range of Hawaiian reef fish species (Hobson 1972).

Diel movement behaviour (identified through manual tracking data or excursions away from the stationary receiver array) was only exhibited by seven of the 15 fish tracked in the East Kleinemonde Estuary (although all of these fish exhibited diel cycles in their presence/absence and/or average receiver data series). This may be a result of certain individuals making insufficient diel position shifts to show significant movements, or that these animals made movements on a scale undetectable by the array within this system; however, it is consistent with other species that exhibit individual behavioural variation in movement patterns. Such intra-specific variability in movement behaviour has been described for numerous fishes, e.g. galjoen *Dichistius capensis* (Attwood and Bennett 1994), snapper (Hartill *et al.* 2003), spotted grunter *Pomadasys commersonnii* (Childs *et al.* 2008a) and dusky kob *Argyrosomus japonicus* (Cowley *et al.* 2008), highlighting the importance of understanding movement behaviour at the individual level (Aebischer *et al.* 1993, Egli and Babcock 2004, Codling 2008).

Tidal-associated movement patterns

The absence of tidal movement cycles (12.4 h) in the fish tagged in East Kleinemonde Estuary was to be expected, as this system remained closed and was not influenced by tidal exchange. According to Chabot and Watson (2010), circatidal rhythms are usually restricted to organisms inhabiting tidal environments. Tidal cycles were, however, detected in the fish from the permanently open Kariega and Sundays estuaries, and occurred in either one or both data series for most fish from these two systems.

Palmer (1973) introduced the term ‘circalunadian’ (which Chabot and Watson 2010 more recently termed ‘circalunidian’), to describe the lunar day, representing the 24.8-h cycle required for the earth to complete one full rotation on its axis, relative to the moon’s position, encompassing two full

tidal cycles (12.4 h). He suggested that the two tidal cycles observed approximately each day in many organisms may in fact comprise a single bimodal circalunadian (24.8-h) cycle, rather than two separate tidal (12.4-h) oscillators. As such, cycles at 12.4 and 24.8 h are both tidal, and under the influence of the moon's orbit of the earth. Based on Palmer's (1973) explanations, it is proposed that the circalunadian peaks (24.8 h) identified in the closed East Kleinemonde Estuary, in the absence of tidal water movement or movement of fish at tidal (12.4 h) cycles, were in response to the level of moonlight, rather than the gravitational force of the moon or the direct physical effects associated with tidal fluctuation, which itself is driven by the lunar-day cycle (Morgan 2001).

The greater prevalence of movements associated with circalunadian (24.8 h) and circatidal (12.4 h) cycles in the average receiver data series of the Kariega Estuary fish than in those of the fish from the Sundays Estuary, suggests that the tidal and lunar-day effects are of greater importance in the former. This is supported by the presence/absence data series, in which the 12.4-h tidal-associated movements in the Sundays Estuary fish were commonly only ranked third, fourth or fifth, whereas in the Kariega Estuary tidal movements were mainly dominant or secondary. This is most likely a result of the differences in bathymetry in the two systems. In the Sundays Estuary, most sandbanks remain submerged on most low tides, allowing fish to access the shallow areas at any time of the diel cycle, similar to that identified in the East Kleinemonde Estuary. However, in the Kariega Estuary, the main sandbank becomes exposed on the spring and neap low tides (see Figure 3.2, Chapter 3), restricting access to certain tidal states only. As a result, white steenbras in this estuary are forced into a behavioural pattern influenced both by tide and by time of day. Colton and Alevizon (1983) found a similar result for bonefish *Albula vulpes* at Grand Bahama Island, where the fish exhibited movements with the tide, although movement behaviours differed somewhat between two geographically proximal areas. The authors ascribed these differences to bottom topography, food distribution and predation.

Movements associated with the spring/neap cycle were more common in the Sundays Estuary than the Kariega Estuary, particularly in the presence/absence data series. This may be due to the absolute depths occurring on the low tides across the spring/neap cycle. In the Kariega Estuary, the main sand bank area is exposed on all low tides, whereas in the Sundays Estuary, the main areas of sandbank become exposed only on spring low tides, which may affect these fish on a spring/neap periodicity. Lunar and spring-neap cycles were more prevalent in the average receiver location data series than the presence/absence data series, in both the Kariega and Sundays estuaries, suggesting that the lunar and spring/neap cycles had a greater influence on axial, than transverse movements.

This is likely a result of differences in the distance that marine conditions penetrate the estuary during different lunar phases (e.g. the distance that a salt wedge moves up the estuary would be greater on the spring high tide), thereby affecting the axial position of the fish (and thus the average receiver location) to a greater extent than the presence/absence of the fish. Such results suggest that changes in the mouth dynamics of an estuary may significantly influence the movement patterns of white steenbras, or at least the ability of the tidal and spring neap cycles to influence their movement, which may also be true for other species. This is evident in the Sundays Estuary, where the progressive deposition of silt in the mouth has resulted in decreased flow and scouring within the estuary. There is also evidence of higher tides (i.e. a greater estuary volume) during spring high and low tide phases, and lower tides (and a smaller estuary volume) during neap high and low phases, due to the time required for total water exchange on a spring high tide exceeding that allowed by the narrow and shallow estuary mouth (personal observation).

Exploration of the effects of tide on the movement of white steenbras provided further evidence of multiple behavioural traits, with some individuals making frequent up- and down-estuary movements, while others showed strong station-keeping behaviour. This appears to be a common trend, highlighting both the occurrence of intraspecific variability in behaviour, and the long-term residency of the species. Interestingly, the individuals that exhibited strict station-keeping behaviour did not exhibit a winter shift in high-use area, suggesting that the fish follow either a resident behaviour, or one in which some exploration takes place, with little 'switching' between behaviours.

The higher numbers of 'significant' movements (i.e. movements spanning at least 1 km between detection ranges of the start and end receivers) amongst the Kariega fish were not simply an artefact of a longer study period in this estuary, as evidenced by the higher monthly average number of movements per fish in this system. There may be two explanations for this. Firstly, the fish in the Kariega Estuary may simply be undertaking more movements, possibly in order to feed more efficiently. Secondly, the more frequent occurrence of these movements in the Kariega Estuary may not be due to variable frequencies of movement, but rather due to the movements within this system being of generally shorter duration, therefore allowing more movements to meet the "maximum 6.2-h duration" criterion. The results of the tidal analyses support both theories. Firstly, the greater prevalence of tidal-associated movements in the Kariega Estuary fish, indicated by the Fourier analysis, suggested that the tidal influence on this system is greater than on the Sundays Estuary, with the regular tidal exposure and inundation cycles of the main sandbank and feeding areas driving a tidal-associated movement pattern in fish in the Kariega Estuary. Secondly, the fish in

the lower reaches of the Kariega Estuary, where the majority of time was spent, were exposed to considerably higher current speeds than those in the lower reaches of the Sundays Estuary (see Tables 3.3 and 3.4, Chapter 3). Fish in the Kariega Estuary may, therefore, be forced to complete any extensive movements within a tidal phase, to avoid having to move against the stronger currents.

Further evidence to support this notion is provided by the high proportions of movements in the Kariega Estuary that were made in the direction of the tidal movement, compared to those made against the tide. The high proportions of movements within the Sundays Estuary made spanning two tidal phases, and the lower proportions of movements made with the tidal movement further indicate the lesser effect of the tide in this system. Furthermore, many of the 'significant' movements in the Sundays Estuary were made in the middle and upper reaches, where current speeds were considerably lower than in the lower reaches of the estuary. The results, therefore, suggest that in areas of high current speed, the white steenbras undertake shorter duration movements that are completed within a single tidal phase, allowing movements with the tide. White steenbras in the Heuningnes Estuary were observed to shift their position up and down the estuary with the direction of tidal flow (Mehl 1973). This type of behaviour may be an adaptation to fluctuating environmental conditions, with tidal-associated movement decreasing the magnitude of the fluctuations. Movement with the tide also allows an animal to explore a greater area of estuarine habitat, with reduced energy consumption (Almeida 1996), with the most common driving reasons behind tidal movements being feeding and predator avoidance (Vinagre *et al*. 2006). Such behaviour is common among estuarine-associated fishes. Snapper were observed to make small-scale movements with the tide in Mahurangi Harbour Estuary, New Zealand (Hartill *et al*. 2003), and black bream *Acanthopagrus butcheri* exhibited movements of direction and magnitude correlated to the direction and magnitude of the tidal change in Little Swanport Estuary, Tasmania, Australia (Sakabe and Lyle 2010). Childs *et al*. (2008a) recorded tidal-associated movements of spotted grunter in the Great Fish Estuary, South Africa. In the same estuary, Næsje *et al*. (in press) recorded tidal-associated movement in dusky kob, although these fish alternated between tidal-associated movement patterns and station-keeping behaviour, a strategy which the authors attributed to optimising feeding.

Despite the high number of movements undertaken, particularly in the Kariega Estuary, and the presence of tidal cycles detected by the Fourier analyses, the low average numbers of movements made per month in each estuary (approximately one movement per eight tidal phases and 24 tidal phases in the Kariega and Sundays estuaries, respectively), suggests that extensive up- and down-

estuary movements do not comprise a critical component of the behaviour of juvenile white steenbras in these two estuaries. Alternatively the energetic costs or predation risks associated with such movements may outweigh the benefits. Station-keeping behaviour may be expected for a species that feeds on sedentary organisms, as is the case with white steenbras (Mehl 1973, Bennett 1993b). What then, is the cause of the observed tidal cycles in the Fourier analyses? This may be best explained by the Fourier analysis results themselves. As the average receiver location metric was aimed at identifying axial estuarine movements, it was expected that tidal influence would be greater on that metric than on the presence/absence metric. The fact that this was not observed suggests that white steenbras distribution along the length of the estuary is influenced less by axial tidal water movement, and more by the changes in depth and associated cycles of exposure and inundation. Tidal influence, therefore, appears to manifest as transverse (movements between shallow banks and channels), rather than axial, changes in position, as shown by the night-time home ranges in the shallow areas of the East Kleinemonde Estuary, and the high tide use of the intertidal sandbanks in the Kariega Estuary.

It appears, then, that the prevalent behaviour is that of station-keeping, exhibited by some individuals all the time and by others most of the time. Most fish exhibited only small-scale movements between shallow sandbanks and deeper channel areas, associated with tidal inundation cycles. It also appears that when white steenbras do undertake movements, particularly in areas of high current speed, such as in the lower reaches of the Kariega Estuary, they are generally in the direction of the tidal movement, while in areas of lower current speeds movements are less strictly associated with the tides. However, the occurrence of movements, even of low frequency, against the direction of the tidal movement suggests that the fish are capable of moving against the tide when necessary.

4.5 Conclusions

The apparent winter upriver shift in the high-use areas of some individuals, and the strong diel behaviour identified through the circular statistics analysis highlight the fact that movement, area use and distribution are temporally dynamic, emphasizing the importance of long-term data collection and the collection of data at multiple temporal scales (Nathan *et al*. 2008). Single series spectral (Fourier) analysis, using the Fast Fourier Transform, allowed for the identification of cyclical rhythms in the movements of white steenbras in estuaries, thereby providing a basis for further, more in-depth environmental analyses. The tool is thus useful for exploratory analyses and identification of movement rhythms in estuarine fishes.

Diel movement was found to be the dominant cyclical pattern, followed by tidal-associated movement that was exhibited by fewer individuals. The diel pattern is created by fish moving into the shallow littoral zone at night to feed, and seeking refuge in the deeper channel areas during the daytime, although the possibility of daytime feeding cannot be discounted. This diel behavioural pattern is therefore hypothesised to be driven by both feeding and predator avoidance. The extent to which these two factors drive the observed diel movement pattern in white steenbras could be directly assessed through simultaneous tracking of the positions, movement patterns and cyclical patterns of white steenbras and the major predatory fishes within an estuary, to quantify predator-prey interactions; as well as a diel analysis of stomach contents or telemetric assessment of physiological state, to describe feeding patterns.

A behavioural pattern was identified in the permanently open Kariega Estuary, which is characterised by extensive intertidal sandbanks, in which movements onto the shallow banks were driven by both the diel cycle and cycles of tidal inundation. In the Sundays Estuary, which is characterised by subtidal sandbanks, tidal behaviour was considerably less prevalent, with fish able to utilise the banks following a diel rhythm, at any tidal state. However, despite the relatively frequent occurrence of tidal-associated movements, the spatial extent of these movements was small, in the order of one to two kilometres.

The observation of individual variability in the cyclic movement patterns of juvenile white steenbras, as observed in their patterns of area use and home range (see Chapter 3), highlights the importance of studying movement at the individual level (Able and Grothues 2007b, Codling 2008). Similarly, the variability in results among estuaries of different type highlights the importance of management of estuaries as individual units.

The types of environmental processes observed to influence the movements of juvenile white steenbras in estuaries, such as the diel cycle and tidal inundation cycles, and possibly the seasonal changes in water temperature, suggest that the factors influencing movement patterns of white steenbras in estuaries work in a complex synergistic manner (Marshall and Elliot 1998). Negative anthropogenic effects on the estuarine habitat and influences on these environmental processes may cause complex repercussions for species utilising these habitats. Therefore, estuaries should be managed in such a way as to ensure the maintenance of ecosystem functioning and the natural range of dynamic states (Whitfield and Bruton 1989, Bennett 1993b).

Chapter 5

Factors affecting distribution in estuaries

5.1 Introduction

Estuaries are highly dynamic environments, within which physical conditions, such as salinity, temperature, current speed and turbidity (among others), may fluctuate substantially (Whitfield 1990). Such fluctuations are often of high magnitude and can be acute, both spatially and temporally, and may have considerable effects on the distribution and movements of species utilising estuaries (Cyrus and Blaber 1987, Whitfield 1998, Marshall and Elliot 1998, Sackett *et al*. 2008). It is therefore important to understand which environmental variables influence the distribution and area use of fishes within estuaries, the extent to which each variable is influential and the mechanism underlying each. The previous chapter identified strong diel cycles in the movement of juvenile white steenbras in the East Kleinemonde, Kariega and Sundays estuaries and, to a lesser extent, tidal cycles in the latter two (permanently open) estuaries. However, despite these patterns, the fish exhibited predominantly station-keeping behaviour. This suggests an ability to tolerate fluctuating environmental conditions, particularly with the fish being resident in the lower reaches of estuaries where environmental fluctuations may be most pronounced. However, it was felt that it was still necessary to determine whether prevailing environmental conditions affected the distributions of the fish within these estuaries.

Acoustic telemetry has been used extensively to study the distribution and movements of fishes in estuaries. Numerous such studies have provided evidence of variability among individual fish; for example, snapper *Pagrus auratus* (Hartill *et al*. 2003), spotted grunter *Pomadasys commersonnii* (Childs *et al*. 2008a) and dusky kob *Argyrosomus japonicus* (Cowley *et al*. 2008). However, intraspecific variability in movement behaviour among estuaries of different type has rarely been assessed. Estuaries differ in physiological and hydrodynamic conditions, such as mouth state, bathymetry and tidal prism, geographic location, climatic conditions (such as mean annual rainfall), and biotic characteristics, such as the presence of submerged macrophyte beds, the density of benthic invertebrates and presence or absence of large predators, which collectively define how that individual system functions, and it is likely that no two estuaries function identically (Whitfield 1998). Consequently, it is intuitive that movement behaviour within a species would also differ in certain aspects among individual estuarine systems, or at least among different types of estuaries (Vasconcelos *et al*. 2010). Such inter-estuary variability would have considerable implications for

estuarine and fisheries management, and would mean that movement behaviour observed within one type of estuary should not simply be inferred for other estuarine systems, particularly those varying in characteristics such as estuary type, size, freshwater input and mouth state. Assessment within a range of geographically proximal estuaries of different type would provide a more comprehensive understanding of the factors that influence the distribution and area use of a species within estuaries (Vasconcelos *et al*. 2010). The range of estuarine conditions observed in the four estuaries in which telemetry studies were conducted (see Chapter 3) provided a unique opportunity to assess factors affecting movement within estuaries, and a comparative assessment of the movement patterns of a single species across estuary types.

5.1.1 Aims and objectives

The aim of this chapter was to assess the environmental variables driving the observed distribution and area use patterns of white steenbras in the Great Fish, East Kleinemonde, Kariega and Sundays estuaries, using acoustic telemetry data and environmental data. The specific objectives were to:

i. Assess the effect of substrate type on the white steenbras distribution in each estuary; and
ii. Assess the effects of different environmental variables on distribution in each estuary.

5.2 Methods and materials

Passive acoustic telemetry data (presented in Chapter 3) and environmental data were used to assess the effects of different environmental variables on the distribution of the tracked fish in the different estuaries. Three analyses were conducted; the first was an assessment of whether certain substrate types were used disproportionately more than others, the second was an assessment of whether the different environmental variables recorded at positional fixes for each fish (during manual tracking) showed deviation from an expected random distribution, and the third was a comparison of environmental data recorded at fish positional fixes (during manual tracking) and those recorded at fixed stations within each estuary. Due to logistical constraints, manual tracking could not be conducted in the Sundays Estuary, and fixed stations for recording environmental data could not be conducted in the East Kleinemonde or Sundays Estuary.

5.2.1 Substrate type

The effect of substrate type on the distribution and area use of white steenbras was assessed in the East Kleinemonde, Kariega and Sundays estuaries by determining the proportions of time spent by each individual in areas of different substrate type, relative to the proportions of each substrate

available at the landscape level (i.e. the study estuary). The Great Fish Estuary was not considered due to the short study duration. Aebischer *et al*. (1993) estimated habitat use as the proportion of detections made within each substrate type. However, as individuals are expected to minimise their time spent out of optimal resource areas (Fauchald and Tveraa 2006), it was felt that the proportions of time spent in areas of each substrate type would better reflect the contribution of each substrate type to the animal's fitness, than absolute numbers of detections (Block and Brennan 1999 in Simcharoen *et al* 2008). In order to determine the proportions of each substrate available, each estuary was divided into a sand zone, a transition zone of mixed sand and mud, and a mud zone. Divisions were based on assessments of estuarine species distributions (Cowley and Whitfield 2001, Wooldridge and Bezuidenhout 2007) and visual assessment of substrate type. Sand zones were defined by clean, coarse-grained sand sediments and mud zones by fine-grained silt. Areas comprising both coarse- and fine-grained sediments were classified as zones of mixed sand and mud.

Using Chi-square contingency tables, the proportions of time spent by each individual in the vicinity of receivers positioned in areas of sand, mud or mixed sand and mud substrate were compared to the overall proportions of these substrate types available in each estuary, to determine whether time spent associated with certain substrate types was significantly disproportionately greater than others (Katnik and Wielgus 2005). Then, to determine which substrate type was responsible for significant Chi-square values at the individual level, the "affinity" of each fish for each substrate type was estimated using a modified approach to the 'Habitat Affinity Index' (HAI) described by Monaco *et al*. (1998). HAI values were calculated for each of the three substrate types, for each individual, as follows:

$$HAI_{habitat} = (p - r)/r \text{ , if } p \leq r, \text{ or}$$

$$HAI_{habitat} = (p - r)/(1 - r); \text{ if } p \geq r,$$

where p was calculated as the proportion of time spent by each fish over each substrate type, and r was determined as the proportion of each substrate available within each estuary. The HAI produces values ranging from -1, indicating no time spent over that substrate, to +1, indicating exclusive use of that substrate. Positive HAI values indicate affinity for that substrate type, while negative values indicate avoidance (Monaco *et al*. 1998).

East Kleinemonde Estuary

Wooldridge and Bezuidenhout (2007) identified two different invertebrate communities within the East Kleinemonde Estuary; those species associated with sandy substrates, occurring predominantly

between the mouth and the bridge (approximately 800 m), and those associated with mud substrate occurring predominantly up-estuary of the bridge. The fact that sand prawns *Callianassa krausii* are found in abundance in the latter region (Terörde 2005) suggested an area of sand/mud transition up-estuary of the bridge (approximately 500 m), including the shallow littoral zone against the north west bank. The mud zone in this system was deemed to start at the end of this shallow littoral area (see Figure 3.4, Chapter 3), approximately 1.3 km from the mouth.

Kariega Estuary

Visual assessment of the substrate in the Kariega Estuary confirmed the presence of sandy substrate to approximately 2.6 km from the mouth, up-estuary of which the sand becomes mixed with riverine mud (see Figure 3.6, Chapter 3). Grange *et al*. (2000) suggested that, as a result of low freshwater input into this estuary, marine sediments are deposited up to approximately 3.5 km from the open mouth. Beyond this, mud rapidly becomes the dominant substrate type, and this point (3.5 km from the mouth) was taken as the upper limit of the mixed substrate zone.

Sundays Estuary

Owing to the considerably greater volume of freshwater inflow, deposition of marine sediments in the Sundays Estuary is restricted to approximately 1.5 km from the mouth (Swart 1986). However, there is considerable deposition of aeolian dune sand, resulting in a broad transition zone of mixed substrate, where the western bank of the estuary, up to approximately 4.0 km from the mouth, is comprised of sandy substrate, while the eastern bank becomes predominantly mud after about 2.5 km from the mouth. The sand zone of this estuary was thus deemed to comprise the area from the mouth to 2.5 km, the transition zone comprised the area between 2.5 and 4.0 km, and the mud zone comprised the area beyond 4 km from the mouth.

5.2.2 Physico-chemical environment at fish positional fixes

Environmental data recorded at positional fixes for each fish whilst manual tracking in the Great Fish, East Kleinemonde and Kariega estuaries (see Chapter 3), included bottom salinity, bottom water temperature, bottom turbidity, current speed and water depth. Each variable was binned into suitable categories, depending on the particular variable. The probability that the contribution of each bin was significantly different from the median contribution was assessed by means of a two-tailed binomial test, conducted in the R statistical package (R Development Core Team 2010), with a Bonferroni adjustment to reduce the likelihood of a type I error (Childs *et al*. 2008b).

5.2.3 Fish positions in relation to the physico-chemical environment at fixed stations

In addition to the environmental data recorded at positional fixes, the same variables were recorded at a number of fixed stations in each of the studied estuaries, on each manual tracking day (see Chapter 3, Figures 3.3 and 3.6). Data were compared by means of the Kruskal-Wallis ANOVA, due to non-normality (Shapiro-Wilk $p < 0.010$ in most cases). Comparisons were made between each fixed station and each individual fish, as well as among each fixed station and all fish combined, within each estuary. This analysis was conducted on environmental data collected at fish positional fixes and at the fixed stations in the Great Fish and Kariega estuaries. The East Kleinemonde was excluded from this analysis, as fixed-station environmental data were not recorded. All analyses were conducted in Statistica 10.0.

5.3 Results

5.3.1 Substrate type

Assuming a random distribution of fish relative to substrate type, proportions of time spent in each substrate zone would be expected to reflect the proportions of each substrate available. Within the East Kleinemonde, Kariega and Sundays estuaries, the proportions of total estuarine area comprising each substrate differed considerably, although in all three estuaries the dominant substrate type was mud (Table 5.1). In the East Kleinemonde Estuary, the proportions of sand and mixed substrates were similar, and only slightly less than that comprised of mud, while in the Kariega and Sundays estuaries mud comprised approximately 75% and 55%, respectively, of available habitat.

Table 5.1: Total surface area (m^2) of each estuary, and proportions (m^2 and %) of each estuary comprised of sand, mixed sand and mud, or mud

Estuary	Total area	Sand area		Mixed area		Mud area	
	(m^2)	(m^2)	(%)	(m^2)	(%)	(m^2)	(%)
East Kleinemonde	298 200	85 880	28.8	99 600	33.4	112 720	37.8
Kariega	1 577 180	313 100	19.9	106 200	6.7	1 157 880	73.4
Sundays	1 757 650	573 280	32.6	223 990	12.7	960 380	54.6

The proportions of time spent in areas of different substrate type were significantly different to the proportions of substrate type available in their respective estuaries, for all 39 white steenbras tracked in the East Kleinemonde, Kariega and Sundays estuaries (Table 5.2). The HAI showed that 12 individuals (30.8%) spent disproportionately more time over sand substrate, and 10 individuals (25.6%) spent disproportionately more time over mud substrate, while 17 individuals (43.6%) spent disproportionately more time over mixed sand and mud (Table 5.2).

Table 5.2: Proportions of time (%) spent over sand, mixed sand and mud, and mud substrates, Chi-square values and level of significance (* = significant at 5%, ** = significant at 1% level), and dominant substrate (+) based on the HAI, for individual white steenbras in the East Kleinemonde (EKM, ^{S,L} = short- and long-period transmitters, respectively), Kariega (KAR) and Sundays (SUN, ^{A,B} = fish captured in vicinity of receivers 4 and 2, respectively) estuaries

Estuary	Fish ID	Sand (%)	Mixed (%)	Mud (%)	Chi-square		Sand	Mixed	Mud
EKM	2001^{S}	59.4	28.2	12.4	50.5	**	+		
EKM	2002^{S}	74.9	24.6	0.6	112.7	**	+		
EKM	2003^{S}	36.7	62.3	1.0	62.9	**		+	
EKM	2004^{S}	32.4	62.5	5.1	54.1	**		+	
EKM	2005^{S}	100.0	0.0	0.0	247.2	**	+		
EKM	3759^{L}	5.6	93.1	1.3	160.4	**		+	
EKM	3760^{L}	9.6	42.6	47.8	18.1	**			+
EKM	3761^{L}	6.9	91.7	1.3	153.8	**		+	
EKM	3762^{L}	51.9	19.3	28.8	26.6	**	+		
EKM	3764^{L}	7.1	91.5	1.4	152.4	**		+	
EKM	3765^{L}	3.3	20.2	76.5	67.3	**			+
EKM	3766^{L}	35.5	64.5	0.0	68.3	**		+	
EKM	3768^{L}	3.5	19.6	76.9	68.2	**			+
EKM	3769^{L}	4.9	41.4	53.8	28.6	**			+
EKM	3770^{L}	4.6	8.9	86.5	100.9	**			+
EKM	*Mean*	29.1	44.7	26.2	7.4	*		+	
EKM	*Mean*^{S}	60.7	35.5	3.8	66.0	**	+		
EKM	*Mean*^{L}	13.3	49.3	37.4	15.9	**		+	
KAR	2036	61.3	30.7	8.1	229.4	**	+		
KAR	2037	52.4	37.6	10.0	249.6	**	+		
KAR	2038	50.8	46.0	3.2	344.5	**		+	
KAR	2039	100.0	0.0	0.0	403.7	**	+		
KAR	2040	99.7	0.3	0.0	400.8	**	+		
KAR	2041	99.7	0.3	0.0	400.7	**	+		
KAR	2042	43.4	56.1	0.6	461.3	**		+	
KAR	2043	100.0	0.0	0.0	403.7	**	+		
KAR	2045	93.4	6.2	0.5	344.7	**	+		
KAR	*Mean*	77.8	19.7	2.5	262.8	**	+		
SUN	64989^{A}	1.5	50.9	47.6	144.9	**		+	
SUN	64990^{A}	3.4	3.7	92.9	59.5	**			+
SUN	64991^{A}	0.0	0.1	99.9	82.5	**			+
SUN	64992^{B}	55.8	18.7	25.5	34.8	**	+		
SUN	64993^{B}	29.4	70.4	0.1	315.9	**		+	
SUN	64994^{B}	7.3	85.8	6.9	480.5	**		+	
SUN	64995^{B}	34.8	65.2	0.0	270.9	**		+	
SUN	64996^{B}	3.5	96.5	0.0	630.8	**		+	
SUN	64997^{B}	5.4	50.6	44.1	137.1	**		+	
SUN	64998^{B}	39.6	60.4	0.0	234.3	**		+	
SUN	64999^{B}	45.1	54.9	0.0	198.9	**		+	
SUN	65000^{B}	34.8	65.2	0.0	270.6	**		+	
SUN	65001^{A}	5.3	10.9	83.8	38.7	**			+
SUN	65002^{A}	0.0	0.0	100.0	83.0	**			+
SUN	65003^{A}	3.0	2.0	95.0	65.7	**			+
SUN	*Mean*	17.5	42.5	40.0	80.4	**		+	
SUN	*Mean*^{A}	2.2	11.3	86.5	47.2	**			+
SUN	*Mean*^{B}	27.9	63.8	8.3	244.6	**		+	

In the East Kleinemonde Estuary, the site at which fish were captured and tagged influenced the results. Fish tagged in the mouth region spent on average disproportionately more time in areas of sandy substrate ($p < 0.001$), while those tagged above the bridge spent on average disproportionately more time in areas of mixed substrate ($p < 0.001$). The mean of time spent by all fish in the East Kleinemonde Estuary was also greatest over mixed substrate ($p = 0.025$). In the Kariega Estuary, time spent by most individuals and the mean time across all fish was disproportionately greater over sandy substrate ($p < 0.001$), which reflected the capture site substrate for all tagged fish. In the Sundays Estuary, the mean proportions of time were disproportionately greater over mixed substrate, reflecting the pattern exhibited by most individuals in this estuary ($p < 0.001$). Here, the capture site again influenced the results. The majority of fish captured in the vicinity of receiver 4 spent disproportionately more time in areas of muddy substrate, while those captured in the vicinity of receiver 2 spent disproportionately more time over mixed substrate ($p < 0.001$ in both cases).

5.3.2 Physico-chemical environment at fish positional fixes

Environmental variables recorded at positional fixes for each fish during manual tracking in the Great Fish, East Kleinemonde and Kariega estuaries indicated that white steenbras are able to tolerate a range of environmental conditions (Table 5.3).

Table 5.3: Environmental variables recorded at positional fixes during manual tracking in the Great Fish (GFR), East Kleinemonde (EKM) and Kariega (KAR) estuaries, showing mean (± SD) values, with ranges for each presented below the means (S = surface, B = bottom)

Estuary (S/B)		Salinity	Temperature (ºC)	Current speed ($m.s^{-1}$)	Turbidity (FTU)	Depth (m)
GFR	S	5.6 (± 5.2)	21.3 (± 1.1)	0.29 (±0.16)	78.8 (±49.0)	0.92 (± 0.5) 0.3 – 3.5
	S	0.0 – 25.0	18.0 – 23.3	0.03 – 0.66	19.3 – 206.0	
	B	9.6 (± 8.2)	20.6 (± 1.3)	0.15 (± 0.10)	87.2 (± 47.7)	
	B	0.0 – 30.0	17.5 – 23.3	0.01 – 0.42	2.7 – 211.0	
EKM	S	27.0 (± 1.1)	22.6 (± 2.6)	-	-	1.74 (± 0.86) 0.46 – 4.09
	S	19.0 – 29.0	14.9 – 27.4	-	-	
	B	27.5 (± 0.9)	22.1 (± 2.7)	-	-	
	B	26.0 – 30.0	14.6 – 27.3	-	-	
KAR	S	37.7 (± 0.7)	17.6 (± 2.0)	0.27 (± 0.12)	4.6 (± 1.7)	2.75 (± 1.07) 0.37 – 6.75
	S	36.0 – 39.0	14.0 – 21.5	0.08 – 0.54	1.8 – 11.0	
	B	38.0 (± 0.7)	17.6 (± 2.0)	-	4.6 (± 1.5)	
	B	36.0 – 40.0	13.5 – 21.5	-	2.3 – 12.0	

Salinity

Bottom salinities recorded at positional fixes for each fish during manual tracking differed widely among estuaries (Figure 5.1). In the Great Fish Estuary, significantly more positional fixes were made at salinities from 0 to 5 (two-tailed binomial tests), although values up to 30 were recorded. There were significantly fewer positional fixes made at salinities greater than 25, despite salinity reaching 36 in parts of the estuary, during the study. In the East Kleinemonde Estuary, salinity recorded at fish positional fixes ranged from 26 to 34, although significantly more positional fixes were made from > 26 to 30, and significantly fewer at salinities outside of this range. In the Kariega Estuary, salinity in parts of the estuary reached 46, as a result of the reverse salinity gradient; although significantly more (85%) positional fixes were made in the salinity range of 36 to 38, and none at salinities exceeding 40.

Temperature

The ranges of bottom temperatures recorded at fish positional fixes were similar within each estuary (Figure 5.1). In the Great Fish Estuary, there were significantly more positional fixes made in the range > 18 to 22°C, and significantly fewer at temperatures of 18°C or less. Similarly, in the East Kleinemonde Estuary, there were significantly fewer positional fixes made at temperatures of 18°C or less, and the range > 22 to 26°C contributed significantly more positional fixes, while temperatures above this were significantly under-represented. In the Kariega Estuary, significantly fewer positional fixes were made below 14°C, or above 22°C, with most falling in the range > 16 to 18°C.

Turbidity

As a result of the differences in estuary type and conditions, the turbidity values recorded at positional fixes differed considerably between the Great Fish and Kariega Estuaries (Figure 5.1). However, in both estuaries, fish were found most often at lower bottom turbidities. In the Great Fish Estuary, where turbidity recorded at the fixed stations ranged from 3.7 to 273 FTU, significantly fewer positional fixes were made above 200 FTU, while the range 40.1 to 80 FTU contributed a significantly greater proportion of positional fixes. Despite fixed station turbidity reaching a maximum of only 14 FTU in the Kariega Estuary, significantly more positional fixes were made at lower turbidity classes (2.0 – 6.0 FTU). Turbidity data were not recorded in the East Kleinemonde Estuary.

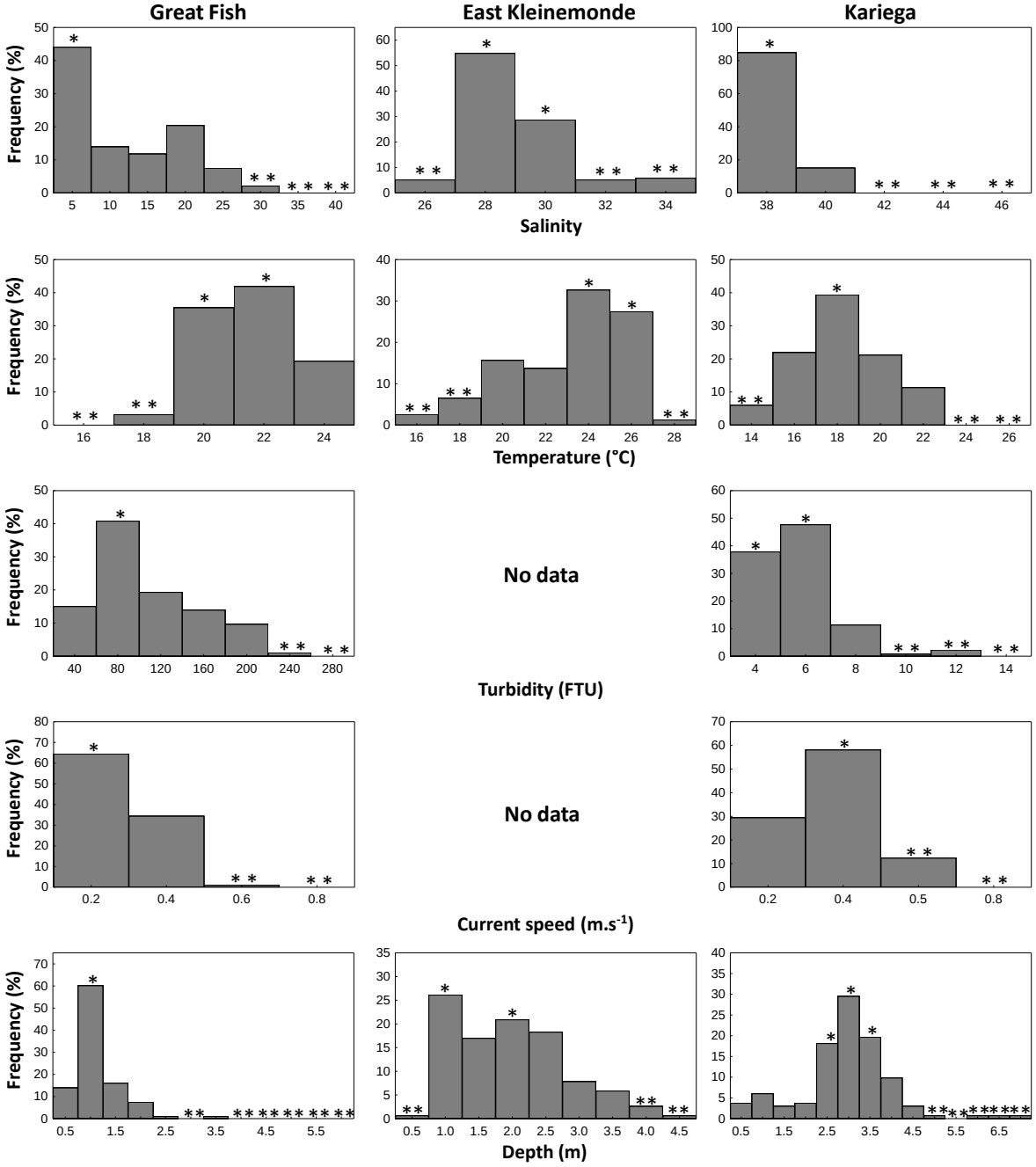

Figure 5.1: Frequency distributions (% of positional fixes) of bottom salinity, bottom temperature °C, bottom turbidity FTU, current speed (m.s^{-1}, Great Fish = bottom current, Kariega = surface current) and depth (m) recorded at all fish positional fixes made during manual tracking in the Great Fish, East Kleinemonde and Kariega estuaries. X-axis values represent upper limit of each bin. Categories represented with * indicate significantly higher contributions, and those with ** significantly lower contributions than the median for all bins (two-tailed binomial test, with Bonferroni adjustment)

Current speed

Current speed was measured near the substrate in the Great Fish Estuary. However, due to instrument failure, this current meter could not be used in the Kariega Estuary, and current was measured only at the surface (see Methods and materials, Chapter 3). In both estuaries, significantly more positional fixes were made in the lower current speed categories, 0.0 to 0.2 $m.s^{-1}$ in the Great Fish Estuary and 0.21 to 0.4 $m.s^{-1}$ in the Kariega Estuary, while the higher current speeds, exceeding 0.4 $m.s^{-1}$, contributed significantly lower proportions of positional fixes (Figure 5.1). Current speed was not applicable in the East Kleinemonde Estuary, as the estuary mouth remained closed during the manual tracking period of the study.

Depth

In the Great Fish Estuary, the shallow depth category > 0.5 to 1.0 m contributed significantly more to the total number of positional fixes (approximately 60%), while depths greater than approximately 3.5 m contributed significantly fewer (Figure 5.1). In the East Kleinemonde Estuary, two separate depth classes contributed significantly greater proportions of positional fixes (> 0.5 to 1.0 and > 1.5 to 2.0 m), while significantly fewer positional fixes were made at depths 0.5 m or less, or greater than 3.5 m. In the Kariega Estuary, significantly more positional fixes were made in the depth range of > 2.0 to 4.0 m, while depths greater than 4.5 m contributed significantly fewer.

5.3.3 Fish positions in relation to the physico-chemical environment at fixed stations

Great Fish Estuary

Environmental variables recorded at positional fixes in the Great Fish Estuary were most similar to those recorded at fixed station 6, in the vicinity of receiver 6, which represented a high use area for the white steenbras tracked in this estuary (see Chapter 3). In this estuary, fixed station salinity remained relatively similar from stations 1 to 5 (Figure 5.2a), beyond which salinity decreased rapidly. Bottom salinities recorded at positional fixes were significantly lower than those recorded at stations 1 to 5, but not significantly different to those at stations 6 or 7 (Table 5.4). Salinities recorded for all fish combined were also significantly lower than stations 1 to 5, and significantly higher than at station 8 (Figure 5.2a). The exception was station 4, where recorded salinities were not significantly different to stations 6 or 7, or to those recorded for each fish or all fish combined.

Bottom water temperature followed the opposite trend to salinity, with recordings relatively similar from receiver 1 to 5 (although temperatures at station 4 were again more similar to those at station 6), beyond which an increasing trend was observed. Temperatures recorded at fish positional fixes

were not significantly different from those recorded at stations 6 to 8, in the middle to upper reaches (Figure 5.2b). Individual fish, and all fish combined, were located in significantly higher temperatures than those recorded at stations 1 to 5 (Table 5.4).

Bottom turbidities recorded at stations 1 to 5 were significantly lower than at stations 7 and 8. Four fish in the Great Fish Estuary were found in significantly higher turbidity conditions than those recorded at receiver 1, while one fish (Fish 92) was located in significantly lower turbidities than those recorded at stations 7 and 8. Bottom turbidities recorded for all fish combined reflected both these patterns, being significantly higher than turbidities recorded at station 1, and significantly lower than at stations 7 and 8 (Figure 5.2c). There were few significant differences between bottom turbidities recorded for individual fish and those recorded at stations 2 to 6 (Table 5.4).

There were few significant differences in current speeds, whether recorded at fixed stations or at individual fish positional fixes, although the current speeds recorded at receiver 5 were significantly lower than those recorded at positional fixes for all fish combined (Figure 5.2d). Only one current speed was recorded at station 7, due to the depth exceeding that suitable for the current meter.

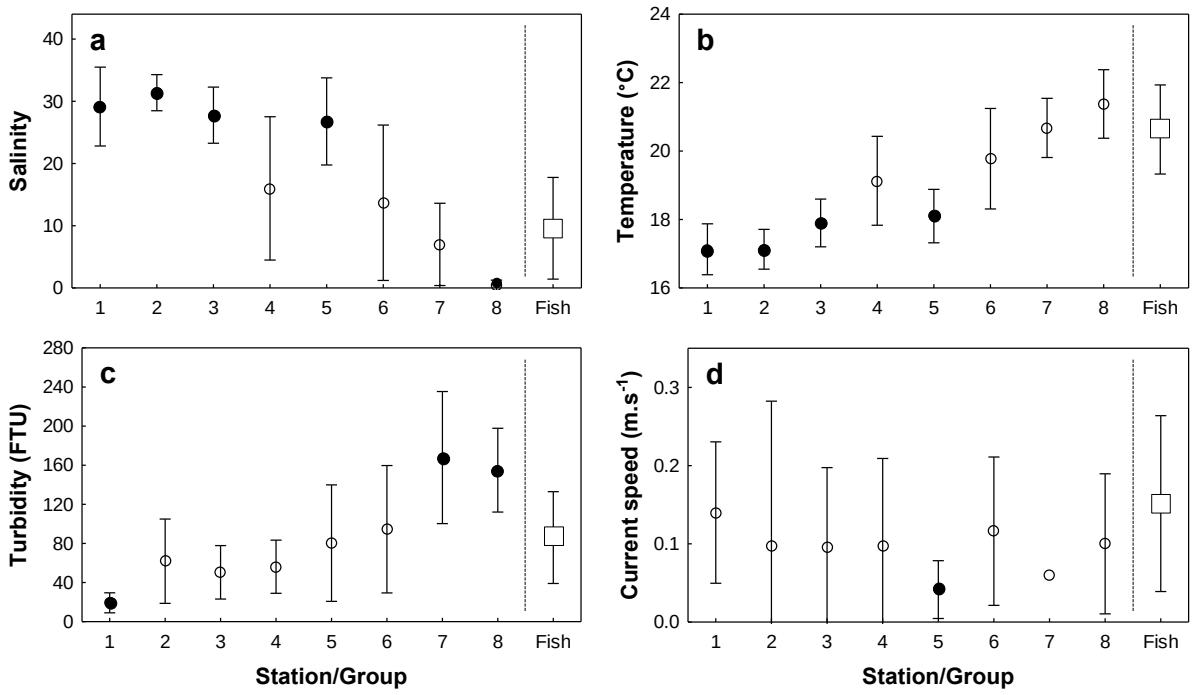

Figure 5.2: Mean (±SD) a) bottom salinity, b) bottom temperature (°C), c) bottom turbidity (FTU), d) bottom current ($m.s^{-1}$) and e) depth (m) values recorded at the eight fixed stations, and at positional fixes for all fish combined (Fish), in the Great Fish Estuary. Solid black means represent stations significantly different to those recorded at fish positional fixes ($p < 0.01$ in all cases)

Table 5.4: *Post-hoc* pairwise comparisons of mean ranks from the Kruskal-Wallis ANOVA (p-values, ns = not significant), between environmental variables recorded at fixed stations, and those recorded at positional fixes made for each fish and for all fish combined, in the Great Fish Estuary (comparisons between stations are not presented)

Fish ID	Fish 82	Fish 83	Fish 84	Fish 86	Fish 87	Fish 88	Fish 92	All fish
Bottom salinity (Kruskal-Wallis ANOVA p < 0.001)								
Station 1	ns	0.006	< 0.001	0.011	< 0.001	0.022	ns	< 0.001
Station 2	ns	< 0.001	< 0.001	0.001	< 0.001	0.002	0.036	< 0.001
Station 3	ns	0.018	0.002	0.028	< 0.001	ns	ns	< 0.001
Station 4	ns	ns	ns	ns	ns	ns	ns	ns
Station 5	ns	0.041	0.004	ns	0.002	ns	ns	< 0.001
Station 6	ns	ns	ns	ns	ns	ns	ns	ns
Station 7	ns	ns	ns	ns	ns	ns	ns	ns
Station 8	0.039	ns	ns	ns	ns	ns	ns	0.030
Bottom temperature (Kruskal-Wallis ANOVA p < 0.001)								
Station 1	0.002	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.031	< 0.001
Station 2	0.002	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.034	< 0.001
Station 3	ns	0.005	0.001	0.005	< 0.001	0.008	ns	< 0.001
Station 4	ns	ns	ns	ns	ns	ns	ns	ns
Station 5	ns	0.014	0.003	0.012	0.002	0.021	ns	< 0.001
Station 6	ns	ns	ns	ns	ns	ns	ns	ns
Station 7	ns	ns	ns	ns	ns	ns	ns	ns
Station 8	ns	ns	ns	ns	ns	ns	ns	ns
Bottom turbidity (Kruskal-Wallis ANOVA p < 0.001)								
Station 1	ns	0.004	< 0.001	ns	< 0.001	0.003	ns	< 0.001
Station 2	ns	ns	ns	ns	ns	ns	ns	ns
Station 3	ns	ns	ns	ns	0.017	ns	ns	ns
Station 4	ns	ns	ns	ns	ns	ns	ns	ns
Station 5	ns	ns	ns	ns	ns	ns	ns	ns
Station 6	ns	ns	ns	ns	ns	ns	ns	ns
Station 7	ns	ns	ns	ns	ns	ns	0.002	0.020
Station 8	ns	ns	ns	ns	ns	ns	0.002	0.024
Bottom current speed (Kruskal-Wallis ANOVA p = 0.016)								
Station 1	ns	ns	ns	ns	ns	ns	ns	ns
Station 2	ns	ns	ns	ns	ns	ns	ns	ns
Station 3	ns	ns	ns	ns	ns	ns	ns	ns
Station 4	ns	ns	ns	ns	ns	ns	ns	ns
Station 5	ns	ns	ns	ns	0.039	ns	ns	0.009
Station 6	ns	ns	ns	ns	ns	ns	ns	ns
Station 7	ns	ns	ns	ns	ns	ns	ns	ns
Station 8	ns	ns	ns	ns	ns	ns	ns	ns

Kariega Estuary

Environmental variables recorded at the five fixed stations in the Kariega Estuary fluctuated widely throughout the estuary (Figure 5.3). Spatial trends were observed in salinity, temperature and turbidity, which increased, and current speed, which decreased, beyond station 2. Data recorded at fish positional fixes in this estuary generally reflected conditions intermediate of those recorded at stations 2 and 3, which represented the high use area within this estuary (see Chapter 3).

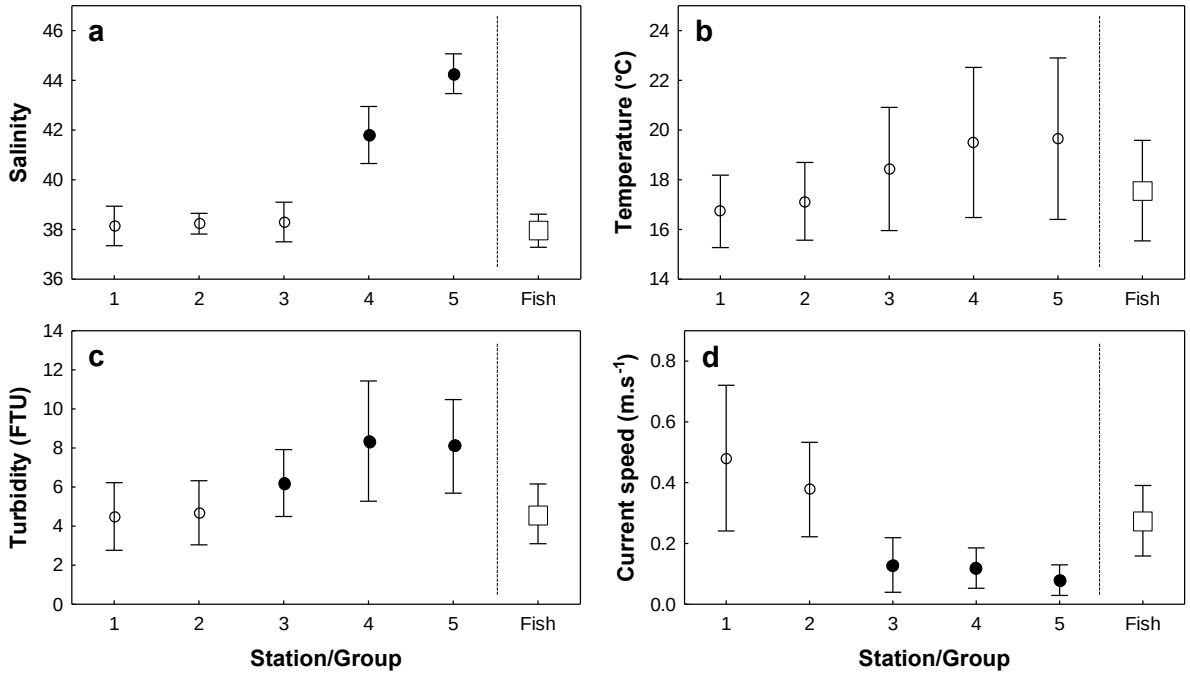

Figure 5.3: Mean (±SD) a) bottom salinity, b) bottom temperature (°C), c) bottom turbidity (FTU), d) surface current ($m.s^{-1}$) and e) depth (m) values recorded at the five fixed stations, and at positional fixes for all fish combined (Fish), in the Kariega Estuary. Solid black means represent stations significantly different to those recorded at fish positional fixes ($p < 0.01$ in all cases)

Positional fixes for each individual fish and all fish combined were recorded at significantly lower bottom salinities than stations 4 and 5 (Figure 5.3a, Table 5.5). There were, however, no significant differences between any of the fish positions and stations 1, 2 or 3. Salinities recorded at stations 1 to 3 were significantly lower than salinities at stations 4 and 5.

There were no significant differences between bottom water temperatures recorded for each individual fish or all fish combined and any station (Table 5.5). However, temperatures recorded at station 1 were significantly lower than those at stations 4 and 5 (Figure 5.3b).

Positional fixes for most individuals were made in significantly lower bottom turbidities than those recorded at stations 4 and 5, although there were no significant differences between salinities recorded for any of the individual fish and stations 1, 2 or 3 (Table 5.5).

Similarly, turbidities recorded at stations 1 to 3 were significantly lower than those recorded at stations 4 and 5. There was a significant difference, however, between bottom turbidities recorded for all fish combined and those recorded at stations 3, 4 and 5 (Figure 5.3c, Table 5.5).

Stations 1 and 2 exhibited significantly stronger surface currents than stations 3 to 5 (Figure 5.3d). Surface current speeds recorded at positional fixes for each individual fish were significantly higher than at receiver 5, with no significant differences from any other stations (Table 5.5). For all fish combined, currents recorded at positional fixes were significantly higher than those recorded at stations 3 to 5, but not significantly different to those at stations 1 and 2.

Table 5.5: *Post-hoc* pairwise comparisons of mean ranks from the Kruskal-Wallis ANOVA (p-values, ns = not significant), between environmental variables recorded at fixed stations, and those recorded at positional fixes, for each individual fish and for all fish combined, in the Kariega Estuary (comparisons between stations are not presented)

Fish ID	Fish 2036	Fish 2037	Fish 2038	Fish 2039	Fish 2040	Fish 2041	Fish 2042	Fish 2043	Fish 2045	All fish
Bottom salinity (Kruskal-Wallis ANOVA p < 0.001)										
Station 1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 3	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 4	< 0.001	0.012	< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Station 5	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Bottom temperature (Kruskal-Wallis ANOVA p = 0.094)										
Station 1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 3	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 4	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 5	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Bottom turbidity (Kruskal-Wallis ANOVA p < 0.001)										
Station 1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 3	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.012
Station 4	0.024	0.002	0.043	ns	0.037	0.002	0.003	ns	0.022	< 0.001
Station 5	0.040	0.003	ns	ns	ns	0.003	0.006	ns	0.036	< 0.001
Surface current speed (Kruskal-Wallis ANOVA p < 0.001)										
Station 1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Station 3	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.002
Station 4	ns	ns	ns	ns	ns	0.029	ns	ns	ns	< 0.001
Station 5	0.002	0.007	0.038	0.027	0.014	< 0.001	0.004	0.003	0.005	< 0.001

5.4 Discussion

5.4.1 Substrate

In a hierarchically-structured habitat, such as an estuary, it is expected that an animal would move in such a way as to minimise the probability of leaving a more optimal patch or habitat type to enter one that is less optimal or unfavourable (Fauchald and Tveraa 2006). However, within an estuary, particularly those with predominantly sand and mud substrates, a distinct division between substrates is unlikely, and two substrates are likely to meet in an area of transition comprising a mixture of both (Dalrymple and Choi 2007). It can also be expected that the extent and position of such mixed substrate transition areas vary considerably among estuaries, affected by factors such as freshwater inflow, flooding, estuary mouth status, marine sediment deposition, longshore sediment transport or aeolian sand deposition.

Similarly, estuarine organisms are unlikely to have abrupt distribution limits, and are likely to show gradual changes in density from one substrate type to another. Disproportional use, however, of one substrate type by most individuals over another substrate type, relative to the proportions of each substrate available at the landscape level, would indicate affinity for, and some ecological benefit of, that substrate type to their overall fitness (Monaco *et al*. 1998, Block and Brennan 1999 in Simcharoen *et al*. 2008). The key question is does each individual allocate the time it spends over each substrate type in proportion to the availability of that substrate, and if not which is the most dominant substrate used, and why?

The majority of individuals spent disproportionately more time over mixed substrate, than areas of homogenous sand or mud, although there was considerable individual variability in the substrate predominantly used. This was influenced by the habitat at the capture site, with most fish (59%) spending disproportionately more time in the substrate type associated with their capture site, which was to be expected, due to the high level of site fidelity shown by white steenbras in all three estuaries (see Chapter 3). This suggests that substrate type is not the primary environmental factor directly affecting the distribution of these fish in estuaries. Common to all estuaries was that distribution was associated with areas of shallow sandbanks or mudbanks, or shallow littoral areas of mixed sand and mud. As these shallow banks support high densities of macrobenthic invertebrates (Wooldridge and Bailey 1982), it is more likely that the observed distributions are proximately driven by availability of prey organisms, which in turn is likely driven by substrate type.

Estuaries provide an important source of food and shelter for juvenile fishes (Bennett and Branch 1990). At the juvenile life stage, food availability and predator avoidance are the most important factors affecting survival; therefore, it may be expected that prey availability is one of the most important factors influencing distribution (McArthur and Pianka 1966, Fretwell and Lucas 1970), and thus affecting the distribution of juvenile fishes within estuaries (Sheppard *et al*. 2011). A component of availability is accessibility, and individuals are likely to associate with areas where prey organisms are more easily accessible (de Villiers *et al*. 1999). This may be related to the size of the fish, the size of the prey organisms and whether the prey organisms are epibenthic or infaunal. It is also likely that the diversity of prey organisms is higher in the transition zone of mixed substrate type (Teske and Wooldridge 2001), where the distributions of sand- and mud-associated species overlap, such as sand prawn and mud prawn *Upogebia africana*, providing a greater variety of prey organisms. Therefore, white steenbras would possibly obtain little benefit by favouring either sand or mud over the other, unless prey availability differed considerably between these substrate types.

The higher proportion (33%) of individuals in the Sundays Estuary, than in the East Kleinemonde (27%) or Kariega estuaries (0%), that spent significantly more time in the section of estuary comprised predominantly of muddy substrate may be related to higher densities of suitable prey items in this area. The start of the mud zone in this estuary is characterised by gently sloping muddy estuary banks and high densities of mud prawn (personal observation). Such an interaction between predator and prey species could be tested by simultaneously assessing the distributions of the predator, in this case white steenbras, and their predominant prey items, relative to the different substrate types available, to identify the factors driving the observed fish distribution.

In contrast, the East Kleinemonde Estuary is characterised by an absence of mud prawn, due to the closed mouth, as mud prawn have an obligatory marine larval phase (Wooldridge and Loubser 1996). However, in this estuary, there is an abundance of sand prawn in the zone of mixed sand and mud (Terörde 2005), providing an important food source in this zone. Although sand prawn densities are highest in the lower reaches of this estuary (Terörde 2005), the proportions of individuals in this estuary predominantly associated with the three substrate zones were roughly equal. This may be an indication that prey items of suitable size are more dense or readily available in the softer sediments of the mixed substrate zone, than in the harder, coarser sediments of the sand zone. This may be an important factor for smaller fish, and would provide further support for the notion of an ontogenetic down-estuary shift in white steenbras distribution, as proposed in Chapter 3.

In the Kariega Estuary, all fish spent disproportionately more time in areas of sandy substrate, indicating an affinity for sand in this estuary. The sandbank adjacent to the high use area, therefore, provides an important source of invertebrate prey items. The low use of the middle reaches of this estuary, despite this area supporting high densities of a potential prey source, the bivalve *Solen cylindraceus* (Hodgson 1987), suggests that some physico-chemical barrier exists further up this estuary. Therefore, the affinity for sandy substrates may be influenced by environmental conditions in other parts of the estuary, particularly the hypersaline conditions in the middle and upper reaches. The Sundays Estuary, in contrast, is characterised by a gradual salinity gradient, decreasing from the mouth, thereby allowing the movement of white steenbras further up this estuary than in the Kariega Estuary. This inter-estuary variability in distribution indicates that distribution within estuaries relative to substrate type is also affected by other environmental variables. Overall, it appears that the distribution of white steenbras relative to substrate type, within the different estuaries studied, is determined largely by biotic (mainly prey availability) and abiotic factors specific to each estuary, with no over-riding dominance of a single substrate type.

The distributions of spotted grunter in the East Kleinemonde Estuary (O'Connell 2008) and of juvenile dusky kob (Griffiths 1997a) and spotted grunter (Childs *et al*. 2008a) in the Great Fish Estuary were similarly attributed to prey availability and density. Vasconcelos *et al*. (2010) found the macrozoobenthos to be an important factor affecting the distribution of fishes within estuaries in Portugal. Cowley *et al*. (2008) suggested that estuarine-associated fishes that prey on non-mobile benthic organisms are likely to exhibit resident behaviour, as has been observed for white steenbras, and that the distribution of these species is likely centred around areas of optimal prey availability.

5.4.2 Environmental variables influencing distribution

The wide ranges of salinity (0 - 40), temperature (13.5 to 27.4 °C), current speed (0 to 0.66 $m.s^{-1}$) and turbidity (1.8 to 211 FTU) recorded at positional fixes, in the different estuaries, provide evidence that white steenbras is able to tolerate a wide range of environmental conditions, as described by Whitfield (1998). The ranges observed were influenced by the different types of estuary studied. In the three permanently open estuaries, white steenbras exhibited predominantly station-keeping behaviour, and where tidal-associated movements were observed these were on a small spatial scale (see Chapter 3), confirming their tolerance to widely and rapidly fluctuating environmental conditions. Despite this tolerance, there was evidence that the distribution of fish within the different estuaries was significantly non-random in relation to certain environmental conditions.

Salinity

Salinity is suggested to be one of the primary environmental variables influencing fish distributions in estuaries, due to the species-specific physiological limitations to its tolerance (Whitfield 1983, Vasconcelos *et al*. 2010). Juvenile white steenbras are good osmoregulators, with a wide salinity tolerance range (> 0 to 35, Whitfield *et al*. 1981, Whitfield 1998). Salinities recorded during manual tracking in the Great Fish (0 - 30, mean 9.6 ± 8.2) and Kariega (36 – 40, mean 38.0 ± 0.7) estuaries reflected those of the fixed stations in the upper and lower reaches, respectively, which was expected due to the fish using small home ranges within each estuary (see Chapter 3). However, the ranges used were markedly different between the two estuaries, due to the vastly different salinity regimes in the two systems. In estuaries exhibiting overlapping salinity ranges, it would be expected that fish would have been predominantly found within the same range of salinities in both estuaries. However, even where recorded salinity ranges did overlap, i.e. those in the East Kleinemonde and Great Fish estuaries, the salinity ranges within which most fish were located did not overlap at all. The results suggest that salinity is not the primary environmental variable driving white steenbras distribution, at least in the latter two estuaries.

In the Great Fish Estuary, white steenbras were consistently located in the oligohaline upper reaches, where the salinity was significantly lower than at stations closer to the mouth. Mehl (1973) recorded adverse physiological stress responses in white steenbras after being transferred from estuary water to freshwater, including cessation of feeding, increased haematocrit levels, subepidermal haemorrhaging and mortality, and Bennett (1985) recorded white steenbras mortalities in the Bot Estuary, after prolonged periods of unusually low salinity (3), and predominantly low temperature (16°C). Furthermore, Harrison and Whitfield (2006) found that relative abundances of white steenbras in estuaries were positively correlated with salinity, suggesting that white steenbras distribution would be expected to be associated with higher salinity levels. These results suggest that the use of the upper reaches in the Great Fish Estuary is not a response to optimal salinity, but rather some other more favourable environmental condition associated with this area. However, the species has been observed to tolerate prolonged low salinity conditions (Mehl 1973), and did not suffer mortalities during a flood event in the Sundays Estuary in January 1995, when numerous euryhaline marine, estuarine and freshwater species did (Whitfield and Paterson 1995). Tolerance of the low salinity conditions in the upper reaches of the Great Fish Estuary is likely facilitated by the artificially elevated conductivity levels as a result of the Orange-Fish River interbasin transfer scheme (Whitfield *et al*. 1994). As a result, osmotic stress on euryhaline marine species may be reduced (Whitfield and Wood 2003), allowing increased penetration of such

species to the river-estuary interface and into the river beyond the tidal influence (James *et al*. 2007b). Sediments in this estuary are washed out during flood events, but are replaced by sand deposited in the upper reaches and mud in the lower reaches during low flow conditions (Whitfield *et al*. 1994). The distribution in the upper reaches of this estuary was, therefore, likely influenced by the position of a large sandbank in the area, deposited after a flood event (Childs *et al*. 2008a), and benthic macrofauna that may have been associated with that sand bank.

The low variability in salinities at which white steenbras were located in the East Kleinemonde Estuary is a reflection of the uniformity of the salinity regime of this small temporarily open/closed estuary, rather than a result of avoidance of higher or lower salinities.

The physico-chemical environment of the Kariega Estuary differs considerably from those in the East Kleinemonde and Great Fish estuaries. Here, significantly lower salinities recorded during manual tracking than those recorded in the middle and upper reaches, and the restricted up-estuary movement (Chapter 3), suggest that the distribution of white steenbras in the Kariega estuary relative to salinity is not random. Mean salinity increased from 38.3 (± 0.8) at receiver 7, approximately 6 km from the mouth, to 41.8 (± 1.1) at receiver 11, 11 km from the mouth, and to 44.2 (± 0.8) at receiver 15, 14.5 km from the mouth. As less than 1% of white steenbras activity was observed beyond receiver 7 (Chapter 3), it appears that the upper boundary of the white steenbras distribution in this estuary is limited by the hypersalinity in the middle to upper reaches. The salinities recorded in this area exceed the maximum salinity tolerance (35) reported for white steenbras (Whitfield 1998). Mehl (1973) recorded white steenbras in salinities reaching 50 in the Heuningnes Estuary, although in that estuary more suitable conditions may not have been available.

Temperature

Temperature has been identified as an important factor affecting the structuring of estuarine fish communities (Whitfield 1998, Marshall and Elliot 1998), and can be an important factor affecting the distribution and movement of fishes (Beitinger and Fitpatrick 1979). Temperature was found to be the primary abiotic factor influencing the movements of spotted grunter in the Great Fish Estuary, South Africa (Childs *et al*. 2008b). In the current study, bottom temperatures recorded at fish positional fixes in the Great Fish, East Kleinemonde and Kariega estuaries were similar, with a relatively high level of overlap among the ranges in which fish were commonly located; > 18 to 24°C, > 14 to 22°C and > 18 to 26°C in the three estuaries, respectively. Although these broad ranges overlapped, the modal peaks in each did not. In the Great Fish and East Kleinemonde estuaries, the

modal peaks were towards the higher temperatures in their respective ranges, suggesting that higher temperatures may be more suitable. Conversely, however, Harrison and Whitfield (2006) found the relative abundance of white steenbras in estuaries to be negatively correlated with temperature. In the Kariega Estuary, the modal peak was towards the lower end of the range recorded, and considerably lower than the modal peaks in the other two estuaries, reflecting the dominant marine influence in the lower reaches of the former. Furthermore, temperatures recorded for all individuals and all fish combined in the Kariega Estuary showed no significant differences to any of the five fixed stations. Overall, the results suggest that temperature was not the dominant factor affecting distribution or area use within these three studies.

Turbidity

In addition to factors such as temperature and salinity, turbidity has been observed to affect fish distribution in estuaries (e.g. Cyrus and Blaber 1987, Whitfield *et al*. 1994). Turbidity levels recorded at fish positional fixes in both the Great Fish and Kariega estuaries reflected those recorded in the middle and lower reaches of the two estuaries, respectively, although the ranges of turbidity recordings in the two estuaries did not overlap. These two estuaries are characterised by vastly different freshwater inflow levels, with the freshwater-dominated Great Fish Estuary generally highly turbid, while the freshwater-deprived Kariega Estuary generally exhibits particularly low turbidity levels. Significantly more positional fixes were made at low turbidities in the Great Fish Estuary (41 – 80 FTU), suggesting that higher turbidities may be unfavourable. It is also possible that excessive turbidity limits the depth of photosynthesis (Day 1951), limiting primary production, and thus lowering benthic macrofaunal biomass in these areas. The fact that the highest turbidity recorded in the Kariega Estuary was lower than the lowest recorded in the Great Fish Estuary suggests that turbidity should have little influence in the Kariega Estuary, and that the significantly lower number of positional fixes at higher turbidities in the Kariega Estuary was a result of the fish not utilising the middle and upper reaches, again, likely a result of the hypersaline conditions in these areas.

Current speed

In the Great Fish and Kariega estuaries, the majority of positional fixes were made at current speeds below 0.4 $m.s^{-1}$, while those at fixed stations in both estuaries reached 0.8 $m.s^{-1}$. The significantly higher proportions of detections made at lower current speeds indicate that higher current speeds, as observed at fixed stations, may be less favourable for white steenbras. However, there were few significant differences between current speeds recorded for individual fish, and each station in the

Great Fish or Kariega estuaries. As such, it is unlikely that current speed is a factor driving the distribution of white steenbras in these estuaries.

Depth

The wide ranges of depth recorded at fish positional fixes, particularly in the Kariega Estuary, reflect the movements from the channel onto the shallow banks when the tide is sufficiently high. Fish in the Great Fish Estuary were located at considerably shallower depths than in the Kariega Estuary, and at daytime positional fixes in the East Kleinemonde Estuary. This reflects the use of the shallow sand bank in the upper reaches of the Great Fish Estuary. It is possible that turbidity plays a role in the avoidance of visual predators, and that in the more turbid Great Fish Estuary, the fish are able to utilise shallower areas, due to decreased possibility of avian predation, than in the less turbid East Kleinemonde and Kariega estuaries. The bimodal distribution of depths recorded during manual tracking in the East Kleinemonde Estuary reflects the diel differences in depth usage, recorded during daytime and night-time tracking sessions.

5.5 Conclusions

Environmental variables, such as temperature, turbidity and salinity have been shown to influence the movements and distribution of fishes in estuaries (e.g. Beitinger and Fitzpatrick 1979, Cyrus and Blaber 1987, Whitfield 1998, Marshall and Elliot 1998, Sackett *et al*. 2007). However, most variables analysed during the current study apparently fell within favourable ranges for white steenbras over large portions of the estuaries, and were shown to have little or no effect on the distribution of the species within these estuaries, with the species adapted to widely variable conditions.

Although it appeared that salinity was not a largely influential factor in the distribution of white steenbras within the different estuaries, hypersalinity appeared to act as a barrier to the upper limit of the distribution in the Kariega Estuary. Temperature had little effect on the distribution of white steenbras in most estuaries, although it is possible that the lower temperatures recorded at the mouth of the Great Fish Estuary influenced the lower distribution of white steenbras within this system. Similarly, high turbidity appeared to limit the upper distribution of white steenbras in the Great Fish Estuary, but had no apparent influence on distribution in the other estuaries. Turbidity may play a role in the depth that white steenbras can safely use, while still avoiding avian predation, while current speed appeared to have little effect on the longitudinal distribution of white steenbras, although the dominance of the lower current speed bins suggests that white steenbras may move closer to the edges of the estuary during periods of strong flow, where currents speeds

are likely to be reduced (Day 1951). Depth appeared not to restrict the distribution of the tagged fish in any of the estuaries studied, although depth utilised was strongly influenced by time of day, and individuals appeared to enter shallower areas in the more turbid Great Fish Estuary.

The individual variability observed in affinity for different substrate types suggests that the distribution of juvenile white steenbras in estuaries is not directly driven by substrate type. The variability among estuaries suggests that the effect of substrate type is an indirect effect, driven by differential environmental characteristics within the different estuaries. It is likely that the observed distribution of white steenbras in these estuaries is driven more by prey availability and the distribution of prey items (Cowley and Whitfield 2001), and thereby indirectly by substrate type, which has a direct influence on the diversity of benthic invertebrate taxa (Teske and Wooldridge 2001, Wooldridge and Bezuidenhout 2007), and the accessibility of prey items (de Villiers *et al*. 1999). The diversity and density of prey associated with each substrate type are likely to vary considerably among estuaries, based on differences in abiotic characteristics, such as hydrodynamics, mouth state, estuary size and freshwater inflow. The overall disproportional use of mixed substrates is likely a strategy to optimise access to prey resources, and distributions coinciding with optimal prey availability (Cowley *et al*. 2008).

Considerable variability in distribution and the environmental variables influencing distribution was observed among estuaries of different type. Although this provides evidence of wide tolerance ranges of white steenbras to numerous environmental variables, this highlights the drawbacks of extrapolating results from one estuary to another, particularly among estuaries of different scale or type (Turpie *et al*. 2004, Vasconcelos *et al*. 2010). Inter-estuary variability in fish behaviour and space use patterns, as well as other factors, such as ichthyofaunal community composition and ecological functioning suggest that estuaries should be managed as individual units (Griffiths 2001).

Chapter 6

Coastal movements

6.1 Introduction

Successful management and conservation of important fishery species require empirical knowledge on movement and migration (Kerwath *et al*. 2005), particularly for estuarine-dependent coastal species that are of social, ecological or economic value, or conservation concern (Able and Grothues 2007a). However, information on recruitment, movement patterns, residency and estuarine dependence for many coastal fishery species, both in South Africa and globally is lacking (van der Elst and Adkin 1991, Bellquist *et al*. 2008). The frequency and geographic scale of individual movements among coastal regions can affect community structure and population dynamics (Jones 2005), as well as the level of genetic mixing (Turchin 1998). Therefore, understanding movement and area use patterns can provide essential information on the species' ecology (Meyer *et al*. 2000) and help to identify the mechanisms responsible for observed coastal population structure and genetic stock structure (Able and Grothues 2007a). Movement behaviour can also determine the effectiveness of management measures aimed at the protection of a species (Attwood *et al*. 2007).

The collapsed status of the white steenbras stock (Lamberth and Mann 2000) has resulted in part from ineffective management regulations. Conventional catch restrictions, such as daily bag and minimum size limits have failed to protect the species, meaning that alternative management measures are necessary. Marine protected areas (MPAs) have been advocated by numerous authors for the improved protection of coastal fish species (Roberts and Polunin 1991, Buxton 1993, Attwood and Bennett 1995a, Roberts 1998, Hilborn *et al*. 2004, Mann *et al*. 2006), and were identified as a management option to facilitate the recovery of overexploited and collapsed linefish species in South Africa (Griffiths *et al*. 1999). However, the effectiveness of individual MPAs has rarely been quantified, largely due to a lack of knowledge on the movement patterns of the species targeted for protection (Lembo *et al*. 2002, Attwood and Cowley 2005). The potential suitability of MPAs for the protection and rehabilitation of the white steenbras stock(s) remains unknown.

Cowley (1999) reported on a preliminary investigation into the movement of white steenbras tagged with conventional dart tags and recaptured in a long-term research programme in the Tsitsikamma National Park MPA, from 1995 to 1999. The study found that the majority of white steenbras recaptured were resident, although some larger individuals exhibited considerably greater

movements. Coastal residency would indicate that MPAs could be effective for this species (Cowley 1999), while large-scale migratory behaviour (if this is the case) would suggest otherwise.

Based on seasonal catch data and gonad development in different coastal regions, Bennett (1993b) proposed that white steenbras undertake an annual spawning migration from May to June from a summer aggregation period in the Western Cape Province to the vicinity of the southern Transkei, where spawning takes place in July and August. However, this is largely speculative and has not been confirmed. Therefore, in order to determine the potential suitability of MPAs, so that appropriate management measures can be implemented to ensure adequate protection of white steenbras at all life stages and during spawning aggregations, an understanding was required of the level of residency and the frequency and spatial extent of dispersal and large-scale migrations in this species.

6.1.1 Research approach and data sources

Two commonly used methods for assessing movement of fishes are conventional dart tagging and acoustic telemetry. The advantages and disadvantages of each, and the merits of employing these two techniques in conjunction are addressed in Chapter 2.

Conventional dart tagging

Conventional dart tagging has been successfully used to assess movements of a range of coastal fish species, for example black sea bass *Centropristis striata* in Great Bay Estuary, New Jersey, USA (Able and Hales 1997), Nassau grouper *Epinephelus striatus* in the central Bahamas (Bolden 2000), and galjoen *Dichistius capensis* in South Africa (Attwood and Cowley 2005). The strength of this technique is in the low cost and ease of application, allowing high numbers of fish to be tagged. Long-term research-based fish tagging programmes and the widespread and high-effort nature of the recreational shore fishery in South Africa provide a good platform for the tagging and recapture of high numbers of fish of a range of species.

Passive acoustic telemetry

Passive acoustic tracking has also been used to assess coastal movements of numerous fishery species, such as kelp bass *Paralabrax clathratus* at Santa Catalina Island, California, USA (Lowe *et al*. 2003) and red roman *Chrysoblephus laticeps* in South Africa (Kerwath *et al*. 2007a). Passive telemetry allows the automated long-term and potentially continuous collection of fish movement data, such as long-term residency and seasonal movement patterns (Heupel *et al*. 2006, Hedger *et al*. 2010b), and can provide information on movements between different environments (Childs *et*

al. 2008a). Acoustic telemetry can provide information in a number of ways. For example, data may be obtained on presence and absence of individuals, such as daytime presence and night-time absence, indicating a diel movement pattern, as observed for juvenile white steenbras in estuaries (see Chapter 3). Telemetry data can also provide information on the periodicity of movements, such as those associated with the tides, or information on high use areas, such as essential habitats within estuaries. However, telemetry can also act in the same way as conventional tagging, by providing "recapture-type" data, at specific localities. This type of "recapture" effort that is provided by an array of passive receivers is continuous and is not restricted to times when anglers are fishing, allowing continuous data collection over long periods. By employing an array of stationary receivers in the inshore zone along the shoreline of a large coastal embayment, it was possible to assess coastal residency and small-scale coastal movements within the bay, to complement the findings of the conventional tagging analysis.

Based on the strengths of the two techniques, acoustic telemetry and conventional dart tagging used in conjunction would provide a more robust assessment (Zeller and Russ 1998), and a number of studies have done this (e.g. Taylor *et al*. 2006, Abecasis *et al*. 2009, Afonso *et al*. 2009). This chapter employed conventional dart tagging to assess the level of residency and the rate of dispersal in the coastal zone for white steenbras at late juvenile, sub-adult and adult life stages, in conjunction with passive acoustic tracking to provide continuous "recapture" effort, in order to assess movements and residency within a large coastal embayment, and movements between estuarine and marine environments.

6.1.2 Aims and objectives

The overall aim of this chapter was to assess the coastal movement patterns of white steenbras, and dispersal from selected key localities. Specific objectives were to:

i. Describe coastal movements using data collected from four dedicated long-term conventional dart tagging programmes;
ii. Evaluate the effects of (a) geographic location, (b) coastal habitat, (c) fish length (age), (d) time at liberty, (e) density, and (f) seasonality, on movement patterns; and
iii. Describe short-term movements of sub-adult and adult individuals within a coastal embayment and into nearby estuaries using acoustic telemetry.

6.2 Methods and materials

6.2.1 Conventional dart tagging

Conventional dart tagging and recapture data for assessment of coastal dispersal patterns of white steenbras were obtained from four ongoing long-term shore-based coastal fish monitoring programmes, conducted at different spatial scales; the De Hoop Marine Protected Area inshore fish tagging programme, the Tsitsikamma National Park and proposed Greater Addo Elephant National Park coastal fish tagging programmes, as well as the Oceanographic Research Institute's National Tagging Project. Two of these programmes are centred within well-established MPAs, and a third programme is conducted within a proposed MPA, each with the aim of assessing residency within and dispersal from the specific MPA (Figure 6.1).

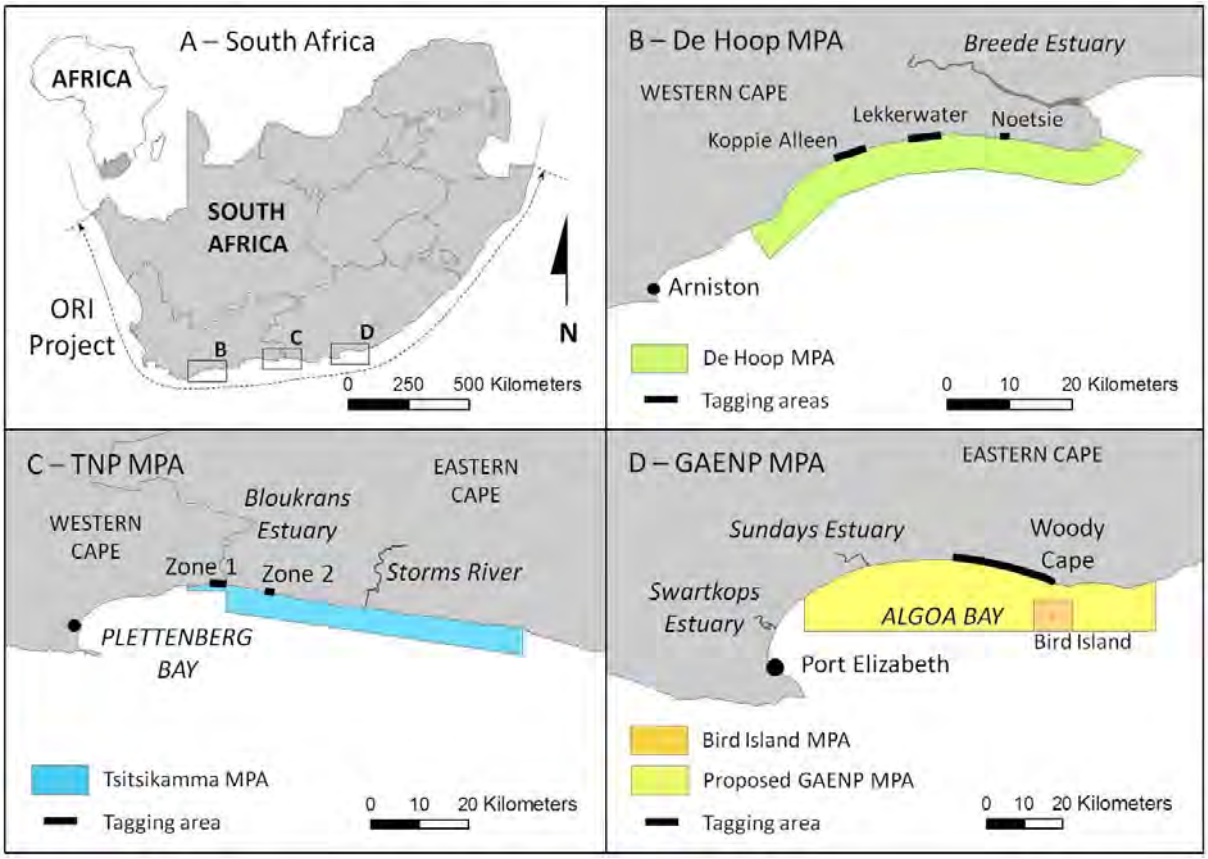

Figure 6.1: Study areas of A) the ORI National Tagging Project that spans the entire South African coastline, and the three research-based tagging programmes; B) De Hoop MPA, C) Tsitsikamma National Park (TNP) MPA, and D) proposed Greater Addo Elephant National Park (GAENP) MPA

The three MPA-based programmes are roughly evenly spaced within the species' core distribution, and the ORI project spans the entire distribution of the species, providing a dataset that was representative of movements throughout its distributional range. The widespread operation along most of the coastline and the high level of effort exerted in the South African shore fishery provided a high level of recapture effort. Tagging and recapture data in the De Hoop, Tsitsikamma and proposed GAENP MPAs, were recorded by researchers, allowing for trustworthy and accurate position recording, fish measurement and species identification (Attwood and Cowley 2005). The long-term nature of the programmes, particularly in the De Hoop MPA and the ORI project, spanning more than 25 years, allowed for assessment of movement patterns over the long-term, providing more representative information on the species life history. These data, therefore, provided a long-term, high quality, robust and reliable dataset, on which to base the analyses of coastal movement patterns.

De Hoop MPA tagging programme

The De Hoop MPA inshore fish tagging programme was initiated in 1984, one year prior to proclamation of the MPA, by Dr Colin Attwood (then of Marine and Coastal Management, currently University of Cape Town), aimed at the study of galjoen *Dichistius capensis*. The programme is focussed on two areas within the De Hoop MPA, namely Koppie Alleen and Lekkerwater, each approximately 3.4 km long, and separated by a distance of 11 km (Attwood 2003) (Figure 6.1). Because recreational angling within the MPA is not permitted, recaptures inside the MPA were restricted to the two research fishing areas, and a third area (Noetsie), situated approximately 9 km east of Lekkerwater, where additional research angling had been conducted for collection of biological samples. The study began with monthly four- to five-day tagging fieldtrips to Koppie Alleen, but was subsequently changed to alternate trips between Koppie Alleen and Lekkerwater from 1987 to 1995, after which it was reduced to three trips per site per year (Attwood and Cowley 2005). The programme administration was later taken over by Ms Lieze Swart in 2008 (Department of Environmental Affairs), and is ongoing. The shoreline in the two areas consists mainly of sandy beaches and interspersed patchy wave-cut aeolianite rock platforms, and is exposed to high energy wave action. The patchy reefs are all shallow and, due to the wind- and wave-driven dynamic nature of the surf zone in the area, are regularly covered and uncovered by shifting sand (Attwood 2003). All angling is conducted by experienced anglers. The De Hoop tagging data are submitted to ORI, for inclusion in the ORI project database, from which data for the current study were extracted (Maggs and Bullen 2010).

Tsitsikamma MPA tagging programme

The Tsitsikamma National Park coastal fish tagging programme was initiated to determine the level of residency of important fishery species within, and the level of dispersal from, the MPA, and to assess catch-per-unit-effort (CPUE) within the MPA over the long term. The programme was initiated in 1995 by researchers from the Department of Ichthyology and Fisheries Science (Rhodes University) and taken over 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 programme initially comprised six five-day field trips annually, which was decreased to four trips annually from 1997 until 2005. From 2006 until 2010, there were two trips annually (summer and winter), but this was increased again to quarterly trips in 2011. The study area includes approximately 5 km of coastline towards the western end of the Tsitsikamma MPA, between the Bloukrans and Klip estuaries (Figure 6.1). The coastline at Tsitsikamma is dominated by steeply shelving, exposed cliffs (Tilney *et al*. 1996). The shoreline is rugged, consisting of steep, rocky ridges, which extend into the subtidal, with some small "pocket" sandy beach areas and numerous sand-filled gulleys (Hanekom *et al*. 1989, Attwood and Cowley 2005), and is exposed to strong wave action (Cowley *et al*. 2002). All angling and tagging is conducted by experienced research anglers who have been trained to handle and tag fish. Angling in the Tsitsikamma MPA took place throughout the 5-km tagging zone (zone 1), allowing recaptures anywhere within this stretch of coastline. For the period 1998 to 2000, angling was also conducted in a second zone to the west of the Lottering Estuary, in close proximity to zone 1 (Figure 6.1). In addition, recreational angling was permitted within a 3-km stretch of the Tsitsikamma MPA, adjacent to the rest camp at Storms River in the centre of the MPA (Hanekom *et al*. 1997), until 2000 when this area was closed to angling.

Proposed Greater Addo Elephant National Park MPA tagging programme

The proposed Greater Addo Elephant National Park (GAENP) MPA coastal fish tagging programme is an ongoing programme, established in 2005 by Dr Paul Cowley, of the South African Institute for Aquatic Biodiversity. The programme is aimed at the assessment of the coastal residency and dispersal patterns of important coastal fishery species, and is focussed on the Woody Cape area of coastline towards the eastern end of Algoa Bay, and falls within the footprint of the proposed GAENP MPA. The programme is comprised of bimonthly two- to three-day research angling field trips, to a section of shoreline extending approximately 30 km along the coastline (Figure 6.1). The subtidal habitat is predominantly sand, with some areas of mixed sand and rock, and sandstone reefs. Unlike angling in the De Hoop MPA, tagging and recapture effort were exerted across a wide area, allowing recaptures to be made at a range of distances from the tagging site. Angling and

tagging are conducted by experienced anglers. Although the area falls within the proposed GAENP MPA, recreational angling is still permitted, allowing recaptures to be made by recreational anglers outside of dedicated tagging field trip periods.

Oceanographic Research Institute National Tagging Project

The Oceanographic Research Institute's (ORI) National Tagging Project (ORI project) is an ongoing nationwide programme that was initiated in 1984, and is administered by the South African Association for Marine Biological Research. The programme differs from the De Hoop, Tsitsikamma and proposed GAENP MPA programmes, in that all fishing and tagging are conducted by member volunteers from around the South African coastline, who participate as a hobby during recreational angling. Recaptures are also frequently reported by even by non-member recreational anglers. The high numbers of ORI members and participants in the South African recreational fishery allows for high numbers of fish, from a wide range of species, to be tagged and recaptured, and the nature of the programme and the recreational fishery allow for geographically widespread angling effort for tagging and recapture. As such, recaptures of fish tagged in this programme can be made at almost any point along the coastline (Figure 6.1). Thus, the programme differs from the previous three programmes, as it assesses general coastal movement patterns, rather than dispersal from a central tagging point. A data report detailing all white steenbras tagged and recaptured in the ORI project (Maggs and Bullen 2010) was complied specifically for the current study.

Dart tagging

The fish handling and dart tagging procedures in the proposed GAENP, Tsitsikamma and De Hoop tagging programmes were consistent. Captured fish were placed on a wet PVC vinyl measuring stretcher, measured to the nearest mm fork length (FL) and/or total length (TL), and tagged with a uniquely numbered plastic dart tag (Type A: 114 mm × 1.6 mm Ø, or Type B: 89 mm × 1.6 mm Ø, Hallprint, Australia). Tags were inserted according to the guidelines of Attwood (1998). Tags were inserted into the dorsal musculature of the fish, with a sharp hollow applicator, ensuring that the tag is firmly anchored behind a dorsal vertebral spine (Cowley *et al*. 2002). Fish tagged during these programmes were released at their capture localities. Tagging of fish as part of the ORI project is conducted by the members of the public (recreational anglers). Although guidelines for the correct handling and tagging of fish are provided, the standardisation of the tagging and handling process cannot be guaranteed, and is likely not the case. However, the comparable recapture rates of most fish and the high numbers of tagged fish that are recaptured in this programme suggest that this is a suitable and reliable method to provide a large sample size.

Dart tagging data analysis

Recapture distances

Tagging and recapture localities for the De Hoop MPA and ORI project are based on a series of 1-km "coastal localities" between the Mozambique border in the east, and the Namibia border in the west, as defined in the ORI project (van der Elst and Penney 1995). Each locality is numbered, according to its distance, in kilometres, from the northern Mozambique border, and each capture and recapture event is allocated to one of these coastal localities. However, there are only 772 coastal localities defined in the ORI project database. Therefore, not every 1-km stretch of coastline is uniquely defined. Consequently, it is possible that two localities (although consecutive "defined" localities) may be separated by a distance greater than 1 km, in which case a fish captured or recaptured at a position between localities will be allocated to the nearest locality defined on the database. This results in a potential decrease in the resolution and accuracy of the data (Attwood and Cowley 2005). Of the 771 distances between neighbouring localities, the greatest distance is 53 km. However, 98% of the distances between neighbouring defined localities are less than 20 km, 92% less than 10 km, and 80% are 5 km or less. The modal distance is 1 km, and the median distance is 2 km, suggesting that error in position estimation is rarely more than 1 or 2 km, sufficiently low for studying longshore movement patterns and migrations. Distances between capture and recapture locations in the De Hoop MPA and ORI project are thus calculated as the distances between coastal localities. Tagging and recapture positions of fish tagged in the Tsitsikamma and proposed GAENP MPAs were recorded using GPS accuracy, and distances between capture and recapture events were calculated as the distance along the coastline between the two positions.

Effect of coastal region on the level of dispersal

The coastline within the distribution range of white steenbras was divided into seven coastal regions (1 – West Coast, 2 – Cape Agulhas, 3 – Mossel Bay, 4 – Tsitsikamma, 5 – Algoa Bay, 6 – Transkei, 7 – KwaZulu-Natal) (Figure 6.2). These regions were defined based on geographical landmarks, such as capes, or political boundaries that would historically have affected the distribution of recreational shore fishing, such as the boundaries of the Transkei region. The proportions of fish in each region that were recaptured within the respective tagging region or that dispersed to the other coastal regions were calculated, to determine the level of dispersal and residency on a regional scale. This analysis was limited to the ORI project data, due to its widespread nature.

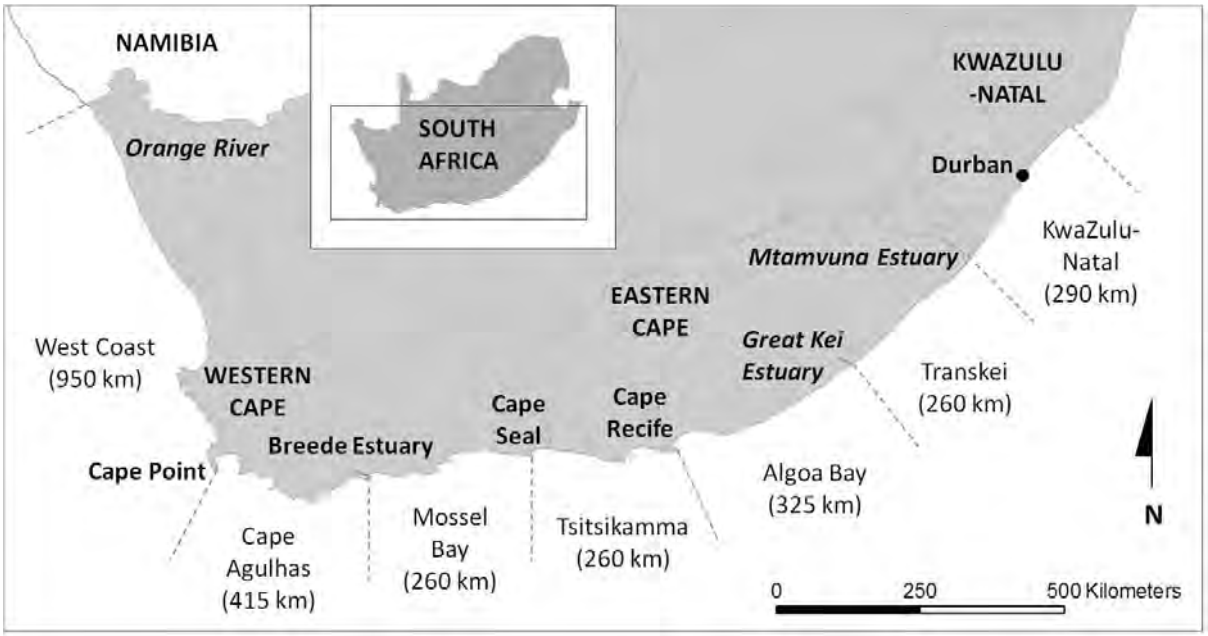

Figure 6.2: Map of the South African coastline, showing the different coastal regions (and lengths, km) as defined in the analyses, from the West Coast to KwaZulu-Natal

Effect of time at liberty on distance moved

The distances between capture and recapture locations for fish in each study were statistically compared to the times 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.

Effect of size (age) at recapture on distance moved

Recapture distances for all fish measured at the time of recapture were compared to the size (and age) of the fish, using linear regression, to determine whether fish size (or age) influenced the scale of movements undertaken. For this analysis, fork lengths were converted to ages, by means of an age-length equation (Mehl 1973), where:

$$age(years) = \frac{ln\left(1 - \frac{FL}{1283}\right)}{-0.1008} + 0.22$$

Juvenile fish were defined as those less than 450 mm FL, based on the suggested size at first attainment of sexual maturity of 390 mm standard length (Day 1981 in Whitfield 1990) and about 450 mm FL (Bennett 1993b). Sub-adult fish were defined as those between 450 and 600 mm FL and adult fish as those greater than 600 mm FL (Bennett 1993b).

Effect of habitat on distance moved

The effect of habitat type on observed recaptures was assessed, by comparing recapture rates and distances, between studies with varying shoreline habitat. Data for this analysis were drawn from the Tsitsikamma MPA and proposed GAENP MPA programmes only, as these provide accurate information on the habitat and accurate position-recording at each capture and recapture site.

Firstly, the proportions of recaptures made in areas of rocky, sandy or mixed (sand and rock) habitats were calculated, based on habitat recorded at the time of recapture. The proportions of the three habitats available within each area were estimated from coastal habitat type, based on Harris *et al*. (2011). Secondly, an assessment of habitat type was conducted, based on the 'Habitat Affinity Index' (HAI) described by Monaco *et al*. (1998) (as presented in Chapter 5 for estuarine substrate type affinity). This analysis was used to compare the proportions of white steenbras captured in each of the three habitats, to those available within each study area. HAI values were calculated for each of the three substrate types, within the two study areas, as follows:

$$HAI = (p - r)/r \text{ , if } p \leq r, \text{ or}$$
$$HAI = (p - r)/(1 - r); \text{ if } p \geq r,$$

where p was calculated as the proportion of fish that were captured over each habitat, and r was determined as the proportion of each habitat available within the study area. Positive HAI values indicate affinity for that habitat, while negative values indicate avoidance (Monaco *et al*. 1998).

The frequency distributions of recapture distances of fish tagged in the Tsitsikamma MPA and proposed GAENP MPA programmes were then compared, to determine whether habitat type influenced recorded recapture distances.

Effect of fish density on the level of dispersal and recapture distance

The effect of density on dispersal and recapture distance was assessed in the De Hoop, Tsitsikamma and proposed GAENP MPA tagging programmes, by comparison with white steenbras CPUE (as a proxy for density) obtained during shore angling in the respective MPA.

Effect of season on recapture location

The effect of seasonality on movements was assessed in two ways. Firstly, monthly proportions (%) of recaptures made in each of the coastal regions (1 – West Coast, 2 – Cape Agulhas, 3 – Mossel Bay, 4 – Tsitsikamma, 5 – Algoa Bay, 6 – Transkei, 7 – KwaZulu-Natal, Figure 6.2) were calculated, to detect possible trends in the proportions of recaptures that would support the theory of a winter migration (after Bennett 1993b). 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 should be based on short times at liberty, to detect seasonal effects. Therefore, recaptures of fish that were at liberty for less than three months (Attwood and Cowley 2005) were extracted for this analysis.

6.2.2 Acoustic telemetry

As a complement to the conventional dart tagging studies, an acoustic telemetry study was designed and implemented, to provide continuous monitoring effort to assess coastal residency and small-scale movements of white steenbras in a coastal embayment. An array of 11 acoustic receivers (Vemco, models VR2 and VR2W) was positioned throughout Algoa Bay, in the Eastern Cape Province, including inside the Coega and Port Elizabeth harbours (Figure 6.3). Receivers were positioned in such a way as to detect residency of the acoustically tagged fish in the vicinity of the tagging site at Woody Cape, within the proposed GAENP MPA, as well as potential movements into and out of Algoa Bay. An additional receiver was positioned approximately 2 km offshore of the Kowie Estuary, to the east of Algoa Bay, in an area well known for white steenbras, to detect potential eastward movements from Algoa Bay.

An additional aim of the telemetry study was to determine the level of connectivity between marine and estuarine environments, and thus provide information on the level of estuarine dependence of late juvenile to large adult life stages. To achieve this, acoustic receivers were positioned in pairs within the mouths of eight permanently open estuaries (Great Fish Estuary in the east to the Kromme Estuary in the west) that either enter, or are adjacent to Algoa Bay (Figure 6.3). These estuaries spanned a greater length of coastline (approximately 300 km) than the marine receiver array, and thus had the potential to provide additional information on longshore coastal movements.

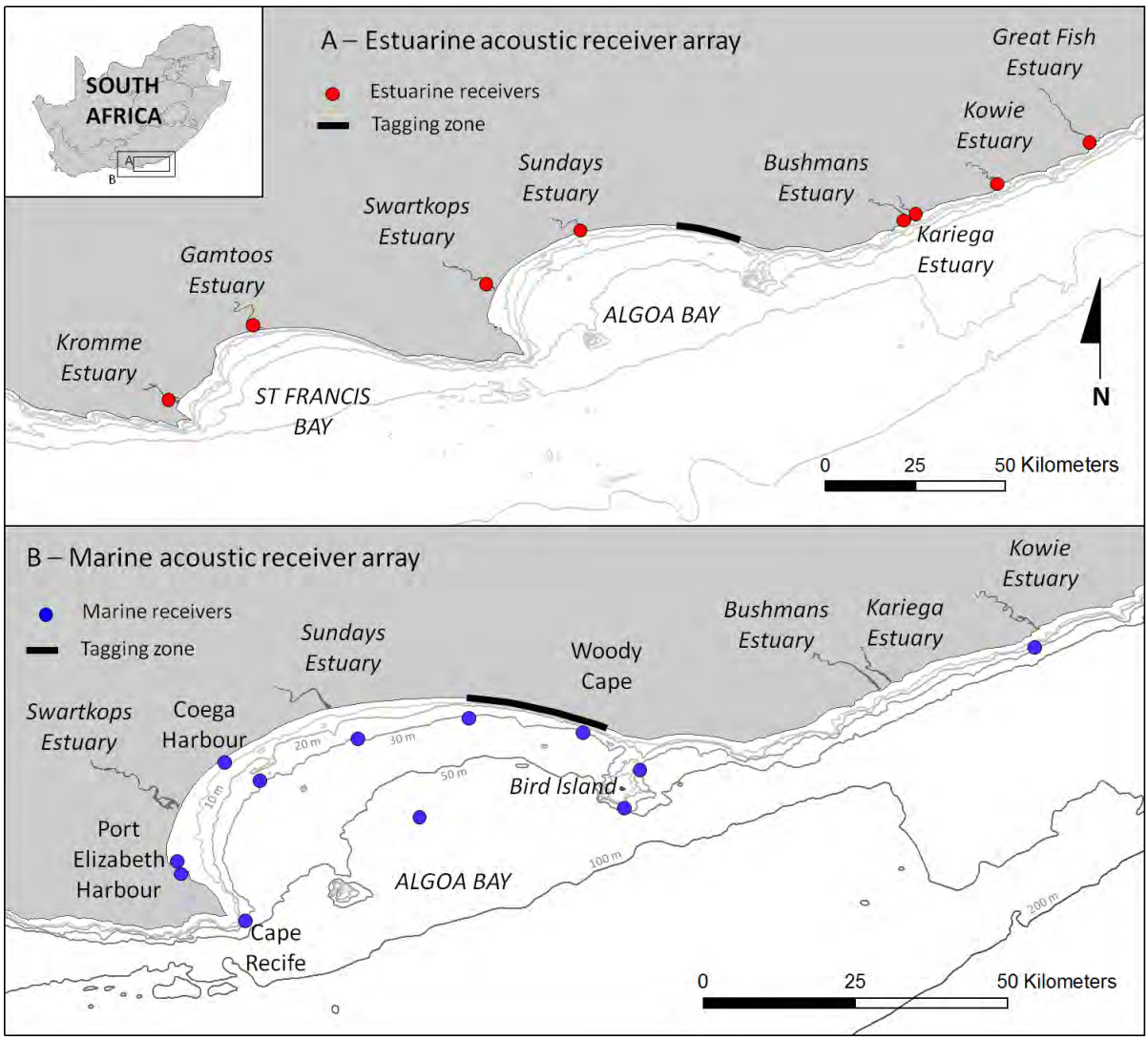

Figure 6.3: Map of the general study area for the telemetry study conducted in Algoa Bay, showing a) the array of acoustic receivers positioned in the eight permanently open estuaries within the study area, and b) the array of acoustic receivers positioned in the marine environment

Fifteen white steenbras ranging from 401 to 623 mm FL (mean = 497 ± 60 mm) were captured by hook and line from December 2008 to February 2009 (Table 6.1). Most were sub-adult fish (450 – 600 mm FL), with one fish considered as late juvenile (< 450 mm FL) and two as adult fish (> 600 mm FL). The fish were surgically equipped with Thelma MP-13 acoustic transmitters (diameter 13 mm, length 31 mm, weight 11.4 g in air and 7.3 g in water, estimated battery life 781 days) with a random nominal delay of 30 to 90 seconds between transmissions, according to the methods described in Chapter 3. Two additional adult fish, of 830 and 960 mm FL, were captured in July and October 2010, respectively, and surgically equipped with Vemco V16-4L acoustic transmitters (diameter 16 mm, length 68 mm, weight 25 g in air and 11 g in water, estimated battery life 1 248 days), with a random nominal delay of 50 to 130 s. All transmitters transmitted at a frequency of 69 kHz.

Table 6.1: Capture, surgery and transmitter details for the white steenbras surgically equipped with acoustic transmitters in the Woody Cape study area in the proposed GAENP MPA

Fish ID	Capture date	FL (mm)	TL (mm)	Surgery duration (mm:ss)	Transmitter type
2019	03-12-08	462	515	07:02	Thelma MP-13 (30 – 90s)
2020	03-12-08	455	510	04:37	Thelma MP-13 (30 – 90s)
2021	03-12-08	460	514	04:23	Thelma MP-13 (30 – 90s)
2022	04-12-08	512	573	06:16	Thelma MP-13 (30 – 90s)
2025	04-12-08	459	518	03:36	Thelma MP-13 (30 – 90s)
2023	06-12-08	401	458	03:21	Thelma MP-13 (30 – 90s)
2024	06-12-08	459	517	05:16	Thelma MP-13 (30 – 90s)
2026	06-12-08	482	541	03:38	Thelma MP-13 (30 – 90s)
2027	07-12-08	499	557	04:50	Thelma MP-13 (30 – 90s)
2028	14-02-09	527	592	02:56	Thelma MP-13 (30 – 90s)
2029	14-02-09	606	685	02:02	Thelma MP-13 (30 – 90s)
2030	14-02-09	493	556	03:43	Thelma MP-13 (30 – 90s)
2031	14-02-09	460	519	04:43	Thelma MP-13 (30 – 90s)
2032	14-02-09	554	613	02:43	Thelma MP-13 (30 – 90s)
2033	14-02-09	623	708	04:06	Thelma MP-13 (30 – 90s)
65062	31-07-10	960	1042	02:30	Vemco V16-4L (50 – 130s)
65069	02-10-10	830	890	07:40	Vemco V16-4L (50 – 130s)

6.3 Results

6.3.1 Conventional dart tagging

At the time of analysis, 5 775 white steenbras had been tagged with conventional dart tags, of which 292 (5.1%) were recaptured. Most of the fish (n = 3 355) were tagged in the ORI project, while 1 551 were tagged in the De Hoop MPA, 388 in the Tsitsikamma MPA and 481 in the Woody Cape area of the proposed GAENP MPA research programmes (Table 6.2).

Table 6.2: Numbers of white steenbras tagged and recaptured in the De Hoop, Tsitsikamma, proposed GAENP and ORI tagging programmes (excludes fish recaptured on multiple occasions)

Tagging programme	No. tagged	Recaptures		Distance travelled (km)			Days at liberty		
		No.	%	Mean	Min	Max	Mean	Min	Max
De Hoop	1 551	86	5.5	33.5	0.0	620	327	2	1 660
Tsitsikamma	388	24	6.3	38.0	0.0	460	351	0	1 660
GAENP	481	23	4.8	29.7	0.1	205	307	10	721
ORI project	3 362	159	4.7	45.1	0.0	554	261	0	2 262
Total	*5 782*	*292*	*5.1*	*39.9*	*0.0*	*620*	*292*	*0*	*2 262*

Recaptures were made from Cape Point to KwaZulu-Natal, spanning most of the core distribution of the species. Recapture rates were similar in all studies, ranging from 4.7 to 6.3%, excluding multiple recaptures. Ten fish in total were recaptured twice, while one of these was recaptured three times.

De Hoop MPA recaptures

The majority (85%) of the 86 recaptures emanating from this tagging programme was made within the De Hoop MPA, with 72% of fish being recaptured within their respective tagging zone (Figure 6.4). Thirty-six fish were tagged and recaptured at Lekkerwater in the centre of the MPA, and 26 at Koppie Alleen, with two individuals at each site having been recaptured twice (all four fish recaptured both times at their tagging site). Only four individuals moved between tagging sites, two in each direction. Eleven fish moved 9 km east from Lekkerwater, and one moved 20 km east from Koppie Alleen, to Noetsie, remaining within the MPA. Only 13 fish (15%) were recaptured outside of the MPA, at distances ranging from 31 to 620 km from the respective tagging site (Figure 6.4). False Bay (336 km) and Algoa Bay (620 km) represented the furthest recapture areas west and east of the MPA, respectively.

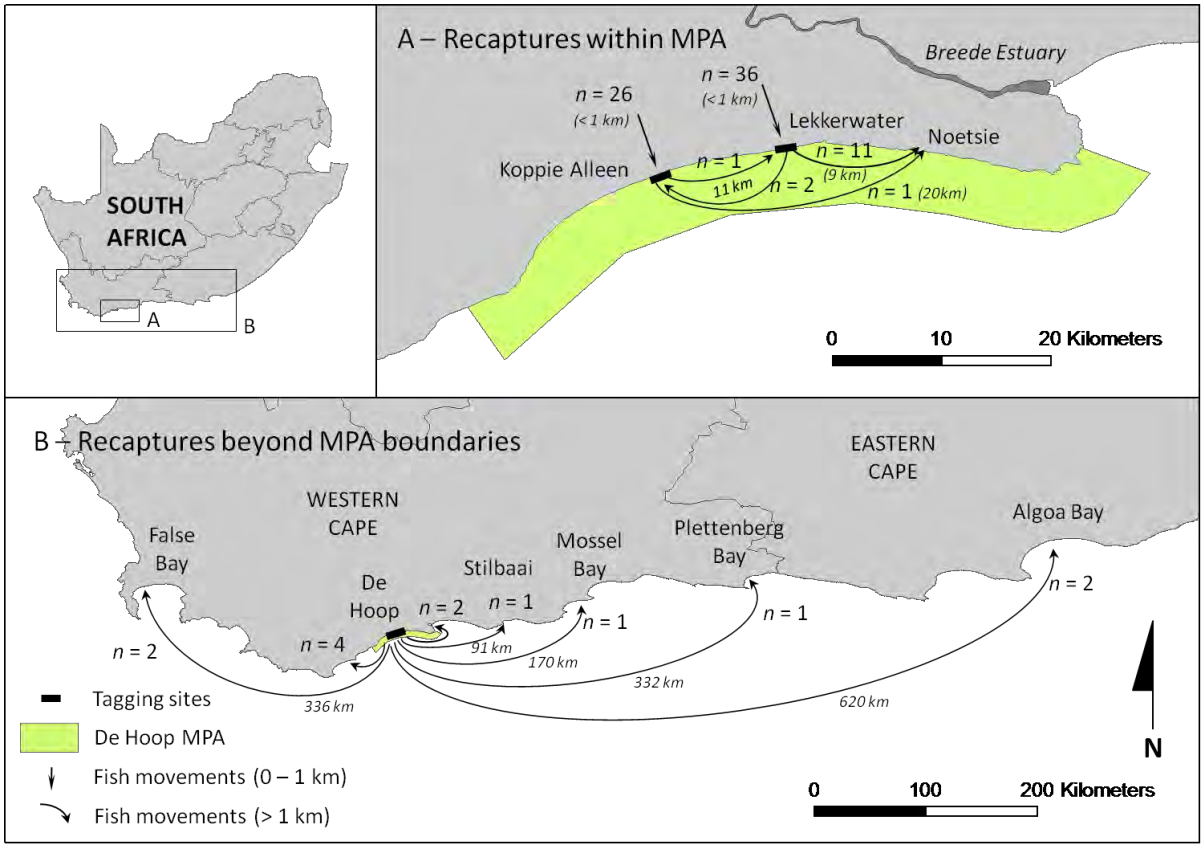

Figure 6.4: Movements of 86 recaptured white steenbras from the De Hoop tagging programme. Arrows connect tagging and recapture locations

Tsitsikamma MPA recaptures

Fifteen of the 24 recaptures (62.5%) were made within the Tsitsikamma MPA, 14 of which were recaptured within 1 km of the tagging site, and one at Storms River, approximately 30 km east of the tagging zone. Two of these fish were recaptured twice, with both recaptures for each fish taking place at the tagging site. A third fish was recaptured once at its tagging locality, but recaptured a second time 1 km east of its tagging site. Four individuals (16.7%) moved west to Nature's Valley, to a sandy beach outside of the MPA adjacent to the Groot Estuary (west), representing distances between 6 and 10 km. One of these fish was recaptured twice at Nature's Valley. The remaining five recaptures (20.8%) were made outside the MPA, at distances ranging from 25 km to 460 km from the tagging site. The greatest movements west and east were to Plettenberg Bay (25 km) and East London (460 km), respectively (Figure 6.5).

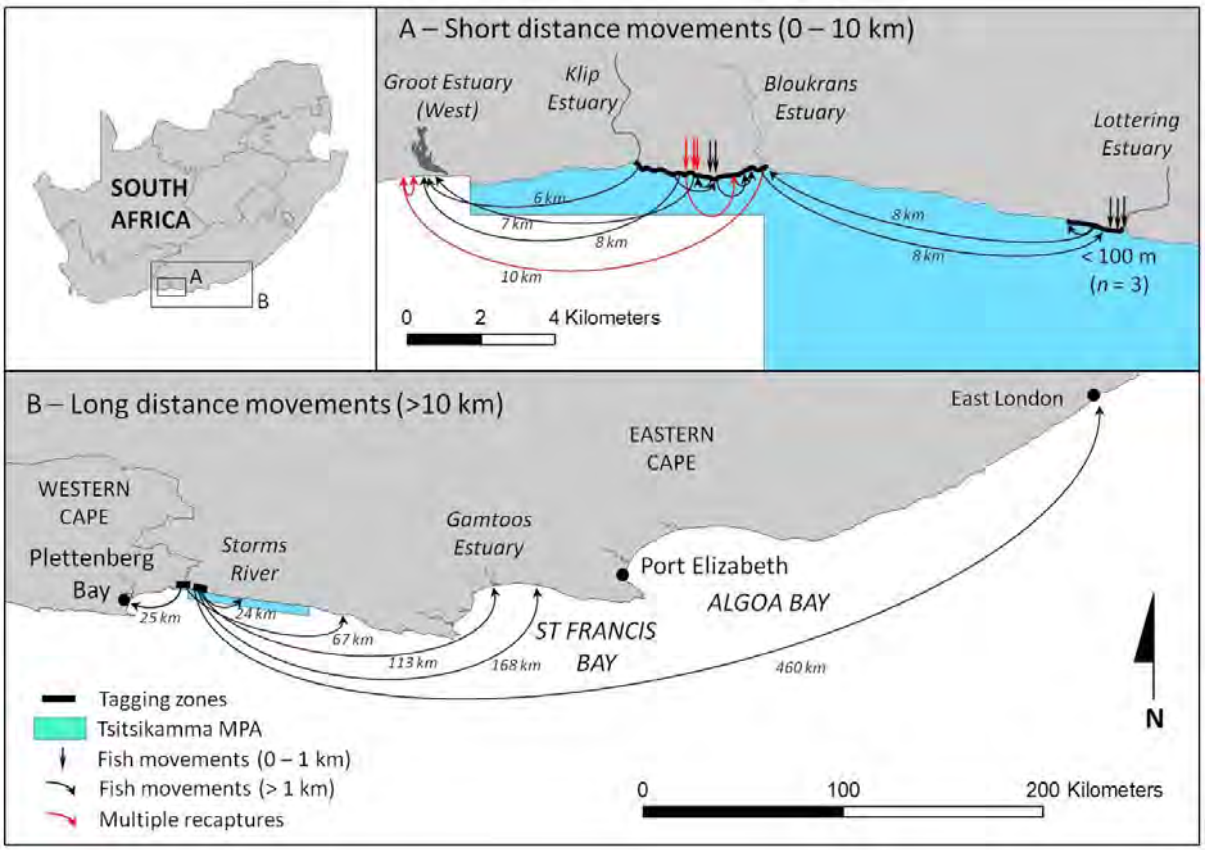

Figure 6.5: Movements of 24 recaptured white steenbras from the Tsitsikamm tagging programme. Arrows connect tagging and recapture locations, red arrows indicate individuals recaptured multiple times

Greater Addo Elephant National Park MPA recaptures

Of the 481 white steenbras tagged in the proposed GAENP MPA tagging programme, 23 were subsequently recaptured (4.8% recapture rate). Nineteen recaptures (82.6%) were made within the footprint of the proposed GAENP (Figure 6.6), with recapture distances in this area ranging from 0.05 to 29 km (mean distance = 5.1 ± 7.8 km), and seven fish being recaptured within 1 km of their respective tagging site. Only four individuals were recaptured outside of the proposed MPA, with maximum displacements of 205 km west to Oyster Bay, and 180 km east to East London (Figure 6.6).

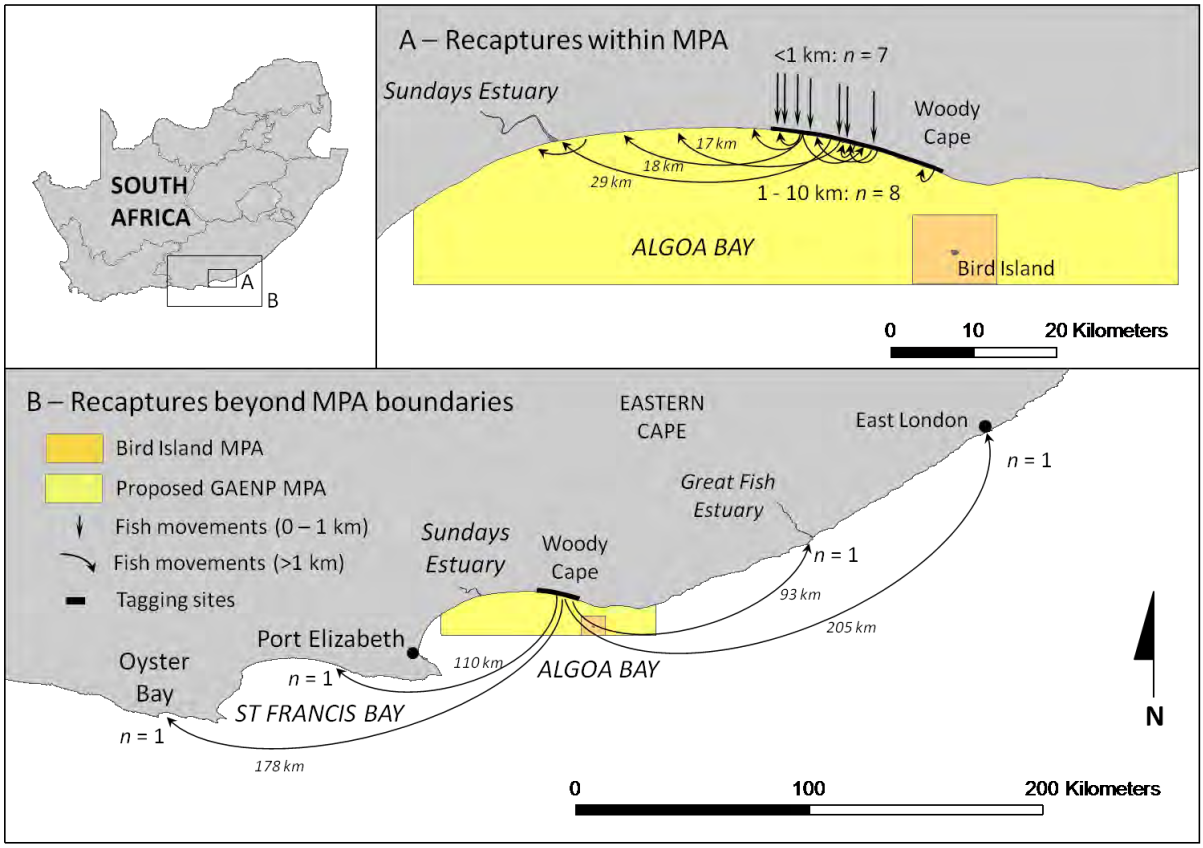

Figure 6.6: Movements of 23 recaptured white steenbras from the GAENP tagging programme. Arrows connect tagging and recapture locations

ORI project recaptures

By the end of 2010, 3 355 white steenbras had been tagged from the Berg Estuary in the west to Scottburgh in the east, of which 159 (4.7%) were recaptured (Figure 6.7). Recaptures were made from False Bay in the west, to Umgeni Estuary, near Durban, in the east, spanning approximately 1 700 km of coastline. Most recaptures (102, 64.2%) were made at the site of capture (i.e. 0 – 1 km displacement). These recaptures were made from False Bay, to Qora Estuary near Mazeppa Bay. Nine fish (5.7%) were recaptured between 1 and 10 km from the tagging site, while 28 (17.6%) and

20 (12.6%) fish, respectively, were captured between 10 and 100 km, and more than 100 km, from the tagging locality (Figure 6.7). Four fish were recaptured twice, and one fish three times, with all recaptures made at the tagging site.

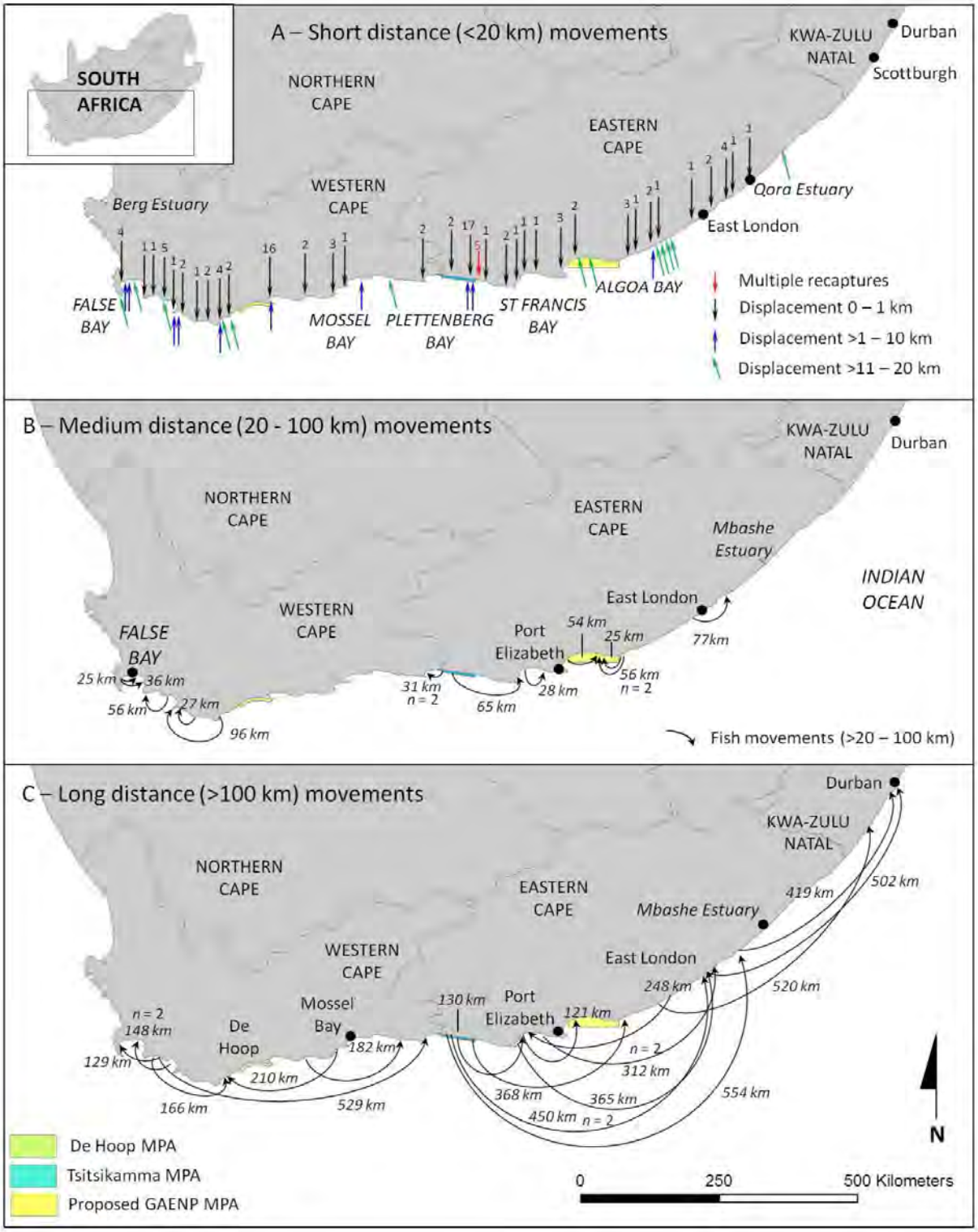

Figure 6.7: Movements of 159 recaptured white steenbras from the ORI tagging programme. Arrows connect tagging and recapture locations

Large-scale movements (> 100 km) were recorded in the Western Cape (n = 7) and Eastern Cape (n = 10) provinces, of up to 529 and 554 km, respectively. There was also evidence of connectivity among different coastal regions, between False Bay (south west coast) and the Tsitsikamma region (south coast), between the Tsitsikamma region and the Algoa Bay and Transkei coastal regions (south east coast), and between the Eastern Cape Province and KwaZulu-Natal. However, there were no long distance displacements recorded crossing between the Eastern and Western Cape provinces, and no evidence of individuals moving between False Bay, known to be a summer aggregation area, and the vicinity of the white steenbras spawning grounds in the Transkei (Bennett 1993b) (Figure 6.7).

Recapture distances and direction of movement

The frequency distributions of distances moved (i.e. the distance between tagging and recapture localities) from each tagging programme were similar, particularly in the Tsitsikamma, De Hoop and ORI programmes. In these three studies, the majority of recaptures (ranging from 58 to 68%) were made within 1 km of the tagging sites, with very few recaptures made between 1 and 5 km from the tagging sites. The results from the GAENP showed relatively fewer individuals recaptured within 1 km, when compared to the other three studies, and relatively more individuals recaptured from > 1 to 5 km from the tagging site (Figure 6.8).

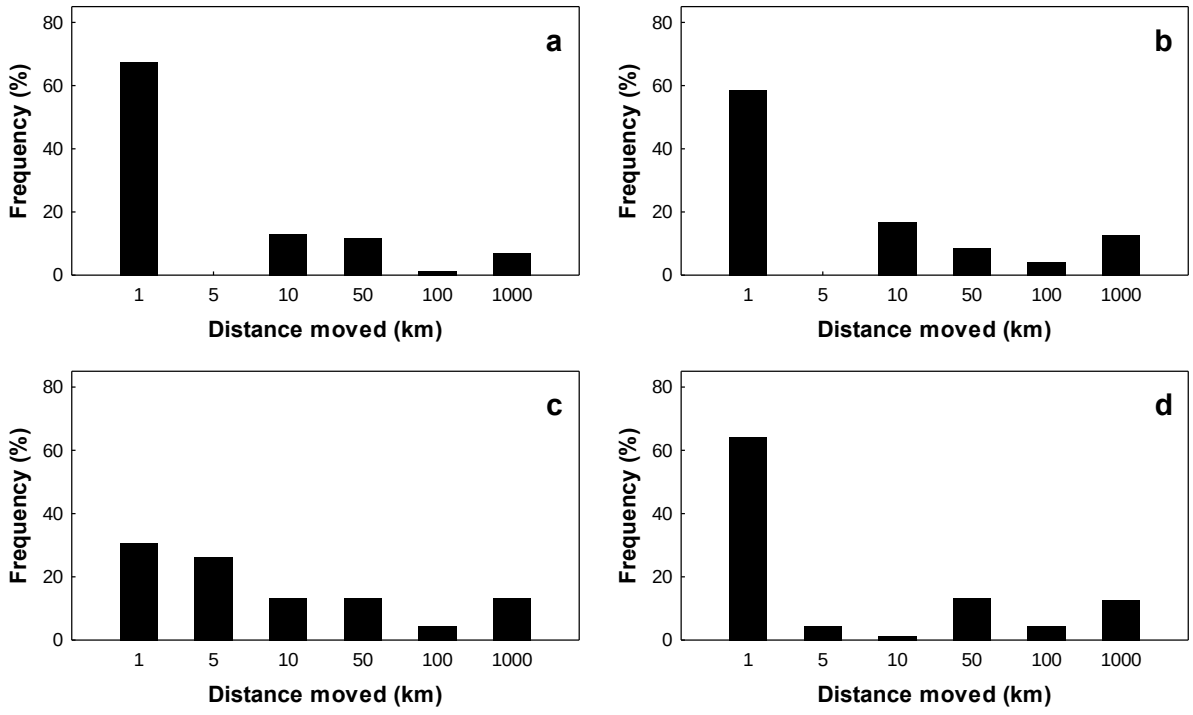

Figure 6.8: Frequency distributions of distances moved (km, values represent upper limit of distance bins), for fish tagged in the a) De Hoop, b) Tsitsikamma, c) GAENP and d) ORI tagging programmes

It is likely that the proportions of recaptures falling into the two lowest recapture distance bins (i.e. 0 to 1 km and > 1 to 5 km) would be influenced by the differences in both the habitat and the resolution at which tagging and recapture localities were recorded, in the different tagging programmes. The frequency distributions of recaptures in the four programmes were thus compared graphically, in two ways; i) with the 0 to 1 km and > 1 to 5 km recapture distance bins presented separately (Figure 6.9 a) and ii) with the number of distance bins reduced so that recapture distances from 0 to 1 km were included in the 0 to 5km bin (Figure 6.9 b). Data are similarly presented for all fish (n = 292) (Figure 6.9 c and d).

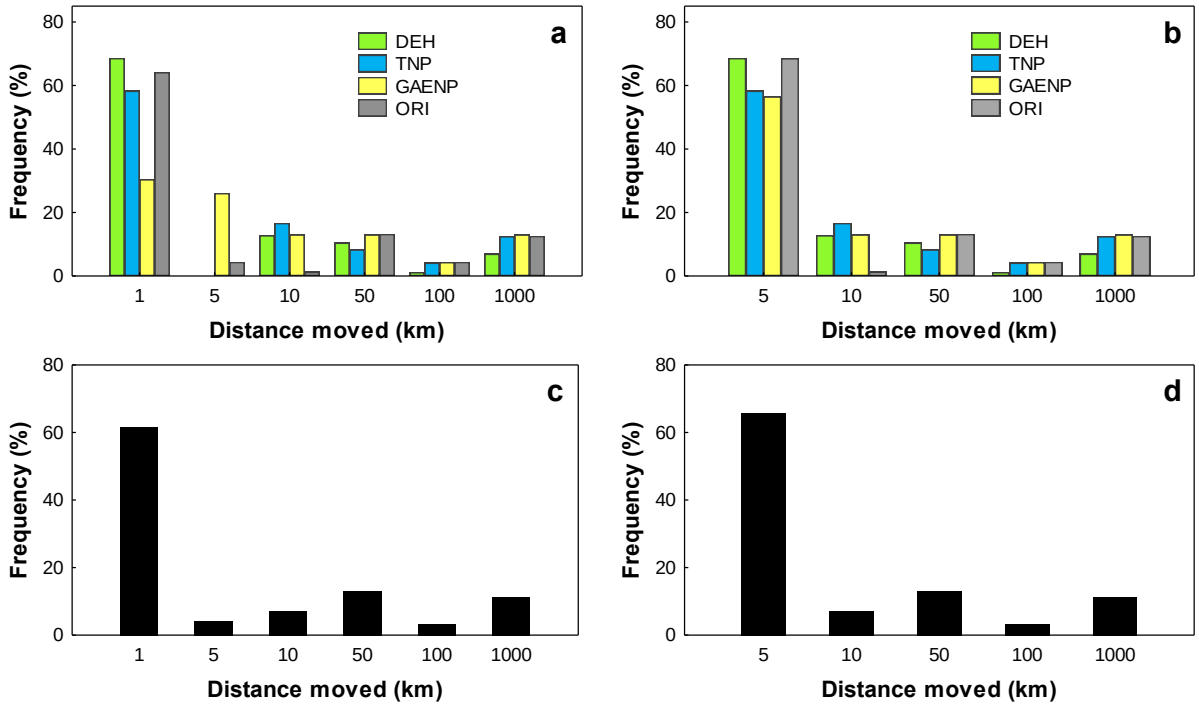

Figure 6.9: Frequency distributions of distances moved (km) for fish from each tagging programme, showing 0 to 1 km and > 1 to 5 km recapture distances a) separately and b) combined; as well as for all fish recaptured (n = 292) showing the two distance bins a) separately and d) combined

This confirmed that observed variability among tagging programmes was predominantly a result of the proportions of shorter distances moved, with recapture frequencies in the 'reduced-bins' distributions showing remarkable similarity among the four programmes. The majority of recaptures in all four programmes were made within 5 km of the tagging site. Dispersal from the tagging site was recorded for fewer individuals, although some individuals made large-scale movements, up to 620 km, and the frequency and magnitude of these movements were greater in an eastward direction from the tagging site (Figure 6.10).

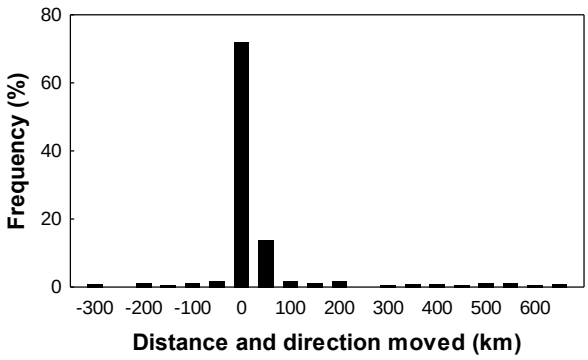

Figure 6.10: Frequency (%) distribution of distances moved (n = 292), including direction of movement along the coast. Negative and positive values represent westward and eastward movements, respectively, and values represent the upper limits of the distance bins

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

Size of fish at tagging

The length frequency distributions (%) of the fish that were measured at the time of tagging in the ORI project (n = 2 615) were similar in each coastal region, although the proportions of larger fish (> 600 mm FL) were higher in the Transkei coastal region (Figure 6.11a). The mean sizes of fish tagged in the ORI project in each of the coastal regions were also similar, although the mean size appeared to be higher towards the West Coast and Transkei coastal regions (Figure 6.11b).

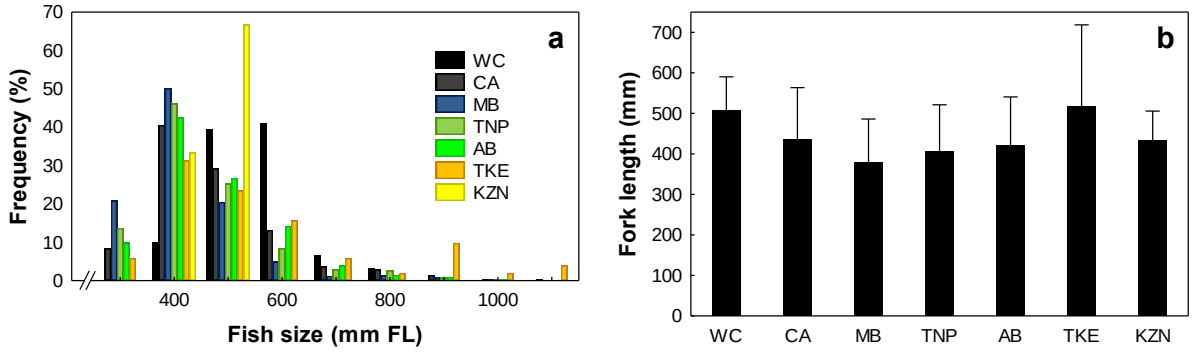

Figure 6.11: Lengths of fish (mm FL) that were measured at the time of tagging in the ORI project (n = 2 615), showing a) length frequency (%) distribution by coastal region, and b) mean size (± SD) by region (WC – West Coast, CA – Cape Agulhas, MB – Mossel Bay, TNP – Tsitsikamma, AB – Algoa Bay, TKE – Transkei, KZN – KwaZulu-Natal)

Effect of coastal region on levels of dispersal and residency

The high proportions of fish tagged in the ORI project in each coastal region that were recaptured within the tagging region provided strong evidence of residency on a regional scale. None of the white steenbras tagged along the west coast was recaptured, and no recaptures from elsewhere were made in this region. Similarly, no white steenbras tagged along the KwaZulu-Natal coast were recaptured. At least 85% of fish tagged in the Cape Agulhas, Mossel Bay, Tsitsikamma and Algoa Bay regions were recaptured within their tagging region (Figure 6.12). Fish tagged in the Transkei region showed the greatest proportion of "dispersal", although this was based on three recaptures only.

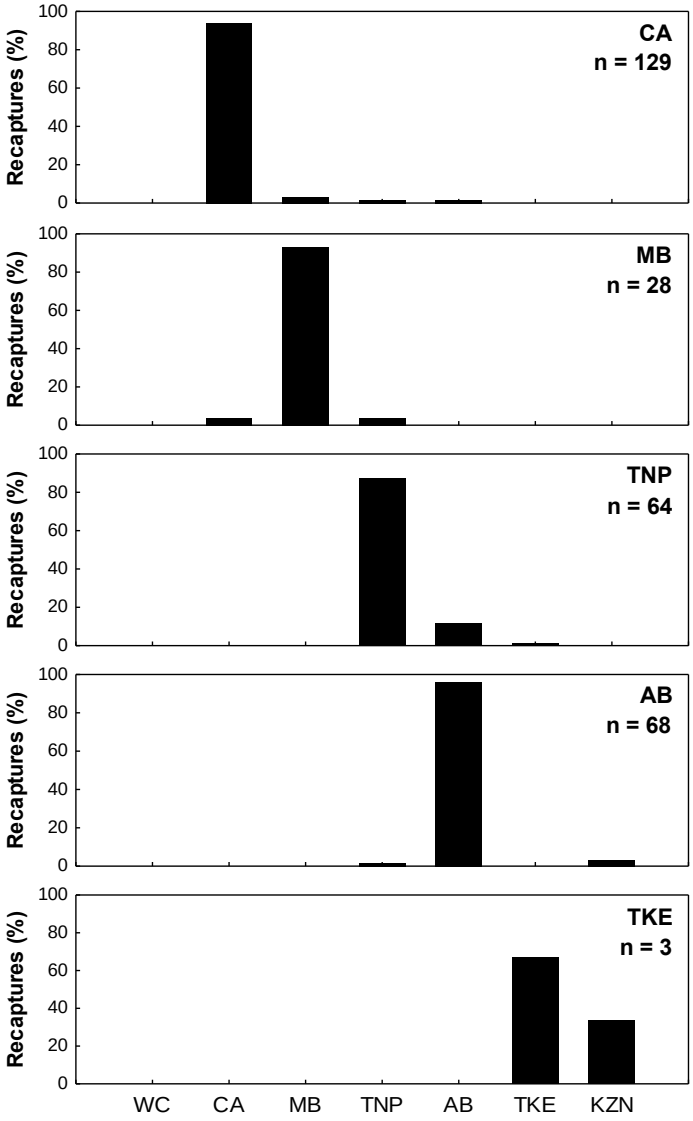

Figure 6.12: The regional distribution (%) of all recaptures (n = 292) from all four tagging programmes, for fish tagged in the different coastal regions (WC – West Coast, CA – Cape Agulhas, MB – Mossel Bay, TNP – Tsitsikamma, AB – Algoa Bay, TKE – Transkei, KZN – KwaZulu-Natal). There were no recaptures of fish tagged along the west coast

The mean distance moved by fish recaptured within each region increased sharply from west to east, although only three fish each were recaptured in the Transkei and KwaZulu-Natal (Figure 6.13).

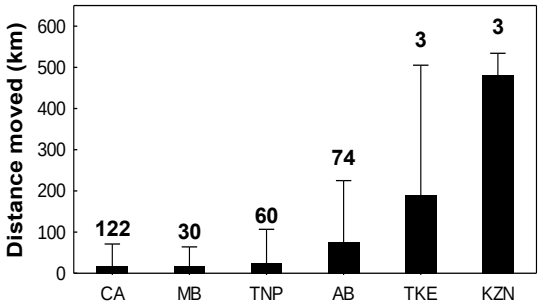

Figure 6.13: Mean (± SD) distance moved (km) for all fish recaptured (n = 292) from all four tagging programmes, by coastal region (CA – Cape Agulhas, MB – Mossel Bay, TNP – Tsitsikamma, AB – Algoa Bay, TKE – Transkei, KZN – KwaZulu-Natal). West Coast was excluded as there were no recaptures made in this area. Sample sizes are presented above each plot

Effect of fish size (and age) on distance moved

Of the 292 white steenbras recaptured, 207 (254 to 900 mm FL) were reliably measured at the time of recapture. Most of these in each of the four programmes (64 to 90%) and overall (78%) were juveniles or sub-adults, smaller than the size at which 50% sexual maturity is attained (± 600 mm FL) (Figure 6.14).

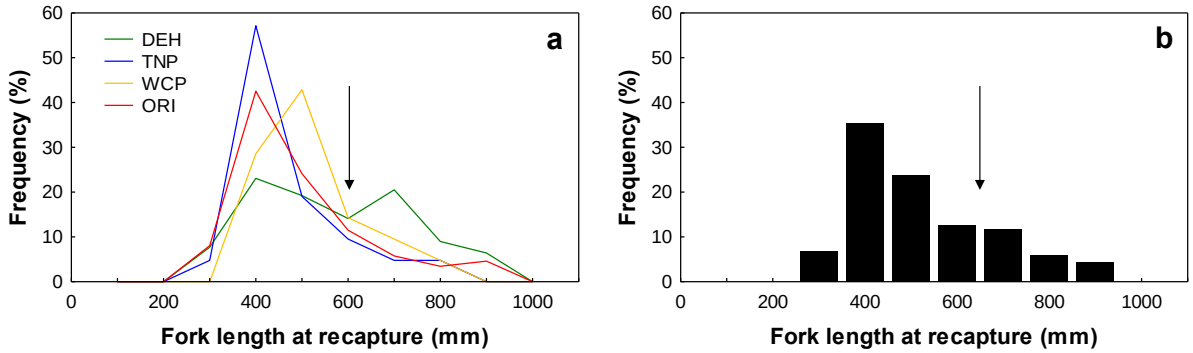

Figure 6.14: Fork length (mm) for fish measured at the time of recapture, for a) each study, and b) all studies combined (n = 207). The arrow indicates approximate size at sexual maturity

Fish having moved greater distances were characterised by greater minimum and mean sizes (mm FL) and ages at the time of recapture (Table 6.3). Distances moved also differed significantly among size classes (Kruskal-Wallis ANOVA, $p < 0.001$) (Figure 6.15). Sub-adult (> 450 to 600 mm FL) and adult (> 600 mm FL) fish undertook significantly greater movements than juveniles (≤ 450 mm FL) ($p < 0.001$). Distances moved by the two largest size classes were not significantly different ($p > 0.500$).

Table 6.3: Mean (±SD) fork lengths (mm) and length ranges, and mean (±SD) ages (years) and age ranges of white steenbras recaptured within various distance bins (n = 207)

Distance moved	Number measured	Mean (±SD) size (mm FL)	Size range (mm FL)	Mean (±SD) age (years)	Age range (years)
0 – 1 km	140	430 (± 132)	254 – 840	4.4 (± 1.7)	2.4 – 10.8
>1 – 10 km	28	518 (± 154)	282 – 865	5.6 (± 2.2)	2.7 – 11.3
>10 – 100 km	22	534 (± 128)	347 – 837	5.7 (± 1.8)	3.3 – 10.7
>100 km	17	668 (± 167)	410 – 900	7.9 (± 2.9)	4.0 – 12.2

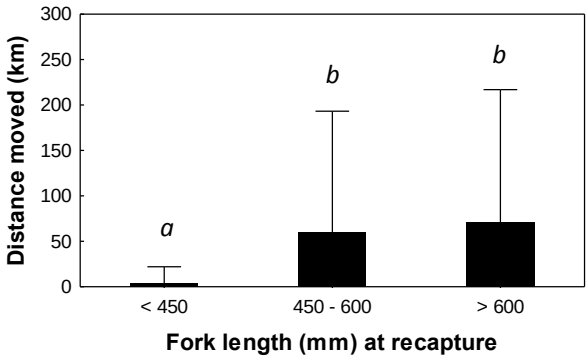

Figure 6.15: Mean (±SD) distance moved (km), by size class (mm FL), for all fish measured at recapture in all programmes (n = 207). Different letters (*a*, *b*) indicate significantly different size classes

Linear regression showed a weak but significant positive correlation between distance moved (km) and (i) fish length (mm FL) (R^2 = 0.148, p < 0.001), and (ii) age (years, estimated from recapture FL) (R^2 = 0.170, p < 0.001), for all fish measured at the time of recapture (n = 207) (Figure 6.16). This trend was also observed for the De Hoop, Tsitsikamma and ORI datasets separately (p < 0.001 in all cases, data not presented).

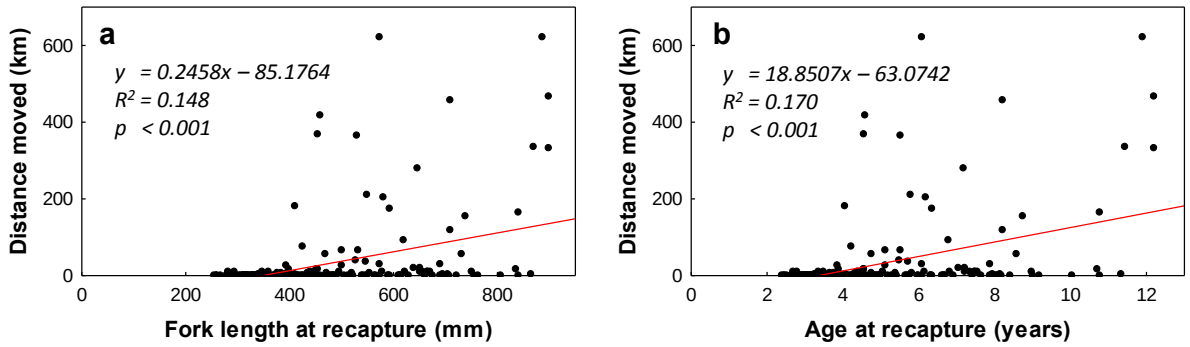

Figure 6.16: Linear regression of distance moved (km) against a) size (mm FL) at recapture, and b) age (years) estimated from FL, for all fish measured at the time of recapture (n = 207)

Effect of time at liberty on distance moved

Times at liberty between tagging and recapture ranged widely (Figure 6.17), with some fish recaptured on the same day as being tagged (in the Tsitsikamma MPA and ORI project), and ranging up to 2 262 days (ORI project). The mean times at liberty were, however, similar among programmes, ranging from 261 to 351 days. When time at liberty for all fish recaptured (n = 292) was graphed against distance moved, with easterly displacements presented as positive distances and westerly displacements presented as negative distances, no clear trend was evident, with a large proportion of recaptures made at zero displacement, up to 1 293 days after tagging (Figure 6.18).

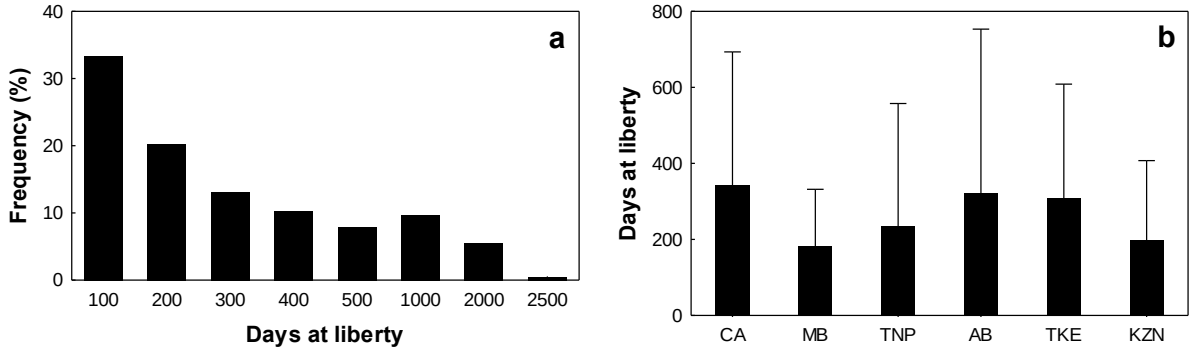

Figure 6.17: Time at liberty (days) for all fish recaptured (n = 292), expressed as a) a frequency (%) distribution, and b) as mean days at liberty (± SD) by coastal region (CA – Cape Agulhas, MB – Mossel Bay, TNP – Tsitsikamma, AB – Algoa Bay, TKE – Transkei, KZN – KwaZulu-Natal). West coast is excluded as there were no recaptures made in this area

However, linear regression showed a significant, although weak (R^2 = 0.0886, p < 0.001), positive correlation between distance moved and the number of days at liberty for all fish (Figure 6.18).

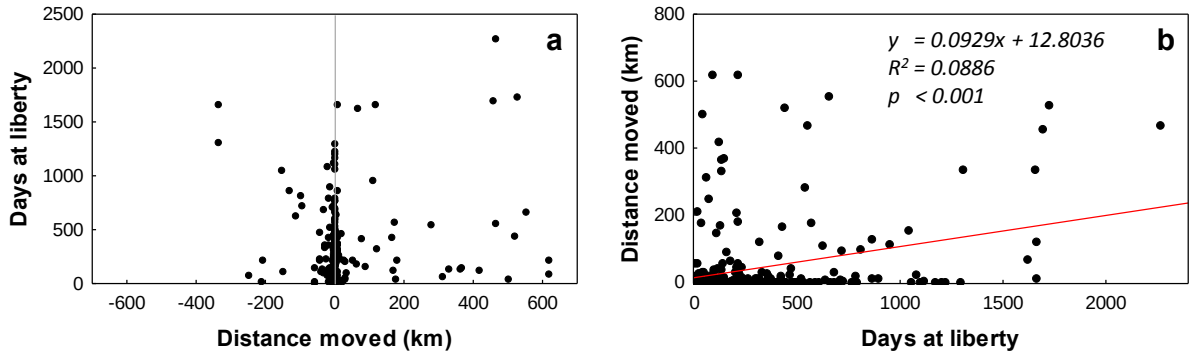

Figure 6.18: Time at liberty (days) graphed against recapture distance (km) for all fish (n = 292) presented in the form of a) a scattergram (positive distances represent easterly displacements and negative distances represent westerly displacements), and b) a linear regression analysis of recapture distance against time at liberty (days)

Effect of habitat on distance moved

From 1995 to 2008, 457 white steenbras were captured in the two fishing zones in the Tsitsikamma (TNP) MPA, and the substrate at the capture site was recorded for 415. Despite the substrate in this study site being predominantly mixed sand and rock (52%) and rock (41%), with small patches of sandy substrate interspersed among rock, the majority of these white steenbras were captured over sandy substrates (40%) or substrates of mixed sand and rock (33%), with 27% caught in rocky habitat. From 2005 to 2011, 560 white steenbras were captured as part of the long-term monitoring programme in the proposed GAENP MPA, of which 94% were captured over sandy substrate, with the rest caught along shores of mixed sand and rock. This study area is dominated by sandy shoreline (90%), with some mixed sand and rock (8%), and negligible rock. The HAI values indicated an affinity for sandy habitats in both study areas (TNP: 0.35, GAENP: 0.34), and negative HAI values indicative of avoidance of rocky habitats (TNP: - 0.32, GAENP: - 0.3) and habitats of mixed sand and rock (TNP: - 0.37, GAENP: - 0.74).

In the proposed GAENP MPA, the proportion of white steenbras recaptured within 1 km of the tagging site was considerably less than that in the Tsitsikamma MPA, although the proportion was considerably higher for fish recaptured > 1 km to 5 km away, in the former study (Figure 6.8). When these two distance bins are combined (Figure 6.9), the two datasets indicate remarkably similar behaviour. Therefore, it appears that the habitat in the Tsitsikamma MPA restricted the frequency of small-scale movements between 1 km and 5 km.

Effect of fish density on distance moved

The mean (± SD) distances moved by fish tagged in the proposed GAENP, Tsitsikamma and De Hoop MPAs were 29.7 km (± 58.7), 38.0 km (± 101.0) and 33.5 km (± 111.4), respectively. Using CPUE as a proxy for density, the corresponding values were 16.6 fish.100 angler hours^{-1}, 3.19 fish.100 angler hours^{-1} and 3.14 fish.100 angler hours^{-1}, respectively (see Chapter 8). Graphical representation of these estimates showed no relationship between CPUE and the mean distance moved (Figure 6.19a). The recapture rates were also unrelated to CPUE (Figure 6.19b), with recapture rates of 4.8%, 5.5% and 6.3%, in the proposed GAENP, De Hoop and Tsitsikamma MPAs, respectively.

Proportions of fish recaptured at different distances from the tagging sites were similar (Figures 6.8 and 6.9), although fewer fish in the proposed GAENP MPA were recaptured within 1 km, and no fish in the De Hoop and Tsitsikamma MPAs were recaptured between 1 and 5 km from the tagging site. CPUE in the proposed GAENP MPA of 16.6 fish.100 angler hours^{-1}, was considerably higher than in

the De Hoop (3.19 fish.100 angler hours^{-1}) and Tsitsikamma (3.14 fish.100 angler hours^{-1}) MPAs, indicating a possible relationship between CPUE (density) and the proportions of fish either remaining within 1 km of a particular location, or moving to locations > 1 to 5 km away (Figure 6.19 c and d).

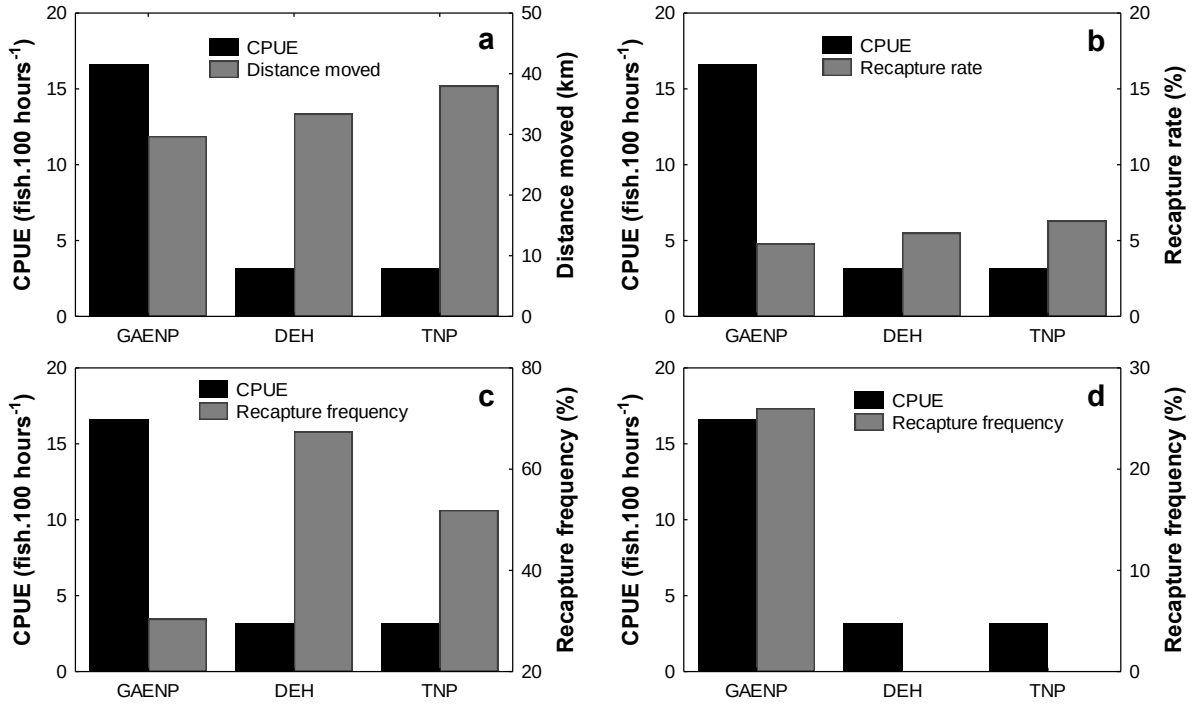

Figure 6.19: Comparative CPUE (fish.100 angler hours^{-1}) and a) mean recapture distance (km), b) recapture rate (%), c) proportions (%) of recaptures made from 0 to 1 km from the tagging site, and d) proportions (%) of recaptures made > 1 to 5 km from the tagging site. The sample units (n = 3) in all comparisons are the individual tagging programmes (GAENP – Greater Addo Elephant National Park MPA, DEH – De Hoop MPA, TNP – Tsitsikamma MPA)

Effect of seasonality on recapture location

Monthly proportions (%) of recaptures made in each of the coastal regions (1 – West Coast, 2 – Cape Agulhas, 3 – Mossel Bay, 4 – Tsitsikamma, 5 – Algoa Bay, 6 – Transkei, 7 – KwaZulu-Natal) showed no obvious seasonal trends (Figure 6.20), although peaks in certain areas could be identified. There was a broad peak (spanning six months) in recaptures made in the Cape Agulhas region, from late winter to early summer (July to December), although there was an anomalous modal peak in May. The Mossel Bay region exhibited a large peak in December, and a lower broad peak from April to June, and the Tsitsikamma region showed a similar bimodal trend, with a peak from April to June and a second from September to December. The Algoa Bay region showed a single broad peak, from

October to February. Only three recaptures each were made in the Transkei and KwaZulu-Natal regions; these were made from April to June, and in September and December, respectively.

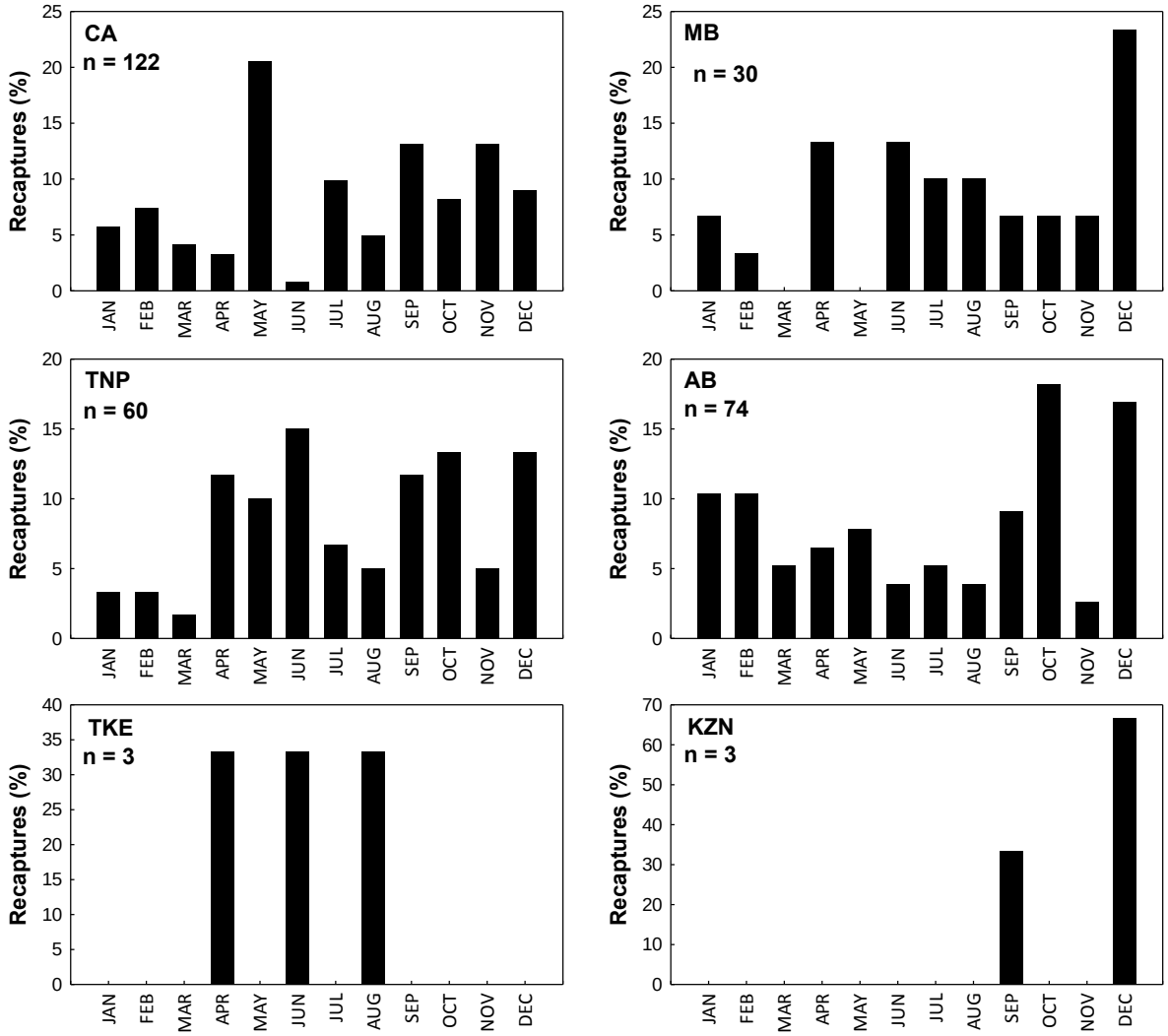

Figure 6.20: Monthly proportions (%) of recaptures made in different regions (CA – Cape Agulhas, MB – Mossel Bay, TNP – Tsitsikamma, AB – Algoa Bay, TKE – Transkei, KZN – KwaZulu-Natal)

Monthly proportions of movement directions for fish at liberty for up to three months are presented in Figure 6.21, for all years combined. From January to April the proportional directions of movements were similar. However, from March to June the proportions of recaptures made of fish that had moved westward decreased, while the proportions of fish recaptured further east of their tagging sites remained high. All recaptures made in July represented fish that had remained resident. From August to November, the majority of recaptured fish had moved in a westerly direction, until December, when the proportions of eastward movements had again increased, reflecting that of January.

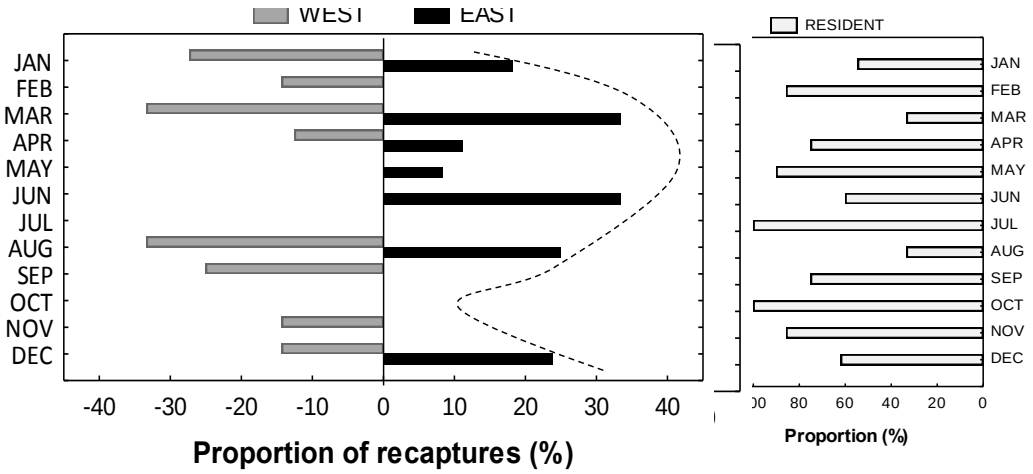

Figure 6.21: Monthly proportions of recaptures for fish at liberty for up to three months (n = 91), for fish that moved westward (negative proportions), eastward (positive proportions) or remained stationary

6.3.2 Acoustic telemetry

Seven of the 17 white steenbras (41%) surgically equipped with acoustic transmitters in the marine environment were subsequently detected, some on multiple occasions (maximum = 5), either on the marine receiver array (2 fish), on a harbour receiver (3 fish), on an estuarine receiver (3 fish), or through being recaptured in the surf zone by recreational anglers (2 fish), or a combination of these (3 fish). Most of the movements were detected within Algoa Bay, but four individuals also made long distance movements and were recorded outside of the bay (Figure 6.22).

Fish 2020 (455 mm FL) was acoustically tagged at Woody Cape on 3 December 2008 and subsequently recaptured in the surf zone by a recreational shore angler in East London, approximately 180 km east of the tagging site, 31 days later. Although this fish was not detected on any receivers in the array, the recorded movement between tagging and recapture localities was included in the conventional dart tagging dataset of the proposed GAENP MPA programme.

Fish 65069 (830 mm FL) was tagged on 2 October 2010. The fish was detected for a short period, 181 days later, on a receiver positioned inshore of Bird Island at a depth of 25 m, approximately 13 km offshore from the tagging site.

Fish 2024 (459 mm FL) was tagged on 6 December 2008 and detected 346 days later (November 2009) on the receiver inside the Coega Harbour, approximately 50 km west of the tagging locality. A total of 97 detections was made during the 2 hours spent in the vicinity of this receiver.

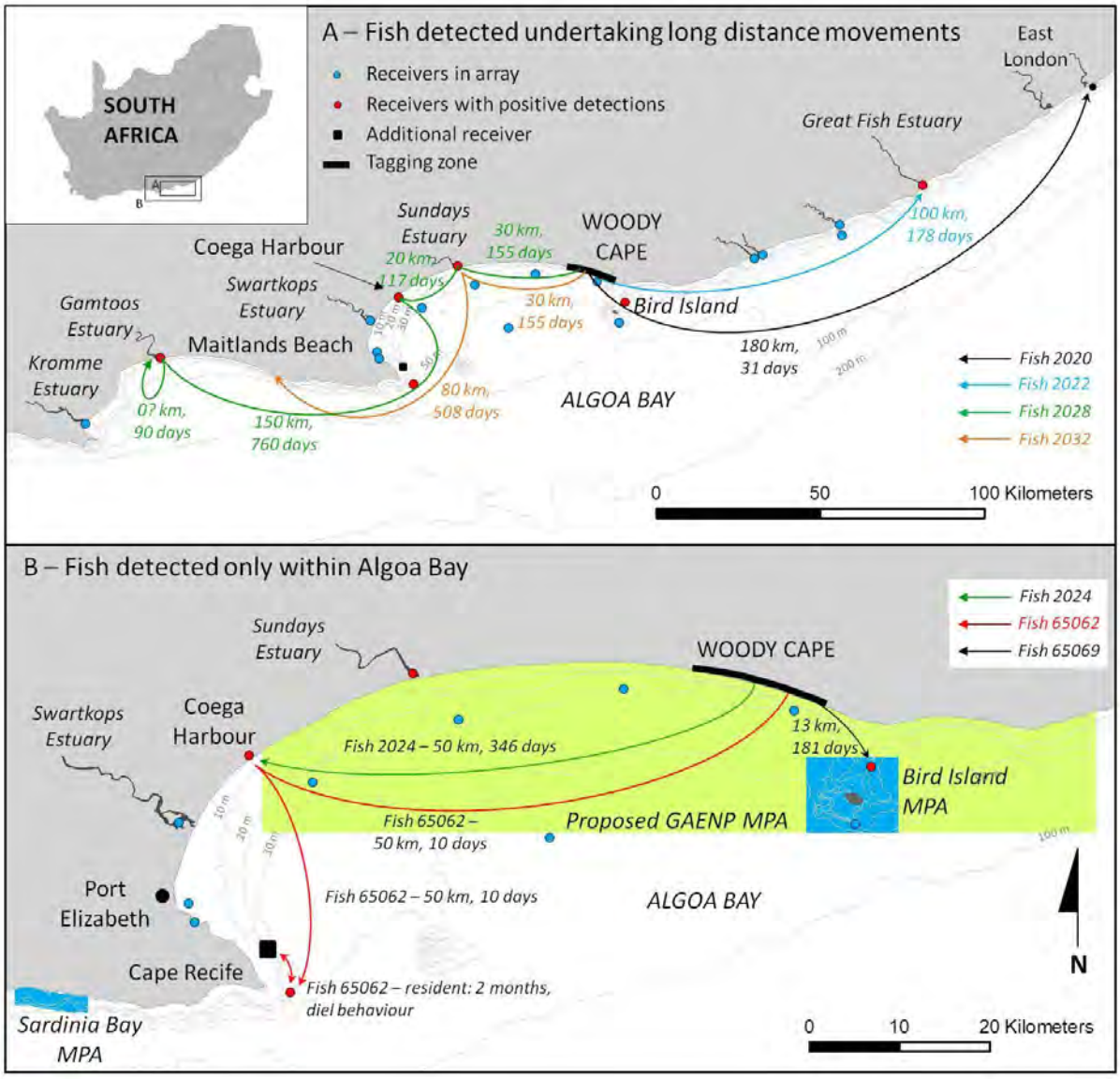

Figure 6.22: Movements of seven white steenbras tagged with acoustic transmitters at Woody Cape, in the proposed GAENP MPA

Fish 65062 (960 mm FL), tagged on 31 July 2010, was detected ten days later in the Coega Harbour, approximately 50 km west of the tagging locality. Four detections were made, within approximately half an hour, before the fish moved out of receiver range. The fish was detected four days later by the receiver positioned off Cape Recife, at the western point of Algoa Bay, approximately 80 km west of the tagging site. The fish was detected on this receiver intermittently for a period of 68 days, during which time 1 264 detections were made. During the same period, the fish was also detected on a nearby receiver deployed as part of an unrelated study on elasmobranchs in Algoa Bay, on which 47 detections were made. The mean time between periods of detection at each of these two receivers, which are approximately 6 km apart, was 20 hours and 25 minutes (range 2 hours 24 minutes – 4 days 7 hours). With the exception of a single detection made at approximately 01:00, all

detections on this additional receiver were made between 08:00 and 18:00. Conversely, with the exception of a single detection made at approximately 10:00, all detections on the Cape Recife receiver were made between 17:00 and 07:00.

Fish 2022 (512 mm FL) was tagged on 4 December 2008 and detected 178 days later in the Great Fish Estuary, approximately 100 km east of the tagging locality. The fish entered the estuary in the late afternoon, and left at first light the following morning.

Fish 2028 (527 mm FL) was tagged on 14 February 2009 and detected 155 days later in the Sundays Estuary. This represented a movement of at least 30 km west along the coastline, and this fish ventured approximately 12 km upriver from the mouth (this estuary had 16 receivers deployed at the time, for the estuarine telemetry study). This fish also entered the estuary in the late afternoon, and left in the early hours of the morning. This fish was detected approximately 20 km further west almost four months later (November 2009) in the Coega Harbour. The sequence of detections suggests two separate overnight visits, separated by 8 days, with the fish entering the harbour in the late afternoon on both occasions. However, it is also possible that the fish entered the harbour and moved deep into the harbour, with the apparent absence period representing a movement beyond the range of the receiver, within the harbour. The fish was then detected 476 days later, in the Gamtoos Estuary, 150 km west of the tagging site, representing the greatest movement west, and the second longest movement overall. The fish remained in the estuary for less than three hours (around midnight), during which time 113 detections were made, before leaving the estuary. The fish was subsequently detected in the Gamtoos Estuary again, 90 days later. The fish again entered and departed at night, although during this second visit it moved at least 3 km up the estuary, where it remained for four days before leaving.

Fish 2032 (554 mm FL), tagged on 14 February 2009, was detected in the Sundays Estuary, 30 km west of the tagging site, in June 2009, 113 days after being tagged. This fish also covered the 30 km coastal stretch, but only ventured about 2 km up the estuary from the mouth. The fish entered early afternoon and left a few hours later. This fish was recaptured by a recreational shore angler 508 days after being tagged, in the surf zone approximately 80 km west of the Sundays Estuary, outside of Algoa Bay.

6.4 Discussion

Research-based tagging and monitoring programmes within three MPAs allowed for the collection of trusted, accurate high resolution movement and dispersal data from three localities spanning the core distribution of white steenbras. In addition, the nationwide ORI project provided a high number of recaptures to support the findings of the three research-based programmes. Conventional dart tagging and recapture studies require a high number of fish to be tagged, in order that sufficient tagged fish are recaptured to detect persistent trends (Attwood and Cowley 2005). The widespread distribution of tagged and recaptured fish, the long-term nature of the tagging programmes, and the capture and tagging of 5 782 white steenbras, with 292 recaptures, allowed for a thorough assessment of white steenbras coastal movements. Despite differences in the numbers of fish tagged and recaptured, the different programmes yielded similar results. The overall recapture rate of 5.1% was similar to shore-angling recapture rates of tagging studies conducted on other coastal fish species in South Africa (e.g. Brouwer *et al*. 2003, Attwood and Cowley 2005).

The lower rate of recapture reporting and the greater (fishery) effort outside of protected areas, when compared to research angling within, have the potential to bias the proportions of recaptures made outside of protected areas negatively and positively, respectively. Attwood and Cowley (2005) accounted for this by incorporating a correction factor into the estimation of recapture rates for galjoen *Dichistius capensis* captured outside of the De Hoop and Tsitsikamma MPAs. However, in the current study, the close agreement in the recapture rates and frequency distributions of recapture distances obtained from the three research programmes with those in the ORI project, based outside of MPAs, suggested that application of a (subjective) correction factor was not necessary.

The recapture distances of fish tagged in each of the four studies were in close agreement, providing a high level of confidence in the results. The majority of recaptures in all four programmes were made within 5 km of the tagging location (most within 1 km), providing strong evidence of resident behaviour in all study areas. It would appear that the dominant behaviour in the coastal zone is residency, although a number of fish undertook large-scale coastal movements between tagging and recapture events. This agrees with the results obtained by Cowley (1999) in the Tsitsikamma MPA from 1995 to 1999.

The multiple detection events for the fish tagged with acoustic transmitters, combined with angler recaptures, provided considerably more data per individual than the recaptures of fish tagged with conventional dart tags, highlighting the value of acoustic telemetry to complement conventional

tagging programmes. The "time at liberty" between detections/recaptures ranged from four days to 508 days, at an average of 165 days (± 172). Furthermore, "recaptures" made by the acoustic receivers allowed the fish to continue moving after recapture, whereas most recaptures of dart tagged fish made by recreational anglers resulted in mortality, and the consequent prevention of any further data collection. This fact was evident in the telemetry results presented, with three of the detected fish having been detected/recaptured on more than one occasion, with multiple detections on each occasion. One fish (Fish 2028) was detected on four separate occasions, before being recaptured in the recreational shore fishery.

The array of passive acoustic receivers spanning Algoa Bay and the adjacent estuaries made it possible to collect movement data on the acoustically-tagged fish well beyond the study area in the proposed GAENP MPA, and based on the spatial scale of the estuarine and marine receiver arrays it was possible to assess coastal movements and residency on a scale of tens to hundreds of kilometres. Fish detected by the acoustic receivers appeared to exhibit a similar type of behaviour to the dart-tagged fish that were recaptured, with a proportion being detected within the bay up to almost a year after tagging, and some undertaking large-scale coastal movements out of the bay.

6.4.1 Conventional dart tagging

Resident behaviour and small-scale movements

Overall, the dominant behaviour was residency, with 61% of fish recaptured within 1 km of their respective tagging site. Times at liberty for fish remaining resident ranged from 0 to 1 293 days, providing evidence of long-term phylopatric behaviour. The fact that those individuals recaptured on multiple occasions were generally recaptured at the initial tagging site, or at a previous recapture location, further highlights the long-term nature of this residency. In the ORI project, recaptures made at the tagging locality occurred along most of the white steenbras core distribution, indicating that this behaviour is consistent throughout its range and not restricted to certain areas (Figure 6.7 a). This was confirmed by the similarly high levels of residency within each of the seven coastal regions, with low levels of dispersal between regions. The observed similarity in results suggests that the coastal region in which the fish are tagged has little effect on the movements of this species.

Residency is one of the most common behaviours in fishes (Attwood 2002) and is prevalent among other local sparids, for example 90% of adult carpenter *Argyrozona argyrozona* recaptures were made in the same location within the Tsitsikamma MPA (Brouwer *et al*. 2003), and 96 to 100% of the recaptures of blacktail *Diplodus sargus*, zebra *Diplodus cervinus hottentotus* and bronze bream

Pachymetopon aeneum were made within a short section of coastline within the Tsitsikamma MPA (Cowley *et al*. 2002). Red roman exhibited a high level of residency within the Goukamma and Tsitsikamma MPAs (Kerwath *et al*. 2007b), with at least 85% recaptured within 500 m of the tagging site in both areas. Similarly, juvenile white musselcracker *Sparodon durbanensis* showed a high level of residency within the De Hoop and Tsitsikamma MPAs with almost 100% of recaptures made within 1 km of the tagging sites (Watt-Pringle 2009). The ecological advantages of resident behaviour include familiarity with food resources and increased foraging efficiency, knowledge of locations of refugia, and immunity against local diseases (Eristhee and Oxenford 2001, Attwood 2002), which ultimately enhance the success of the population (Harden Jones 1968).

The results of the DE Hoop, Tsitsikamma and ORI tagging programmes were in close agreement, with at least 58% of fish in each study recaptured within 1 km of the respective tagging site. Only 4% of recaptures in the ORI programme were made between 1 and 5 km from the tagging site and none in the De Hoop or Tsitsikamma programmes in this range. Although it was not possible, nor intended, to estimate reliable home ranges for the recaptured white steenbras, the high proportion of recaptures made within 1 km on either side of the tagging location suggests that home ranges of most fish are unlikely to span more than about 2 km of coastline.

The proportions of recaptures made in the proposed GAENP MPA within 1 km and from > 1 km to 5 km were almost equal. The discrepancy among tagging programmes in the proportions of recaptures made within these categories is likely a consequence of the distribution of angling effort, the resolution of position recording and the distribution of habitat types within each study site. In the De Hoop MPA, all recaptures made within the tagging sites were allocated to the respective 1-km ORI coastal locality codes (either Koppie Alleen or Lekkerwater). Therefore, within-site movements (maximum 3 km) would have been recorded as 0 to 1 km displacements, and because angling within the MPA was restricted to the two tagging sites, separated by 11 km, it was not possible for recaptures to be made at distances between 1 and 11 km from either tagging site (except for 9 km east from Lekkerwater to Noetsie), which explains the lack of recaptures within this range in De Hoop MPA. In the ORI tagging programme, release and recapture positions are recorded at a similar resolution to the De Hoop MPA tagging programme; therefore, it is likely that in the event of a fish having been recaptured at a position along the coast for which there is no defined ORI locality code, that the nearest locality was allocated. This may mask short distance movements, between 1 and 5 km, underestimating the size of the 'home range' area used (Attwood and Cowley 2005). In the proposed GAENP MPA tagging programme, tagging effort is more widespread, and angling effort

may be exerted at any point along the approximately 30-km study area. Furthermore, tagging and recapture positions in this and the Tsitsikamma programmes were recorded with GPS accuracy, rather than simply allocating the recapture position to a coastal locality, as in the ORI tagging programme, allowing recaptures to be recorded accurately at any distance (within the study area) from the tagging locality.

Large-scale movements

Although the dominant behaviour appeared to be residency (0 to 1 km, 62%), there were some individuals in each tagging programme that were recaptured at considerable distance from their tagging sites. Overall, 11% of fish were recaptured more than 100 km from their tagging site providing evidence of large-scale migrations, up to 620 km, and mixing among coastal regions. In total, 15% moved more than 5 km west, and 19% more than 5 km east.

However, of the 13 recaptures made of fish tagged in the ORI project in the Eastern Cape Province, which did not remain resident, only one fish moved westwards, with the rest moving to a position further east along the coastline. Similarly, large-scale movements undertaken by adult white musselcracker were also predominantly in an eastward direction (Watt-Pringle 2009). Brouwer (2002) provided evidence of red steenbras *Petrus rupestris* undertaking easterly spawning migrations from the Agulhas Bank with the onset of sexual maturity, but suggested that these were one-way movements, and that return migrations were unlikely. Therefore, the predominantly eastward movements of the recaptured white steenbras may be consistent with the onset of migratory behaviour towards the spawning grounds in the Transkei (Bennett 1993b).

It is interesting to note that no recaptures of white steenbras, tagged in any study, were made west of Cape Point, and a handful of recaptures were made as far east as KwaZulu-Natal. The recaptures in KwaZulu-Natal are surprising, as this is outside of the species' core distribution (Lamberth and Mann 2000). However, the low number of recaptures within KwaZulu-Natal, despite the high recreational shore angling effort in this province (Brouwer *et al*. 1997), confirms the low abundance of white steenbras in this region. Although recreational shore angling effort along the west coast is considerably lower than that in KwaZulu-Natal (Brouwer *et al*. 1997), the lack of recaptures along the west coast suggests that there may be little ecological benefit for white steenbras to migrate to the west coast, or to return to the west coast after having migrated eastwards.

White steenbras are recorded along the west coast, although there are few estuaries within this region to support juvenile populations. Furthermore, water temperatures along the west coast are predominantly low (≤ 15°C) (Christensen 1980). Attwood and Cowley (2005) suggested that the infrequent occurrence of galjoen in the upwelling area between South Africa and Namibia is caused by the low survivorship of the eggs of this species at such low temperatures. This may also be true for white steenbras. Based on historical catches, it is also possible that the low numbers of white steenbras recorded along the west coast are an artefact of overfishing, rather than environmental conditions (SJ Lamberth, DAFF, pers. comm.).

The low frequency of occurrence of white steenbras along the west coast has been confirmed by a number of studies. The species was absent from two seine net studies of the fish community within the Langebaan Lagoon (Whitfield *et al*. 1989, Clark 2007). Bennett (1993a) reported declining white steenbras catches in the beach-seine fishery along the west coast between Cape Point and Cape Columbine from 1983 to 1991, and Hutchings *et al*. (1999) recorded zero white steenbras in experimental marine and estuarine gill-net catches along the west coast, between Cape Point and the Olifants River Mouth, from 1997 to 1999. White steenbras also did not feature in shore-angler catches along the west coast, in an extensive survey of the South African recreational shore fishery (Brouwer *et al*. 1997). However, environmental conditions along the west coast can result in sporadic recruitment and nodal fish distributions, which are often not reflected in such surveys, and white steenbras catches in the legal gill-net fisheries in estuaries such as the Berg are often underreported (SJ Lamberth, DAFF, pers. comm.). Therefore, it is possible that white steenbras are present in greater numbers along the west coast than these surveys suggest.

Effect of coastal region on fish size and level of dispersal

Size frequency distributions of fish tagged in the ORI project were similar among coastal regions throughout the white steenbras distribution, although the proportions of larger fish (> 600 mm FL) were greater in the Transkei catch. There was a trend of larger fish, on average, tagged along the West Coast and Transkei regions, with lower mean sizes tagged in regions in between. This supports the notion of adult aggregation areas in the south Western Cape and Transkei, but also reflects the greater abundance of nursery areas (estuaries and associated coastal zone) in between. However, the proportions of fish tagged within each region that were recaptured within the same region were similar (88 to 96% in all but the Transkei region), suggesting that the coastal region had little effect on resident behaviour. The lower proportion of fish that were tagged and recaptured within the Transkei region was as a result of the low sample size of fish tagged in this region (n = 3).

Effect of fish size (and age) on distance moved

The high level of residency in the surf zone of fish up to about 500 mm FL, and the considerably longer-distance movements of larger fish agreed with the findings of Bennett (1993b). This author suggested that white steenbras are resident in shoals, ranging within restricted sections of sandy and mixed sand and rock shoreline until sexual maturity is reached, after which they extend their range into deeper waters and begin to undertake large-scale migrations. This would explain the offshore movement of Fish 65069, tagged at 830 mm FL (± 10 years old), to Bird Island, and that of Fish 65062, tagged at 960 mm FL (± 14 years old) to an area off Cape Recife peninsula, to depths between approximately 12 and 25 m. Similar patterns were observed for two other local sparids. Red steenbras exhibit residency in shallower water (in this case < 50 m) as juveniles, and move into deeper areas (> 50 m) with the onset of sexual maturity (Smale 1988), and carpenter *Argyrozona argyrozona* exhibit an increase in depth as a function of fish size (Griffiths and Wilke 2002).

These results confirm the change in behaviour with the onset of sexual maturity, and that the behaviour of white steenbras in the coastal zone is largely determined by the size (or age) of the fish, with larger fish exhibiting a considerably greater scale of coastal movements than smaller individuals. Such ontogenetic shifts from residency to migratory behaviour have been documented in other coastal sparids in South Africa, such as red steenbras (Smale 1988, Brouwer 2002), and white musselcracker (Watt-Pringle 2009), and are generally indicative of adult spawning migrations. Bennett (1993b) proposed that adult white steenbras undertake annual spawning migrations, between a summer aggregation along the west and south west coasts and winter spawning grounds in the Transkei, along the east coast, but simultaneously cautioned that the results were speculative. The increased level of dispersal and the extent of coastal movements made by the larger fish recaptured in the dart tagging programmes presented in the current study support this notion.

Numerous South African linefish species adopt a life history approach that includes an annual migration up the east coast to spawn in the Transkei or KwaZulu-Natal (Hutchings *et al*. 2002a). Juvenile red steenbras are resident, while adults undertake spawning migrations to the Transkei area, with spawning taking place in late winter, although there is also evidence of a spawning stock off the south coast of South Africa (Smale 1988, Brouwer 2002). White musselcracker also exhibit residency as juveniles, and undertake spawning migrations up the east coast as adults (Watt-Pringle 2009). Shad *Pomatomus saltatrix* appear to migrate up the east coast to KwaZulu-Natal to spawn during spring, after which return migrations to coastal areas further south west are observed (van der Elst 1976), and adult geelbek *Atractoscion aequidens* migrate from western and southern Cape

waters to KwaZulu-Natal, following the annual *Sardinops sagax* "sardine run", where spawning also takes place in spring (Griffiths and Hecht 1995). The warmer waters of the Transkei and KwaZulu-Natal enhance the growth rates of the eggs and larvae, and the movement eastwards allows the eggs and larvae to drift south west along the coastline (Griffiths and Wilke 2002). This is particularly advantageous for estuarine-dependent species, such as white steenbras and leervis *Lichia amia*, as spawning further up the east coast allows recruitment into estuaries along the south east and south coasts, which are more dense than in areas further west (Bennett 1993b). This pattern of eastward migration up the South African east coast to spawn thus appears to be the most successful strategy in this environment, and the ecological advantage is indicated by the high number of South African linefish species exhibiting this life history style (Hutchings *et al*. 2002a).

Is there evidence for a spawning migration in white steenbras?

The results from the current study support Bennett's (1993b) migration theory to a certain degree, as the larger individuals showed a greater tendency to migrate, and undertook larger movements, on average. Also, a large proportion of recaptures was made east of the tagging site, with most of these fish roughly the size at which sexual maturity is attained. The mean distance moved by fish recaptured within each of the different coastal regions increased substantially from west to east, until a maximum in the Transkei, indicating that individuals recaptured in the Transkei had migrated considerable distances eastwards.

Based on Bennett's (1993b) proposed spawning migration, and considering that more than 1 500 white steenbras larger than 500 mm FL have been tagged along the coastline, if a large proportion of the adult stock was migrating annually between the summer and winter aggregation areas, it would be expected that the recapture information would confirm the connectivity between the south west coast summer aggregation area and the Transkei winter spawning grounds. However, despite 70 recaptures of fish of this size, widespread within the white steenbras core distribution, with time at liberty of up to 1 653 days, this was not the case.

Although the level of dispersal among regions was low, large-scale movements recorded in the different tagging programmes confirmed the connectivity among coastal regions for the larger fish. Long-distance movements of fish tagged in the De Hoop MPA provided evidence of connectivity between De Hoop MPA and False Bay to the west, and Plettenberg Bay to the east, spanning most of the Western Cape Province. Long-distance recaptures also confirmed connectivity between the Tsitsikamma MPA and the Transkei, spanning the entire coastline of the Eastern Cape Province.

However, evidence of connectivity between the Western and Eastern Cape provinces by means of long-distance movements, was restricted to just two individuals, both tagged in the De Hoop MPA. This is particularly evident in the recaptures made in the ORI programme, where no large-scale movements between these provinces were recorded, with movements appearing to represent two separate areas of movement (Figure 6.7 c). These results posed a number of questions.

1. Do all mature fish migrate to Transkei to spawn? The movements of an adult fish tagged with an acoustic transmitter (Fish 65062) provide some interesting insight. This fish was the largest of the 17 white steenbras acoustically tagged (960 mm FL), and substantially larger than the size at 50% sexual maturity. This fish was detected in Coega Harbour, 50 km west of the tagging site, ten days after tagging and then at Cape Recife, approximately 30 km from the Coega Harbour, four days later, where it remained resident for more than two months. This was surprising, as the period of residency within Algoa Bay spanned the period from late July to late October, coinciding with the spawning season (Bennett 1993b). While the possibility that the effects of the tagging process prevented this fish from migrating to spawn in the subsequent spawning season cannot be discounted entirely, the evidence suggests that not all mature fish aggregate in the Transkei during the spawning season. Watt-Pringle (2009) reported that not all adult white musselcracker migrate to spawn along the east coast, and that localised spawning was observed in other parts of its distribution range. Garratt (1988) advocated that pelagic spawning predatory linefish species in South Africa adopt one of three reproductive strategies; that in which the entire breeding stock migrates to the Transkei or KwaZulu-Natal to spawn (such as shad), that in which a portion of the breeding stock migrates while the rest remains in Eastern and Western Cape waters and spawns locally (such as yellowtail *Seriola lalandi* and blue hottentot *Pachymetopon aeneum*), and that in which the breeding adults do not migrate but spawn under favourable conditions (such as santer *Cheimerius nufar*). In light of this, the following question can be posed.

2. Does spawning take place in Algoa Bay, and/or elsewhere along the coastline? The sizes at which juvenile white steenbras recruit into estuaries along the South African coastline can be used to address this question. Early juvenile recruits tend to increase in size from east to west along the coastline, with recruits recorded from 20 to 30 mm TL in the Sundays Estuary on the south east coast (Beckley 1984), up to 40 mm TL in the Knysna Estuary on the south coast (Whitfield and Kok 1992), and 18 to 50 mm TL in the Kleinmond Estuary on the south west coast (Bennett 1989). The period of peak recruitment is also later annually in estuaries further west, with recruitment peaking in August and September along the south east coast (Beckley 1984), September and October along the south

coast (Whitfield and Kok 1992), and October to November along the south west coast (Bennett 1989). The results suggest that white steenbras recruits within each cohort are spawned over the same period, in the same area, supporting the notion of a single spawning region (Transkei) and season (July to October). Based on this result, another question can be posed.

3. Do all mature fish spawn every year? Commercial beach-seine catches made in False Bay, in the Western Cape Province, from 1991 to 1992, indicated a strong seasonal occurrence of adult white steenbras, with low numbers caught in winter, supporting the proposed migration away from the Western Cape Province in the winter months (Bennett 1993b). The monthly proportions of adults captured and tagged in the ORI project provided further support. However, adult white steenbras are not completely absent from the Western Cape Province in winter, and histological examination showed that the gonads of those adults that were captured had minimal development or had been reabsorbed (Lamberth *et al*. 1995). This result provides evidence that not all white steenbras capable of maturing spawn (or migrate) every year.

The low number of individuals having moved between the Western Cape and Eastern Cape provinces, and the evidence indicating that not all white steenbras migrate to the Transkei or spawn every year, suggest that further assessment of the connectivity of coastal populations is required.

Individual variability

There was considerable individual variability in the distances travelled by fish of the larger size classes, with some (up to 840 mm FL) showing zero displacement. This may be partly caused by the adult white steenbras that remain in False Bay during the winter months (Lamberth *et al*. 1995). Intra-specific variability in behaviour is common among fishes (Dingle 1996) and may be caused by numerous factors, such as social factors, genetic variability or environmental conditions (Attwood 2002). Sex-specific movement patterns have been reported in fishes (e.g. Barrett 1995), although it is not possible to sex white steenbras macroscopically, and considering the congruence in growth rates and size at 50% sexual maturity between the two sexes (Bennett 1993a), and that they are broadcast spawners it is unlikely that sex would have affected the observed movement patterns.

Secondly, this may reflect the high variability in the size or age at which white steenbras mature, with a wide maturation window from 490 mm to 900 mm TL (approximately 450 to 820 mm FL) (Bennett 1993b), or about five to eight years (Attwood and Bennett 1995a); although, this does not explain the large acoustically-tagged adult fish remaining within Algoa Bay over the spawning period.

Thirdly, this may be indicative of behavioural polymorphism, with some fish undertaking large-scale migrations and others exhibiting resident behaviour. Such behaviour has been observed in other coastal fishes in South Africa, such as red steenbras, red stumpnose *Chrysoblephus gibbiceps*, santer (Griffiths and Wilke 2002) and dusky kob (Griffiths and Attwood 2005). Similar results were also observed in other areas; for example, painted comber *Serranus scriba* in Palma Bay Marine Reserve, Mallorca Island, Medirranean Sea (March *et al*. 2010), and barred sand bass *Paralabrax nebulifer* in Catalina Marine Life Reserve, Santa Catalina Island, California (Mason and Lowe 2010). Griffiths and Wilke (2002) provide a summary of a wide range of species from different families exhibiting such a split, with different proportions of zero-displacement and longer-distance recaptures. These authors ascribe such a pattern to one of two possibilities: either behavioural or genetic polymorphism within the population or occupation of home ranges by individual fish, with all or most fish undertaking small-scale exploratory movements. Similarly, Attwood and Cowley (2005) present two possible movement behaviour models for galjoen; polymorphism and a "tourist" model, under which an individual fish may exhibit residency at one of a few home ranges and nomadic movements among these, at different times, dictated by environmental conditions. The similarity in results obtained in tagging studies at different localities discounts the possibility of behavioural polymorphisms. Genetic analyses presented in the following chapter suggest that genetic polymorphism is unlikely, although this was not specifically addressed.

The fact that certain individuals recaptured on multiple occasions showed variable movement patterns in subsequent intervals at liberty (i.e. one recapture of zero displacement and one of a significant movement), suggests that individual sub-adult white steenbras are resident in the coastal zone within a familiar home range, with most or all individuals undertaking infrequent small- to medium-scale movements outside of this home range (which may appear as multiple behavioural traits), with the low proportion of "non-residents" reflecting the low frequency and consequently low probability of capturing or recapturing a fish while undertaking a coastal movement outside of its home range. Such behaviour would allow individuals to remain resident until sexually mature, therefore reaching a suitable size to withstand the stresses of undertaking large migrations (Hutchings *et al*. 2002a). It is also possible that larger individuals undertake regular longshore movements, but that these movements are further offshore, where the fish are not accessible to capture in the shore fishery, consequently resulting in lower recapture rates, and greater variability in distances of recorded movements.

Finally, the most simple explanation is that adult fish may exhibit fidelity to a home range area, albeit on as broad a scale as a particular coastal embayment, to which they return (i.e. homing behaviour) after migrating to spawn. Homing to certain areas after spawning is well-documented in fishes (e.g. Carlson and Haight 1972, Spedicato *et al*. 2005), and is not discounted in this case.

Effect of habitat and fish density on dispersal

The affinity of white steenbras for sandy substrate and the predominance of rocky shoreline and non-contiguous patches of sandy substrate in the Tsitsikamma MPA have forced the white steenbras into small areas, in which they show a high level of residency for extended periods. This was reflected in the vast majority of fish in this MPA that were recaptured within 1 km of the tagging site. In contrast, the proposed GAENP MPA study area is characterised by a large expanse of contiguous sandy shoreline, with some patches of mixed sand and rock. Here, white steenbras are not restricted to small areas, allowing increased home range size and small-scale displacements, and decreased likelihood of being recaptured at the tagging locality. As a result, the proportions of white steenbras recaptured in the proposed GAENP MPA programme up to 1 km and those recaptured from 1 to 5 km were similar. Therefore, habitat has affected the results observed in these two MPAs, and is likely to play a major role in the distribution and behaviour of this species. The effect of habitat on the frequency of short-distance (< 5 km) movements suggests a level of behavioural plasticity (Attwood 2002).

The Ideal Free Distribution theory (Fretwell and Lucas 1970) suggests animals will adjust their distribution according to the availability of and competition for food resources in a way that allows equitable 'fitness' for all individuals. Krebs *et al*. (1973) suggested that populations may exhibit higher levels of residency when density and thus competition are low, but that aggressive behaviour and migration may increase under high density conditions. Two main goals of MPA establishment are to increase fish density within the MPA and increase density of fishes in adjacent areas through density-dependent spill-over (Sale *et al*. 2005). Based on this, it is expected that (at least for some species) local density would influence the proportion of individuals that remain resident and the level of dispersal (Kramer and Chapman 1999). Such an effect may manifest as a higher proportion of individuals recaptured away from the tagging site, in areas of higher density (Attwood and Cowley 2005). Two questions may be asked to determine whether density-dependence is at play.

Firstly, did higher density result in higher mean displacement of recaptured fish? Results from the De Hoop, Tsitsikamma and proposed GAENP MPAs suggested not. Despite substantially higher CPUE in

the GAENP MPA, than in either the De Hoop or Tsitsikamma MPAs, the mean distances moved in each study were similar, and each was characterised by high variability. This suggests that present density has not had an observable effect on the level of dispersal in these three MPAs. Furthermore, the similarity in observed movements between the MPA-based research projects and the ORI project based in open access areas suggests that dispersal rates in these MPAs are similar to those in open areas.

Secondly, did higher densities result in higher frequencies of small-scale movements? The proportions of recaptures made within 5 km of the tagging sites in each of the three MPAs were similar. However, differences were observed in the proportions of fish having moved 0 to 1 km and 1 to 5 km among the three MPAs, suggesting that higher densities in the proposed GAENP MPA may have increased the tendency of white steenbras to undertake small-scale movements away from their home range. As white steenbras tend to shoal in the inshore environment, higher densities may result in localised prey resource depletion, and the consequent need to forage over greater areas. Similarly, the lower proportion of recaptures made from 5 to 10 km in the ORI project, than in the three MPA-based projects, suggests that higher densities within the MPAs may be driving movements in the order of 5 to 10 km, although these may be confounded by higher mean sizes (and thus greater tendency to migrate) of fish recaptured in the De Hoop (519 ± 168 mm FL) and proposed GAENP (471 ± 102 mm FL) MPAs, than those that were tagged in the ORI project (437 ± 141 mm FL). It is also likely that the differences between the proposed GAENP MPA and the De Hoop MPA and ORI project, in terms of the proportions of small-scale movements, result from the lower resolution of position-recording in the latter two programmes (Attwood and Cowley 2005).

Based on these results, there is little evidence that density is driving dispersal of white steenbras, although higher densities may influence the level of short-distance movements. Is this mechanism likely to result in spill-over of white steenbras from MPAs into adjacent fishery areas? This is unlikely, based on the scale of these movements. A similar conclusion was drawn for galjoen, suggesting that MPAs will provide little improvement to the catches of either species in adjacent fished areas (Attwood and Cowley 2005), at least not at the current densities in MPAs.

Effect of time at liberty on distance moved

Attwood and Cowley (2005) predicted that when movement patterns in a species conform to a diffusion-type process, it can be expected that the proportion of recaptures made at the tagging site would decrease over time. Under this model, it is expected that the distance between tagging and

recapture localities would be related to time at liberty. However, in the De Hoop, Tsitsikamma and GAENP tagging programmes, this was not the case, with zero-displacement recaptures made up to 1 293 days at liberty, and the maximum distance moved (620 km), recorded for two fish after just 87 and 208 days at liberty. However, distances moved were positively and significantly correlated with time at liberty, for all fish recaptured. This correlation was weak (R^2 = 0.0886), and may be explained by three factors. Firstly, the frequency distribution of times at liberty was skewed towards shorter durations, as the number of recaptures decreased with increasing time at liberty (as in most tagging studies). This, combined with the high proportion of zero-displacement recaptures, would have skewed the correlation towards high numbers of recaptures with zero displacement and low times at liberty. Secondly, the majority of recaptured fish were juveniles and sub-adults, which exhibited higher levels of residency than adults. Thirdly, the greater the time at liberty, the more the fish would have grown, and thus the greater the likelihood of a fish reaching the size at which migratory behaviour begins, with recapture distance dependent on the size of fish at recapture, rather than time at liberty. Thus, it can be concluded that the observed pattern of movement in white steenbras does not conform to a diffusion process (Griffiths and Wilke 2002), and is driven by the size or age of the fish, and the onset of sexual maturity (Bennett 1993b), rather than the time at liberty. Interestingly, the mean times at liberty appeared to be lower for fish tagged in the Mossel Bay and KwaZulu-Natal regions, and may reflect the level of shore fishing effort (Brouwer *et al*. 1997), and thus vulnerability to capture within these regions. Furthermore, the mean time at liberty for fish > 600 mm FL at the time of tagging was 275 days (± 302 d), with 70% of recaptures made within one year of tagging, suggesting that white steenbras are highly vulnerable to capture soon after reaching maturity.

Effect of seasonality on recapture location

The four seasons relate closely to the spawning period of white steenbras, with a perceived migration occurring in the late autumn and early winter months (May to June), with spawning believed to take place in the Transkei in the winter months (July and August) (Bennett 1993b). Catch data suggest a return migration to the south west coast during spring, where they aggregate, probably for feeding (Penney 1991), over the summer months (Bennett 1993b). Therefore, peak periods of recaptures in each location were assessed to determine whether these agreed with expected peaks in different areas associated with the migration.

Monthly proportions of recaptures made in the different regions of coastline, as defined for this chapter (Figure 6.2), showed no obvious seasonality. However it was possible to tease the trends

from the data in the different regions. Based on Bennett's (1993b) proposed spawning migration, increased proportions of recaptures were expected along the south west coast in the austral summer months, along the Transkei coast in winter and bimodal peaks between these two regions in autumn and spring.

The broad peak in recaptures in the Cape Agulhas region from September to December is consistent with a post-spawning summer aggregation in this region. Peaks in the proportions of recaptures from April to June in the Mossel Bay and Tsitsikamma regions reflect the eastward migration from the south west coast towards the Transkei in the late autumn and early winter months. The almost complete lack of recaptures in the Transkei provides little credibility to any conclusion drawn for this area, although the three recaptures in this area were made from April to August. It is possible that white steenbras may not feed during the spawning aggregation, in which case the number of recaptures would be expected to be low. In the Algoa Bay region, to the west of the Transkei, there was a notable peak over the period October to December, which may be indicative of the return migration in this region in spring to summer. The fact that there was no increase in the proportions of recaptures in autumn or winter, to indicate increased activity in this region at that time of year, suggests that the eastward migration may be further offshore than the westward return migration. The Tsitsikamma and Mossel Bay regions also exhibited peaks from October to December, and in December, respectively, which coincide with the return migration over spring, into summer.

The monthly proportions of fish that were recaptured either further west or further east of their tagging sites within three months of tagging, also followed this trend, with decreasing westward movements and high proportions of eastward movements from March to June, which is consistent with the autumn/winter migration towards the Transkei coast. The greater proportions of westward movements from August to November reflect the return migration to the south west coast.

Overall, the analysis of seasonality provided support for the spawning migration proposed by Bennett (1993b). However, the number of recaptures is highly dependent an angling effort, which is likely to vary considerably, both seasonally and spatially. Furthermore, the number of recaptures of fish greater than the size at which 50% sexual maturity is attained was low. Therefore, an improved understanding of seasonal patterns in movement will require a greater number of recaptures, particularly in the Transkei region, and of adult fish, or an alternative method will be necessary, such as long-term passive acoustic telemetry.

6.4.2 Acoustic telemetry

The movement of Fish 2024, from the tagging site at Woody Cape (in the proposed GAENP MPA) to Coega Harbour, represents a moderate movement (± 30 km) made over a relatively long period (282 days). The movement of this fish (459 mm FL at tagging) at this spatial scale agrees with the conventional tagging results for sub-adult white steenbras (450 – 600 mm FL), and is possibly representative of nomadic movements at this size class, and a degree of residency within Algoa Bay.

The apparent resident behaviour from October 2010 to April 2011 of the larger Fish 65069, measuring 830 mm FL at tagging and thus expected to participate in spawning migrations, may be further evidence of residency within Algoa Bay. This fish may have returned from a 2010 spawning migration, and remained resident between tagging and the offshore detection, prior to the 2011 migration. It is also possible that this individual did not undertake a spawning migration, but remained resident until detection approximately 13 km away at Bird Island, with the offshore movement to Bird Island representing the offshore movement associated with the onset of sexual maturity (Bennett 1993b, Attwood and Bennett 1995a).

Fish 65062 was detected in Coega Harbour and then at Cape Recife, just 14 days after tagging, having travelled at least 80 km, after which it remained resident within Algoa Bay over the spawning season. During this period, the fish exhibited a distinct diel behavioural pattern, reflecting that of the juveniles in estuaries (see Chapter 4), and that of adults in the nearshore zone in False Bay (SJ Lamberth, DAFF, pers. comm.). The fish followed a regular pattern of movement, coinciding with two nearby receivers (± 6 km apart). The Cape Recife receiver (Figure 6.22) was positioned at a depth of approximately 20 m, in an area of sandy substrate, while the additional receiver was positioned at a depth of approximately 12 m, in a sand patch amongst shallow reef, in an area known to have a high density of ragged tooth sharks *Carcharias taurus* (Smale 2002). This area has also been shown to exhibit high densities of sand prawn *Callianassa kraussi* and *C. gilchristi* at depths between about 6 m and 13 m (Cockroft and Tomalin 1987), which forms an important part of the diet of marine white steenbras > 400 mm TL (Bennett 1993b). It is, therefore, proposed that the diel pattern was related to feeding in the shallow sandy area among the reef during the day, where the food resource was more dense, and moving away from this sand/reef area at night to avoid predation.

The movement of Fish 2020 to East London, representing approximately 180 km, provides evidence of larger-scale movements at this life stage. This movement was greater than the mean movement (26 km) of conventionally dart-tagged fish between 400 and 500 mm FL, given the size of the fish at

the time of tagging (455 mm FL). This fish covered the 180 km in no more than 31 days, indicative of a directed movement. However, the fish was considerably smaller than the size at 50% sexual maturity (600 mm FL), suggesting that this movement was not related to a spawning migration.

In contrast, the movement of Fish 2032 from the tagging site at Woody Cape to the Sundays Estuary, and subsequently to Maitlands Beach to the west of Algoa Bay was likely associated with the onset of sexual maturity. This fish was tagged at 554 mm FL, and finally recaptured at a point approximately 80 km west, 621 days after being tagged. While the fish was not measured at the time of recapture, it had almost certainly reached sexual maturity during its 20 months at liberty. Similarly, the movements of Fish 2028, from Woody Cape to the Sundays Estuary and then Coega Harbour (± 50 km) made over almost a year (346 days), suggested residency within the bay, and nomadic small- to medium-scale movements (in the order of tens of kilometres). This fish had most likely reached maturity by the time it was detected in the Gamtoos Estuary, having been tagged 857 days earlier, at 527 mm FL. Therefore, this fish represented movements on a scale consistent with sub-adult white steenbras (450 – 600 mm FL) that were tagged with conventional dart tags, and larger-scale movements consistent with those of conventionally-tagged adults (> 600 mm FL).

It is possible that the movement of Fish 2022, detected 100 km east of the tagging site, in the Great Fish Estuary, was also related to the onset of sexual maturity. This fish was tagged at 512 mm FL and detected in the Great Fish Estuary 178 days later. Therefore, this fish may also have reached sexual maturity during this period at liberty, with the fish migrating east in June, in time for the July/August spawning season (Bennett 1993b).

The movements of individuals from the Woody Cape area in the proposed GAENP MPA into the Sundays Estuary and Coega Harbour, without detections on the inshore receivers, suggest that these movements were made close inshore (surf zone) along the coastline, outside of the detection ranges of the receivers moored at depths between 20 and 30m in the nearshore zone. Bennett (1993b) suggested that white steenbras (roughly 130 – 550 mm FL) in False Bay were confined almost entirely to the surf zone, while a comprehensive inshore small-mesh trawl survey conducted along the South African south and south east coasts produced no white steenbras of this size range deeper than 10 m (Wallace *et al*. 1984b). Unfortunately, due to the highly dynamic substrate and poor receiver detection range in the surf zone, caused by the strong wave action, it was not possible to position a receiver closer inshore.

Three of the seven fish detected after tagging were, at some point, detected on receivers positioned within an estuary. Similarly, three individuals were detected on the receiver within the Coega Harbour. Although these estuarine and harbour visits (n = 9) were recorded for multiple individuals, all were for short periods. Eight of these movements comprised no more than a single overnight stay, with one visit constituting four days. While this provides evidence that sub-adult and adult white steenbras do make use of estuaries, and other sheltered environments, it appears that after having left their estuarine nursery habitats, late juvenile, sub-adult and adult white steenbras lose their dependence on estuarine environments. Cowley *et al*. (2008) and Hindell *et al*. (2008) suggested that directed movements of estuarine-associated fishes from the marine environment back into estuarine/riverine areas typically with reduced salinities may be an attempt to rid themselves of marine parasites. The movement of Fish 2028 into the Sundays Estuary, as far as 12 km from the mouth, may also have been for the purpose of removing parasites. Anecdotal evidence also suggests that white steenbras enter estuaries as adults during periods of extreme cold sea conditions. Although the low number of such detections precluded any statistical investigation, environmental factors (including wind speed and direction, swell size, the presence of coastal trapped waves, water temperature and rainfall) were assessed for anomalous oceanographic or environmental conditions, which may have effected these movements into estuaries. However, there were no such anomalies associated with these dates (WS Goschen, South African Environmental Observation Network, pers. comm.). Considerably greater numbers of detections will be required before such questions can be answered.

While the general behaviour reflected in the telemetry results was long-term residency within the bay, with some larger scale movements, the possibility cannot be excluded that tagged fish moved beyond the boundaries of the receiver array, without detection. Evidence for this was provided by Fish 2020 recaptured by a recreational shore angler in East London, 180 km away, without detection on a receiver. It is also possible that other individuals entered estuaries outside of the range of estuaries monitored in the current study, or were recaptured by recreational anglers, but were not reported. The latter is unlikely, as all transmitters were marked with contact details and the word “Reward”.

The fact that most fish were last detected well before the end of the expected battery life of the transmitter may be a result of most fish having left the bay. Considering that the smallest fish was 401 mm FL at the time of tagging (approximately four years old), by the end of the expected battery

lives of the smaller transmitters (781 days) it is likely that most individuals had reached sexual maturity (approximately 6 years), and could have begun undertaking spawning migrations.

6.4.3 Practical considerations

The agreement in results between the conventional tagging and acoustic telemetry studies highlights the value of employing these two techniques in conjunction. The high proportion of individuals detected on multiple occasions in Algoa Bay confirms the suitability of acoustic telemetry for assessing coastal residency and movements. The fact that recapture rates of white steenbras in the different studies, and overall, were consistent with those from other species of coastal fishes, suggests that conventional dart tagging is a suitable method for assessing the movement patterns of this species.

Tagging programmes involving recreational anglers may draw criticism, due to the potential for poor reporting rates, poor handling and tagging of captured fish, and potentially higher mortality rates. There is currently a high level of under-reporting of recaptures outside of MPAs, of fish tagged as part of the research programmes within MPAs (Lamberth 1996, Attwood and Cowley 2005). This could be evaluated through a study comparing current reporting rates to those reported for tags offering a reward. However, the under-reporting of illegally-recaptured fish within MPAs may be similarly high. Furthermore, the consistency of recapture rates among the De Hoop, GAENP and ORI tagging programmes, and the remarkable consistency in the frequency distributions of recapture distances among studies, suggests that the under-reporting of white steenbras recaptures is insufficient to grossly affect the results. Furthermore, the close agreement of results suggests that the handling of tagged fishes in the ORI tagging programme, by recreational anglers, does not induce a greater mortality rate than in the other two studies. It may also be argued that the distribution of recaptures is dependent on the distribution of effort within the recreational fishery (Griffiths and Wilke 2002). However, the widespread recaptures made throughout the area between Cape Point and the Transkei suggests that this is not the case. The lack of recaptures along the west coast (within the species' distribution) is more likely an artefact of low CPUE in this region (Sauer and Erasmus 1996). What does appear to be a problem, with recaptures made by recreational anglers, is the inaccurate recording of the lengths of fish at the time of recapture. This problem is exacerbated by the fact that many recaptures are made by recreational anglers who are not participants in the tagging programme, and thus, are not aware of what information to record in the event of recapturing a fish, or how to record it accurately.

6.5 Conclusions

The overall aim of this chapter was to describe the coastal movements of white steenbras, using all available conventional tagging data and a dedicated acoustic telemetry study. There was a strong size effect, with juveniles remaining resident in small areas, sub-adults undertaking small-scale coastal movements and most adult fish undertaking large migrations. Residency and small-scale movements suggest that at the juvenile and sub-adult life stages, white steenbras is vulnerable to localised depletion, but simultaneously could be successfully protected by means of MPAs. This should be considered in the management of the species to ensure that sufficient area of suitable habitat for the species is protected. The results highlight the importance of incorporating spatial data into stock status assessments for the management of coastal linefish species (Attwood 2002).

The majority of recaptured fish were juvenile or sub-adult fish, and considering their higher level of residency, would have skewed the overall level of residency. The nature of the habitat (i.e. contiguous sand or sandy patches interspersed among rock), as well as seasonality, influenced the scale of movements, in terms of small-scale movements (≤ 5 km displacements) and direction, respectively. White steenbras density and time at liberty had little influence on the level of dispersal.

Despite the information gained through the conventional tagging and acoustic telemetry studies, there is still a lack of empirical evidence of movement of white steenbras between their aggregation area in False Bay, and the spawning area along the Transkei coast, as advocated by Bennett (1993b). This lack of empirical evidence of movement between these two areas poses the questions of what the scale of coastal migrations might be and what the spatial scale of regional population-level mixing may be, suggesting that further assessments of movement and stock structure are required.

A long-term assessment of white steenbras coastal movements and migrations will be conducted at the national level, as part of the Ocean Tracking Network (OTN) programme. This is an international programme, focussing on large-scale marine animal migrations. In South Africa, large-scale movements will be assessed through an extensive array of acoustic receivers positioned at ecologically important points along the South African coastline. This programme has been initiated, and a number of fishes have already been equipped with acoustic transmitters. The possibility of stock segregation as a result of this apparent lack of regional connectivity is best addressed at the molecular level. The stock structure of the species and the level of population mixing are addressed in the following chapter, using genetic analyses.

Chapter 7

Genetic stock structure

7.1 Introduction

Understanding movement is central to understanding a species' ecology (Meyer *et al*. 2000). However, for many coastal fishery species, movement is not well understood. The results of the previous four chapters have provided important information on the movements of white steenbras in its juvenile, sub-adult and adult life stages, as well as some of the factors that influence its movement. However, despite the conventional tagging and recapture of a high number of white steenbras, some of which moved considerable distances between capture and recapture locations, there is still no empirical evidence of individuals moving between their summer aggregation area in False Bay, and their winter spawning grounds along the Transkei coast, representing their perceived spawning migration. Furthermore, movement studies cannot provide information on the consequences of dispersal at the molecular level (Waples 1998). A suitable approach to assessing movements and connectivity at this level is through the study of population genetics, which can provide valuable information on spatial delineation of genetic stock structure (von der Heyden 2009), and concomitantly on the magnitude and spatial extent of gene flow and connectivity among populations or geographic localities (Waples 1998).

Information on genetic stock structure is a pivotal component in the understanding of a species' ecology and essential for its effective management (Balloux and Lugon-Moulin 2002). However, such information is lacking for numerous important fishery species, in South Africa and elsewhere, including for white steenbras. Informing management decisions for a species such as white steenbras requires a robust understanding of genetic structure and stock delineation, to ensure that each distinct stock or population is suitably managed (Teske *et al*. 2010).

Before being able to identify the stock structure of a species, we need to understand what a genetic 'stock' represents. Numerous definitions have been used, such as "groups of fish of one species that interbreed and hence share a common gene pool" (Milton and Shaklee 1987: 728), or "a group of organisms whose demographic/genetic trajectory is largely independent from other such groups" (Waples 1998: 438). Ovenden (1990) and Begg and Waldman (1999) assert that stock delineation should consider the geographic limits of a group of fish, and characteristics such as self-recruitment,

interbreeding and similarity in life history characteristics. For the purposes of the current study, the term stock refers to non-interbreeding, geographically-distinct populations of the same species.

Adopting a phylogeographic approach can provide insight into whether a species exists as a single stock, or as multiple genetic stocks – a factor that has serious implications for management. Disregarding stock structure can lead to ineffective fisheries management and loss of genetic diversity (Smith *et al*. 1991, Begg and Waldman 1999). Genetic data can also provide baseline measures of historical intraspecific biodiversity against which the effects of exploitation can be measured. This can, in turn, inform management decisions. Understanding population structure and connectivity is also essential for predicting responses to environmental disturbances and the potential effects of climate change on population structure and species distribution (Nicastro *et al*. 2008, Zardi *et al*. 2011), which can lead to more effective management (Waples 1998). By linking life history patterns with oceanographic processes, it is also possible to identify the environmental factors that influence the level of connectivity among geographic regions and their effects on the resultant population structure (Teske *et al*. 2011).

7.1.1 Gene flow and genetic diversity

Within the marine environment, it has traditionally been assumed that there is a relative lack of geographic barriers to migration and dispersal (Billington 2003), when compared to freshwater and terrestrial environments. In addition, life history characteristics that are common among marine species, such as high rates of dispersal during long pelagic egg and larval phases and adult migration, are expected to maintain low levels of intra-specific genetic differentiation (Grant and Bowen 1998). Therefore, marine species have typically been expected to show high levels of gene flow and low genetic differentiation (Waples 1998).

In the South African marine context, population genetics studies have been conducted on a range of organisms. Teske *et al*. (2010) assessed the level of genetic differentiation in red roman *Chrysoblephus laticeps* (Sparidae), and found that despite its sedentary reef-dwelling behaviour, it exists as a single well-mixed stock, exhibiting genetic homogeneity along the eastern and southern coasts. Similar results were found for another sparid, Cape stumpnose *Rhabdosargus holubi*, with a well-mixed population spanning a similar area (Oosthuizen 2006). Spotted grunter *Pomadasys commersonnii* (Haemulidae) was also found to exist as a single well-mixed population (Klopper 2005). A similar, but possibly unexpected, result was observed for a small, rock pool-associated gobiid, *Caffrogobius caffer*. The adults of this species appear to move only on small scales, yet this

species was found to exhibit genetic homogeneity throughout its range from False Bay to east of East London (Neethling *et al*. 2008). This low level of genetic differentiation has also been identified in some marine invertebrates. The squid *Loligo reynaudii* was shown to exhibit genetic homogeneity along the South African south and east coasts, despite distinct spawning aggregations (Shaw *et al*. 2010). The south coast lobster *Palinurus gilchristi* was also observed to exhibit a high level of gene flow and low spatial genetic differentiation (Tolley *et al*. 2005), as was the South African abalone *Haliotis midae* (Evans *et al*. 2004). Therefore, there are numerous marine species along the South African coast that conform to this expected high level of gene flow.

The suggested spawning migration of white steenbras (Bennett 1993b), the dispersal capabilities of the adults documented in the previous chapter and by earlier studies, the exhibition of broadcast spawning and the dispersal of eggs and larvae by means of coastal oceanographic features (Hutchings *et al*. 2002a) suggest that white steenbras should exhibit similarly low levels of spatial genetic differentiation. Therefore, it was expected that analyses of the genetic structure within white steenbras would provide evidence of a single, well-mixed population.

Marine species, however, do not always exhibit large, genetically homogenous populations (Hauser and Carvalho 2008), and examples exist of species exhibiting strong genetic differentiation along the South African coastline. The brown mussel *Perna perna* exhibits two geographically separated and genetically distinct lineages (Zardi *et al*. 2011). The estuarine mud prawn *Upogebia africana* was shown to exist in two genetically distinct, yet slightly geographically overlapping lineages, despite a marine larval phase, during which it may be expected to disperse relatively great distances (Teske *et al*. 2006). The caridean shrimp *Palaemon peringueyi* is characterised by active and passive dispersal capabilities; yet this species was found to exist in three distinguishable genetic clades, coinciding with the biogeographical provinces (Teske *et al*. 2007). Similarly, morphometric comparisons, catch data, tagging studies, spatial variability in growth rates and reproductive biology, and the presence of multiple nursery and spawning grounds showed that silver kob *Argyrosomus inodorus*, is present in a number of discrete stocks along the South African coastline (Griffiths 1997b), although this has not been substantiated by genetic analysis. These results show that there is substantial variability among taxa in terms of their levels of gene flow and population mixing.

This is particularly evident in the case of two closely related hake species *Merluccius capensis* and *M. paradoxus*. These two species occupy partly overlapping distributions along the South African and Namibian coastlines; however, *M. capensis* exhibited genetic homogeneity while *M. paradoxus*

showed significant spatial genetic differentiation based on mitochondrial DNA (mtDNA) sequence data (von der Heyden *et al*. 2007). The highly variable results observed among taxa and closely related species within the South African marine environment highlight the fact that spatial genetic structure cannot simply be inferred from closely related species, or from predictions based on biology or life history, and must be assessed on a species by species basis (Teske *et al*. 2010).

7.1.2 Aim and objectives

The aim of this chapter was to assess the genetic stock structure of white steenbras, to determine whether the species exists as a single stock or multiple stocks. Specific objectives were to:

i. Identify the level and distribution of genetic diversity of white steenbras along the South African coastline;
ii. Test the null hypothesis that white steenbras exists as a single intermixing stock;
iii. Determine the level of genetic differentiation among stocks, and identify the barriers to gene flow, if multiple stocks are identified;
iv. Determine whether genetic divergence is related to geographic distance among sampling localities, by testing the null hypothesis that there is no significant relationship between genetic difference and geographic distance; and
v. Provide information on genetic diversity of juveniles and adults, and of the two life stages combined, and test the null hypothesis that there is no significant genetic differentiation between juvenile and adult white steenbras.

Numerous authors have advocated the use of multiple genetic markers, to elucidate more clearly the genetic polymorphism within a species (Aris-Brosou and Excoffier 1996, Waples 1998, Gompert *et al*. 2006), as different gene regions exhibit independent evolutionary histories (Kaouèche *et al*. 2011). This chapter thus incorporated both mitochondrial DNA (mtDNA) sequencing and genotyping of microsatellite repeat loci in the nuclear genome to provide the information necessary to answer the key questions.

The mitochondrial genome is a circular molecule, comprising between 14 000 and 26 000 nucleotide base pairs in different fish taxa, and is made up of a number of different gene regions. Within the mitochondrial genome, the non-protein coding control region shows considerable variation among individuals among and within populations, and exhibits a relatively high mutation rate (Billington 2003). These characteristics make the control region a particularly useful region for population

genetics studies, resulting in its widespread use in studies of marine fishes (e.g. von der Heyden *et al*. 2007, Liu *et al*. 2010), including multiple studies on sparid species (e.g. Bargelloni *et al*. 2005, Domingues *et al*. 2007, Teske *et al*. 2010). For these reasons, the control region was chosen for the current study, to infer population structure and demographic history of white steenbras.

Microsatellite loci are sections of the nuclear genome, containing multiple repeat motifs of short nucleotide sequences. These repeat motifs may be di-, tri-, tetra-, penta- or hexanucleotide sequence repeats. Each of these segments containing multiple repeats constitutes a single locus, with variable numbers of repeats at a given locus representing different alleles (Goldstein and Pollock 1997). Nuclear DNA is diploid, and a locus may be homozygous (i.e. having inherited the same allele from both parents), or heterozygous (i.e. having inherited different alleles from each parent). Polymorphic loci (i.e. those represented by multiple alleles) provide a means for comparing genetic differentiation among individuals and populations. Multiple polymorphic loci may be identified within a single species (Bhargava and Fuentes 2010), allowing a more robust assessment of genetic differentiation. Microsatellites have been widely used for population genetics studies on marine fishes, and have been used to assess genetic differentiation in numerous sparid species, for example gilthead sea bream *Sparus auratus* (De Innocentiis *et al*. 2004) and striped sea bream *Lithognathus mormyrus* (Sala-Bozano *et al*. 2009).

The merits of assessing both mtDNA and microsatellite variation in conjunction are discussed in Chapter 2. Complementary employment of these two genetic markers can provide an understanding of both historical population demography and contemporary population structure (Lemaire *et al*. 2005, Perez-Ruzafa *et al*. 2006).

7.2 Methods and materials

7.2.1 Sample collection

Genetic samples were collected from eight discrete sites along the South African coastline, representing the white steenbras core distribution (Figure 7.1). Attempts were made to collect at least 25 juveniles (< 350 mm FL) and 25 adults (> 600 mm FL) from each locality, although this was not always possible. Due to its life history, white steenbras juveniles are uncommon west of False Bay and east of East London (Harrison 2003), with these two areas representing the western- and eastern-most juvenile samples, respectively. Due to low capture rates, only 17 adults could be sampled in the East London area, and insufficient in the region of the East Kleinemonde Estuary to constitute a suitable sample of adults in this region.

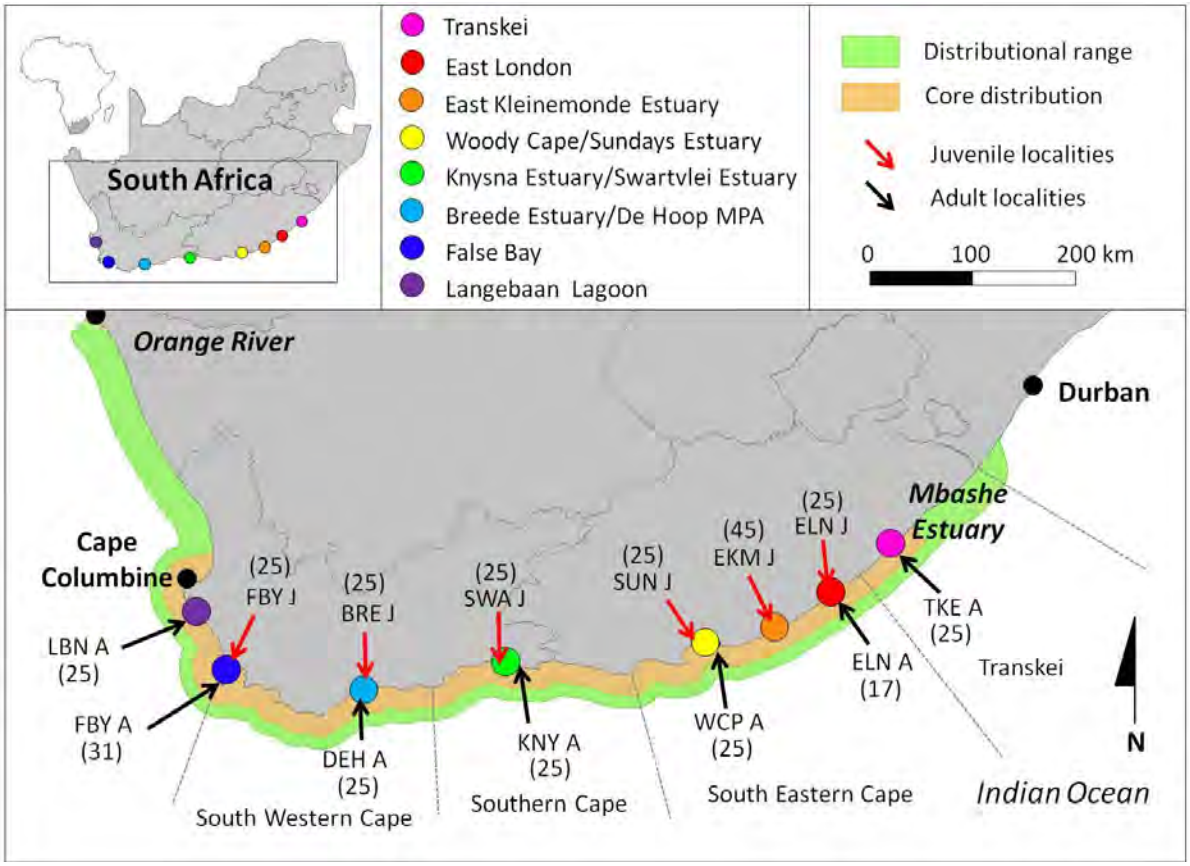

Figure 7.1: Sampling localities for juvenile (J) and adult (A) white steenbras; numbers in parentheses represent sample sizes from each locality (LBN = Langebaan Lagoon, FBY = False Bay, DEH = De Hoop MPA, BRE = Breede Estuary, SWA = Swartvlei Estuary, KNY = Knysna, SUN = Sundays Estuary, WCP = Woody Cape, EKM = East Kleinemonde Estuary, ELN = East London, TKE = Transkei)

For analyses among coastal regions, adult and juvenile samples were grouped as follows: False Bay adults and juveniles; De Hoop MPA and Breede Estuary; Knysna and Swartvlei Estuary; Woody Cape and Sundays Estuary; and East London adults and juveniles. Juvenile samples were collected from estuaries, while adult samples were collected in the marine environment, except Knysna adults that were predominantly captured within the Knysna Estuary. Genetic material was collected in the form of a 10- to 20-mm pectoral fin clipping, and stored in individually labelled vials containing ethanol (99%). Fish captured outside of the fishery were returned unharmed after sampling.

7.2.2 DNA extraction

A sub-sample of fin tissue was taken from each individual (approximately 5 mm × 5 mm). Genetic material was extracted using the commercially available Wizard® Genomic DNA Purification Kit (Promega, USA), following the manufacturer's instructions (Appendix II). Extracted products were stored at 4°C until gel electrophoresis or further mtDNA or microsatellite processing. Extraction

success was determined by subjecting 5 µl of the final extracted product to electrophoresis through 2% agarose gel containing ethidium bromide with 1XTBE buffer, at 100 V for 25 minutes. The gel products were viewed and photographed on an ultraviolet (UV) transilluminator.

7.2.3 Mitochondrial DNA methods

Primer selection

A fragment of the control region from each extracted DNA product was amplified, using standard polymerase chain reaction (PCR) amplification techniques (Saiki *et al*. 1988). This technique requires short sequences of nucleotides (primers) that match conserved regions on either side of the region to be amplified, and through the process of repetitive denaturing of the double-stranded DNA, annealing of the primers to each complementary strand and synthesis of new double strands, the number of copies of the target sequence can be exponentially increased (Campbell *et al*. 1999). Before the target sequence could be successfully amplified, a number of primer pairs, designed for related species (Table 7.1), were tested for PCR amplification of the white steenbras control region, in order to identify a suitable primer pair.

Table 7.1: Forward (F) and reverse (R) primers tested for PCR amplification of the white steenbras control region

Primer name	F/R	Sequence	Source
LPRO-F	F	5’ - AAC TCT CAC CCC TAG CTC CCA AAG - 3’	Summerer *et al*. (2001)
TDK-D	R	5’ - CCT GAA GTA GGA ACC AGA TG - 3’	Lee *et al*. (1995)
ChrysoCytbF	F	5’ - GCA GCA GCA YTA GCA GAG AAC - 3’	Teske *et al*. (2010)
Sparid12SR1	R	5’ - TGC TSR CGG RGC TTT TTA GGG - 3’	Teske *et al*. (2010)
PT	F	5’ - CTT ACT ATC AAC TCC CAA AGC - 3’	Jean *et al*. (1995)
PU	R	5’ - GGG CAT TCT CAC GGG GAT GCG - 3’	Jean *et al*. (1995)

Universal mitochondrial control region primers LPRO-F and TDK-D (Summerer *et al*. 2001, Lee *et al*. 1995) failed to amplify the white steenbras control region, while sequences produced from the products amplified with ChrysoCytbF and Sparid12SR1, designed for red roman (Sparidae, Teske *et al*. 2010), were poor. Primers PT and PU, designed for the black sea bream *Acanthopagrus schlegelii* (Sparidae, Jean *et al*. 1995), produced a clean amplification product for the white steenbras control region and long (> 700 nucleotide bases), clean sequences of high quality. The primers PT (forward) and PU (reverse) were thus selected for this study.

PCR amplification

All PCR reactions were conducted in 50 µl solutions, containing 1X buffer, 3 mM $MgCl_2$, 0.2 µM of each primer, 0.8 mM dNTPs, 0.5 units of DNA Super-Therm Taq Polymerase (Southern Cross Biotechnology, South Africa), and 5 µl of extracted DNA template, made up to the final volume with distilled water. The PCR cycling profile comprised an initial denaturation step at 94°C for 3 minutes, followed by 35 cycles of denaturation at 94°C for 50 seconds, annealing at 56°C for 40 seconds and extension at 72°C for 90 seconds, followed by a final extension step at 72°C for 7 minutes, and hold at 16°C. Amplification was conducted on an Eppendorf Mastercycler thermal cycler (Eppendorf, Germany) or a Hybaid Multiblock system PCR thermal cycler (ThermoScientific). Amplification success was determined using gel electrophoresis as conducted for extracted DNA.

Sequencing

Amplified products were sent to a commercial sequencing facility (Macrogen Inc., Korea) for PCR purification and sequencing. However, approximately 10% of the PCR products were purified and cycle sequenced prior to being sent for commercial sequencing (Appendix III). Purification was done using the QIAquick PCR Purification Kit (Qiagen, Germany), and cycle sequencing with the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, USA), following the manufacturer's instructions.

7.2.4 Microsatellite methods

PCR amplification

The microsatellite markers used in this study were identified by Reid *et al*. (submitted). These authors successfully amplified 15 polymorphic loci in white steenbras, of which nine were isolated from white steenbras, and six through cross-species amplification from three related sparids: four from the hottentot seabream *Pachymetopon blochii,* one from the red roman (*Clat11* from Teske *et al*. 2009), and one from the black spot seabream *Pagellus bogaraveo* (*Pb-OVI-D106* from Piñera *et al*. 2006). These 15 markers were initially included in the current study (Table 7.2). Fourteen of the markers were tetranucleotide repeats, and one (*LLtr004*) was a trinucleotide repeat.

Amplification of microsatellite loci was conducted using the Quantitect® Multiplex PCR Kit (QIAGEN®). For this technique, the forward primers in each primer pair were fluorescently labelled with different colours (Applied Biosystems) to distinguish alleles at the different loci, allowing the simultaneous amplification of multiple loci in a single 'multiplex' reaction, thereby saving substantial time and cost and providing consistent amplification across loci. Where two loci were characterised by non-

overlapping allele size ranges, it was possible to fluorescently label the forward primers of both with the same colour, and combine the two in a single PCR reaction with primers of other colours. In this way, it was possible to amplify all 15 loci for each sample in three multiplex PCR reactions (Reid *et al*. submitted) (Table 7.2).

Table 7.2: Multiplexes 1, 2 and 3, showing the microsatellite loci included in each, the colour with which the forward primer of each was fluorescently labelled and the allele size range of each locus

	Fluorescent Colour	Allele size (number of nucleotide bases): 100 120 140 160 180 200 220 240 260 280 300 320 340 360
Multiplex 1	Blue (6-FAM)	**PBt007** **LLt005**
	Green (VIC)	**LLt006** **PB106**
	Yellow (NED)	
	Red (PET)	**LLt014** **LLt011**
Multiplex 2	Blue (6-FAM)	**LLt007**
	Green (VIC)	**PBt018** **CL011**
	Yellow (NED)	**LLt024**
	Red (PET)	**LLtr004**
Multiplex 3	Blue (6-FAM)	**LLt020**
	Green (VIC)	**PBt013** **LLt002**
	Yellow (NED)	
	Red (PET)	**PBt003**

All reactions were conducted in 10 µl solutions, in 96-well plates. Each reaction contained 5 µl of Quantitect Multiplex PCR Master Mix®, 0.5 µl of diluted DNA template (0.1X), 0.2 pmol of each forward and reverse primer in that multiplex, and made up to the final volume with Quantitect Multiplex deionised water. PCR reactions were conducted in a GeneAmp® 2720 Thermal Cycler or PCR System 9700 (Applied Biosystems). The PCR cycling profile comprised an initial polymerase activation step at 95°C for 15 minutes, then 50 cycles of annealing at 94°C for 60 seconds and extension at 60°C for 90 seconds, followed by a 4°C hold. Amplification success was tested by running 4 µl of each PCR product on a 3% agarose gel in TAE buffer, at 110 V for 20 minutes. Gels included GelRed™ Acid Stain (Biotium). Gel products were viewed and photographed on a UV transilluminator.

GeneScan analysis

Successful PCR products were prepared for GeneScan, by adding 0.1 µl of PCR product from each sample, to 10 µl of formamide containing GeneScan™ 500 LIZ™ Size Standard (Applied Biosystems). Samples were denatured at 95°C for 3 minutes, before GeneScan analysis on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems). The Genetic Analyzer separates the negatively charged particles by size, and fragment lengths are measured by laser recording of relative fluorescence units (RFUs), emitted in relative concentrations by the fluorescently-labelled primers. A synthetic/virtual gel image and an electropherogram were then produced for each sample, indicating allele peaks in base pair lengths according to RFU levels, representing allele sizes for each locus in that multiplex.

7.2.5 Mitochondrial DNA data analysis

Raw mtDNA sequences were cleaned and edited in Chromas Lite version 2.01 (Technelysium Pty Ltd), and aligned manually in Seqman Pro™ (DNASTAR®). A final sequence alignment was produced in Clustal X (Larkin *et al*. 2007), which agreed with the manual alignment. Aligned sequences were imported into DnaSP version 5 (Librado and Rozas 2009) for analyses and output to other analysis software. Analyses in this chapter (for both mtDNA and microsatellites) were grouped by analysis approach, starting with simple descriptive statistics and genetic diversity estimates, followed by comparative analyses of genetic differentiation, then sample clustering-type analyses and finally analyses that incorporate geographic sampling locality information.

Sample grouping

One of the aims of this chapter was to assess the level of white steenbras spatial genetic diversity around the South African coastline, as well as among juveniles and among adults. As such, *a priori* delineation of populations was defined by both age class and by geographic locality. In order to avoid potential masking of genetic differentiation at the geographic locality level by possible differences between juvenile and adult age classes, certain analyses were conducted on two different sample groupings. The first grouping comprised eight locality groups (Figure 7.1), five of which contained juvenile and adult samples, pooled on the basis that they originated from the same section of coastline (exact tests for differentiation showed no significant differences among or between juvenile and adult populations, see results). However, as juveniles were sampled from estuaries, and adults from the nearby surf zone (or, in the case of Knysna adults, from a nearby estuary), it was felt that it was also necessary to treat juvenile and adult populations (within each of the five regions from which both age classes were sourced) as separate groups. This constituted a total of 13 populations (six juvenile and seven adult), representing eight localities.

Genetic diversity

Three indices of genetic diversity were calculated for each group at the locality and population levels: the number of polymorphic or segregating sites (*S*), haplotype diversity (*h*) and nucleotide diversity (π). The number of polymorphic sites represents the number of variable nucleotide positions within the DNA sequence, recorded within each group. Haplotype diversity (also termed gene diversity or allele diversity) is the probability that two individuals drawn at random from a population would have different haplotypes (Billington 2003). This is a measure of the relative frequency of each haplotype in the population (Nei 1978). Nucleotide diversity is a measure of the mean proportion of nucleotide differences between pairs of randomly chosen haplotypes within the population (calculated as the number of nucleotide differences between haplotypes, divided by the number of nucleotide bases in the sequence) (Nei and Tajima 1981). This index represents the probability that individual homologous nucleotides from two randomly drawn haplotypes within a population will be different (Nei and Tajima 1981), by considering both the frequency of haplotypes in the population and the divergence among them (Billington 2003). Diversity indices were calculated in DnaSP version 5.

Haplotype network

Each individual haplotype is unique in its nucleotide sequence, and reflects the mutations that distinguish it from other, similar haplotypes. Thus, haplotypes can be arranged according to their similarity to other haplotypes and, by considering their geographic source, can be used to partition population structure (Posada and Crandall 2001). A median-joining (MJ) haplotype network was created in the Network software version 4.6.0.0 (Fluxus Technology Ltd), to illustrate schematically the relationships among haplotypes. A minimum spanning (MS) network was first created, which simply connects all haplotypes without inferring additional nodes, or creating cycles in the event of ambiguous relationships (Bandelt *et al*. 1999). The MS network is then expanded to create the MJ network by adding additional nodes (which represent either extant unsampled haplotypes or extinct ancestral haplotypes), using a parsimony criterion (Posada and Crandall 2001). However, due to the complexity of the additional relationships in the MJ network, the MS network is presented.

Tests for selective neutrality

Selection acting on a gene under study can lead to misinterpretation of the population demography (Ballard and Whitlock 2004), and falsely indicate the presence of genetic structure. Therefore, genes should be tested for neutrality before making inferences about population genetic structure (Ford 2002). Numerous tests have been developed to test for the presence of selection. While some genes

within the mitochondrial genome are under selection (MacRae and Anderson 1988), the mitochondrial control region is a non-coding region of the mitochondrial genome (Ballard and Whitlock 2004), and is therefore assumed to be selectively neutral (Fu 1997, Liu *et al*. 2010). However, it has been suggested that selection may indirectly act on a neutral locus by virtue of it being linked to a locus under natural selection (Tajima 1989, Fu 1997). Linked selection to deleterious mutations is termed background selection, resulting in loss of mutations, whereas linked selection to advantageous mutations is termed genetic hitch-hiking (Fu 1997). Owing to the possibility of linked selection, tests for selective neutrality have been incorporated into studies of the control region. Because evolution in populations may be affected by numerous natural forces, a single test is unlikely to provide information on all these forces, therefore the employment of multiple tests in conjunction is recommended (Fu 1997). Four analyses were conducted to test for selective neutrality of the region under study.

The first test was the Ewens-Watterson homozygosity test, based on the infinite-alleles model (Wright 1931, Kimura and Crow 1964) and Ewens' (1972) theory of neutral alleles, in which the sum of haplotype frequencies (*F*) can be used to represent the distribution of selectively neutral haplotype frequencies (Watterson 1978). The infinite-alleles model assumes that a mutation can occur at any nucleotide position, thus mutation to any other haplotype has equal probability (Balloux and Lugon-Moulin 2002). The significance of the test is determined as the probability of observing random samples with equal or lower *F*-values than that observed (Excoffier and Lischer 2009).

The second test was that described by Tajima (1989), which is based on the infinite sites model (which assumes all new mutations occur at a new nucleotide position) and assumes that there is no recombination in the gene region under study. From the number of polymorphic sites (*S*) and the average number of nucleotide differences (π), two population mutation rate parameters (θ_S and θ_π) can be calculated, which are incorporated into the computation of Tajima's (1989) *D*-statistic. Under neutral evolution, the two parameter estimates should be in close agreement, and the resulting *D*-statistic should be close to zero. However, in the event of selection on the gene, population non-stationarity or heterogeneity of mutation rates among nucleotide sites, the *D*-statistic may depart from zero (Fu 1997). A coalescent simulation algorithm is then implemented (after Hudson 1990), under the assumption of selective neutrality, to generate random samples, from which the proportion of simulated *D*-statistics that are equal to or less than that observed represents the level of significance (Excoffier and Lischer 2009).

The third test was that of Fu (1997), also calculated under the infinite-site model and the assumption of no recombination. The test statistic F_S is computed for *S'*, which is defined as the probability of a random sample of haplotypes having the same or greater number of alleles than observed in the test population (Fu 1997). The significance of this test is determined as the proportion of multiple random F_S statistics, generated under the null hypothesis of selective neutrality using a coalescent algorithm (from Hudson 1990), that are equal to or less than the observed F_S value (Excoffier and Lischer 2009). Fu (1997) calculated that for F_S, unlike other neutrality tests, the critical point at the 5% level of significance corresponds to the lower 2nd percentile of the distribution, meaning that significance at the 5% level actually corresponds to a greater than 5% probability. Therefore, for the F_S test, the statistic should be considered significant at the 5% level, if the p-value falls below 0.02, not 0.05 (Fu 1997, Excoffier and Lischer 2009). All the above neutrality tests were conducted in Arlequin version 3.5 (Excoffier and Lischer 2009).

The fourth test was that of the parameters *D** and *F**, proposed by Fu and Li (1993), which are suggested to be more powerful tests for neutrality than Tajima's (1989) *D* (Fu and Li 1993, Fu 1997). Mutations occurring in the internal branches of a genealogy represent old mutations, whereas those in the external branches represent more recent mutations. In the presence of purifying or negative selection, deleterious alleles are present in low numbers, therefore an excess of mutations is expected in external branches (i.e. more recent or new mutations) (Fu and Li 1993). Similarly, an excess of mutations in the external branches is expected if an advantageous allele has recently become fixed in the population. Conversely, under balancing selection a deficiency in mutations in external branches is expected. Therefore, comparison of the observed numbers of mutations in external and internal branches with expected numbers in each can be used to test for selective neutrality. The parameters *D** and *F** described by Fu and Li (1993) provide such comparisons. These indices are also believed to be the most powerful for detecting the presence of background selection, although Fu's F_S is more powerful in the presence of genetic hitch-hiking (Fu 1997). Fu and Li's test was conducted in DnaSP version 5.

Population size history by mismatch distribution

The frequency distribution of the observed number of nucleotide differences between all pairs of haplotypes in the sample is termed the mismatch distribution. While this may be a simplistic measure of genetic variability, the shape of the mismatch distribution for samples drawn from a contemporary population can provide insight into the history of that population, reflecting events such as population expansions or declines (Rogers and Harpending 1992). The model is based on

quantitative measures of divergence between all pairs of haplotypes and assumes a random nucleotide substitution process and equal mutation rates for all nucleotide positions. Under the assumption of population equilibrium, a multimodal mismatch distribution is expected (Excoffier and Lischer 2009). Reductions in population size would be expected to exhibit an L-shaped frequency distribution (skewed to the right), while population expansion events would manifest as unimodal distributions (Rogers and Harpending 1992). Assuming a demographic expansion model (population size increase), certain parameters of the expansion are estimated, including the mutation parameters θ_0 (prior to expansion) and θ_1 (after the expansion event), and the time since the expansion event (τ) in scaled coalescent units, based on the mean and variance of the observed mismatch distribution (Excoffier and Lischer 2009). The significance of the mismatch test is then determined based on the sum of squared deviations (SSD) between the parameters of the observed and expected distributions, under the null hypothesis that the estimated parameters are the true parameters, and where the probability is determined as the proportion of SSD values from a number of simulated sets of parameters (n = 1 000 in this case) that are larger than or equal to that observed (Excoffier and Lischer 2009). The analysis was also run under the assumption of a spatial expansion model (population geographic range increase), following a similar method.

Harpending's (1994) raggedness index (*r*) was also calculated, as a measure of the smoothness of the mismatch distribution, and of the goodness-of-fit to the model of population expansion. The index is dependent on the maximum number of observed nucleotide differences between haplotypes, and the frequencies of the mismatch classes (Excoffier and Lischer 2009). The significance of the test is determined as the proportion of simulated SSD values greater than or equal to that observed, as for the mismatch model (n = 1 000 simulations). Mismatch distributions and Harpending's *r* were computed in Arlequin version 3.5.

From the mismatch distribution, it is possible to estimate the time since the most recent common ancestor of the observed haplotypes, and thus the time since the start of a population expansion (Slatkin and Hudson 1991). The time since expansion (T) was calculated as $T = \tau/2u$ (Rogers and Harpending 1992) (where τ is expansion time in scaled coalescent units, and $2u$ = estimated population mutation rate $\mu \times$ number of nucleotide bases in analysed sequence × generation time). Population mutation rates for fish mitochondrial control regions have been estimated at between 3.6% (Donaldson and Wilson 1999, Centropomidae) and 11% (McMillan and Palumbi 1997, teleosts in general) per nucleotide site per million years, while Bargelloni *et al*. (2003) estimated a mutation rate for sparids of approximately 10%. Time since expansion was calculated using all three mutation

rates. The sequenced mtDNA for the current study included 720 bases, and the generation time of 6.0 years was used, based on the age at 50% sexual maturity (Bennett 1993b).

Analysis of molecular variance

Analysis of Molecular Variance (AMOVA, Excoffier *et al*. 1992) was used to estimate indices of genetic structure at different hierarchical levels, based on nucleotide sequence differences of observed haplotypes, and their frequencies. The different levels of assessment were defined in this analysis as *among geographic localities* (n = 8 localities, Figure 7.1), *among populations within localities* (5 of 8 geographic localities had two populations – East London, Woody Cape/Sundays, Knysna/Swartvlei, Breede/De Hoop, False Bay), and *within individual populations*, i.e. inter-individual (n = 13 separate populations). AMOVA was also used to test for genetic differences between juvenile and adult populations. Hierarchical levels included *among groups* (n = 2 groups: juvenile and adult), *among populations within groups* (n = 7 adult populations, n = 6 juvenile populations) and *within populations* (n = 13 populations). A matrix of Euclidean squared distances between haplotypes was created from nucleotide sequence differences, the covariance of which was assessed at the different levels of genetic structure using a non-parametric permutation procedure (Excoffier and Lischer 2009). At each level, 10 000 permutations were conducted, to test the significance of covariance components and fixation indices. AMOVA analyses were conducted in Arlequin version 3.5.

Population differentiation

Exact probability tests of population differentiation were conducted to test the null hypothesis of no genetic differentiation (Raymond and Rousset 1995) between groups, at both the locality and population levels. Using this test, it is possible to test for non-random distribution of individuals between pairs of groups. This test extends the 2 × 2 contingency table of Fisher's exact test to an $R \times C$ (rows × columns) contingency table of groups × haplotypes. Using a Markov chain technique, values in randomly selected cells are then adjusted to create different table states whilst keeping row and column totals constant, with the Markov chain following a random walk, "visiting" all possible contingency tables. The significance of the test is determined as the proportion of tables visited that have an equal or lower probability than the observed table (Raymond and Rousset 1995). The significance criterion (α) was set at 0.05. A total of 100 000 steps were conducted in the Markov chain, with 10 000 dememorisation steps. These tests were conducted in Arlequin version 3.5. The exact test provides only a qualitative test of pairwise differences; therefore, Raymond and Rousset (1995) suggest that this test does not eliminate the need to calculate pairwise fixation indices (F_{ST}) among groups, which can provide quantitative comparisons.

Pairwise population comparisons (F_{ST})

Magnitudes of genetic differentiation were assessed between localities and between populations by pairwise comparisons of haplotype frequencies. Genetic differences are presented as pairwise fixation indices (F_{ST}, Wright 1951), with F_{ST} corresponding to the variance among haplotype frequencies within the pair of samples, standardised by the mean haplotype frequency among all localities/populations (Weir 1996), calculated under the infinite-alleles model (Wright 1931, Kimura and Crow 1964). The significance of each observed pairwise F_{ST} value was calculated by permutation (10 000 permutations) of the haplotypes between groups and determined as the proportion of permutations that provide an F_{ST} value equal to or greater than that observed. Analyses were conducted in Arlequin version 3.5.

Isolation by distance

In a species exhibiting average dispersal distances per generation that are on smaller scales than the species distribution range, it might be expected that genetic differentiation between geographic localities would increase with distance (Dupanloup *et al*. 2002), as the probability of gene flow decreases – a pattern known as isolation by distance (Slatkin 1993). A Mantel test (Mantel 1967) was used to test for a correlation between pairwise genetic differences and geographic distances between locality groups. A matrix of pairwise F_{ST} values, calculated between localities, was created and correlated with a similarly constructed matrix of geographic distances (km). Rows and columns of one matrix were then permuted (10 000 times) while the other matrix was kept constant. The significance of the test was determined by the proportion of permuted correlation coefficients (R) equal to or greater than the R observed. The analysis was conducted in Arlequin version 3.5.

Spatial analysis of molecular variance

Spatial genetic variability was further investigated at the locality level, using SAMOVA version 1 (Spatial Analysis of Molecular Variance, Dupanloup *et al*. 2002). SAMOVA is an adaptation of the AMOVA (Excoffier *et al*. 1992) that considers the geographic positions (latitude and longitude coordinates) of localities, and uses a simulated annealing procedure to delineate the sampling localities into groups that provide the greatest *among group* variability. The analysis randomly allocated the eight localities to K groups (K is user-defined), and variance components were calculated at the *among groups*, *among localities within groups* and *within localities* levels. One locality was then drawn randomly from one of the groups and allocated to another, and the AMOVA variance components were recalculated. This step was repeated 10 000 times, and to ensure that the result was not biased by the initial grouping, the entire process was repeated 100 times. The

best grouping of localities was then taken as that which produced the greatest index of variance *among groups of localities* (F_{CT}) (Dupanloup *et al*. 2002). The analysis requires more than one group, and at least one group with more than one locality; therefore, six analyses were run, with *K* ranging from 2 to 7 (i.e. $1 < K < 8$). SAMOVA attempts to group geographically adjacent localities, although this is not always the case (particularly when there is low genetic differentiation among populations within groups). In such cases the grouping may not be biologically meaningful (Neethling *et al*. 2008).

7.2.6 Microsatellite DNA analysis

Data processing

The raw data files (containing electropherograms of allele peaks) created by the GeneScan software were manually scored in the programme GeneMarker version 1.95 (SoftGenetics® *LLC*), which identified the most likely alleles at each locus based on peaks in RFUs. Alleles were checked and scored by accepting the true alleles and removing any spurious peaks or those associated with fluorescent "pull-up" from other dye colours. Once all loci for each sample had been successfully scored, the respective alleles at each locus for each individual were exported to a matrix of paired allele sizes. Four individuals with missing data for more than three loci were removed prior to further analyses.

Genetic diversity

Indices of genetic diversity were calculated for each microsatellite locus, and for the eight sampling localities. The numbers of microsatellite alleles recovered at each sampling locality were averaged across all loci, as a measure of genetic diversity for each locality. Mean allelic richness was also calculated for each locus across all localities, as well as for each locality across all loci, in the programme FSTAT 2.9.3 (Goudet 1995, 2001). Observed and expected heterozygosities (proportions of heterozygous genotypes) were calculated for each locus across all sampling localities, as well as for each locus within each locality, in Arlequin 3.5.

Hardy-Weinberg Equilibrium

An exact test was conducted, to test for departure of the observed allele frequencies at each locus from Hardy-Weinberg Equilibrium (HWE). Departure from HWE can indicate that at least one of the assumptions of HWE (random mating, selective neutrality, and lack of genetic structure) have been violated (Weir 1996, Hallerman *et al*. 2003). The test uses a modified Markov chain procedure (with 100 000 steps in the Markov chain and 10 000 dememorisation steps) (Guo and Thompson 1992),

similar to that described for the population differentiation exact test. The significance of the test is determined as the proportion of contingency tables visited that have an equal or lower probability than the observed table. Tests were conducted in Arlequin 3.5.

Linkage disequilibrium

Linkage disequilibrium tests were conducted between pairs of loci across all sampling localities, as well as between pairs of loci within each locality separately, to test for significant non-random association of alleles at different loci. This test is based on a likelihood ratio test, which compares the likelihood of the observed haplotype frequencies under the hypothesis of linkage equilibrium (i.e. no association between loci, calculated as the product of allele frequencies) against those under the hypothesis of linkage disequilibrium (i.e. association between loci, estimated using an Expectation-Maximisation (EM) algorithm) (Slatkin and Excoffier 1996). Significance of the observed likelihood ratio was tested by computing the null distribution of the ratio under the hypothesis of linkage equilibrium, through 16 000 permutations of alleles between individuals at a single locus, and recalculating the likelihood ratio statistic each time (Excoffier and Lischer 2009). The number of initial conditions from which the EM was started was set at 5. This test makes the assumption of HWE, deviation from which may produce a significant likelihood ratio statistic (Excoffier and Lischer 2009). Standard Bonferroni corrections were applied because of multiple statistical tests (Rice 1989).

Population differentiation

Exact probability tests were conducted to test the null hypothesis of no genetic differentiation (Raymond and Rousset 1995) between groups, at both the locality and population levels, as for the mtDNA. This test was also used as an *a priori* test to determine whether different populations in each sampling area showed significant genetic differentiation, or whether juvenile and adult samples within one locality could be pooled and subsequently analysed as a single population (i.e. locality group). Comparisons were made among all thirteen populations separately, among the eight sampling localities (see Figure 7.1 for sampling sites) and between juveniles and adults (the latter was based on the 13 populations grouped into one adult and one juvenile group).

Pairwise population comparisons (R_{ST})

Genetic differences in the microsatellite data were quantified by pairwise comparisons of allele frequencies for each pair of localities (n = 8) and populations (n = 13). The analyses proceeded in a similar fashion to that described for the mtDNA analysis, but were based on the calculation of Slatkin's (1995) R_{ST}, which is analogous to F_{ST} but assumes the stepwise mutation model, in which

every mutation will create a new allele by adding or deleting a microsatellite repeat (Kimura and Ohta 1978). The mutation of microsatellites is assumed to follow this model more closely than the infinite-alleles model (Balloux and Lugon-Moulin 2002). The significance of each observed pairwise R_{ST} value was calculated as described for F_{ST}.

Analysis of molecular variance

Genetic variability in the microsatellite data was analysed by AMOVA (Excoffier *et al*. 1992), which assessed differences in allele frequencies at different hierarchical levels. The analysis proceeded in a similar manner, and at the same grouping levels, as described for the mtDNA, but was run under the stepwise mutation model (Ohta and Kimura 1973), which considers the actual sizes of alleles, as opposed simply to allele frequencies (Excoffier and Lischer 2009). Furthermore, because microsatellite DNA is diploid, AMOVA is able to assess variability at a fourth level, *within individuals*. AMOVA was also used to test for genetic differences between juvenile and adult populations, as described for the mtDNA analysis.

Relatedness

Genetic variability was further analysed by estimating the level of relatedness between pairs of individuals (based on allele frequencies), defined as the "average frequency that two homologous alleles, one sampled from each individual, are identical by descent" (Ritland 2000: 1196). Pairwise comparisons of all individuals from the global sample were calculated using three methods-of-moments relatedness estimators (those of Queller and Goodnight 1989, Ritland 1996 and Lynch and Ritland 1999), implemented in the Genalex software package version 6 (Peakall and Smouse 2006). Variances in estimates of pairwise relatedness were calculated within each of the eight sampling localities, and compared among localities by non-parametric Kruskal-Wallis ANOVA (performed in Statistica 10), based on recommendations by Ritland (2000). Mean within-locality relatedness estimates were also calculated for each locality, and statistically compared to overall relatedness within the global sample, using a permutation procedure. Significance of the estimate for each locality was determined as the probability of the observed mean being greater than that estimated by 9 999 permutations (Peakall and Smouse 2006).

Population assignment

An assignment test was run to assign each individual in the global sample to one of the eight original sampling localities, based on the individual's genotype and the allele frequencies of each sampling population (juveniles and adults pooled within each) (Paetkau *et al*. 1995, 1997). The likelihood that

an individual was from a certain source population was determined as the estimated frequency of its specific genotype at each locus in the respective source population (Banks and Eichert 1999). For each individual, this was estimated across all loci, as the log of the product of the estimated probabilities at each locus (Peakall and Smouse 2006). The individual was then assigned to the population for which the maximum likelihood for that individual was observed (Waser and Strobeck 1998). The analysis was run in Genalex, adopting the "leave one out" approach, in which the individual being assigned was excluded from the allele frequency estimation of its original sampling population. This is done to remove the potential bias created by one population having the individual's genotype already present (Waser and Strobeck 1998). The analysis was also run in Arlequin, which does not adopt this approach, and allele frequencies in each population were simply calculated from the observed allele frequencies of all original members (Excoffier and Lischer 2009).

Factorial correspondence analysis

Factorial correspondence analysis (FCA) is a multivariate distance-based clustering method, which can be used to spatially explore variability among samples in a multivariate dataset (Seldin *et al*. 2006). The technique differs slightly in approach from the more commonly used principal components analysis (PCA), in that FCA explores multiple contingency tables (created from tables of allele frequencies), to create a correspondence matrix. Each population can then be treated as a group of individual points in an ordination space that has as many dimensions as there are alleles at each locus (Seldin *et al*. 2006). The FCA determines a deviation vector (in terms of magnitude and direction) defining how each individual deviates from the centre of the ordination space, which is determined as the centre of the coordinates of all individuals. The analysis then decomposes these individual deviation vectors into three dimensions, which can be presented spatially (graphically), as a set of deviations from the expected overall values (Seldin *et al*. 2006). This creates a three-dimensional ordination space, in which individuals influenced by similar factors would display similar divergences. The FCA analysis was run for four groupings, to spatially represent the variation in microsatellite allele frequencies of individuals from the eight sampling localities, the 13 populations, and separately for adults and juveniles, in the programme Genetix 4.05.2 (Belkhir *et al*. 1996 - 2004).

Structure analysis

A Bayesian model-based clustering method, implemented in the programme Structure 2.3.3 (Pritchard *et al*. 2000), was used to infer population structure from observed multilocus microsatellite genotypes in the global sample. The analysis uses a Markov chain Monte Carlo method to probabilistically assign individuals exhibiting similar genotypes to one or more of a hypothetical

number of discrete putative populations (*K*), which is user-defined, but in reality is unknown. The term "population" in this sense does not refer to the 13 sampling populations described, but rather to hypothetical groups of individuals. The analysis assumes that each individual has drawn some proportion of its genotype from ancestors in each of the *K* populations and attempts to assign individuals to one or more populations, based on allele frequencies, in such a way that HW and linkage equilibrium are maintained (Pritchard *et al*. 2000). The analysis incorporated the assumptions of two models available in the Structure software. The first was the *admixture ancestry model*, which allows for mixed ancestry, and the second was the *correlated allele frequencies model*, which assumes that each of the *K* populations has undergone independent drift from a common hypothetical ancestral population, thereby expecting that allele frequencies may be similar among populations (Falush *et al*. 2003). These two models were selected based on the results of the previous analyses, and the null hypothesis that white steenbras is present as a single well-mixed population, in which allele frequencies are expected to be similar among geographic localities. Two separate analyses were run, the first with no prior information on the locality from which each individual was sampled, and the second including the locality information (n = 8 localities).

Values of *K* tested in the present study ranged from *K* = 1, representing a single well-mixed population, to *K* = 8, representing the eight sampling localities. For each value of *K*, 20 iterations were conducted, from which the mean log probability that the observed set of genotypes in the global sample was drawn from the *K* populations was estimated. Each iteration consisted of 100 000 burnin steps, and an additional 100 000 steps in the Markov chain. The mean probabilities were compared among values of *K*, by means of a Kruskal-Wallis ANOVA, to determine whether there were significant differences. Tukey's post hoc test was used to identify the sources of the variability. The most probable number of real populations present was taken as the value of *K* that maximised the log probability (Falush *et al*. 2003), and accounted for the greatest variability in the data (Pritchard *et al*. 2010).

Isolation by distance

To test for isolation by distance (Slatkin 1993) in the microsatellite data, a Mantel test (Mantel 1967) was performed in Arlequin version 3.5. A matrix of pairwise F_{ST} values was created. These F_{ST} values were then adjusted to Slatkin's linearised genetic distance, which is calculated as $F_{ST}/(1 - F_{ST})$, taking negative F_{ST} values to be zero (Slatkin 1995). The analysis then proceeded in the same way as described for the mtDNA.

Spatial autocorrelation

Spatial autocorrelation analysis (Smouse and Peakall 1999) was used to test whether genotypes sampled from populations in close proximity were genetically more similar than those further apart. This analysis treated all loci per individual as one combined genotype, which had the effect of decreasing stochastic allele-to-allele and locus-to-locus noise. First, a covariance matrix of Euclidean squared distances was created from pairwise genetic distances between individuals. Similar (reduced) correlation matrices were also created for all pairs of individuals sampled within a certain distance class from each other, and were correlated against the overall correlation matrix (Smouse and Peakall 1999). Significance testing for autocorrelation at each distance class was determined using a permutation procedure, by permuting the individuals randomly within the initial correlation matrix, 9 999 times. Any distance classes showing mean autocorrelation coefficients (*R*) outside of the confidence interval obtained (higher or lower) can be deemed to exhibit significant spatial genetic structure (i.e. a two-tailed test). The significance of the assessment for positive (i.e. a one-tailed test) spatial autocorrelation at a distance class was determined as the probability of observing a higher correlation coefficient than that obtained from the 9 999 permutations. Secondly, a confidence interval was calculated for the observed correlation coefficient at each distance class, using 1 000 bootstrap trials. If the bootstrap confidence interval did not straddle the null distribution ($R = 0$), positive spatial autocorrelation at that distance was inferred (Peakall and Smouse 2006).

Assessments were conducted at the locality level (n = 8 localities) and population level (n = 13 populations), and for juveniles (n = 6 populations) and adults (n = 7 populations) separately. For this assessment, three different distance classes were used. In the first analysis distance classes of 100 km were used, based on the minimum distance between sampling localities. The second categorisation of distances was based on logical geographical divisions between sampling localities, i.e. between localities separated by long stretches of coastline. The third analysis was run with distance classes defined in such a way that the numbers of pairs of populations within each distance class were equal.

7.3 Results

7.3.1 Mitochondrial DNA

Mitochondrial control region sequences were successfully generated for 307 white steenbras, and could be confidently read for 720 nucleotide bases (709 when gaps were excluded). These 307 individuals comprised 174 haplotypes including gaps, and 169 haplotypes when gaps were excluded, and a total of 143 polymorphic sites were recorded (Table 7.3). Diversity indices, *S*, *h* and π, were fairly consistent among localities and populations. Haplotype diversity in all groups and populations, as well as overall, was high (range: 0.960 – 1.000), as a result of the high numbers of haplotypes observed. Nucleotide diversity in all localities and populations, as well as overall, was also relatively high (range: 0.009 - 0.013, or 0.9 – 1.3%).

Table 7.3: Genetic diversity indices calculated from 720-base pair mtDNA control region sequences for 307 individuals (n = 8 localities/13 populations), showing numbers of sequences (*N*), polymorphic sites (*S*), haplotypes (*H*), private haplotypes (*P*) and mean number of nucleotide differences between sequences (*k*), as well as haplotype (*h*) and nucleotide (π) diversities (TKE, EKM and LBN represent locality and populations levels, as they are represented by juveniles or adults only)

	Locality/ Population	*N*	*S*	*H*	*P*	*k*	*h*	π
Locality	ELN	40	73	29	20	8.831	0.979	0.013
	WCP/SUN	50	68	37	17	8.543	0.980	0.012
	KNY/SWA	47	61	40	18	7.067	0.988	0.010
	BRE/DEH	44	64	35	21	7.734	0.979	0.011
	FBY	55	71	47	27	6.692	0.985	0.009
Population	TKE A	25	51	23	8	9.193	0.993	0.013
	EKM J	25	53	24	11	9.090	0.997	0.013
	LBN A	21	48	18	10	9.152	0.990	0.013
	ELN A	15	36	12	5	8.114	0.971	0.012
	ELN J	25	63	22	13	9.363	0.987	0.013
	WCP A	25	53	20	6	9.010	0.980	0.013
	SUN J	25	47	21	10	8.240	0.987	0.012
	KNY A	25	47	22	9	6.937	0.987	0.010
	SWA J	22	45	21	8	7.351	0.996	0.010
	BRE J	21	42	18	9	7.476	0.986	0.011
	DEH A	23	52	19	11	8.150	0.960	0.011
	FBY A	30	50	25	18	6.143	0.996	0.009
	FBY J	25	51	25	8	7.397	1.000	0.010
	Overall	*307*	*143*	*169*	-	*8.036*	*0.985*	*0.011*

Haplotype network

The minimum spanning haplotype network (Figure 7.2) indicated the presence of a few common haplotypes, and a high number of rare haplotypes. Haplotypes 1 (28 individuals) and 2 (15 individuals), separated by six mutations, were the most common and were represented by seven and six of the geographic localities, respectively. Haplotype 1 formed the centre of a star-like topology, from which numerous haplotypes branched, and which was well represented by all eight sampling localities. Haplotype 2 formed the centre of a small, second cluster (indicated by the dashed polygon), in which all eight sampling localities were also represented. A long external branch extended from the main clade (represented by the solid polygon) including haplotypes differing by up to 17 mutations, although within this clade all eight geographic localities were again represented. The network indicated little association between haplotype genealogy and geographic location.

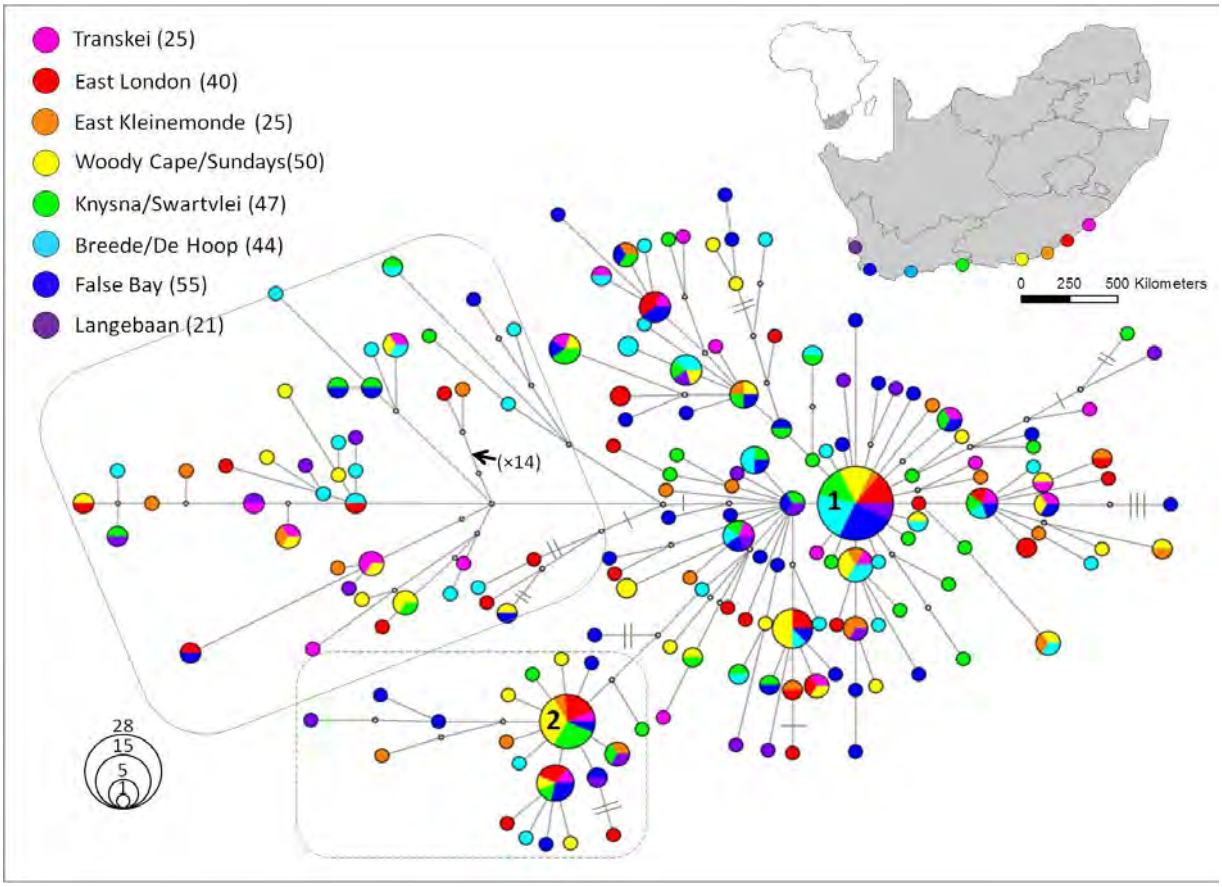

Figure 7.2: Minimum spanning network of 174 haplotypes identified from 307 mitochondrial control region sequences, from eight geographic localities (locality sample sizes represented in parentheses, colours indicate sampling localities). Common haplotypes 1 and 2 are labelled and sizes of circles are proportional to haplotype frequencies. Intermediate nodes represent unsampled extant haplotypes or ancestral haplotypes and branches indicate one mutational step, with additional steps indicated by the number of transverse bars (×14 indicates a branch with 14 mutational steps)

Tests for selective neutrality

Watterson's *F*-statistic was close to the expected *F*, for every locality and population, with no significant departures from neutrality. Conversely, Tajima's *D* was negative for all localities and populations, and showed significant departure from neutrality for most individual localities, and significant departure overall at the locality level. Fu's F_S values were negative and departed significantly from neutrality (at α = 0.02) for all localities and most populations, and overall at both levels. Seven of the eight localities and 11 of the 13 populations showed non-significant *D** and *F** values, although overall both values departed significantly from neutrality at both levels. The results of the four analyses were, therefore, not in agreement (Table 7.4).

Table neutrality 7.4: Tests for selective neutrality, conducted on 720-base pair mitochondrial control region sequences, for the eight localities and 13 populations (n = 307 individuals, ns = not significant, significant values are highlighted in bold)

Group	Watterson's		Tajima's		Fu's		Fu and Li's			
	F	*p*	*D*	*p*	F_S	*p*	*D**	*p*	*F**	*p*
Locality										
TKE	0.043	1.000	-1.27	0.100	-15.64	**0.000**	-2.09	ns	-2.16	ns
ELN	0.043	0.714	-1.75	**0.018**	-14.05	**0.000**	-2.29	ns	-2.50	ns
EKM	0.043	1.000	-1.43	0.068	-15.49	**0.000**	-1.70	ns	-1.89	ns
WCP/SUN	0.040	0.963	-1.55	**0.039**	-21.48	**0.000**	-2.05	ns	-2.23	ns
KNY/SWA	0.033	0.996	-1.74	**0.023**	-25.05	**0.000**	-2.61	< 0.05	-2.75	< 0.05
BRE/DEH	0.041	0.997	-1.67	**0.030**	-24.69	**0.000**	-2.04	ns	-2.27	ns
FBY	0.033	1.000	-2.03	**0.007**	-25.10	**0.000**	-2.04	ns	-2.27	ns
LBN	0.052	1.000	-1.33	0.072	-11.17	**0.000**	-1.56	ns	-1.72	ns
Overall	0.041	0.959	*-1.60*	***0.045***	*-19.08*	***0.000***	-4.64	< 0.02	-3.96	< 0.05
Population										
TKE A	0.057	0.883	-1.27	0.092	-15.64	**0.000**	-2.09	ns	-2.16	ns
ELN A	0.081	1.000	-1.22	0.101	-2.66	0.095	-1.12	ns	-1.32	ns
ELN J	0.043	1.000	-1.69	**0.022**	-12.45	**0.001**	-1.79	ns	-2.06	ns
EKM J	0.093	0.505	-1.43	0.050	-15.49	**0.000**	-1.70	ns	-1.89	ns
WCP A	0.046	0.891	-1.39	0.062	-7.02	**0.009**	-1.69	ns	-1.87	ns
SUN J	0.067	1.000	-1.37	0.083	-9.49	**0.001**	-1.10	ns	-1.38	ns
KNY A	N.A.	N.A.	-1.75	**0.024**	-13.58	**0.000**	-2.88	< 0.05	-2.98	< 0.05
SWA J	0.053	0.980	-1.59	**0.031**	-14.46	**0.000**	-2.05	ns	-2.23	ns
BRE J	0.052	1.000	-1.42	0.070	-10.31	**0.000**	-1.22	ns	-1.50	ns
DEH A	0.053	0.492	-1.63	**0.043**	-7.74	**0.008**	-2.14	ns	-2.32	ns
FBY A	0.043	1.000	-1.97	**0.007**	-16.87	**0.000**	-2.54	< 0.05	-2.77	< 0.05
FBY J	0.050	1.000	-1.83	**0.018**	-21.91	**0.000**	-2.35	ns	-2.57	ns
LBN A	0.059	0.734	-1.33	0.068	-11.17	**0.001**	-1.56	ns	-1.72	ns
Overall	-	-	*-1.53*	*0.052*	*-12.22*	***0.009***	-4.64	< 0.05	-3.96	< 0.05

Population size history by mismatch distribution

The expected mismatch distributions calculated under the demographic expansion model (population size increase) and the spatial expansion model (geographic range increase) showed negligible difference, as did the upper and lower bounds around the expected distribution; therefore, the results presented are restricted to those of the demographic expansion model (mean = 8.15, variance = 24.05) (Figure 7.3).

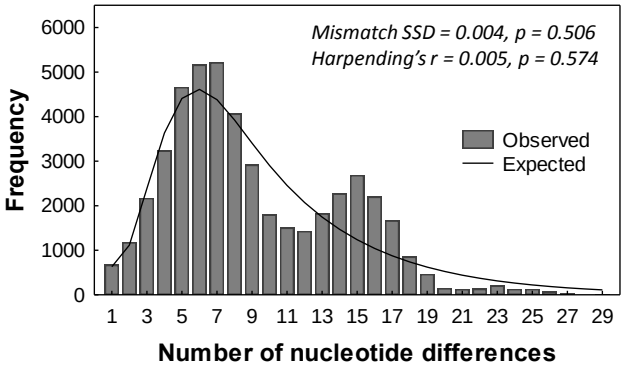

Figure 7.3: Observed (bars) and expected (line) mismatch distributions (under the sudden expansion model) of the frequency distribution of pairwise nucleotide differences between all pairs of haplotypes (mean = 8.15, variance = 24.05, n = 174 haplotypes, mismatch p = 0.506)

The mismatch distribution was distinctly bimodal, which usually indicates a population at equilibrium (Rogers and Harpending 1992). The shape of the distribution, therefore, was not characteristic of a model of population expansion, which is expected to be unimodal. However, despite the bimodal nature of the distribution, the sum of squared deviations, i.e. the departure of the observed distribution from that expected under a population expansion, was not significant (SSD = 0.004, p = 0.506), meaning that the null hypothesis of a population expansion cannot be rejected. Harpending's (1994) raggedness index *r* was low (0.005), usually associated with smoother, unimodal distributions (Excoffier and Lischer 2009), and the non-significance of this estimate (p = 0.574) suggests a good fit of the observed data to the model of population expansion. Based on an estimated τ of 3.35, and mutation rates of 3.6, 10 and 11% (Donaldson and Wilson 1999, Bargelloni *et al*. 2003, McMillan and Palumbi 1997), time since population expansion in white steenbras (rounded to nearest 100 years) was estimated at 21 500, 7 700 and 7 000 years, respectively.

Analysis of molecular variance

The AMOVA provided estimates of differentiation, variance and associated significance for comparisons of genetic diversity at three hierarchical levels (*among geographic localities*, *among populations within localities*, and *within populations*), as well as the percentage contribution of each level to overall observed variation. The *within populations* level contributed certainly the greatest percentage of variation, while those *among localities* and *among populations within localities* were negligible (Table 7.5). Observed genetic differentiation *within populations* (p = 0.947) and *among populations within localities* did not differ significantly from the null distribution (p = 0.999). However, there was significant departure *among localities* from the null hypothesis of no significant genetic variation (p = 0.007), although the level of variation (F_{CT} = 0.010) was low (Table 7.5).

Table 7.5: AMOVA results, to determine the level of mtDNA genetic variance among geographic localities (n = 8), among populations within localities (n = 5 localities each represented by two populations) and among individuals within separate populations (n = 13)

Source of variation	Deg. of freedom	Sum of squares	Variance component	Percent variation	Fixation index	p
Among localities	7	28.12	0.0417	1.02	F_{CT} 0.010	0.007
Among populations	5	12.38	-0.0698	-1.71	F_{SC} -0.017	0.999
Within populations	294	1205.36	4.0999	100.69	F_{ST} -0.007	0.946
Total	*306*	*1245.86*	*4.0718*	*100.00*		

AMOVA to test for differences among juvenile and adult populations showed no significant differences at any level, and low (negative) fixation indices (Table 7.6). This result reinforces the results of the previous analysis that most variation occurs within individual populations.

Table 7.6: AMOVA results, to determine the level of mtDNA genetic variance between juvenile and adult groups (n = 2), among populations within the juvenile and adult groups (n = 5 localities each represented by two populations) and among individuals within separate populations (n = 13)

Source of variation	Deg. of freedom	Sum of squares	Variance component	Percent variation	Fixation index	p
Between groups	1	2.32	-0.0074	-0.18	F_{CT} -0.002	0.881
Among populations	11	38.17	-0.0266	-0.66	F_{SC} -0.007	0.908
Within populations	294	1205.36	4.0999	100.84	F_{ST} -0.008	0.946
Total	*306*	*1245.86*	*4.0657*	*100.00*		

Population differentiation and pairwise population comparisons (F_{ST})

Locality level

In order to further explore the genetic differentiation observed in the results of the AMOVA, exact tests of differentiation and pairwise population comparisons (based on F_{ST}) were conducted at the locality and population levels, to identify more accurately the groups contributing to the observed variability. At the locality level, 25 of the 28 pairwise comparisons showed no significant genetic differentiation, based on the exact tests (Table 7.7). Three significant pairwise comparisons were observed, those between East London and Breede/De Hoop (p = 0.041), between East London and Langebaan (p = 0.043), and between Langebaan and Woody Cape/Sundays (p = 0.040).

Table 7.7: P-values for pairwise exact tests for genetic differentiation between localities (n = 8), based on 720-base pair mtDNA sequences (boldface values indicate significant differences)

	TKE	ELN	EKM	WCP/SUN	KNY/SWA	BRE/DEH	FBY
ELN	0.121	-	-	-	-	-	-
EKM	0.874	0.147	-	-	-	-	-
WCP/SUN	0.479	0.434	0.245	-	-	-	-
KNY/SWA	0.547	0.292	0.715	0.652	-	-	-
BRE/DEH	0.116	**0.041**	0.248	0.213	0.579	-	-
FBY	0.474	0.801	0.370	0.303	0.996	0.683	-
LBN	0.674	**0.043**	1.000	**0.040**	0.767	0.530	0.653

However, pairwise genetic comparisons based on F_{ST} showed no significant differentiation between pairs of localities and all F_{ST} values were low (Table 7.8). The highest F_{ST} values at the locality level were observed between False Bay and Transkei (0.015, p = 0.088), and between False Bay and Woody Cape/Sundays (0.015, p = 0.051)

Table 7.8: Pairwise F_{ST} values (above diagonal) and associated p-values (below diagonal) between localities (n = 8 localities, no significant differences)

	TKE	ELN	EKM	WCP/SUN	KNY/SWA	BRE/DEH	FBY	LBN
TKE		-0.007	-0.012	-0.008	0.006	-0.002	0.015	-0.013
ELN	0.651		-0.015	-0.012	-0.002	-0.001	0.000	-0.007
EKM	0.749	0.946		-0.010	0.002	0.000	0.009	-0.015
WCP/SUN	0.667	0.977	0.807		0.003	0.002	0.015	-0.015
KNY/SWA	0.227	0.540	0.337	0.274		-0.001	-0.007	0.000
BRE/DEH	0.443	0.455	0.400	0.286	0.428		0.007	0.002
FBY	0.088	0.393	0.144	0.051	0.872	0.145		0.021
LBN	0.703	0.614	0.792	0.899	0.381	0.336	0.052	

Population level

At the population level, there were 78 possible pairs of populations, of which only one showed significant differentiation, that between False Bay adults and Transkei adults (p = 0.035) (Table 7.9). Furthermore, pairwise genetic comparisons showed no significant differences between pairs of populations and all F_{ST} values were low (Table 7.10). The highest F_{ST} values at the population level were between False Bay adults and Woody Cape adults (0.024, p = 0.065), and between False Bay adults and Langebaan adults (0.025, p = 0.070). An exact test between juvenile and adult samples also showed no significant difference between groups (p = 0.644 ± 0.018).

Table 7.9: P-values for pairwise exact tests for genetic differentiation between populations (n = 13), based on 720-base pair mtDNA sequences (boldface values indicate significant differences)

	TKE A	ELN A	ELN J	EKM J	WCP A	SUN J	KNY A	SWA J	BRE J	DEH A	FBY A	FBY J
ELN A	0.761	-	-	-	-	-	-	-	-	-	-	-
ELN J	0.633	0.901	-	-	-	-	-	-	-	-	-	-
EKM J	0.878	0.518	0.828	-	-	-	-	-	-	-	-	-
WCP A	0.734	0.598	0.813	0.655	-	-	-	-	-	-	-	-
SUN J	0.756	0.745	0.776	0.724	0.767	-	-	-	-	-	-	-
KNY A	0.406	0.782	0.507	0.785	0.816	0.671	-	-	-	-	-	-
SWA J	0.962	0.842	0.882	0.950	0.680	0.865	0.932	-	-	-	-	-
BRE J	0.596	0.128	0.677	0.584	0.435	0.606	0.538	0.363	-	-	-	-
DEH A	0.069	0.198	0.261	0.267	0.108	0.205	0.323	0.908	0.111	-	-	-
FBY A	**0.035**	0.563	0.758	0.073	0.224	0.194	0.225	0.693	0.063	1.000	-	-
FBY J	0.996	0.944	0.964	0.970	0.842	0.643	0.991	1.000	0.799	0.178	0.169	-
LBN A	0.675	0.371	0.558	1.000	0.246	0.206	0.675	1.000	0.576	0.864	0.338	1.000

Table 7.10: Pairwise F_{ST} values (above diagonal) and associated p-values (below diagonal) between populations (n = 13 populations, no significant differences)

	TKE A	ELN A	ELN J	EKM J	WCP A	SUN J	KNY A	SWA J	BRE J	DEH A	FBY A	FBY J	LBN A
TKE A		-0.021	-0.005	-0.012	-0.018	-0.007	0.006	-0.008	-0.006	-0.013	0.021	-0.002	-0.013
ELN A	0.847		-0.017	-0.032	-0.030	-0.034	-0.012	-0.026	-0.017	-0.015	0.004	-0.009	-0.023
ELN J	0.553	0.837		-0.012	-0.015	-0.013	-0.002	-0.011	-0.009	-0.007	0.006	-0.018	-0.004
EKM J	0.744	0.995	0.806		-0.017	-0.015	0.002	-0.013	-0.010	-0.006	0.008	0.002	-0.015
WCP A	0.908	0.974	0.905	0.896		-0.019	0.006	-0.014	-0.013	-0.010	0.024	0.000	-0.023
SUN J	0.591	0.981	0.846	0.854	0.935		-0.001	-0.020	-0.006	-0.005	0.010	-0.004	-0.018
KNY A	0.257	0.661	0.481	0.360	0.269	0.418		-0.018	-0.003	-0.005	-0.003	-0.023	0.000
SWA J	0.599	0.932	0.783	0.800	0.771	0.933	0.917		-0.019	-0.020	-0.013	-0.014	-0.013
BRE J	0.521	0.722	0.704	0.685	0.719	0.529	0.502	0.895		-0.024	0.000	0.000	-0.009
DEH A	0.760	0.705	0.647	0.568	0.673	0.525	0.531	0.937	0.980		0.002	-0.004	-0.003
FBY A	0.078	0.330	0.237	0.220	0.065	0.178	0.523	0.873	0.411	0.342		-0.006	0.025
FBY J	0.459	0.645	0.966	0.368	0.427	0.517	0.997	0.868	0.410	0.490	0.625		0.006
LBN	0.707	0.840	0.492	0.800	0.953	0.850	0.394	0.712	0.577	0.422	0.070	0.265	

Isolation by distance

The isolation-by-distance analysis showed no association between pairwise genetic differentiation (pairwise F_{ST} values) and geographic distance between localities, and linear regression showed no significant correlation between variables (p = 0.393, R^2 = 0.0005) (Figure 7.4).

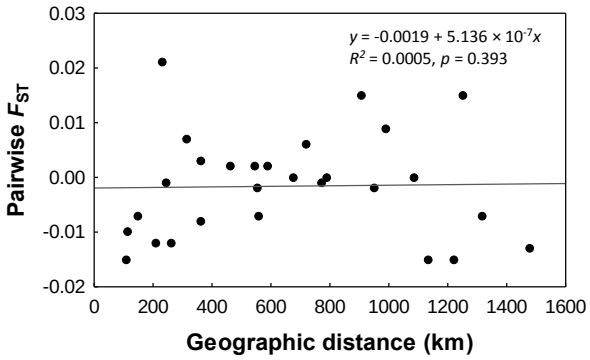

Figure 7.4: Scatterplot of pairwise F_{ST} values for the mtDNA data and geographic distance (km), to assess isolation by distance, at the locality level (n = 8 localities)

Spatial analysis of molecular variance

The SAMOVA analyses showed significant *among groups* variability ($p < 0.05$ in all cases), although similarly low F_{CT} was observed for all *K* values, and variability at the *among groups* level contributed less than 2% to overall variability in each SAMOVA. F_{CT} ranged from a minimum of 0.010 for *K* = 2 groups of localities, increasing gradually to a maximum of 0.013 for *K* = 6 groups, after which it decreased for *K* = 7 groups. For the *K* = 6 grouping (i.e. maximum *among groups* variability), four localities were represented as individual groups, while the East Kleinemonde and East London localities were grouped, and the Woody Cape/Sundays and Langebaan localities were grouped, despite the latter two localities being geographically separated by three other (ungrouped) localities (Figure 7.5). For *K* = 2 to 5, the False Bay and Knysna/Swartvlei localities were grouped, and for *K* = 2 to 6, Woody Cape/Sundays and Langebaan localities were grouped. The groupings had little biological meaning.

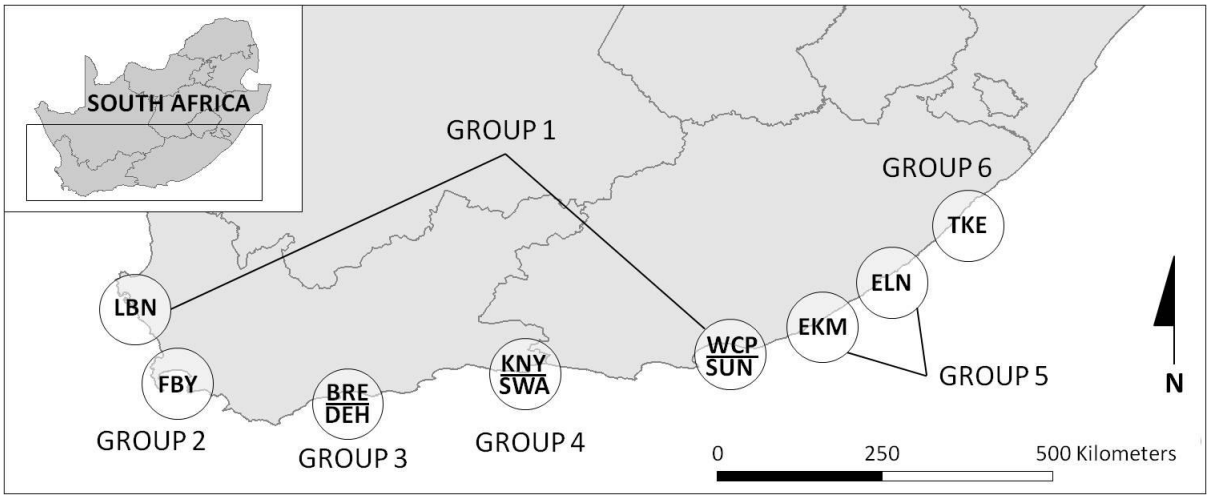

Figure 7.5: Grouping of sampling localities for *K* = 6 groups, as determined by SAMOVA as the grouping representing maximum *among groups* variability

Synthesis of mitochondrial DNA results

In order to relate the observed results to biological meaning more simply, certain parameters were plotted in a way that they could provide more information and facilitate biological interpretation (Figure 7.6).

Haplotype diversity (*h*) represents an index of genetic diversity, which has been shown in some species to decrease with distance from the spawning locality as haplotypes are lost due to larval-phase mortality or due to individuals not dispersing to the edge of the range (Matthee *et al*. 2007). However, *h* remained high throughout the white steenbras core distribution (Figure 7.6a), even in the localities furthest from the suggested spawning area in the Transkei (Bennett 1993b). Similarly, it may be expected that the number of private haplotypes (those found exclusively within a single sampling locality) would decrease with distance from the spawning site, although again this was not the case for white steenbras (Figure 7.6b).

Under complete panmixia, it is expected that haplotype frequencies within each locality would be consistent, while in the case of geographically-isolated populations or a geographic barrier to gene flow one might expect different regions not to share the same common haplotypes. The most common haplotype (haplotype 1) was present in samples from Langebaan to East London (Figure 7.6c), throughout most of the range of the study, providing evidence of historical gene flow among geographic regions. Similarly, although its contribution decreased considerably west of Knysna, the second most common haplotype (haplotype 2) was present from Transkei as far west as False Bay.

To further illustrate the level of gene flow, the pairwise F_{ST} values between the western-most (Langebaan) and eastern-most (Transkei) localities and all other localities are presented (Figure 7.6d), to determine whether the most distant localities exhibited greater genetic differentiation as a result of edge effects (Johannesson and André 2006). Langebaan (black bars) was most different to its neighbouring locality, False Bay, and showed very low differentiation with all other localities. The greatest genetic differentiation between Transkei (grey bars) and other localities was also with False Bay, while Transkei and Langebaan, at the two geographic extremes showed a negative pairwise F_{ST} (as with most other pairwise values), indicating negligible genetic differentiation.

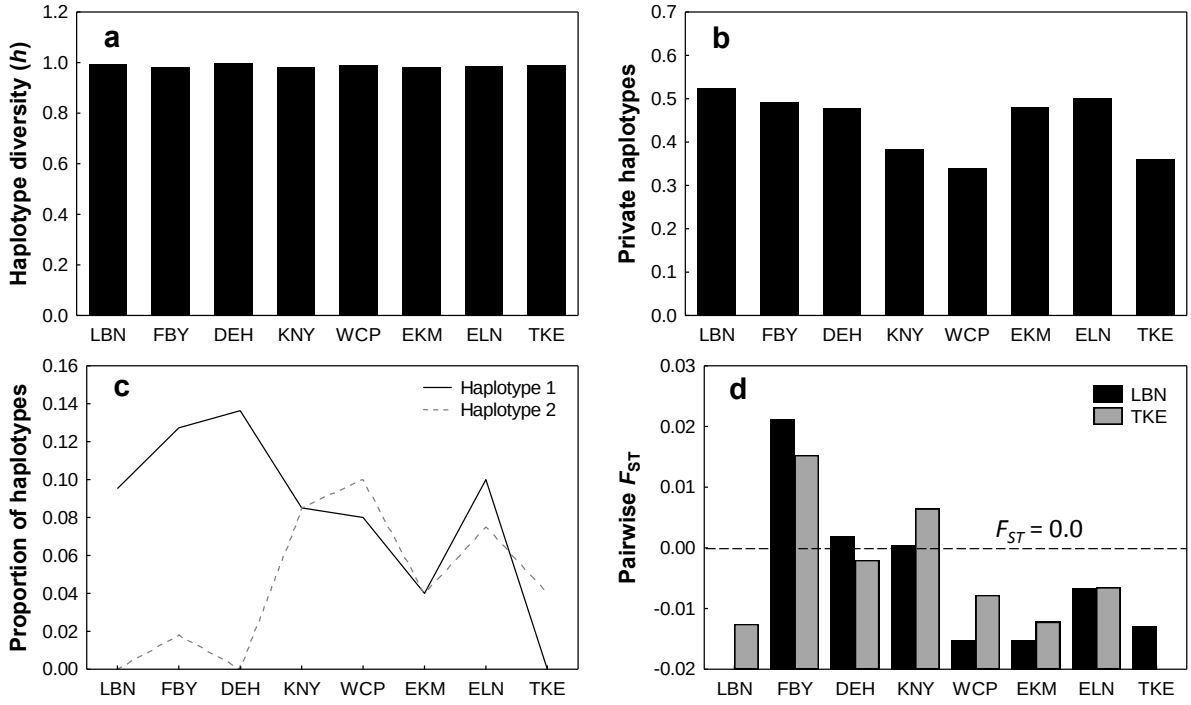

Figure 7.6: Summary of selected genetic analysis parameters recorded for each geographic locality, to facilitate interpretation of results: a) haplotype diversity (*h*), b) proportion of sequences in each locality representing private haplotypes, c) proportions of sequences in each locality representing the two most common haplotypes (haplotypes 1 and 2), and d) pairwise F_{ST} values recorded between the western-most (Langebaan, LBN) and eastern-most (Transkei, TKE) localities and each of the other localities, with the dotted line representing F_{ST} = 0.0; (for localities with juvenile and adult samples the two age classes were pooled; DEH represents Breede Estuary/De Hoop MPA, KNY represents Knysna/Swartvlei Estuary, and WCP represents Woody Cape/Sundays Estuary

7.3.2 Microsatellite DNA

Genetic diversity, Hardy-Weinberg Equilibrium and linkage disequilibrium

Initially 15 microsatellite markers were tested and preliminary analyses indicated that *PBt007, LLt024* and *PBt013* differed significantly from HWE and amplified poorly. These loci were thus excluded from further analyses, and are not discussed further. The mean number of microsatellite alleles (N_A) recovered at each of the remaining 12 loci ranged from 4.00 (*PBt018*) to 15.74 (*PBt003*). Similarly, mean allelic richness (A_R) at each locus ranged from 3.32 (*PBt018*) to 12.65 (*PBt003*). Observed heterozygosities (H_O) were close to those expected (H_E) under the HWE, for all loci except *CL011* (H_O = 0.48, H_E = 0.65). This locus also produced the only high F_{IS} estimate, indicating a heterozygote deficiency (Bahri-Sfar *et al*. 2000) and departure from HWE (Perez-Ruzafa *et al*. 2006) (Table 7.11).

Table 7.11: Summary statistics for 12 microsatellite loci, showing total number of alleles per locus (*N*) observed in the global sample, mean (± SD) number of alleles (N_A) and mean (± SD) allelic richness (A_R) averaged across all eight localities, and observed and expected heterozygosities (H_O and H_E), inbreeding coefficient (F_{IS}) and Hardy-Weinberg exact test p-value (*HWE*), for the global sample

Locus	*N*	N_A		A_R		H_O	H_E	F_{IS}	*HWE*
LLt005	6	5.00	(± 0.00)	4.82	(± 0.12)	0.66	0.70	0.07	0.55
LLt006	14	9.88	(± 0.35)	8.72	(± 0.43)	0.82	0.87	0.06	0.08
PB106	13	10.38	(± 0.92)	8.94	(± 0.59)	0.83	0.87	0.04	0.71
LLt014	11	8.50	(± 0.93)	7.58	(± 0.37)	0.83	0.85	0.03	0.35
LLt011	14	11.25	(± 1.49)	9.27	(± 0.74)	0.82	0.83	0.01	0.92
LLt007	15	10.00	(± 1.51)	8.23	(± 0.59)	0.83	0.83	0.00	0.23
PBt018	5	4.00	(± 0.76)	3.32	(± 0.42)	0.40	0.42	0.03	0.12
CL011	6	5.00	(± 0.93)	4.33	(± 0.69)	0.48	0.65	**0.27**	**0.00**
LLtr004	8	6.25	(± 0.46)	5.61	(± 0.26)	0.74	0.76	0.03	0.56
LLt020	19	13.38	(± 1.69)	11.13	(± 0.86)	0.91	0.90	-0.01	0.27
LLt002	14	11.50	(± 0.93)	9.95	(± 0.48)	0.89	0.88	-0.01	0.44
PBt003	25	15.75	(± 2.76)	12.65	(± 0.84)	0.91	0.91	0.00	0.18

Significant departure from HWE ($p < 0.001$) was observed overall for one locus only, *CL011* (Table 7.11). This locus also exhibited departure from HWE within five of the eight localities separately (data not presented). Locus *LLt005* showed departure from HWE in two localities, loci *LLt011*, *LLt007* and *LLt002* showed no departure from HWE, and the remaining eight loci each showed departure from HWE in one locality. After standard Bonferroni correction, departure from HWE was observed in three loci; *PB106* in East London, *LLt020* in East Kleinemonde and *CL011* in the Woody Cape/Sundays and Breede/De Hoop localities.

Values of N_A across all loci were lowest in Transkei and Langebaan, likely due to their lower sample sizes (Fritsch *et al*. 2007) (Table 7.12). Estimates of A_R and F_{IS} showed no trends among localities. Mean H_O values (averaged across loci within each locality) were close to H_E for all localities, although all were slightly reduced, reflecting the influence of the lower-than-expected H_O of locus *CL011*.

Table 7.12: Summary statistics for the eight localities (n = sample size per locality, N_A, A_R, H_O and H_E refer to mean number of alleles, mean allelic richness and observed and expected heterozygosities averaged across all 12 loci (± SD), F_{IS} = inbreeding coefficient estimated across all 12 loci)

Locality	n	N_A		A_R		H_O		H_E		F_{IS}
TKE	25	8.17	(± 2.89)	7.62	(± 2.66)	0.72	(± 0.20)	0.78	(± 0.17)	0.08
ELN	41	9.42	(± 3.78)	7.96	(± 2.91)	0.79	(± 0.17)	0.80	(± 0.12)	0.01
EKM	41	9.08	(± 3.40)	7.81	(± 2.76)	0.76	(± 0.17)	0.79	(± 0.14)	0.05
WCP/SUN	48	10.00	(± 4.07)	8.15	(± 2.91)	0.76	(± 0.21)	0.79	(± 0.15)	0.05
KNY/SWA	48	9.50	(± 3.87)	7.86	(± 2.78)	0.75	(± 0.18)	0.79	(± 0.16)	0.04
BRE/DEH	47	9.67	(± 4.56)	7.98	(± 3.25)	0.77	(± 0.18)	0.79	(± 0.13)	0.02
FBY	55	9.75	(± 4.16)	7.87	(± 2.98)	0.77	(± 0.13)	0.79	(± 0.14)	0.02
LBN	25	8.33	(± 3.11)	7.80	(± 2.93)	0.72	(± 0.18)	0.78	(± 0.14)	0.08

Linkage disequilibrium was observed in 99 of the 528 pairwise locus comparisons (8 localities × 66 pairs), although only 10 remained significant after Bonferroni correction. These were observed in all localities except East Kleinemonde. Significant pairs were not consistent across localities and included all but three loci (*CL011, LLtr004* and *LLt020*). In the global sample, 9 of the 66 pairwise comparisons showed significant linkage disequilibrium (Table 7.13), although only five remained significant after Bonferroni correction (two of which involved *CL011*). Therefore, no loci were excluded due to linkage disequilibrium; however, *CL011* was excluded due to departure from HWE.

Table 7.13: Tests for pairwise linkage disequilibrium, for all pairs of loci, across all eight localities (boldface values indicate significant differences)

Locus	Llt005	LLt006	PB106	LLt014	Llt011	LLt007	PBt018	CL011	LLtr004	LLt020	LLt002
LLt006	0.429										
PB106	**0.000**	0.649									
LLt014	0.224	0.194	0.051								
Llt011	**0.000**	0.183	**0.000**	0.734							
LLt007	0.756	0.481	0.390	0.062	0.761						
PBt018	0.877	0.281	0.633	0.976	0.222	0.591					
CL011	0.159	0.204	0.757	0.583	0.444	**0.047**	**0.000**				
LLtr004	0.306	0.766	0.343	0.845	**0.045**	0.106	0.222	0.931			
LLt020	0.348	0.265	0.355	0.111	0.962	0.134	0.149	0.308	0.914		
LLt002	0.323	0.207	0.447	0.884	0.745	0.164	0.318	0.533	0.650	**0.001**	
PBt003	0.301	0.887	0.567	0.585	0.077	0.927	0.765	0.717	0.370	**0.000**	**0.001**

Population differentiation and population comparisons (R_{ST})

Population level

Pairwise population exact tests revealed no significant differentiation between populations (Table 7.14). Similarly, pairwise comparisons based on R_{ST} also revealed no significant differences between populations (Table 7.15). The highest R_{ST} value at the population level, observed between the Langebaan adults and the Swartvlei juveniles, was R_{ST} = 0.015 (p = 0.126).

Table 7.14: P-values for pairwise population exact tests of genetic differentiation, based on 11 microsatellite loci, between populations (n = 13, no significant differences)

	TKE A	ELN A	ELN J	EKM J	WCP A	SUN J	KNY A	SWA J	BRE J	DEH A	FBY A	FBY J
ELN A	0.541	-	-	-	-	-	-	-	-	-	-	-
ELN J	0.496	1.000	-	-	-	-	-	-	-	-	-	-
EKM J	0.261	0.586	0.535	-	-	-	-	-	-	-	-	-
WCP A	0.475	1.000	1.000	0.513	-	-	-	-	-	-	-	-
SUN J	0.490	1.000	1.000	0.516	1.000	-	-	-	-	-	-	-
KNY A	0.449	1.000	1.000	0.537	1.000	1.000	-	-	-	-	-	-
SWA J	0.490	1.000	1.000	0.533	1.000	1.000	1.000	-	-	-	-	-
BRE J	0.482	1.000	1.000	0.522	1.000	1.000	1.000	1.000	-	-	-	-
DEH A	0.467	1.000	1.000	0.492	1.000	1.000	1.000	1.000	1.000	-	-	-
FBY A	0.231	0.570	0.468	0.243	0.503	0.507	0.504	0.505	0.523	0.492	-	-
FBY J	0.503	1.000	1.000	0.547	1.000	1.000	1.000	1.000	1.000	1.000	0.503	-
LBN A	0.485	1.000	1.000	0.502	1.000	1.000	1.000	1.000	1.000	1.000	0.500	1.000

Table 7.15: Pairwise R_{ST} values (above diagonal) between populations (n = 13), based in 11 microsatellite loci, and associated p-values (below diagonal, no significant differences)

	TKE A	ELN A	ELN J	EKM J	WCP A	SUN J	KNY A	SWA J	BRE J	DEH A	FBY A	FBY J	LBN A
TKE A		-0.001	-0.005	0.007	-0.015	-0.009	-0.006	-0.018	-0.016	-0.004	-0.011	-0.012	0.007
ELN A	0.330		-0.008	-0.007	-0.019	-0.007	-0.001	-0.007	-0.021	0.012	-0.012	-0.017	0.006
ELN J	0.485	0.522		-0.005	-0.015	-0.018	-0.004	0.003	0.000	0.004	-0.016	0.003	-0.017
EKM J	0.226	0.575	0.590		-0.010	0.009	0.004	0.008	-0.009	0.013	-0.008	-0.010	0.010
WCP A	0.851	0.824	0.912	0.801		-0.025	-0.016	-0.005	-0.005	-0.009	-0.019	-0.006	-0.024
SUN J	0.583	0.462	0.907	0.205	0.979		-0.013	-0.004	-0.014	-0.003	-0.006	0.002	-0.002
KNY A	0.485	0.329	0.474	0.285	0.913	0.776		0.006	0.004	-0.016	-0.006	0.001	-0.014
SWA J	0.925	0.493	0.311	0.221	0.484	0.468	0.211		-0.015	0.010	-0.010	-0.011	0.015
BRE J	0.903	0.879	0.387	0.746	0.463	0.787	0.250	0.885		0.005	-0.020	-0.014	0.000
DEH A	0.427	0.172	0.306	0.168	0.643	0.419	0.908	0.173	0.244		0.004	0.005	-0.005
FBY A	0.717	0.631	0.928	0.740	0.975	0.542	0.505	0.700	0.986	0.249		-0.015	0.001
FBY J	0.728	0.757	0.298	0.796	0.471	0.270	0.291	0.749	0.843	0.219	0.914		0.003
LBN A	0.200	0.229	0.918	0.195	0.988	0.386	0.854	0.126	0.358	0.515	0.340	0.254	

Locality level

Pairwise population exact tests revealed no significant differentiation between juvenile and adult samples within each of the five localities represented by both ($p > 0.50$ for all five comparisons). Thus, juvenile and adult populations could be pooled within each sampling locality (Balloux and Lugon-Moulin 2002). At the locality level, with juvenile and adult samples within each locality pooled, there were no significant pairwise genetic differences (Table 7.16).

Table 7.16: P-values for pairwise population exact tests of genetic differentiation, based on 11 microsatellite loci, between localities (n = 8, no significant differences)

	TKE	ELN	EKM	WCP/SUN	KNY/SWA	BRE/DEH	FBY
ELN	0.497	-	-	-	-	-	-
EKM	0.264	0.529	-	-	-	-	-
WCP/SUN	0.543	1.000	0.481	-	-	-	-
KNY/SWA	0.567	1.000	0.488	1.000	-	-	-
BRE/DEH	0.568	1.000	0.508	1.000	1.000	-	-
FBY	0.331	0.485	0.242	0.465	0.483	0.512	-
LBN	0.471	1.000	0.503	1.000	1.000	1.000	0.569

Pairwise genetic comparisons based on R_{ST} also showed no significant differences between geographic localities (n = 8 localities), and all pairwise R_{ST} values were low, showing high genetic similarity. The highest R_{ST} value at the locality level (R_{ST} = 0.010, p = 0.192) was observed between East Kleinemonde and Langebaan (Table 7.17).

Table 7.17: Pairwise R_{ST} values (above diagonal) between localities (n = 8), based in 11 microsatellite loci, and associated p-values (below diagonal, no significant differences)

	TKE	ELN	EKM	WCP/SUN	KNY/SWA	BRE/DEH	FBY	LBN
TKE		-0.002	0.007	-0.006	-0.015	-0.013	-0.007	0.007
ELN	0.407		-0.004	-0.007	-0.001	-0.001	-0.004	-0.008
EKM	0.231	0.596		0.005	0.003	-0.001	-0.005	0.010
WCP/SUN	0.566	0.774	0.207		-0.005	-0.003	0.002	-0.008
KNY/SWA	0.965	0.419	0.243	0.643		-0.007	-0.005	-0.002
BRE/DEH	0.928	0.397	0.428	0.495	0.861		-0.005	-0.005
FBY	0.660	0.567	0.661	0.215	0.652	0.652		0.005
LBN	0.191	0.660	0.192	0.675	0.423	0.581	0.210	

Analysis of molecular variance

An AMOVA conducted on the microsatellite data showed no significant genetic variability at any of the four hierarchical levels tested (*among geographic localities*, *among populations within localities*, *among individuals within populations* or *within individuals*), with low levels of genetic differentiation at all levels, although most of the variation was observed *within individuals* (Table 7.18).

Table 7.18: AMOVA results, to determine the level of microsatellite genetic variability among geographic localities (n = 8), among populations within localities (n = 5 localities each represented by 2 populations), among individuals within populations (n = 13), and within individuals (n = 330)

Source of variation	Deg. of freedom	Sum of squares	Variance component	Percent variation	Fixation index	*p*
Among localities	7	20.487	-0.005	-0.160	F_{CT} -0.0016	0.852
Among populations	5	16.837	0.001	0.020	F_{SC} 0.0002	0.413
Among individuals	317	1058.142	-0.017	-0.050	F_{IS} -0.0050	0.716
Within individuals	330	1112.500	3.371	100.640	F_{IT} -0.0064	0.763
Total	*659*	*2410.391*	*3.350*			

An AMOVA to test for differences among juvenile and adult populations also showed no significant differences at any level, and again most variation was observed *within individuals* (Table 7.19).

Table 7.19: AMOVA results, to determine the level of microsatellite genetic variability between juvenile and adult groups (n = 2), among populations within the juvenile and adult groups (n = 6 juvenile populations and 7 adult populations), among individuals within separate populations (n = 13), and within individuals (n = 330)

Source of variation	Deg. of freedom	Sum of squares	Variance component	Percent variation	Fixation index	*P*
Between groups	1	3.262	0.001	0.020	F_{CT} 0.0002	0.396
Among populations	11	34.061	-0.005	-0.140	F_{SC} -0.0014	0.843
Among individuals	317	1058.142	-0.017	-0.500	F_{IS} -0.0046	0.724
Within individuals	330	1112.500	3.371	100.620	F_{IT} -0.0062	0.765
Total	*659*	*2410.391*	*3.350*			

Relatedness

The relatedness analyses showed low pairwise relatedness between individuals within the global sample for all three indices, although relatedness coefficients in some comparisons reached maxima of 1.00, 0.50 and 0.83 for the Queller and Goodnight (1989), Ritland (1996) and Lynch and Ritland (1999) indices, respectively. Within each locality, mean pairwise estimates and associated variances were consistently low for all three indices (Table 7.20), and Kruskal-Wallis ANOVAs showed no significant differences among localities for the Ritland (1996) or Lynch and Ritland (1999) indices. Significant differences were, however, observed for the Queller and Goodnight (1989) index ($p = 0.008$). Tukey's post hoc test indicated that False Bay exhibited significantly higher pairwise relatedness than East London ($p = 0.003$) and Breede/De Hoop ($p = 0.017$); although the mean relatedness for all groups was less than 0.01. None of the eight sampling localities showed overall within-locality relatedness coefficients significantly greater than the permuted means (Table 7.20).

Table 7.20: Numbers of individuals per locality (n), numbers of within-population pairwise comparisons (*NC*), means and variances (σ^2) of each of the relatedness indices, and the within-population means and p-values for the eight sampling localities, based on 11 microsatellite loci

			Queller and Goodnight (1989)		Ritland (1996)		Lynch and Ritland (1999)		Within-localities	
Locality	n	*N*C	Mean	σ^2	Mean	σ^2	Mean	σ^2	Mean	*p*
TKE	25	300	0.009	0.027	-0.001	0.002	0.000	0.003	18.61	0.102
ELN	41	820	-0.019	0.021	-0.002	0.002	-0.003	0.003	17.51	0.897
EKM	41	820	-0.006	0.022	0.001	0.003	0.001	0.003	18.23	0.246
WCP/SUN	48	1128	-0.009	0.021	-0.004	0.002	-0.004	0.002	18.08	0.395
KNY/SWA	48	1128	-0.002	0.019	-0.003	0.001	-0.004	0.002	18.13	0.332
BRE/DEH	47	1081	-0.014	0.021	-0.002	0.002	-0.002	0.002	17.76	0.747
FBY	55	1485	0.005	0.020	-0.002	0.002	-0.002	0.003	17.69	0.825
LBN	25	300	-0.001	0.022	-0.001	0.002	<0.001	0.003	18.65	0.082

Population assignment

The population assignment analysis showed no separation of individuals into discrete populations. All pairwise comparisons (n = 28 pairs) of the likelihood of assignment of individuals from each of two populations to one or the other population showed completely overlapping likelihoods, with the likelihoods of assignment to either population roughly even for all pairs of sampling localities (Figure 7.7). In these plots, discrete populations would show separate distributions associated more strongly with opposite axes, while distribution along a diagonal taken through the origin indicates even likelihood of assignment to either population.

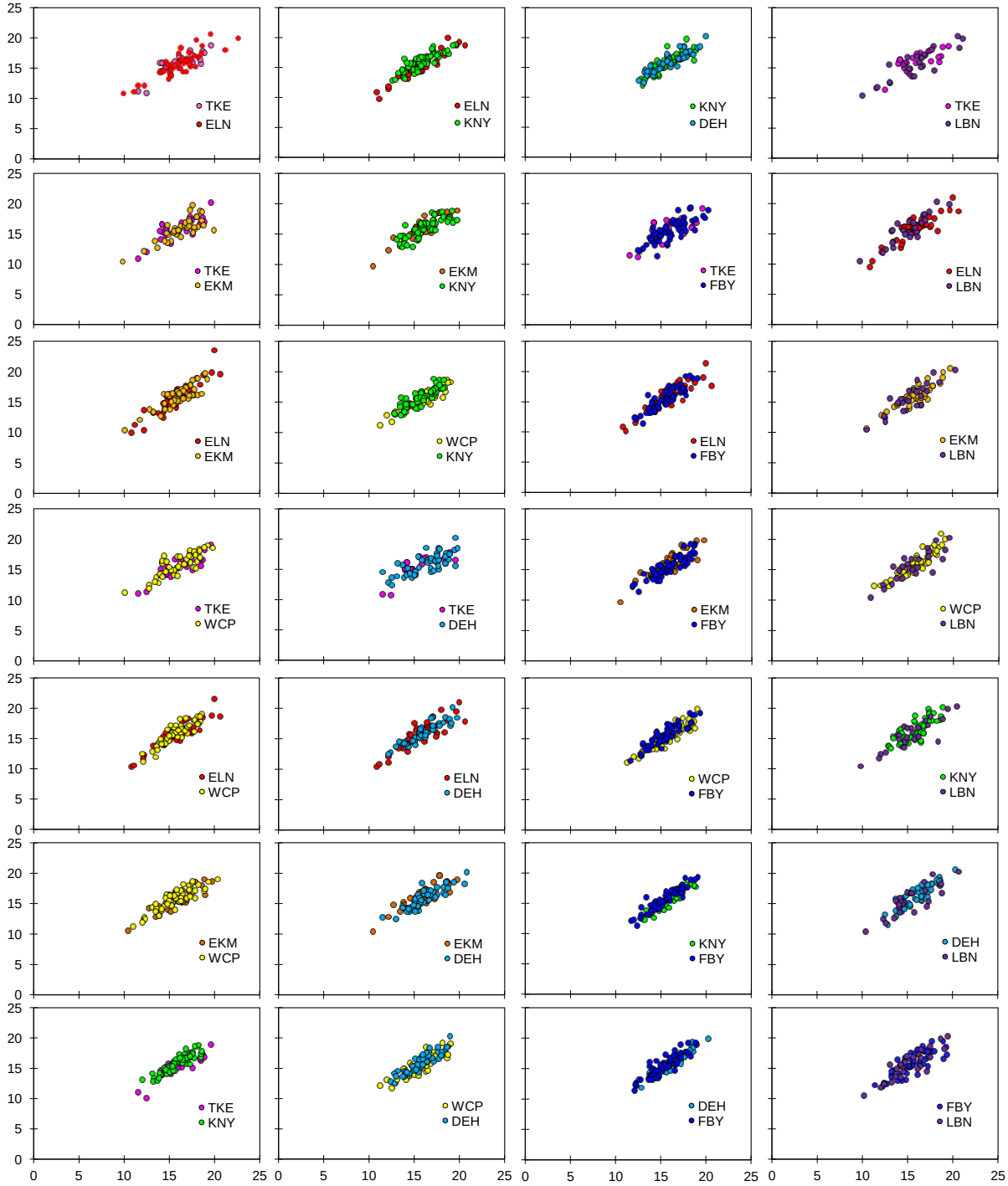

Figure 7.7: Pairwise likelihood assignment plots, created from the population assignment analysis, for the eight sampling localities (locality colours are consistent with those of the sampling localities in Figures 7.1 and 7.2). Each axis in each plot represents the likelihood of assignment to one of the two populations. Discrete populations would be distributed towards higher values on separate axes, while distribution along the diagonal indicates similar likelihood of assignment to either population

The population assignment analysis run in Genalex, using the "leave one out" approach, was unable to correctly assign most individuals to their original sampling localities, based on allele frequencies, which is expected when there are low levels of genetic differentiation (Waser and Strobeck 1998). No population had more than 20% of its original members assigned correctly, with a mean proportion of correct assignments across localities of only 10.0% (± 5.7%) (Figure 7.8a). In contrast, the population assignment analysis run in Arlequin, not adopting the "leave one out" approach, was able to successfully assign the majority of individuals to their original sampling localities (Figure 7.8b). For this analysis, the best assignment of original sampling locality members to the correct population was 80%, with a mean successful assignment across the eight sampling localities of 68.5% (± 9.4%).

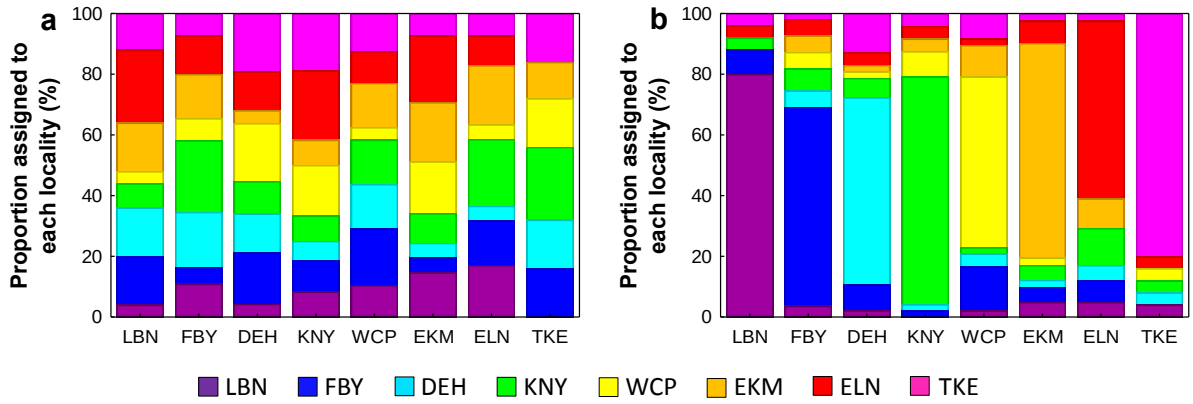

Figure 7.8: Proportions (%) of individuals sampled from each of the original sampling localities assigned (based on most likely allele frequencies) to each of the eight putative localities, a) adopting the "leave one out" approach as calculated in Genalex, and b) not adopting the "leave one out" approach as calculated in Arlequin

Factorial correspondence analysis

Factorial correspondence analysis was conducted on four different groupings of samples; eight sampling localities, thirteen populations, six juvenile populations and seven adult populations. In all four analyses there was no clustering or distinct separation of any of the groups. Results of the FCA conducted on the eight sampling localities, as well as the six juvenile populations are presented. These two groups were chosen as the overall aim of this chapter was to identify white steenbras genetic differentiation among coastal regions, and distinct clustering of juvenile genotypes associated with the geographical sampling locations would indicate spatial genetic structure. The results of the other two analyses showed similar results, and these are not presented.

The FCA showed no distinct separation of any of the eight localities (Figure 7.9a). Figure 7.9b shows an expansion of the centre of the ordination space, in which most of the samples were situated. The Transkei locality distribution was slightly offset along axes 2 (y-axis) and 3 (z-axis), while Langebaan and East Kleinemonde were slightly shifted to the left, and Breede/De Hoop to the right, along axis 1 (x-axis), although most samples in these four groups overlapped with the majority of samples from the other localities.

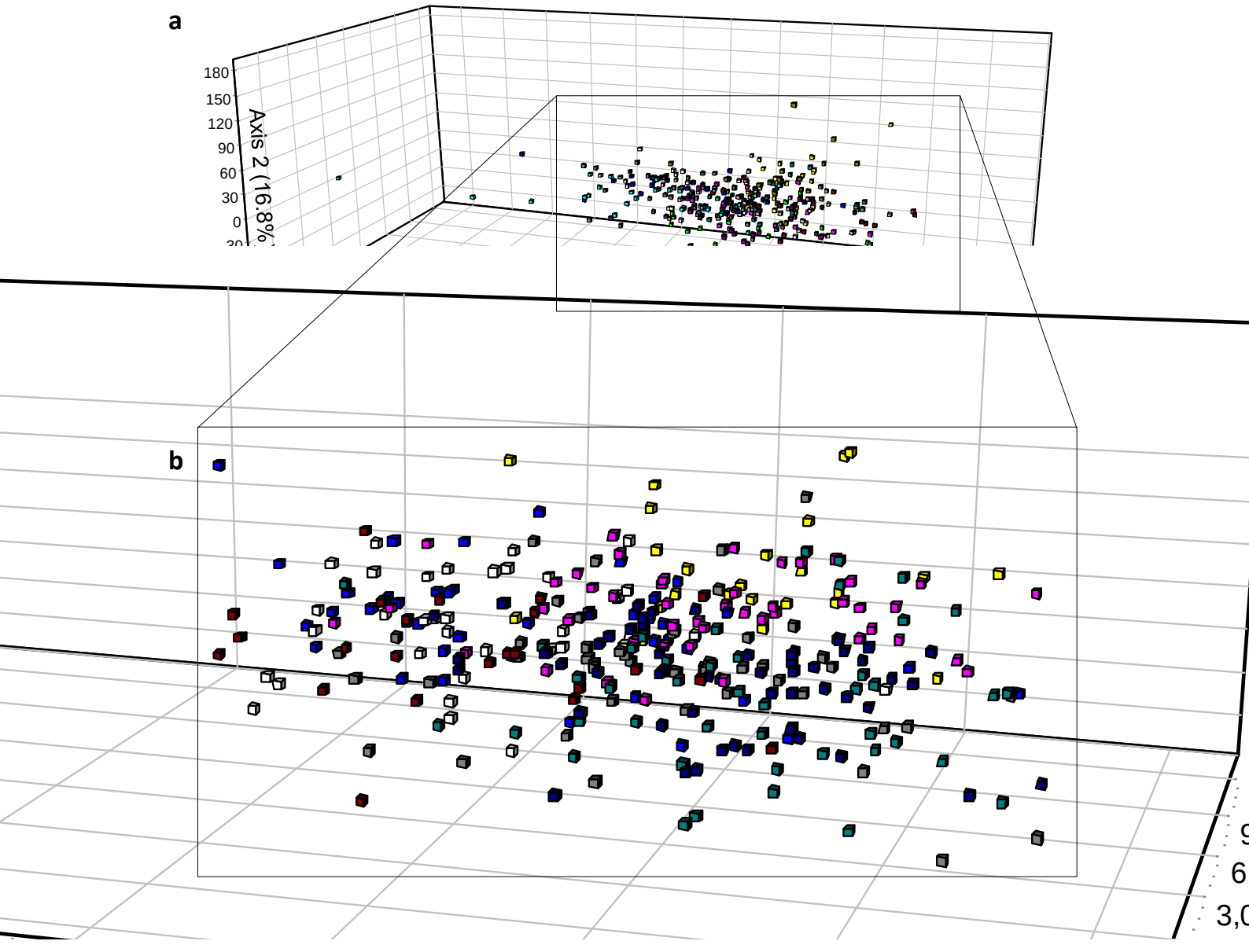

Figure 7.9: Factorial correspondence analysis of genotypes from the eight localities (juveniles and adults pooled within the five sites with both classes), based on allele frequencies of 11 microsatellite loci (the programme does not provide an option to edit colours, therefore locality colours do not match those of Figures 7.1 or 7.2)

The FCA ordination plot of the juvenile samples (represented by six populations) also showed no distinct separation of any of the groups (Figure 7.10a). Figure 7.10b shows an expansion of the centre of the ordination space, in which most of the samples were situated. In this analysis, the East Kleinemonde population showed a slightly shifted distribution along axis 1 (x-axis), when compared to the other groups. The Breede group separated out slightly along axes 2 (y-axis) and 3 (z-axis), while the False Bay genotypes showed a slight shift along axis 2 (y-axis), when compared to the other groups. Again, however, most genotypes from all groups overlapped in the centre of the ordination space, showing little spatial genetic differentiation among juvenile white steenbras.

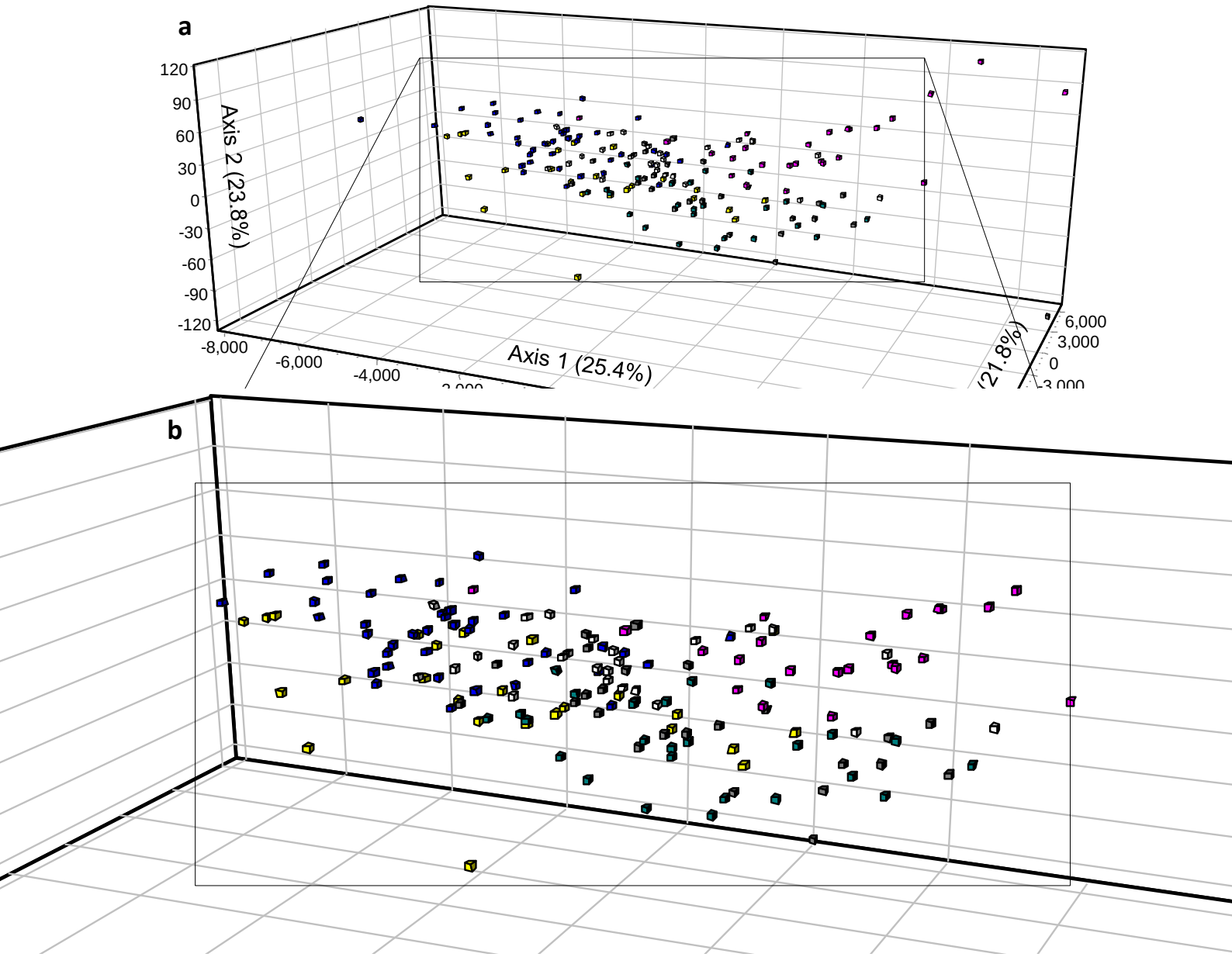

Figure 7.10: Factorial correspondence analysis of juvenile samples, based on allele frequencies of 11 microsatellite loci (colour codes do not match those of Figure 7.9)

Structure analysis

The Structure analysis was aimed at estimating the probability that the global sample was drawn from a number of putative populations (*K*), given the observed genotypes. The highest probability was observed for *K* = 1, in both analyses (without and with prior locality information, Figure 7.11), indicating that the overall sample (n = 330 juvenile and adult individuals from 8 sampling localities) is most likely representative of a single population. The results of the Kruskal-Wallis ANOVA showed that there were significant differences in probability estimates among *K*-values ($p < 0.001$). Tukey's post hoc tests identified significant differences for the first analysis (no prior information) between *K* = 1 and *K* = 4 to 8, and for the second analysis (with prior information) between *K* = 1 and *K* = 3 to 8, but in neither case was the probability of *K* = 1 significantly different to the probability of *K* = 2.

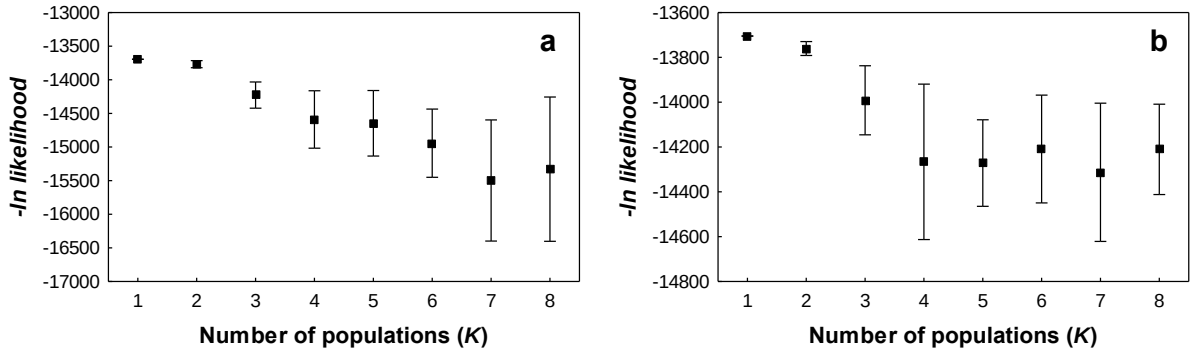

Figure 7.11: Mean (± SD) probability (negative log likelihood) of the data for each value of *K* (user-defined numbers of putative populations), run with a) no prior information on sample localities, and b) including prior information on sample localities

In addition, the Structure software outputs graphs displaying the estimated individual admixture proportions (i.e. proportions of an individual's genome that are attributed to each of the *K* putative populations). These individual admixture proportions, for *K* = 1 to 8, were remarkably similar among the eight sampling localities, indicating similar probabilities for individuals in all sampling localities of coming from any of the *K* populations, which is expected when populations are not genetically discrete. Figure 7.12 represents these admixture proportions for each analysis (a – h represent analyses for *K* = 1 to 8, respectively), with each of the 330 individuals represented as a single multicoloured vertical line, with the proportions of each different colour representing the proportion of membership of that individual to each of the *K* putative populations. The figure also indicates that admixture proportions of individuals did not vary among the original sampling localities, which further indicates the similar likelihood of individuals within each locality of having been drawn from each of the *K* putative populations.

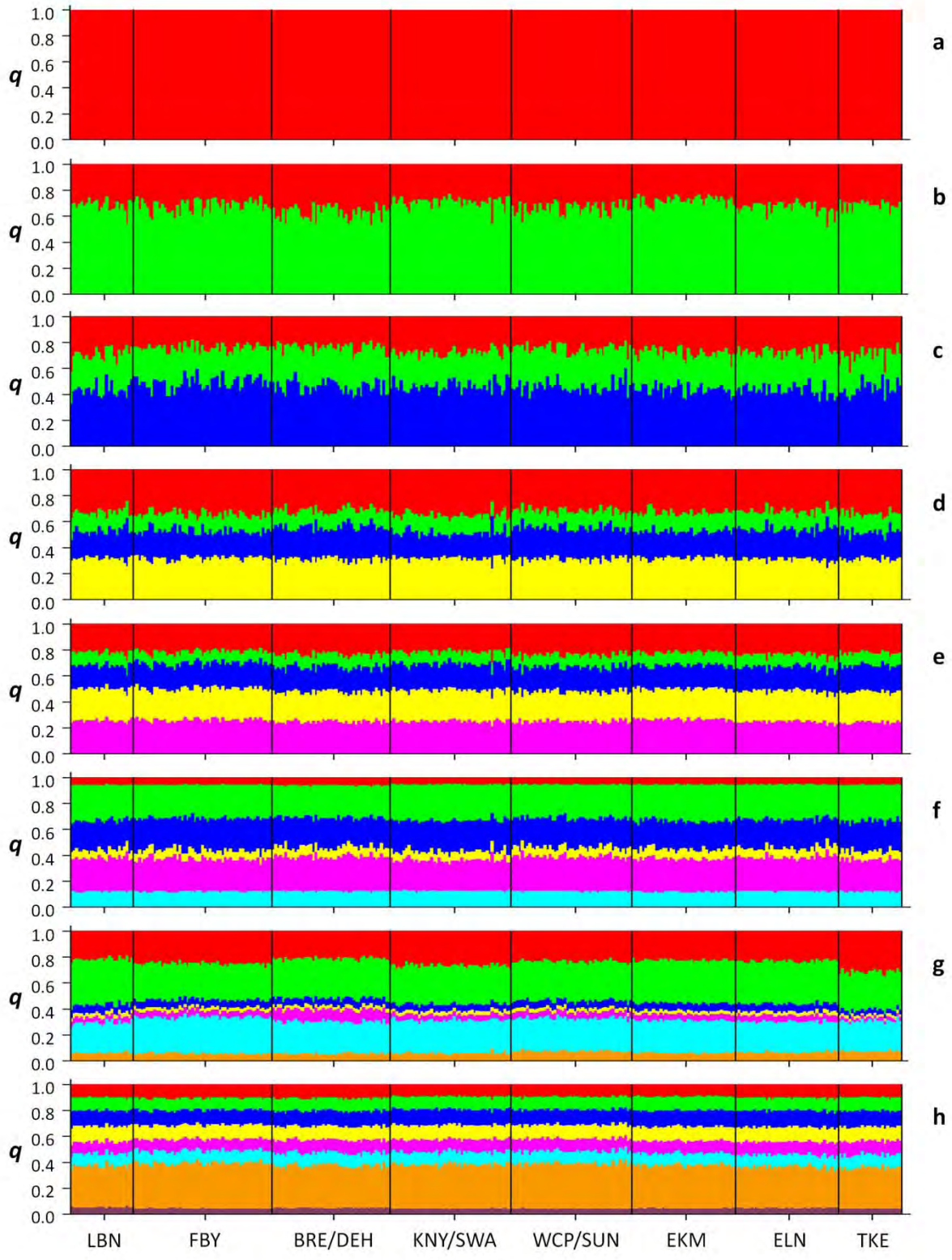

Figure 7.12: Plots of individual admixture proportions (*q*) from each of the putative populations for *K* = 1 to 8 (a - h), with each hypothetical population in each plot represented by a different colour. Each plot is comprised of 330 vertical lines, each representing one individual (x-axis), with individuals grouped by original sampling locality

Isolation by distance

As with the mtDNA, the isolation-by-distance analysis of the microsatellite genotypes showed that there was no association between pairwise genetic differentiation (Slatkin's 1995 linearised F_{ST}) and pairwise geographic distance (Figure 7.13), and linear regression showed no significant correlation between the two variables (p = 0.227, R^2 = 0.022).

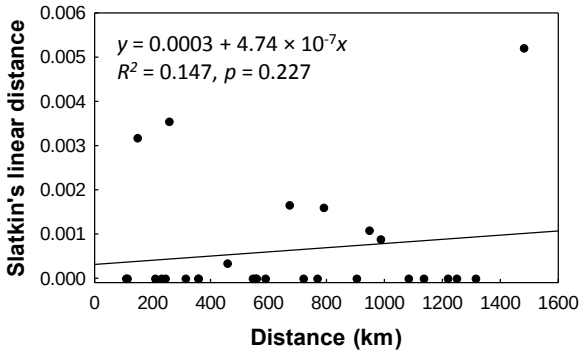

Figure 7.13: Scatterplot of Slatkin's (1995) linearised F_{ST} values for the microsatellite data, based on 11 loci, plotted against geographic distance (km) to assess isolation by distance, at the locality level (n = 8 localities)

Spatial autocorrelation

Correlation coefficients (*R*) calculated for the different distance classes showed no spatial autocorrelation at any distance class, for analyses run at the locality level (n = 8 localities), population level (n = 13 populations), or for separate analyses of adults (n = 7 populations) or juveniles (n = 6 populations) (Figure 7.14, a – d). Similarly, the analyses with distance classes defined logically by large geographic breaks between sampling localities, and with distance classes defined to ensure equal sample sizes in each, showed no significant autocorrelation at any distance (Figure 7.14, e and f). The non-significant probability of the estimated *R* at each distance class (p > 0.05 in all cases) being greater than that determined by permutation indicated no positive spatial autocorrelation in any distance class, in any of the six analyses. Bootstrap confidence intervals showed no departure from the null hypothesis of no positive spatial autocorrelation (*R* = 0), except in two cases. These were observed at the 340 to 440 km distance class in the analysis in which distance classes were defined based on logical geographic divisions (Figure 7.14e), and at the 267 to 382 km distance class in the analysis with equal sample sizes in each class (Figure 7.14f). Significant negative spatial autocorrelation was also observed in the 120 to 200 km distance class in the analysis with logical distance classes (Figure 7.14e).

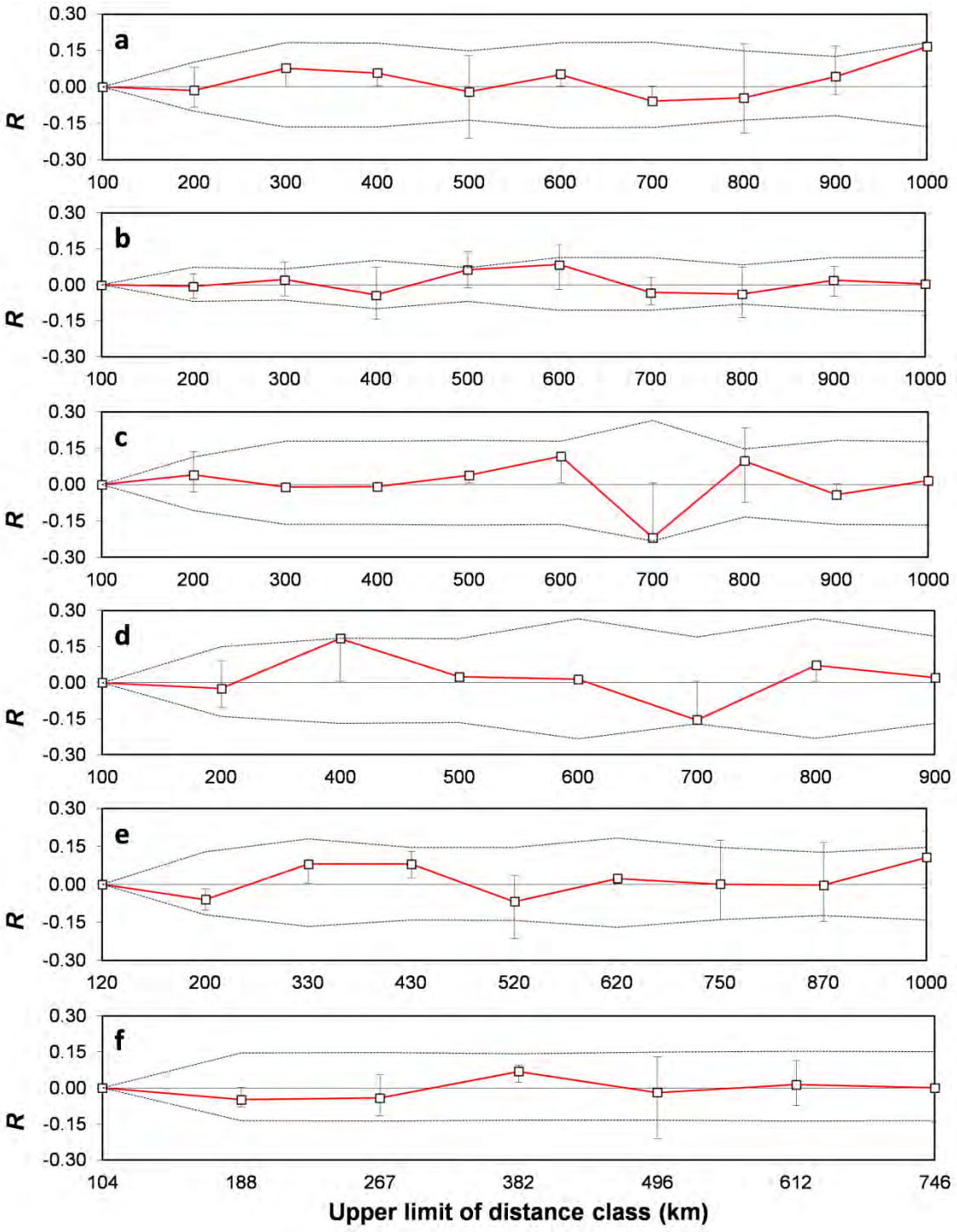

Figure 7.14: Spatial autocorrelation analyses for a) 8 localities, b) 13 populations, c) 7 adult populations, d) 6 juvenile populations, e) logical geographic delineation, and f) equal sample sizes in each distance class (note x-axes of d – f have different spatial scales). Red lines join estimated correlation coefficients (*R*, white markers) at each distance class. Dotted lines represent the 95% confidence interval around *R*, outside of which *R* would denote significant spatial autocorrelation (two-tailed). Bootstrap error bars around *R* that do not straddle *R* = 0 indicate deviation from the null hypothesis of no positive spatial autocorrelation, x-axis)

Synthesis of microsatellite results

Selected microsatellite results were also plotted in such a way as to facilitate the transfer of statistical results to biological meaning. Expected heterozygosity (H_E) indicated high levels of genetic diversity and showed remarkable similarity across all sampling localities, with negligible declines in the two edge populations (Figure 7.15a). The inbreeding coefficient (F_{IS}) was low for all localities, showing low within-locality genetic similarity when compared to overall genetic similarity (Figure 7.15b). The two highest F_{IS} values were observed in Langebaan and Transkei, which (although at the two geographic extremes) were represented by the lowest sample sizes, while the lowest F_{IS} was observed for False Bay, with the largest sample size. Most individuals were "mis-assigned" in the population assignment analysis (Figure 7.15c), with the maximum of 19% (in the East Kleinemonde locality) correctly assigned to their original sampling locality. In terms of pairwise R_{ST} values, Transkei (black bars) showed the greatest genetic differentiation to Langebaan (i.e. the two most distant localities), while Langebaan (black bars) showed the greatest differentiation to East Kleinemonde. All R_{ST} values were low, with no significant differences, and no geographic trend (Figure 7.15d).

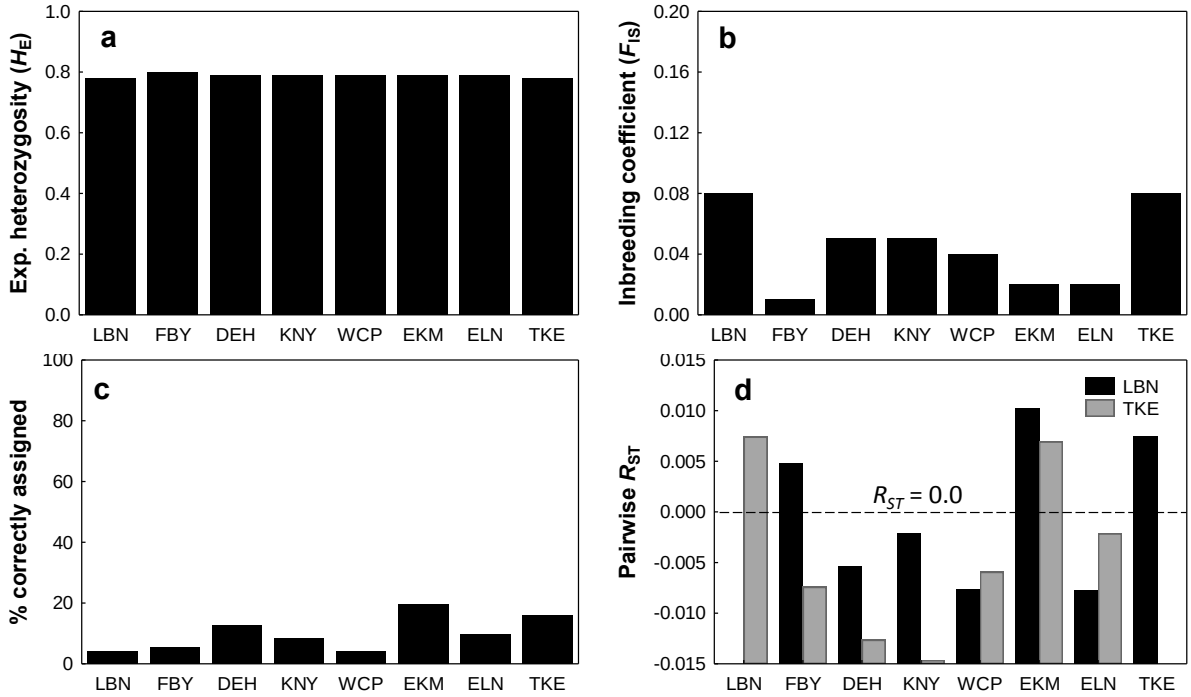

Figure 7.15: Summary of selected microsatellite analysis results recorded for each geographic locality; a) expected heterozygosity (H_E), b) inbreeding coefficient (F_{IS}), c) percentage of individuals correctly assigned to their original sampling localities, and d) pairwise R_{ST} values recorded between the western-most (LBN) and eastern-most (TKE) localities and each of the other localities, with the dotted line representing R_{ST} = 0.0. For localities with juvenile and adult samples the two age classes were pooled; DEH represents BRE/DEH, KNY represents KNY/SWA and WCP represents WCP/SUN

7.4 Discussion

There is a general lack of information on the genetic stock structure of fish species in South African waters, and the white steenbras is no exception. There is also a lack of empirical evidence of the adult spawning migration. This chapter has combined mitochondrial and microsatellite DNA analyses to determine the genetic stock structure of the white steenbras, and provide further ecological information to augment that obtained through other techniques.

7.4.1 Summary statistics, genetic diversity indices and historical population demography

Genetic diversity

Haplotype diversity was high in all localities, with no geographic trend. Nucleotide diversity was also consistent among localities and moderately high, indicating a high level of genetic diversity (Nei and Tajima 1981). Overall, haplotype and nucleotide diversity for the white steenbras control region fell within the range observed for other marine fishes (Grant and Bowen 1998) (Table 7.21).

When compared to other South African sparids, genetic diversity was similar to that of the territorial reef-dwelling red roman (Teske *et al*. 2010), yet higher than that recorded for Cape stumpnose *Rhabdosargus holubi* (Oosthuizen 2006). The striped seabream *Lithognathus mormyrus* exhibited similar haplotype diversity but considerably higher nucleotide diversity (Sala-Bozano *et al*. 2009). In the Eastern Atlantic and Mediterranean Sea, the latter species exhibited lower haplotype diversity, but higher nucleotide diversity (Bargelloni *et al*. 2003) than white steenbras, indicative of relatively fewer haplotypes but greater genetic variability among them. When compared to sparids in other areas, white steenbras genetic diversity was similar to *Spondyliosoma cantharus,* but higher than *Pagrus pagrus*, *Dentex dentex* and *Pagellus bogaraveo* in the Eastern Atlantic and Mediterranean Sea (Bargelloni *et al*. 2003). The differences between white steenbras and these other species may be a result of differences in local oceanographic conditions and geological and climatic histories.

Compared to other South African marine species, diversity indices were higher than those of the shallow- and deep-water hakes *Merluccius capensis* and *M. paradoxus*, respectively (von der Heyden *et al*. 2007), but remarkably similar to those obtained for banded goby (Gobiidae), a southern African endemic with low levels of adult movement (Neethling *et al*. 2008). The similarity of white steenbras with banded goby and the red roman in terms of genetic homogeneity across their ranges, despite vastly different life history strategies, is likely a result of dispersal during their long larval phases (Teske *et al*. 2010), suggesting that the distribution of genetic diversity is largely influenced by oceanographic conditions.

When compared to other estuarine-associated fishes, white steenbras genetic diversity was lower than that of the white seabream *Diplodus sargus* in the Northeast Atlantic and Mediterranean Sea (Domingues *et al*. 2007). The spotted grunter in South Africa (Klopper 2005) and Australian barramundi *Lates calcarifer* in Northern Australia (Chenoweth *et al*. 1998) exhibited lower haplotype diversity but higher nucleotide diversity than white steenbras, indicating greater variability among haplotypes. The higher nucleotide diversity observed in the spotted grunter is possibly due to the large population size occurring around the South African coastline, resulting in lower loss of genetic diversity due to drift, and the consequent accumulation of mutations over time (Klopper 2005), whereas the higher nucleotide diversity in Australian barramundi is caused by the strong spatial genetic structuring (Chenoweth *et al*. 1998).

Table 7.21: Haplotype diversity (*h*) and nucleotide diversity (π) indices for population studies on selected fishes, based on mitochondrial control region sequencing

Species	*h*	π	Source
Southern Africa			
Lithognathus lithognathus	0.997 - 1.00	0.009 - 0.013	Current study
Lithognathus mormyrus	0.967	0.051	Sala-Bozano *et al*. (2009)
Chrysoblephus laticeps	1.0	0.005 – 0.011	Teske *et al*. 2010
Caffrogobius caffer	0.965	0.0100	Neethling *et al*. (2008)
Rhabdosargus holubi	0.89 – 0.96	0.0048 – 0.0064	Oosthuizen 2006
Hippocampus capensis	0.46 - 0.84	0.0029 - 0.00461	Teske *et al*. (2003)
Merluccius capensis	0.85 – 0.88	0.0057 – 0.0063	von der Heyden *et al*. (2007)
Merluccius paradoxus	0.44 – 0.57	0.0011 – 0.0015	von der Heyden *et al*. (2007)
Pomadasys commersonnii	0.968 – 0.987	0.021 – 0.023	Klopper (2005)
Atlantic and Mediterranean Sea			
Thunnus thynnus	0.986	0.0179	Boustany *et al.* (2008)
Diplodus sargus	0.85 – 1.0	0.024 – 0.036	Domingues *et al*. (2007)
Spondyliosoma cantharus	0.94 – 0.98	0.016 – 0.018	Bargelloni *et al*. (2003)
Pagrus pagrus	0.35 – 0.53	0.003 – 0.006	Bargelloni *et al*. (2003)
Dentex dentex	0.49 – 0.67	0.008 – 0.049	Bargelloni *et al*. (2003)
Pagellus bogaraveo	0.069 – 0.52	0.0004 – 0.005	Bargelloni *et al*. (2003)
Lithognathus mormyrus	0.62 – 0.90	0.012 – 0.017	Bargelloni *et al*. (2003)
Pacific			
Gadus macrocephalus	0.41 – 0.71	0.0002 – 0.0012	Liu *et al*. (2010)
Lateolabrax maculatus	0.96 – 1.0	0.008 – 0.015	Liu *et al*. (2006)
Lateolabrax japonicus	0.96 – 1.0	0.027 – 0.035	Liu *et al*. (2006)
Australia			
Lethrinus miniatus	0.610 – 0.980	0.004 – 0.200	van Herwerden *et al*. (2009)
Lutjanus sebae	0.690 – 0.920	0.0032 – 0.0076	van Herwerden *et al*. (2009)
Lutjanus carponotatus	0.658 – 0.881	0.003 – 0.013	Evans *et al*. (2010)
Plectropomus maculatus	0.889 – 0.984	0.003 – 0.017	Evans *et al*. (2010)
Lates calcarifer	0.763 – 0.933	0.0269 – 0.0598	Chenoweth *et al*. (1998)

Genetic diversity estimated using polymorphic microsatellite loci was high, for all localities and overall, as for the mtDNA. Of the 15 loci initially tested, four were excluded at different stages of the analyses. *PBt007* and *LLt024*, isolated in *Pachymetopon blochii* and white steenbras, respectively (Reid *et al*. submitted), and *PB106* isolated in *Pagellus bogaraveo* (Piňera *et al*. 2006) were excluded partway through the study due to poor amplification and departure from HWE. *CL011*, originally isolated in red roman (Teske *et al*. 2009), was later excluded due to departure from HWE. Therefore, it seems that for white steenbras, loci isolated from related species performed less successfully. For the remaining loci, observed heterozygosities (H_O) matched those expected (H_E). Genetic diversity, in terms of mean number of alleles, mean allelic richness and observed heterozygosity, was remarkably consistent among sampling localities, showing little evidence of spatial genetic variability.

While H_O is likely to vary widely, depending on the species (even within a species), the specific loci scored, the number of loci scored and the sample sizes obtained (Fritsch *et al*. 2007), those observed for white steenbras (0.72 – 0.79) were consistent with those of numerous other fishes, for example sea bass *Dicentrarchus labrax* (0.75 – 0.80, Fritsch *et al*. 2007), and Japanese eel *Anguilla japonica* (0.75 – 0.86, Han *et al*. 2010), and fell within the ranges of others, such as red snapper *Epinephelus morio* (0.49 – 0.92, Zatcoff *et al*. 2004) and coho salmon *Oncorhynchus kisutch* (0.55 – 0.91, Beacham *et al*. 1995). When compared to other sparids, white steenbras H_O was higher than those observed for the white sea bream (0.31 to 0.51, Perez-Ruzafa *et al*. 2006), but similar to those observed for gilthead sea bream *Sparus aurata* (0.74 to 0.86, De Innocentiis *et al*. 2004) and striped sea bream (0.62 to 0.87, Sala-Bozano *et al*. 2009), in the western Mediterranean and Atlantic Ocean. However, H_O (0.72 – 0.79), N_A (8.17 – 10.0) and A_R (7.72 – 8.15) in the different localities were all slightly lower than those estimated for red roman along the South African coastline (Teske *et al*. 2010) (H_O: 0.78 – 0.89, N_A: 8.29 – 15.0, A_R: 8.20 – 8.65).

Population size and demographic history

Climatic oscillations and major glaciations during the Pleistocene period are likely to have caused population expansion and decline events (Grant and Bowen 1998), which would have shaped the contemporary population structures of most extant species (Excoffier 2004). Grant and Bowen (1998) suggested that a combination of high haplotype diversity and relatively high nucleotide diversity (> 0.005) are indicative of secondary contact between previously differentiated allopatric lineages, or a long evolutionary history in a large stable population. Conversely, Neethling *et al*. (2008) suggested that nucleotide diversity of 0.010 is low, and combined with high haplotype diversity reflects a population expansion associated with low genetic differentiation.

Allopatric white steenbras populations are unlikely, given the high larval dispersal capability, and the migratory adult life stage. However, historical catch data from Namibia indicate catches beyond the northern limit of its published distribution range, the mouth of the Orange River (Smith and Smith 1986). The possibility of a secondary spawning aggregation in this region has been suggested, but that overexploitation during the 20th century reduced this stock to non-viability (SJ Lamberth, DAFF, pers. comm.). However, pairwise genetic comparisons showed no evidence of genetic differentiation among localities, and all sampling localities were represented in the main clade and smaller clade of the haplotype network, suggesting that the presence of extant allopatric lineages is unlikely.

Much about the demographic history of a population can be inferred from the shape of its mismatch distribution (Rogers and Harpending 1992). The bimodal shape of the white steenbras distribution closely reflected those simulated by Aris-Brosou and Excoffier (1996) for populations at stationarity and with homogeneity of mutation rates among nucleotide sites. However, Harpending's (1994) raggedness index (0.005) was low, indicative of a historical population expansion (Excoffier and Lischer 2009), and not dissimilar to other South African marine species, spotted grunter (0.005), dusky kob *Argyrosomus japonicus* (0.001, Klopper 2005) and red roman (0.020, Forget 2007). Consistent with this was the non-significant departure of the observed distribution from that expected under population expansion. A similar non-significant bimodal distribution was observed for Japanese sea bass *Lateolabrax japonicus*, which the authors interpreted as population expansion (Liu *et al*. 2006). Therefore, the bimodal shape of the distribution may reflect historical population stationarity, with the larger left-hand peak indicating a more recent population expansion. The non-significance of the departure from a unimodal distribution is likely a result of the magnitude of this peak, which could be interpreted as an L-shaped distribution and, therefore, population expansion after a decline event (Rogers and Harpending 1992). It appears, therefore, that the population exhibited a long period of stationarity, followed by a population decline and subsequent expansion. Historical population expansions have also been inferred from the mismatch distributions of other South African marine fishes; for example, Cape stumpnose (Oosthuizen 2006), shallow-water hake (von der Heyden *et al*. 2007), banded goby (Neethling *et al*. 2008) and red roman (Teske *et al*. 2010). The significant negative values of Tajima's (1989) *D* and Fu's (1997) F_S provide further evidence of an expanding population (Tajima 1989, Aris-Brosou and Excoffier 1996).

The notion of a post-decline expansion is supported by the haplotype network (Figure 7.2). The high frequencies of rare haplotypes, which are mutational derivatives of a few common haplotypes, has been observed in the mtDNA control regions of numerous fish species (Billington and Hebert 1991),

for example red snapper *Lutjanus campechanus* (Camper *et al*. 1993), red drum *Sciaenops ocellatus* (Gold *et al*. 1993), white seabream (Bargelloni *et al*. 2005) and shallow-water hake (von der Heyden *et al*. 2007). The star-like morphology of the main clade of the network and the high number of rare haplotypes (which represent new mutations) are indicative of a population expansion (Slatkin and Hudson 1991, Fu and Li 1993). There was also one long external branch, with up to 17 mutational steps. Fu and Li (1993) suggested that an excess of mutations in the external branches can indicate the presence of negative selection. However, selection is likely to result in low genetic diversity indices, such as those observed for Pacific cod *Gadus macrocephalus* (Liu *et al*. 2010), which were considerably lower than those observed for white steenbras (Table 7.21). A topology with a few common haplotypes and high numbers of rare haplotypes, and a long external branch with high numbers of mutations, was also observed for red roman (Teske *et al*. 2010). These authors proposed that the external branch may have been the result of a separate genetic lineage. The possibility of an extant second genetic lineage of white steenbras is unlikely, based on the migratory adult life stage and the restricted range of this species. However, this possibility cannot be discounted altogether (Grant and Bowen 1998, Teske *et al*. 2010).

The estimated time since the start of the white steenbras population expansion, 21 500 to 7 000 years before present, is consistent with values from other South African marine taxa, such as 14 800 to 9 900 years for red roman (Forget 2007), 23 000 to 4 500 years for shallow-water hake (von der Heyden *et al*. 2007) and 11 400 to 4 600 years for deep-water hake (von der Heyden *et al*. 2010). Similarly, Tolley *et al*. (2005) estimated time since population expansion in south coast rock lobster at between 10 600 and 5 300 years. It must be noted here that time since population expansion was estimated based on τ, which is taken as the mode of the mismatch distribution (Rogers and Harpending 1992). Furthermore, these times are based on mutation rates inferred from other species, and that confidence limits around these estimates are broad. However, they still provide a realistic estimate of time since expansion. The agreement among taxa provides testimony to this. Other than the upper estimates of 21 500 years for white steenbras and 23 000 years for shallow-water hake, most South African species cited here showed times since expansion approximately within the last 15 000 years. This roughly coincides with the glacial Holocene temperature increase of about 5.5°C (Sachs *et al*. 2001, von der Heyden *et al*. 2010). Expansions occurring within the last 10 000 years would have occurred since the end of the last glaciation period (von der Heyden *et al*. 2007). The concordance in South Africa, among a range of species (from crustaceans to teleosts), provides evidence that the population structures of marine organisms within this region have been shaped by similar biogeographical factors (Bremer *et al*. 2005), such as historical climatic conditions.

Tests for selective neutrality

Although the mitochondrial control region is considered not to be subject to natural selection (Liu *et al*. 2010), tests for selective neutrality have been incorporated into studies of this gene region, as the control region may be affected through the process of linked selection (Tajima 1989, Fu 1997). These tests, however, are all based on certain assumptions, such as stationary populations, no migration, and homogeneity of mutation rates at different nucleotide sites (Tajima 1989, Fu and Li 1993, Aris-Brosou and Excoffier *et al*. 1996, Fu 1997), many of which are unrealistic for natural populations (Excoffier *et al*. 1992). As such, neutrality tests are sensitive to violations of these assumptions (Aris-Brosou and Excoffier 1996, Ford 2002) and, as a result, have largely become regarded in the literature more as tests for demographic population changes than for selective neutrality (Guinand *et al*. 2004, Neethling *et al*. 2008, van Herwerden *et al*. 2009).

Overall, the four tests for neutrality provided inconsistent results. Wattersons's *F* showed no evidence of selection on the gene region under study, at any level, while roughly half the populations and localities differed significantly from neutrality based on Tajima's *D*, and Fu and Li's *D** and *F** values for most localities and populations were not significant, thus failing to reject the null hypothesis of selective neutrality. Conversely, all estimates of Fu's F_S were significant with large negative values, usually indicative of natural selection (Fu 1997). Although significant estimates of Tajima's *D* are expected in the presence of natural selection, Tajima (1989) cautioned that negative values could be indicative of a population expansion and Aris-Brosou and Excoffier (1996) showed that under sudden expansion of large magnitude, Tajima's *D* can be expected to depart from neutrality. The non-significant estimates could also indicate the absence, or simultaneous presence of both population expansion and heterogeneity of mutation rates at different loci, which have opposing effects on Tajima's *D* (Aris-Brosou and Excoffier 1996). The test described by Fu and Li (1993) is suggested to be among the most powerful for testing for selective neutrality, particularly in the presence of background selection (Fu 1997). Bertorelle and Slatkin (1995) suggested that the neutrality tests of Tajima (1989), Fu and Li (1993) and Fu (1997) may not be appropriate in the presence of heterogeneity of mutation rates, as they are based on the infinite sites model, which assumes homogeneity of mutation rates. Furthermore, Fu (1997) suggested that if the estimates of F_S are significant, while those of *D** and *F** are not, the observed polymorphism is likely a result of population expansion, or possible genetic hitch-hiking. Therefore, the results of the four tests of selective neutrality are more likely an artefact of population expansion, than robust evidence against selective neutrality. Further insight could be provided by the use of additional genetic markers.

7.4.2 Comparative analyses of genetic differentiation

Analysis of molecular variance

AMOVA is designed to delineate the genetic variability in a global sample, and identify the level at which most variability occurs. In the mtDNA, the greatest source of variability was identified within populations (i.e. inter-individual variability), while in the microsatellite loci the greatest variability was recorded within individuals. For the mtDNA, significant genetic variance was identified among geographic localities, although the magnitude of this variance was negligible. Furthermore, the microsatellite loci showed low, non-significant genetic variance among localities, indicating low levels of genetic variability among geographic localities.

The significant variability observed among geographic localities in the mtDNA, but not in the microsatellite loci, might reflect historical rather than contemporary divergence, as mtDNA has been shown to be more suited to assessment of historical population demography, while the latter are more suited to assessment of contemporary population structure (Zhang and Hewitt 2003). For example, microsatellites showed secondary contact and extensive inter-breeding among populations of striped sea bream (sand steenbras) along the South African east coast, for which mtDNA revealed deeply divergent lineages (Sala-Bozano *et al*. 2009). This highlights the value of employing a mitochondrial region and microsatellites to elucidate the patterns of gene flow and stock structure (Lemaire *et al*. 2005).

The variance component at the *among localities* level is determined by the correlations between random haplotypes drawn from each locality and from the entire sample (Excoffier *et al*. 1992). In a global sample exhibiting high haplotype diversity and a high proportion of rare haplotypes, as in the current study, differences among localities might be expected (Excoffier *et al*. 1992). Although some rare haplotypes may be present at few localities, it is more likely that these simply represent alleles that are rare in the species, throughout its distribution. With 174 haplotypes identified and sample sizes ranging from 21 to 55, it was not possible for a single locality to be entirely representative of the haplotypes occurring within the global sample, suggesting that increased sample sizes would render more shared haplotypes among localities, and likely further reduce the already low levels of genetic differentiation. The lack of genetic divergence among localities is supported by the low pairwise F_{ST} values and the isolation-by-distance analysis. This suggests that the observed differences are more likely an artefact of a few quite different haplotypes in one or two populations than evidence of spatial genetic stock structure.

Genetic differentiation and pairwise population comparisons

The level of gene flow in marine organisms is expected to be higher than in freshwater species, as a result of the potential lack of physical barriers to gene flow and characteristically larger population sizes of marine species (Grant and Bowen 1998, Billington 2003). Exact tests for differentiation in the mtDNA showed few significant pairwise comparisons at the locality and population levels, while no significant differences were observed in the microsatellite loci at either level. Furthermore, the low, non-significant F_{ST} and R_{ST} values confirm the lack of differentiation at locality and population levels. Negative F_{ST} and R_{ST} values were common. This can occur when genetic differences are smaller than the observed sampling error, and these values can be interpreted as zero, indicating no restriction to gene flow between groups (Waples 1998). Overall, the results indicate low genetic differentiation and high levels of gene flow in white steenbras throughout its core distribution (Waples 1998).

Similar results were obtained for two other sparids and numerous other taxa along the South African coastline. Cape stumpnose and red roman showed similarly low differentiation between localities, and the authors concluded that there were no barriers to gene flow in either species (Oosthuizen 2006, Teske *et al*. 2010). Von der Heyden *et al*. (2007) drew the same conclusions of panmixia in the shallow-water hake, as did Neethling *et al*. (2008) for banded goby. Spotted grunter, an estuarine-dependent coastal migrant like white steenbras, also showed no significant genetic differentiation between coastal regions (Klopper 2005).

In contrast, most marine invertebrates in South Africa, such as the abalone *Haliotis midae* (Evans *et al*. 2004), the estuarine mud prawn (Teske *et al*. 2006), and the brown mussel *Perna perna* (Nicastro *et al*. 2008, Zardi *et al*. 2011), as well as some fish species, such as the Knysna seahorse *Hippocampus capensis* (Teske *et al*. 2003) and the deep-water hake (von der Heyden *et al*. 2007), exhibited significant genetic differentiation among coastal regions at some point along the South African coastline. The results suggest that taxa characterised by low levels of adult dispersal generally show multiple genetically-distinct populations. Species with high adult dispersal capabilities generally showed higher levels of gene flow (as predicted by Avise *et al*. 1987), suggesting that dispersal at the adult life stage is an important mechanism maintaining gene flow. In some species, larval dispersal alone may be insufficient to maintain genetic homogeneity among coastal regions. The banded goby appears to be an exception, with high levels of gene flow despite low levels of adult dispersal; although this species is thought to have an extended pelagic larval phase, as well as high fecundity and strong post-flexion swimming ability (Neethling *et al*. 2008).

Relatedness

In contrast to the differentiation tests, which provided a measure of the genetic differentiation between groups, the relatedness analyses estimated coefficients of relatedness relative to the global sample (Queller and Goodnight 1989). Overall, there was low intra-population relatedness and no locality was more closely related within than it was to the global sample, providing evidence of a low level of inbreeding within different coastal regions, confirming the lack of spatial genetic structure. Samples from all localities were, therefore, most likely drawn from a single stock (Lynch and Ritland 1999).

7.4.3 Clustering analyses (microsatellites)

Factorial correspondence analysis

In the four sets of groups analysed by FCA (results were only presented for eight sampling localities and for six juvenile populations), there was no evidence of one or more groups showing distinct separation from the rest. Furthermore, the distributions of the individuals along the axes of the FCA ordination, based on differences in allele frequencies, showed no obvious geographic trends in any of the four analyses, thereby providing evidence of a low level of spatial genetic structure and no isolation of populations.

Population assignment

The results of the population assignment analysis which adopted the "leave one out" approach differed considerably from the analysis that did not adopt this approach, indicating that the latter analysis is strongly biased. The results show that the decision whether to include or exclude each individual genotype from the population allele frequency calculations when assigning that individual has a major effect on the outcome. This is a result of the high number of unique genotypes, created by the combination of 11 loci, most of which are highly polymorphic (Waser and Strobeck 1998). When the individual allele frequencies were excluded during this process, the programme was largely unable to assign individuals to their original sampling localities. For all sampling populations, at least one member of the original sample was allocated to every other sampling population, and relatively evenly among localities. The exception was the original Transkei locality, from which no individuals were assigned to the East London or Langebaan populations. Knutsen *et al*. (2003, 2004) were able to successfully assign the majority of Atlantic cod *Gadus morhua* sampled from a range of localities in the Norwegian Skagerrak region to their original sampling localities, which showed significant genetic differentiation. A similar result was obtained for populations of black rockfish *Sebastes melanops* along the coasts of Oregon and Washington (Miller *et al*. 2005). While the

proportions of individuals assigned to each population from each of the original sampling localities varied among localities, the inability to correctly assign individuals to their sampling localities provides evidence of a lack of locality-specific alleles and/or allele frequencies, and a lack of spatial genetic divergence (Paetkau *et al*. 1995), which agrees with results from the relatedness analysis, and the low non-significant R_{ST} values.

Structure analysis

Pritchard *et al*. (2010) suggested that biologists attempting to elucidate the most likely possible number of populations (*K*) should be wary not to overestimate *K*. Rather, the lowest value of *K* that captures the major structure in the data should be accepted (one might in this instance make an analogy to Occam's razor, or the approach of maximum parsimony used in other genetic methods). The Structure analysis indicated that the most likely number of actual populations from which the 330 white steenbras were drawn, was one, indicating a single, well-mixed stock. The Structure analysis has been shown to successfully delineate divergent populations in species exhibiting significant pairwise differentiation, for example northern pike *Esox lucius* (Laikre *et al*. 2005), striped sea bream (Sala-Bozano *et al*. 2009) and the estuarine rainbow smelt *Osmerus mordax* (Bradbury *et al*. 2008), suggesting that the analysis is a reliable technique for identification of the presence of genetic stock structure.

Under the admixture model, i.e. admixture of individuals between sampling localities (Pritchard *et al*. 2000), individuals are assumed to have equal probability of coming from each population, whereas, under the no admixture model, i.e. discrete populations, each individual is expected to have a greater probability of coming from one discrete population than the others. Therefore, based on the previous results indicating that there is a high level of gene flow and low genetic differentiation within white steenbras, it was expected that the estimated posterior probabilities of individuals should be roughly evenly distributed among each of the *k* populations. In most cases this was the observed result. Furthermore, the individual admixture proportions, for $K = 2$ to 8, were consistent among the original eight sampling localities, reflecting the similar proportions of individuals from each population assigned to each sampling locality in the population assignment analysis. A similar result was obtained for red roman sampled from five sites along the South African coastline, including an offshore sampling locality, with the highest probability observed when samples were assumed to be drawn from a single population (Teske *et al*. 2010). The results provide evidence that samples drawn from different coastal regions are not genetically divergent.

7.4.4 Relating genetic results to geographic location

Spatial Analysis of Molecular Variance, isolation by distance and spatial autocorrelation

SAMOVA, isolation by distance and spatial autocorrelation analyses assessed the spatial distribution of genetic differentiation. The SAMOVA grouped non-adjacent localities, having little biological meaning (Dupanloup *et al*. 2002). This is likely a result of the low genetic differentiation among localities, identified by the pairwise F_{ST} values, as the SAMOVA aims to identify maximally differentiated groups (Dupanloup *et al*. 2002). Therefore, the SAMOVA was unable to identify biologically meaningful groups with a greater variability than that observed in the overall sample.

In contrast to SAMOVA, which seeks to identify abrupt genetic divergence, isolation-by-distance and spatial autocorrelation analyses are aimed at detecting genetic differentiation along a gradient. The analyses showed no showed no evidence of isolation by distance, or spatial autocorrelation, reflecting the low and non-significant pairwise F_{ST} and R_{ST} values observed at the locality and population levels. Han *et al.* (2010) found low genetic differentiation and no evidence of isolation by distance in the Japanese eel, which they attributed to adult migration and oceanic dispersal during a long pelagic larval phase. Similarly, Neethling *et al*. (2008) and Teske *et al*. (2010) found no isolation by distance in banded goby and red roman, respectively, and their SAMOVA analyses showed biologically meaningless groupings of non-adjacent sampling localities, confirming the lack of regional clustering of haplotypes. Results for all three species can be ascribed to high levels of gene flow and low genetic differentiation in species that are well-mixed throughout their ranges.

Isolation by distance was identified in three estuarine-associated fishes with pelagic larval phases but low adult dispersal; Australian barramundi in Northwest Australia (Chenoweth *et al*. 1998), white sea bream in the Northeast Atlantic and Mediterranean (Domingues *et al*. 2007) and rainbow smelt on the east coast of Canada (Bradbury *et al*. 2008). In contrast, spotted grunter (Klopper 2005) and white steenbras in South Africa, which exhibit large-scale coastal migrations, showed no isolation by distance, highlighting the role that adult dispersal plays in maintaining gene flow.

Overall, the spatial autocorrelation analyses conducted on the microsatellite genotypes showed little evidence of spatial autocorrelation, showing that individuals sampled from populations within close geographical proximity are not more closely related to those sampled at greater distances (Smouse and Peakall 1999), for the global sample or for juveniles and adults separately. There was, however, some evidence of positive spatial autocorrelation between 330 and 382 km. This distance represents the pairwise comparisons between Woody Cape/Sundays and Transkei, and Woody Cape/Sundays

and Knysna/Swartvlei, which showed pairwise R_{ST} = -0.006 and -0.005, respectively. The fact that both values were effectively zero, and that there were numerous pairs of geographically more proximate localities with greater R_{ST} (with evidence of significant negative spatial autocorrelation between 120 and 200 km), suggests that the observed positive spatial autocorrelation is an artefact of the low overall differentiation. The results are, therefore, not conclusive of positive spatial autocorrelation in the samples. There was also no evidence of spatial autocorrelation in the permutations tests, at any distance class, in any of the analyses.

7.5 Conclusions

Overall, the results of the different analyses for the mtDNA and microsatellite loci were in close agreement, providing evidence of a highly genetically diverse stock, which was confirmed by the AMOVAs as high levels of variability within and among individuals. There was no evidence that genetic diversity decreased with distance from the suggested spawning grounds, and negligible evidence of edge effects causing lower genetic diversity at the limits of the species' core distribution.

Reductions in genetic diversity as a result of overexploitation have been reported for certain marine fish species, for example the orange roughy *Hoplostethus atlanticus* (Smith *et al*. 1991) and New Zealand snapper *Pagrus auratus* (Hauser *et al*. 2002). It is also acknowledged that the fishery effects on genetic diversity may be delayed and, for white steenbras, there is no pre-exploitation baseline estimate of genetic diversity against which current estimates can be compared. However, the high genetic diversity recorded and its congruence with other marine species, as well as the lack of genetic differentiation between juvenile and adult samples suggest that overexploitation of white steenbras has not resulted in reduced genetic diversity in this species. Genetic material extracted from historic samples would be necessary to test this directly.

Conventional dart tagging provided little evidence of white steenbras moving between the Eastern and Western Cape provinces (see Chapter 6). This posed the question of whether these areas were represented by separate stocks, with connectivity restricted by some physical barrier. Griffiths (1997a) and Griffiths *et al*. (2002) identified separate south coast and south east coast stocks of silver kob *Argyrosomus inodorus* and white stumpnose *Rhabdosargus globiceps*, respectively. Similarly, Griffiths and Wilke (2002) recorded a low level of exchange of carpenter *Argyrozona argyrozona* between Tsitsikamma and Mossel Bay. The similarity among species in the region separating distinct stocks suggests separation by a common oceanographic feature, such as the cold water ridge extending offshore from the coast between Tsitsikamma and Mossel Bay (Figure 1.3).

The low pairwise F_{ST} and R_{ST} values, the lack of geographic subdivisions in the haplotype network, the inference of a single population from the Structure analysis, the low F_{IS} values for the microsatellite loci and the failure to correctly assign samples to their source populations confirm the lack of major barriers to gene flow among coastal regions in white steenbras. The lack of isolation by distance confirms the absence of a gradual genetic differentiation across the distribution range. It is likely that gene flow is maintained by adult spawning migrations and larval dispersal, with little post-settlement migration. Therefore, the low number of recaptures of conventionally dart tagged white steenbras representing movements between the Eastern and Western Cape provinces (n = 2) is likely a result of the low proportion of adults recaptured. The observed results, and agreement between mtDNA and microsatellite loci, provide robust evidence of a single, well-mixed stock with high levels of gene flow. Numerous phylogeographic breaks have been observed for marine species in South Africa, such as Cape Point (Teske *et al*. 2011), Cape Agulhas (Evans *et al*. 2004, Teske *et al*. 2006, von der Heyden *et al*. 2008), between Knysna and Cape St Francis (Griffiths 1997b), between Kenton on Sea and Haga Haga (Zardi *et al*. 2011), and between Haga Haga and the Umkomazi Estuary (Teske *et al*. 2006). Therefore, gene flow in white steenbras among coastal regions is unaffected by the geographical or oceanic features that have been identified as barriers to gene flow in other South African marine species.

The results of the genetic analyses cannot directly confirm that adult white steenbras undertake annual spawning migrations between False Bay and the Transkei, nor whether a single spawning event takes place. However, the genetic analyses have shown that white steenbras is present as a single genetic unit. The lack of genetic divergence along the coastline confirms the high levels of connectivity and gene flow throughout the core distribution of the species, and results of this chapter and previous chapters simultaneously oppose the idea of isolated spawning aggregations or discrete populations. The presence of a single, well-mixed stock can improve the resilience of the species and prevent localised extinction that may occur due to unfavourable environmental conditions or through anthropogenic impacts, through mechanisms such as larval dispersal and adult migration.

Management considerations

In the absence of morphological or meristic differences to delineate discrete stocks, white steenbras has always been managed as a single stock. There have, however, been differential commercial and recreational restrictions applied in different geographical areas, such as commercial harvesting in certain areas within the Western Cape Province only (until 2001, when the commercial exemption

for white steenbras was withdrawn and a complete commercial ban imposed). Based on the results of this chapter, white steenbras should be managed as a single stock. This is not, however, to say that management of white steenbras need not consider the genetic implications of these results, as excessive local harvest in one area, particularly areas of known aggregation, is likely to affect the entire stock, and concomitantly those dependent on the resource in other areas. Furthermore, the number of migrants per generation required to mask the signal of inherent stock structure is low, and the actual number of migrants per generation from one area may be insufficient to rebuild a depleted population in another (Hauser and Carvalho 2008). Corrective management will require assimilation of all available biological, ecological and social information pertaining to white steenbras, to effectively address the conservation needs of the species.

Chapter 8

Fishery and management implications

8.1 Introduction

The persistence of a fishery species relies on active and effective management. Regulations should consider environmental and anthropogenic changes and, thus, be dynamic and adaptable in their interpretation and implementation. Effective management requires a comprehensive understanding of the life history of exploited species, as well as information on environmental and anthropogenic threats, factors affecting its life history, distribution, and movement behaviour, and an understanding of its exploitation (for example, the respective fisheries for a species). Thus, information on which to base management decisions should be drawn from all available sources.

The commercial fisheries targeting "linefish" in South Africa have largely been managed through effort (input) restrictions, while the total control of effort in the recreational sector is not possible (Attwood and Farquhar 1999), and recreational fisheries are generally managed through catch (output) restrictions on individual anglers. However, as a result of overexploitation, the stocks of numerous linefish resources in South Africa have collapsed (Griffiths 2000). Technical improvements in fishing equipment, ineffective regulations, continually increasing recreational participation and inadequate enforcement of regulations have all contributed to the observed declines (Penney 1991, McGrath *et al*. 1997, Attwood and Farquhar 1999, Mann *et al*. 2003).

A Linefish Management Protocol (LMP) was implemented in South Africa in 1999 to provide a standardised methodology for assessing the status of linefish stocks. The LMP required that an Operational Management Plan (OMP) be developed for each species, which would clearly define *a priori* the management objectives for the species, the type of stock assessment analysis to be conducted, the type of catch data to be used, and the relevant management actions to be taken, based on the outcomes of the analysis (Griffiths *et al*. 1999). The assessment techniques included single species per-recruit analyses, age-based production models and virtual population analysis.

Van der Elst and Adkin (1991) stated that the stock of white steenbras was "sound", meaning "no immediate concern; no negative trends evident"; "abundant species – not under pressure". However, Bennett (1993a) conducted per-recruit analyses on white steenbras, based on competition shore catch data recorded up to 1991, and reported a spawner biomass per recruit (SB/R) of just 6%

of pristine. According to the guidelines of the LMP, stocks of species with SB/R < 25% should be considered as collapsed (Griffiths *et al*. 1999). Therefore, overexploitation had resulted in the collapse of the white steenbras stock, as early as 1991.

The LMP recommends that stocks are reassessed every three to five years, suggesting that an updated assessment for white steenbras is long overdue. However, standard stock assessment techniques as prescribed in the LMP are not suitable for all species, particularly those targeted by multiple fisheries (Penney 1991), and for many linefish species suitable data are not available (Griffiths *et al*. 1999). Age-structured production modelling requires a reliable estimate of natural mortality, which may be difficult to obtain for many species (Attwood 2003), particularly those occurring in low densities. The lack of recent catch data from the commercial sector and the low numbers of white steenbras recorded during roving creel surveys of the recreational shore fishery precluded the possibility of using standard stock assessment techniques; therefore, an alternative approach was required. In such cases, suitable stock status indicators (for example CPUE relative to historic or protected area values) may be used (Griffiths *et al*. 1999).

The aim of this chapter was to assess the current stock status of white steenbras, to provide baseline information necessary for the corrective management of the species. This was achieved by assimilating available historical and recent white steenbras catch and effort data, from fishery-dependent and fishery-independent sources, and elucidating long-term trends in catch, effort and CPUE relative to historical management measures, in the fishery sectors targeting white steenbras.

8.2 Linefish management in South Africa

Initially fishing control measures in the recreational and commercial sectors were technical (e.g. government-dictated mesh sizes); however, open access to the resources resulted in overharvesting of stocks and it was recommended that participation be restricted, in order to 'control' the effort exerted on the resource. Access restrictions were introduced in the form of licences or permits, initially in the commercial sector but later in the recreational sector as well, without which one was denied legal access to the resource. These restrictions were governed by a series of Sea Fisheries Acts (Hutton and Pitcher 1998). The first legislation to protect South Africa's living marine resources was that of the Sea Fisheries Act 1940, superseded by amended Acts in 1973 and 1988. These Acts were largely technical in nature, detailing institutional requirements, policies and responsibilities. In 1985, a Linefish Management Framework was introduced (Government Gazette No. 9543, December 1984), which included the first catch restrictions for numerous linefish species, aimed at providing

improved protection for those species showing stock declines (Griffiths 2000). Numerous additional regulatory measures were implemented over the years, including amendments to these regulations in response to stock declines, new restrictions such as closed seasons and the proclamation of a number of MPAs, all of which were aimed at decreasing effort in the respective fishery. The Marine Living Resources Act (MLRA, Government Gazette No. 18930) was promulgated in 1998 to provide for equitable access to and sustainable utilisation of living marine resources (Witbooi 2006), and detailed the processes for the allocation of permits and quotas, as well as the setting of catch and effort restrictions.

The linefishery has many participants, including recreational anglers (shore or boat-based along the coasts and in estuaries), full-time commercial fishers (boat-based only), and subsistence fishers, complicating enforcement, management and collection of catch and effort data (Sauer *et al*. 1997). Certain linefish species also form important components of the commercial net fisheries, which has led to conflict among fishery sectors (Lamberth *et al*. 1997). The high number of access points and the wide operational range of the fisheries further complicate their management (Sauer *et al*. 2003).

Governance in the recreational sector and the commercial linefishery is characterised by a series of catch restrictions imposed on licensed fishers, including minimum legal size and maximum daily bag limits, and effort restrictions, through area and seasonal closure. However, in the absence of suitable biological information, regulations specific to most species were based on perceived vulnerability, rather than on sound scientific evaluation, and many of these regulations failed to protect the target species (Griffiths 2000). White steenbras was also historically targeted in a number of commercial net fisheries, including the purse seine, gill-net and beach-seine fisheries. While the regulations differed broadly among fisheries, in terms of catch and effort restrictions, these fishers were also subjected to a range of management interventions, which became increasingly stringent over the years. Nets were first required to be licensed in 1975. A series of strict regulations was implemented in 1983, and again in 1990, including seasonal, area and effort restrictions, and minimum size limits for “angling” species. However, these and subsequent restrictions failed to arrest the declines in the stocks of most linefish species, and a commercial ban was imposed in 2001 on the harvest of white steenbras and other “angling” species (SJ Lamberth, DAFF, pers. comm.). Management regulations that pertained to recreational and commercial linefisheries, and commercial net fisheries, respectively, with some regulations specific to white steenbras, are presented in Tables 8.1 and 8.2. Few attempts have been made to assess the effectiveness of the management measures introduced for linefish species (Attwood 2003).

Table 8.1: Management regulations pertaining to the recreational fishery, with those specific to white steenbras marked with an asterisk (pppd = per person per day)

Year	Regulation	Source
1964	Proclamation of Tsitsikamma MPA	Government Gazette No. 936
1984	Implementation of linefish management framework	Government Gazette No. 9543
	- * Maximum daily bag limit set at 10 pppd	Government Gazette No. 9543
	* Minimum legal size limit set at 40 cm TL	SJ Lamberth pers. comm.
	Proclamation of De Hoop MPA	Tunley 2009
1992	* Maximum daily bag limit decreased to 5 pppd	Attwood and Bennett (1995b)
1996	* Minimum legal size increased to 60 cm TL	Attwood and Farquhar (1999)
1998	Marine Living Resources Act	Government Gazette No. 18930
2000	Proclamation of Dwesa-Cwebe MPA	MLRA (1998)
2002	* Maximum daily bag limit decreased to 1 pppd	Sauer *et al*. (2003)
	Ban on recreational use of vehicles in the coastal zone	Government Gazette No. 22960
2008	Proclamation of Stilbaai MPA including Goukou Estuary	Government Gazette No. 31517
2012	* Current restrictions: 1 pppd ≥ 60 cm TL	

Table 8.2: Management regulations pertaining to the commercial net fisheries

Year	Regulation	Source
<1969	Minimum beach-seine mesh size set at 44 mm	Penney (1991)
1974	Commercial beach-seines registered, limited to 121 nets in False Bay	Penney (1991)
1975	Licensing of commercial beach-seine nets and gill-nets	Hutchings *et al*. (2002b)
	Beach-seine permits allocated for fewer areas	Penney (1991)
	Permits granted to commercial netters only	Penney (1991)
1982	Permits restricted to 84 beach-seine nets in False Bay	Penney (1991)
	Prohibition on catch of “angling” species by pelagic boats	Penney (1991)
	Purse seine fishery prohibited in False Bay	Penney (1991)
1983	Seine netting at night prohibited	Bennett (1993a)
	Winter closed season implemented in beach-seine fishery	Bennett (1993a)
	Minimum size of 40 cm TL implemented for white steenbras	Bennett (1993a)
	75% reduction in beach-seine permits	Bennett (1993a)
	Netting of angling species prohibited outside False Bay and Walker Bay	Penney (1991)
	Permits restricted to 34 nets in False Bay	Penney (1991)
1984	Closed season False Bay (May - October)	Penney (1991)
1988	Number of nets restricted to 29, net length to 275 m in False Bay	Penney (1991)
1989	Area closure of 1 km around Eerste Estuary (False Bay)	Bennett (1992)
1990	Limited seine net rope length to 200 m (W shore of False Bay)	Bennett (1992)
	Limited seine net rope length to 400 m (N shore of False Bay)	Bennett (1992)
1992	Restricted commercial areas within False Bay	Bennett (1993b)
1995	White steenbras ban, but 20 mt exemption for beach-seine fishery	SJ Lamberth pers. comm.
2001	Commercial ban on “Russman” seine and certain “angling” species	SJ Lamberth pers. comm.
	Linefish emergency, 20 mt white steenbras exemption withdrawn	SJ Lamberth pers. comm.

8.3 Trends in catch, effort and catch-per-unit-effort by fishery sector

Smith and Smith (1986) described the distribution of white steenbras from the Orange River in the west, to KwaZulu-Natal in the east, while Lamberth and Mann (2000) suggested that the core distribution is from north of Cape Columbine to the Mbashe Estuary, within which the majority of the stock occurs. However, white steenbras did not feature in shore-angler catches in a survey of the recreational shore fishery along the west coast of South Africa (Lamberth 1996), and Hutchings *et al*. (1999) recorded no white steenbras in experimental marine and estuarine gill-net catches along the west coast, between Cape Point and the Olifants Estuary from 1997 to 1999. It is possible that the core distribution has contracted, with few individuals making use of the west coast. However, recent reports suggest that catches along the Cape west coast have increased over the past couple of years (SJ Lamberth, DAFF, pers. comm.).

8.3.1 Recreational shore fisheries

The recreational shore fishery is one of the largest fisheries in South Africa, supporting an estimated 380 000 participants in 1990 (Bennett 1991). McGrath *et al*. (1997) applied a 2% compound growth rate to an earlier estimate to reach an estimate of 412 000 participants by 1995, which, if extrapolated to 2012, would provide a current estimate of over 575 000 participants. While more recent estimates are not available, there is consensus among researchers and managers that participation in this fishery continues to increase.

Numerous surveys have been conducted to assess the catch, effort, species composition and value of the shore fishery, in different parts of the coastline. While inconsistency in survey techniques, analyses and time periods, as well as different fisher behaviours (e.g. competitive vs. recreational) make these studies unsuitable for direct comparison (Bennett and Attwood 1993), the results nonetheless provide an opportunity to assess trends or major changes over the long term. The results of a number of these studies were used to determine the percentage numerical (and where possible gravimetrical) contribution of white steenbras to overall catch for the period, as well as the species rank relative to other teleosts, and where possible CPUE (fish.100 angler hours^{-1}), for different sections of the South African coastline. Studies conducted in KwaZulu-Natal showed that white steenbras was absent from most catches in the commercial beach-seine fishery (Beckley and Fennessy 1996), the boat-based linefishery (Penney *et al*. 1999) and the recreational shore fishery (Maggs 2010), and where it was present in catches the contribution was negligible. The following analysis therefore focuses on the shoreline from the Orange River in the west, at the Namibia border, to the Mtamvuna Estuary, at the Transkei/KwaZulu-Natal border in the east.

Owing to changes in provincial boundaries and the numerous different coastal regions described in these studies, the naming of coastal regions has become rather complex. For the purpose of this chapter, four coastal sections are defined; the west coast ranges from the Orange River to Cape Point, the south west coast from Cape Point to the Breede Estuary (near the eastern boundary of De Hoop MPA), the south east coast spans the area between the Breede and Great Kei estuaries, and the Transkei coast encompasses the coastline within the boundaries of the former Transkei, from the Great Kei Estuary to the Mtamvuna Estuary at the KwaZulu-Natal border (Figure 8.1).

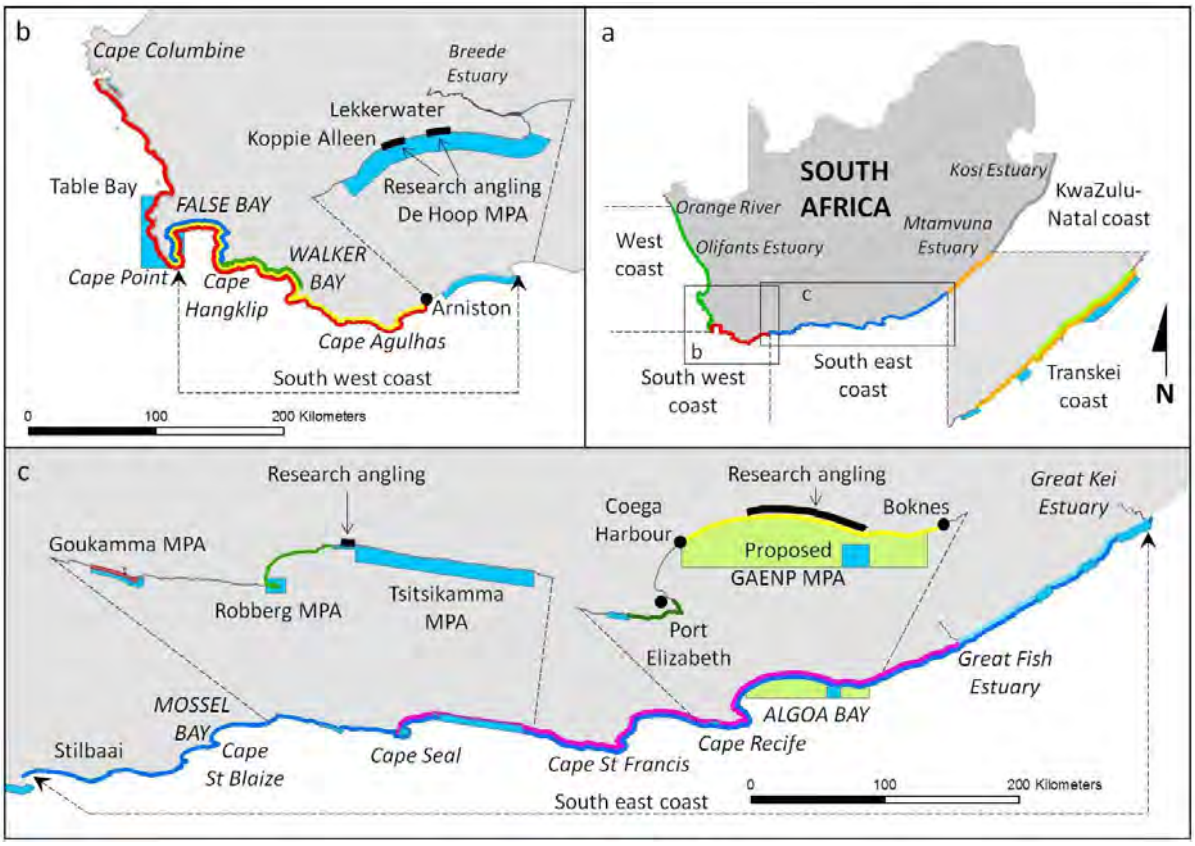

Figure 8.1: Sections of coastline surveyed by the shore fishery surveys discussed (different colours indicate different survey areas), and localities mentioned in text, showing a) the four coastal sections, b) south west coast and part of the west coast, and c) south east coast

A series of roving creel surveys was conducted in the 1990s, along the west coast (Sauer and Erasmus 1996), south west coast (Lamberth 1996), south east coast (Brouwer and Buxton 2002) and Transkei coast (Mann *et al*. 2003), to assess the shore fishery at the national level (Brouwer *et al*. 1997) (Figure 8.1). Numerous localised studies have also been carried out over the years, assessing both recreational and competition shore anglers, and a number of research programmes have been conducted using experimental angling (mainly in MPAs). Data were drawn from these studies to complement the results of the roving creel surveys (Table 8.3).

Table 8.3: Survey locations, dates and number of fish caught (No.), CPUE (fish.100 angler hours^{-1}), contribution (% no. and % kg) and species rank (relative to all teleosts) for white steenbras, for studies that assessed shore angling (research, recreational and competitive) along different regions of the South African coastline (WC = west coast, SWC = south west coast, SEC = south east coast, TKE = Transkei coast)

Region	Geographical range	Dates	Form	No.	CPUE	% (no.)	% (kg)	Rank	Source
WC	Port Nolloth to Cape Point	1994 - 1996	Recreational	-	±0.02	0.2	-	-	Sauer and Erasmus (1996)
SWC	False Bay	1938 - 1985	Competition	866	1.84	17.7	17.8	2	Bennett (1991)
SWC	False Bay and surrounds	1938 - 1985	Competition	4642	±2.00	29.5	31.8	1	Bennett *et al.* (1994)
SWC	Cape Point to Arniston	1994 - 1996	Recreational	68	0.12	4.4	-	3	Lamberth (1996)
SWC	Cape Hangklip to Walker Bay	1995 - 1997	Recreational	-	-	8.0	-	3	Attwood and Farquhar (1999)
SWC	De Hoop MPA (Koppie Alleen)	1984 - 1985	Research	6	0.42	1.1	-	7	Bennett and Attwood (1991)
SWC	De Hoop MPA (Koppie Alleen)	1988 - 1990	Research	50	2.63	1.4	-	3	Bennett and Attwood (1991)
SWC	De Hoop MPA (Lekkerwater)	1988 - 1990	Research	273	8.56	4.1	-	3	Bennett and Attwood (1991)
SWC	De Hoop MPA	1984 - 1992	Research	531	4.68	2.4	-	3	Bennett and Attwood (1993)
SWC	De Hoop MPA	1987 - 2009	Research	1 486	3.19	3.3	-	5	CG Attwood, L Swart (unpubl.)
SEC	Stilbaai to Kei Mouth	1994 - 1996	Recreational	29	0.60	1.0	2.9	11	Brouwer and Buxton (2002)
SEC	Goukamma MPA	1993 - 2002	Recreational	142	0.41	2.1	3.2	7	Pradervand and Hiseman (2006)
SEC	Goukamma MPA	2008 - 2009	Recreational	1	<0.1	0.3	-	15	van Zyl (2011)
SEC	Robberg to TNP western boundary	2003/2004	Recreational	33	0.76	2.8	-	7	King (2005)
SEC	Robberg to Great Fish Estuary	1959 - 1982	Competition	787	-	3.9	3.9	-	Coetzee *et al*. (1989)
SEC	Robberg to Great Fish Estuary	1978 - 1982	Competition	143	0.24	3.3	1.6	-	Coetzee *et al*. (1989)
SEC	Robberg to Great Fish Estuary	1979 - 1982	Competition	131	0.53	2.0	1.2	-	Coetzee *et al*. (1989)
SEC	Tsitsikamma MPA	1964 - 1965	Recreational	36	-	4.4	4.5	7	Hanekom *et al*. (1997)
SEC	Tsitsikamma MPA	1989 - 1991	Research	13	2.80	1.8	-	-	Hanekom *et al*. (1997)
SEC	Tsitsikamma MPA	1991 - 1995	Recreational	65	2.10	2.5	3.9	8	Hanekom *et al*. (1997)
SEC	Tsitsikamma MPA	1998 - 2005	Research	111	1.36	1.3	-	15	Götz *et al*. (2008)
SEC	Tsitsikamma MPA	1995 - 2009	Research	457	3.14	-	-	-	PD Cowley (unpubl.)
SEC	Port Elizabeth (Cape Recife)	1985/1986	Recreational	13	0.28	1.0	2.0	10	Clarke and Buxton (1989)
SEC	Coega Harbour	2006 - 2007	Research	18	0.92	0.4	-	13	Dicken 2010
SEC	Coega Harbour to Boknes	2006 - 2009	Recreational	48	1.29	7.9	-	2	R Chalmers (unpubl.)
SEC	Proposed GAENP MPA	2005 - 2011	Research	560	16.61	20.3	-	1	PD Cowley (unpubl.)
SEC	Great Fish Estuary to Kei Estuary	1982 - 1998	Competition	269	0.20	1.4	1.1	3	Pradervand and Govender (2003)
TKE	Kei Estuary to Mtamvuna Estuary	1997/1998	Recreational	4	0.18	0.6	<1	16	Mann *et al*. (2003)
TKE	Mbolompo Point to Mtamvuna Estuary	1977 - 2000	Competition	18	0.03	<0.1	<0.1	24	Pradervand (2004)

White steenbras has traditionally been considered as one of the most popular recreational shore-angling species in South Africa, being targeted throughout its distributional range (Biden 1948, Mehl 1973). Even following severe stock declines, this species was the target of 6% of all shore angling effort along the South African coastline, and constituted the third most targeted species along the south east (17% of anglers) and south west (9%) coasts, and fifth most targeted (4%) along the west coast (Sauer and Erasmus 1996, Brouwer *et al*. 1997).

West coast

The survey of the shore fishery along the west coast covered more than 900 km of coastline. The total harvest for the study area over the two-year period (1994 – 1996) was estimated at 74 798 fishes. White steenbras was of little importance in the shore fishery over that period, contributing approximately 0.23% (Sauer and Erasmus 1996). The actual numbers of each species recorded were not provided by Sauer and Erasmus (1996); therefore, a crude estimate of white steenbras CPUE was determined by multiplying the percentage contribution of white steenbras to total catch by the overall CPUE for all species, which provided a rough estimate of 0.02 fish.100 angler hours^{-1}. Furthermore, the species was only captured within one of the survey zones, approximately 50 km north of Table Bay, which spanned just one kilometre of shoreline. In the absence of additional literature on the shore fishery along the west coast, this study suggests that white steenbras is not important (or heavily overexploited) as a fishery species along this coastal region.

South west coast

White steenbras was a dominant component and constituted about 30% of shore-angling catches along the south west coast, from 1938 to 1990 (Bennett 1993a). The species also formed the third most common shore-caught species in False Bay from 1984 to 1992 (Lamberth and Bennett 1993), and was the fifth and second most dominant species, numerically and gravimetrically, respectively, captured along the south west coast from 1994 to 1996 (Brouwer *et al*. 1997).

From 1938 to 1960, the species featured poorly in shore-angling catches within False Bay and along the Cape Peninsula (Bennett and Griffiths 1988). The poor catches prior to 1960 largely reflected the restricted distribution of competition angling within the region at this time. However, after 1960, competitive shore angling became more widespread and vehicle access to beaches along the False Bay north shore increased (Penney 1991), with anglers exerting more effort along the sandy and mixed sand and rock shores of False Bay, which resulted in a significant increase in the targeting and catch of shallow-water species, including white steenbras (Bennett 1991, Bennett 1993a). Shore-

angling catches of white steenbras increased steadily until the mid 1970s, by which time the contribution of the species had increased from about 1% of competition shore angling catches to about 20% (Lamberth and Bennett 1993). A similar trend can be assumed for non-competition (purely recreational) shore anglers. Over roughly the same period (1959 to 1982), the mean mass of white steenbras caught in the recreational shore fishery in the then Cape Province (west, south west and south east coasts) increased from 1.8 kg to 3.0 kg (Coetzee *et al*. 1989), which was likely a result of angler distribution shifting to more suitable white steenbras habitat, where large shoals of mature fish became more accessible from the shore. Bennett (1993a) determined that the recreational shore fishery contributed approximately 75% by number and 50% by mass to the total annual catch of white steenbras in South Africa, and during the period 1985 to 1992, accounted for almost 60% numerically of the total white steenbras catch in False Bay (Lamberth *et al*. 1994).

From 1976 to 1985, white steenbras constituted the second most common species in competition shore catches, contributing 18% by number and mass (Bennett 1991). However, despite its important contribution over this period, white steenbras CPUE declined by about 90% after 1975 (Bennett 1991), from 6.0 fish.100 angler hours^{-1} in the 1970s to 2.3 fish.100 angler hours^{-1} by 1984, and to 0.7 fish.100 angler hours^{-1} in the 1990s (Bennett 1993a, Bennett *et al*. 1994, Lamberth 1996). Similarly, the contribution of white steenbras to annual angler catches by mass in the shore fishery of the south west coast decreased from approximately 30% in the 1960s, to 8% in the period 1990 to 1991 and as little as 0.6% by 1994 to 1996 (Lamberth 1996). The observed decline reflects the general decline in abundance of the species, although the effect was likely elevated by a shift in targeting of competition anglers towards cartilaginous species, to gain more points (Taylor 1993). The cause and level of this decline will be further discussed in the C*ommercial net fisheries* section.

Shore angling from Cape Hangklip to Walker Bay, along the south west coast, was conducted at low levels of effort in the first part of the 20th century, rising to a peak by 1950 (Attwood and Farquhar 1999). Catch records from the time of JDF Gilchrist (1897 – 1906), the state marine biologist, indicate sporadic large catches of white steenbras in the commercial linefishery in this region over this period, although it is suggested that these records may reflect line and net caught fish (SJ Lamberth, DAFF, pers. comm.). Data from the National Marine Linefish System showed that by the period 1987 to 1997 white steenbras was absent from the commercial linefishery in this area altogether, providing further evidence for the decline of the species. In contrast, however, from 1995 to 1997, white steenbras was the third most common species caught in the recreational shore fishery in this area, constituting 8% of the total catch (Attwood and Farquhar 1999).

Towards the eastern end of the south west coast is the large, well-established De Hoop MPA, within which a long-term shore angling research programme has been conducted since 1984. Two sites that are situated within the current MPA boundaries were selected for inclusion in the study, prior to proclamation of the MPA in 1985. At the time the study was initiated, one site was heavily exploited by recreational shore anglers, while the other was considered to represent a pristine surf zone ichthyofaunal community, by virtue of its inaccessibility (Bennett and Attwood 1991). Research angling catches made from May 1984 to September 1985 at the exploited site produced a CPUE for white steenbras of 0.42 fish.100 angler hours^{-1}, and it is reasonable to assume that this value was representative of exploited areas in that region of the coastline, outside of MPAs. However, in October 1985, the De Hoop MPA was proclaimed, encompassing 46 km of coastline, including both research fishing areas. After proclamation, white steenbras CPUE in the previously exploited area increased to 1.26 fish.100 angler hours^{-1} by 1988, and to 2.63 fish.100 angler hours^{-1} by 1990 (Bennett and Attwood 1991). During the latter period (1988 to 1990), CPUE in the pristine area was recorded at 8.56 fish.100 angler hours^{-1} (Bennett and Attwood 1991), the second highest for white steenbras anywhere along the South African coastline. The results confirm the protection offered by the MPA to white steenbras resident within the surf zone.

The shoreline of the De Hoop MPA, and likely most of the sandy and mixed sand and rock shoreline along this section of coastline, therefore, constitute important areas for white steenbras. The considerably lower CPUE recorded outside of this MPA, and the CPUE recorded in the exploited area prior to proclamation, suggest that white steenbras along this section of coastline have been heavily depleted. Furthermore, catches of white steenbras within the De Hoop MPA subsequently declined to between 3 and 4 fish.100 angler hours^{-1} by 2009 (Figure 8.2), which has been suggested to reflect the overall stock decline (Lamberth and Mann 2000).

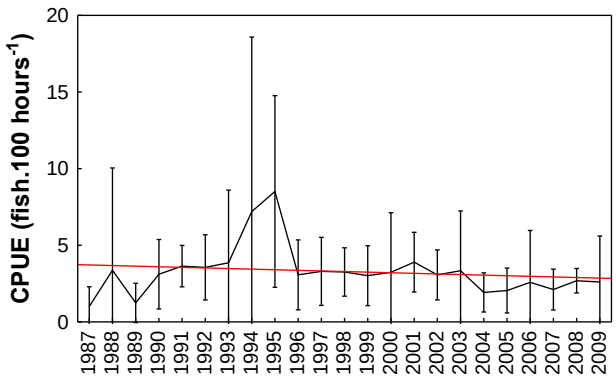

Figure 8.2: Trend in mean (±SD) monthly CPUE (fish.100 angler hours^{-1}) recorded during research angling in the De Hoop MPA over the period 1987 to 2009 (CG Attwood, L Swart, unpublished data)

South east coast

The south east coast, as defined for this analysis, encompasses two existing MPAs (Tsitsikamma and Goukamma), as well as the shoreline of the proposed Greater Addo Elephant National Park (GAENP) MPA, within which dedicated roving creel surveys or research angling have been conducted.

The Tsitsikamma MPA is the oldest and largest of these, and historically had a short section that was open to recreational shore fishing. Observed CPUE of white steenbras from this open section (2.1 fish.100 angler hours^{-1}), from 1991 to 1995, was lower than that (2.8 fish.100 angler hours^{-1}) recorded during experimental research angling in areas of the MPA that have been closed to recreational angling since proclamation in December 1964 (Hanekom *et al*. 1997). However, when compared to historical recreational shore catches made within the MPA in 1964 and 1965, the numerical percentage contribution of white steenbras to total catch had decreased from 4.4% to 2.5% by the period 1991 to 1995 (Hanekom *et al*. 1997). Unfortunately, no effort data were recorded for these historical catches, and CPUE for white steenbras could not be compared among time periods. The results do, however, indicate that the closed areas of the TNP were providing some protection for white steenbras, but that recreational angling within the open section of the MPA, prior to closure, was responsible for a decline in white steenbras relative abundance over the years (Hanekom *et al*. 1997).

A long-term research angling programme was initiated within the Tsitsikamma MPA in 1995 (Rhodes University Department of Ichthyology and Fisheries Science). Angling was conducted between the Klip and Bloukrans estuaries near the western boundary (fishing zone 1) of the MPA (see Figures 6.1 and 6.5, Chapter 6), from 1995 to 2009, and in a second fishing zone at the mouth of the Lottering Estuary, in close proximity to fishing zone 1, over the period 1998 to 2000. Angling in the two zones produced a combined white steenbras CPUE of 3.14 fish.100 angler hours^{-1} (PD Cowley, unpublished data), which suggested that white steenbras abundance within the MPA had increased since that recorded from 1991 to 1995 (Hanekom *et al*. 1997). The trend in annual mean monthly CPUE of white steenbras recorded during the later study showed an initial increase until a peak of more than 9 fish.100 angler hours^{-1} in 1997, although this was followed by a steady decline, reaching zero by 2009 (Figure 8.3a). The catch data for the two fishing zones were separated; to determine whether the catches made over the short period at fishing zone 2 had influenced the overall CPUE recorded (Figure 8.3b). The results indicate that CPUE was considerably higher in fishing zone 2 (8.37 fish.100 angler hours^{-1}) than in fishing zone 1 (2.88 fish.100 angler hours^{-1}); the latter being similar to that recorded in the closed areas from 1991 to 1995 (Hanekom *et al*. 1997). Despite the influence of zone

2 on the overall CPUE from 1998 to 2000, the peak in CPUE was observed in 1997, prior to the period of fishing in zone 2, and the decline in zone 1 after 1997 remains clear. Interestingly, the substrate in fishing zone 2 (which produced a higher CPUE for white steenbras than fishing zone 1) is predominantly sandy, whereas that in fishing zone 1 is predominantly of rock and mixed sand and rock, suggesting an affinity of white steenbras for areas of sandy substrate.

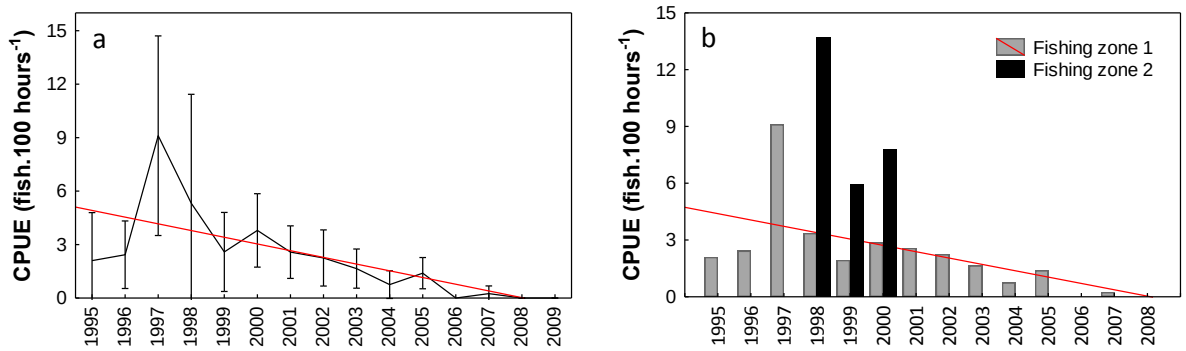

Figure 8.3: Long-term catch data recorded during research angling in the Tsitsikamma MPA over the period 1995 to 2009, showing a) mean (±SD) monthly CPUE (fish.100 angler hours^{-1}) for the two fishing zones combined, and b) mean monthly CPUE for the two fishing zones separately (PD Cowley, unpublished data)

Part of this dataset, spanning the period 1998 to 2005 (i.e. after the peak in 1997), was published by Götz *et al*. (2008), exhibiting a CPUE for white steenbras (in fishing zone 1 only) of just 1.36 fish.100 angler hours^{-1}, which is lower even than that within the previously open section of the MPA, further highlighting the decline since 1997. This may be due to a number of causes. Firstly, the area is near the boundary of the MPA, and catches may be influenced by recreational angling occurring adjacent to the MPA, or this may be evidence of illegal exploitation occurring within the MPA. Alternatively, the lower CPUE of white steenbras during this later period may reflect the overall decline in white steenbras at the stock level (Lamberth and Mann 2000). This phenomenon was observed also in the De Hoop MPA. The result has sombre implications for the management of coastal fishes, if the level of stock decline is so severe that catches even within well-established MPAs have declined.

The second MPA within this region is the Goukamma MPA, which is smaller than the TNP MPA (and the DE Hoop MPA on the south west coast), and remains open to recreational shore angling. Pradervand and Hiseman (2006) recorded a low CPUE for white steenbras of 0.41 fish.100 angler hours^{-1}, from 1993 to 2002, although the species was the seventh most common teleost, contributing 2.1% and 3.2% to the total catch, by number and mass, respectively. This CPUE is similar

to that recorded in the De Hoop MPA, prior to proclamation, and is indicative of the depleted state of the fishery within the area. The high proportion of sand and mixed sand and rock shoreline suggests that the area is suitable for species such as white steenbras. However, the MPA remains open to recreational shore angling, and a recent roving creel survey conducted within the MPA from October 2008 to December 2009 recorded just one white steenbras, and a lower CPUE (<0.1 fish.100 angler hours^{-1}) (van Zyl 2011). The fact that white steenbras CPUE was significantly higher within closed areas of the TNP than open areas, and increased significantly after proclamation of the De Hoop MPA, suggests that the Goukamma MPA has the potential to afford white steenbras considerable protection, if shore angling is prohibited.

As part of the national shore angling survey, a roving creel survey was conducted from 1994 to 1996, from Stilbaai to the Kei Estuary (Brouwer *et al*. 1997, Brouwer and Buxton 2002). During this survey, 29 white steenbras were recorded, with a CPUE of approximately 0.6 fish.100 angler hours^{-1}. This species contributed 1.4 and 2.9% to the total catch, by number and mass, respectively (Brouwer and Buxton 2002). Recreational shore catches of white steenbras made from 2003 to 2004, between the western boundary of the TNP MPA and the western side of the Robberg Peninsula, were similarly low, and showed considerably lower CPUE (0.76 fish.100 angler hours^{-1}, King 2005) than those observed within the TNP MPA. These results provide further evidence of the protection offered by the larger, well-established MPAs. Shore catches made along the Port Elizabeth coastline, in 1985 and 1986, were even lower than those reported by King (2005), with a CPUE of 0.28 fish.100 angler hours^{-1} (Clarke and Buxton 1989). The low CPUE recorded during this survey, however, may be a result of the predominantly rocky shores in the survey area, which are less suitable for white steenbras (Bennett 1993b).

Competition shore angling data from the eastern part of the south east coast showed that white steenbras is generally not a large contributor in these catches. Coetzee *et al*. (1989) provided data on catch card returns made by individual anglers during shore-based angling competitions, between Robberg and the Great Fish Estuary, over a 24-year period (1959 – 1982). While no data were recorded for effort, the overall annual catch of white steenbras among these anglers and the percentage contributions (by number and mass) showed a general increasing trend from about 1967 to 1977, after which catches declined (Figure 8.4). This trend reflects that of the recreational shore fishery within False Bay and along the south west coast over the same period. The increase until the mid 1970s is likely an artefact of improved vehicle access to beaches, and the consequent targeting of species associated with sandy shores. The decline in absolute catch (by number) after the peak in

1977 (Figure 8.4a) is possibly due to the competitive anglers shifting their effort towards elasmobranchs, as was observed elsewhere along the coast (Taylor 1993, Hanekom *et al*. 1997), or may be a result of general overexploitation in this area. The fact that the contribution of white steenbras to the total catch, both numerically and gravimetrically (Figure 8.4b), remained high despite the decrease in actual catch, suggests the latter is more likely; however, in the absence of effort data, such a statement cannot be made confidently.

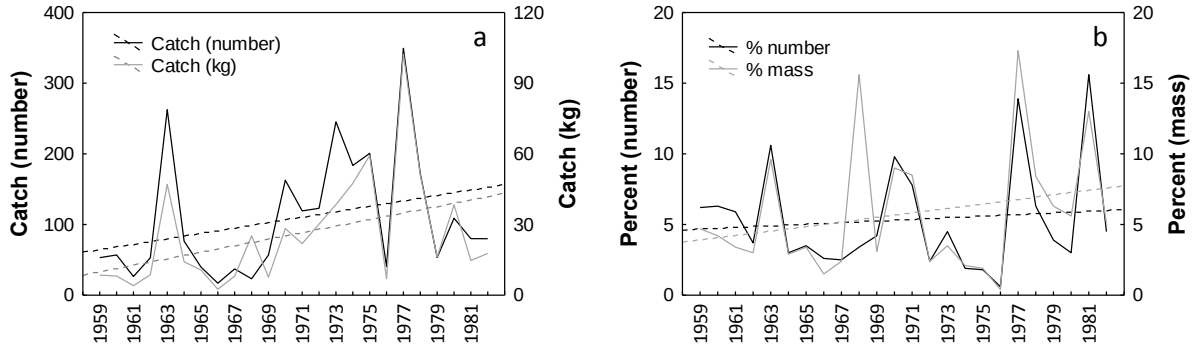

Figure 8.4: Shore angling catch data from individual catch card returns for competition angling from Robberg to the Great Fish Estuary, for the period 1959 to 1982 (after Coetzee *et al*. 1989). Dotted lines represent linear fits to the respective data, to show overall trends

Competition shore angling data are presented for the same region (Robberg to Great Fish Estuary), for the annual competition known as "angling week", for the years 1978 to 1982, in which teams of anglers fished for a set period of one week, in February each year (Coetzee *et al*. 1989). Estimates of CPUE were obtained from the estimated total effort and the numerical catch of white steenbras. Data are also presented for this area, for the period 1979 to 1982, from "postal competitions", in which teams of anglers would fish for a single eight-hour period, and nine such competitions are held annually (Coetzee *et al*. 1989). Overall, white steenbras contributed 3.3% of total catch by number, with a CPUE of 0.24 fish.100 angler hours^{-1} in the angling week catches, and 2.0% by number with a CPUE of 0.53 fish.100 angler hours^{-1} in the postal competitions (Coetzee *et al*. 1989). Similarly, Pradervand and Govender (2003) recorded low CPUE (0.2 fish.100 angler hours^{-1}) and a numerical contribution of only 1.4% to total catch in competition shore angling catches between the Great Fish and Great Kei Estuaries. These competition catches are somewhat lower than those obtained for white steenbras in the recreational shore fishery and research angling elsewhere along the south east coast (Table 8.3). The result is likely an artefact of competitive anglers targeting elasmobranchs to maximise competition points (Hanekom *et al*. 1997); however, it may also indicate lower abundance of white steenbras towards the eastern end of its distribution, due to

overexploitation or less optimal resources for this species, in this area. Interestingly, though, white steenbras constitutes the third most targeted species along the south east coast, being targeted by an estimated 11% of shore anglers (Brouwer *et al*. 1997).

Research angling conducted from 2006 to 2007 in the Coega Harbour, in Algoa Bay, produced a higher CPUE for white steenbras (0.92 fish.100 angler hours^{-1}) than other studies along the eastern part of the south east coast, particularly the competition catches reported by Coetzee *et al*. (1989), although the species contributed only 0.4% numerically to the total teleost catch (Dicken 2010). This low contribution reflects the high abundance of other fishes within the harbour, resulting from the shelter and potentially elevated food levels, when compared to the adjacent marine environment (Dicken 2010). The Coega Estuary flowing into the harbour also provides estuarine cues. The high proportion of white steenbras captured in the harbour (89%) below the size at 50% sexual maturity suggests the use of the harbour as a nursery area. Despite the low absolute number of white steenbras captured, the fact that angling is prohibited within the harbour suggests that this could function indirectly as a protected area for white steenbras and other coastal fish species.

As with the Goukamma MPA, the proposed GAENP MPA in Algoa Bay has potential to provide protection for white steenbras in the surf zone. A roving creel survey conducted along the eastern shoreline of Algoa Bay, including the proposed GAENP MPA, from 2006 to 2009, recorded a CPUE of white steenbras of 1.29 fish.100 angler hours^{-1}, constituting the second most common teleost recorded, and contributing 7.9% to the total catch (R Chalmers, unpublished data). The relatively high contribution of white steenbras to catches along this section of the coastline, and the positive results observed in the TNP and De Hoop MPAs, suggest that once proclaimed the GAENP MPA is likely to contribute significantly to the protection of white steenbras in the surf zone, if the area is closed to shore angling. Furthermore, the higher CPUE of white steenbras along the shoreline of the proposed GAENP MPA than during competition angling or recreational shore angling along other sections of the south east coast (Table 8.3) indicates a possible increase in the abundance of white steenbras in this area.

The suggested increase in white steenbras abundance within this area is confirmed by shore angling as part of a long-term monitoring programme along the eastern shoreline of Algoa Bay (PD Cowley, unpublished data). Research angling, conducted approximately bimonthly, recorded an increasing trend in the CPUE of white steenbras from summer 2005 until early 2011, as well as the highest CPUE recorded for all studies discussed (16.6 fish.100 angler hours^{-1}) (Figure 8.5).

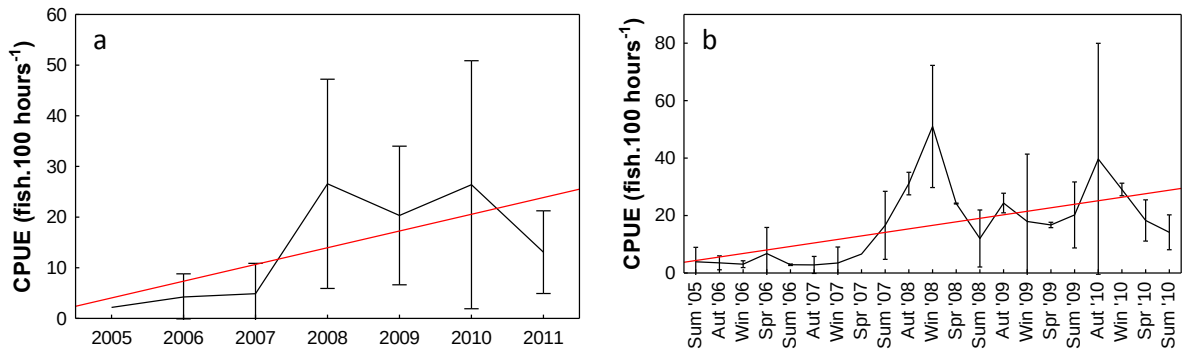

Figure 8.5: Mean (±SD) daily CPUE (fish.100 angler hours^{-1}) of white steenbras recorded a) by year, and b) by season, during research angling within the boundaries of the proposed GAENP MPA

The observed increase in the CPUE of white steenbras over the seven-year period, and the greater CPUE than in other studies presented, may reflect an increase in abundance, caused by a decline in shore angling effort in the region, as a result of the ban on the use of vehicles in the coastal zone imposed in January 2002. This section of coastline is now accessible only on foot, with access points some distance from the shore. Therefore, the "beach driving ban" appears to have contributed to decreasing the overall shore angling effort within this region, and possibly other poorly accessible coastal regions; thereby indirectly contributing to increased abundance of white steenbras. The improved CPUE may be indicative, and provide the first evidence, of a recovery of the white steenbras stock, although this has not been observed in other coastal regions. The considerably higher CPUE recorded during research angling, than that recorded during the roving creel survey (R Chalmers, unpublished data), may also be evidence of under-reporting of catches, particularly fish that are smaller than the minimum legal size.

Attwood (2003) suggested that carrying capacity can be affected by the patchiness of the habitat. Therefore, suitability of this section of coastline may also be due to the predominantly sandy shoreline, with some mixed sand and rock and very little rocky shoreline, as white steenbras exhibits an affinity for sandy shores (see Chapter 6). This suggests that MPAs incorporating a large proportion of sandy substrate may be more suitable for the species.

Transkei coast

White steenbras featured poorly in recreational shore angler catches along the Transkei coast, from 1997 to 1998 (Mann *et al*. 2003), and in competition shore angling catches in the Transkei from 1977 to 2000 (Pradervand 2004), suggesting that the abundance of white steenbras in the Transkei is lower than in coastal regions further west. Recorded CPUE for white steenbras in the Transkei during

these studies (0.18 and 0.03 fish.100 angler hours^{-1}, respectively) are close to the lowest CPUE estimates recorded in all surveys included in the analysis.

The shore fishery at the national level

The results of the studies presented showed generally higher CPUE of white steenbras within MPAs. There was also a general decreasing trend in CPUE towards the ends of the white steenbras distribution, along the west and Transkei (east) coasts (Figure 8.6).

According to Bennett (1993b), white steenbras undertake annual spawning migrations to the Transkei and south east coasts in late winter. Anecdotal evidence suggests that historically white steenbras were sporadically captured in high numbers along the southern Transkei coast over the spawning season. It is possible that the low CPUE estimates of white steenbras in these areas reflect the low density of juveniles and the low numbers of adults present outside of the spawning season, although considering the spawning aggregation, it was expected that shore catches of white steenbras during the survey and competition angling within the Transkei would have been higher. The low CPUE values observed may be a result of under-reporting of catches during the survey. Alternatively, as white steenbras is known as an early morning angling species, it is possible that anglers targeting white steenbras may not have been intercepted during the roving creel survey, which was restricted to daylight hours (Mann *et al*. 2003). However, this is unlikely the case with competition anglers, suggesting that the observation is a result of the general decline in white steenbras abundance, providing evidence of suppressed spawner stock levels.

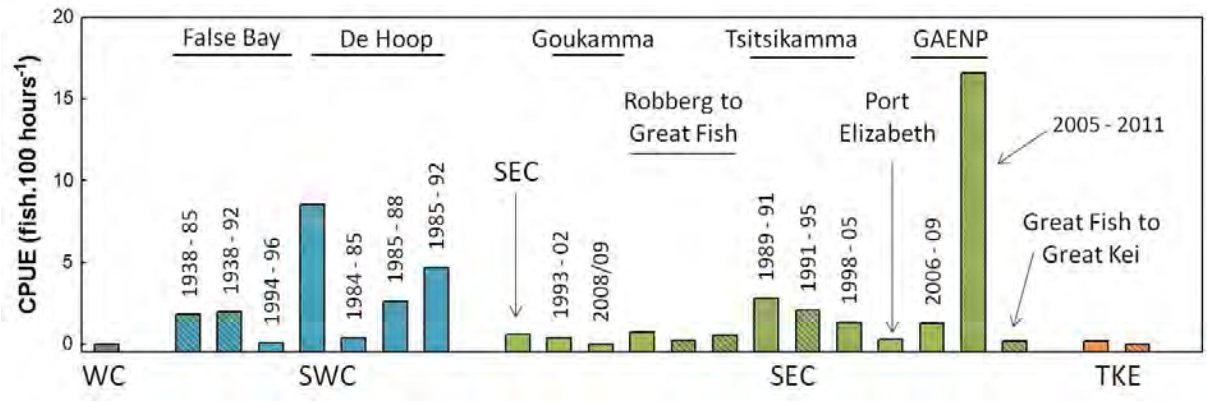

Figure 8.6: White steenbras CPUE (fish.100 angler hours^{-1}), recorded or inferred, from shore fishery surveys along different regions of the South African coastline (WC = west coast, SWC = south west coast, SEC = south east coast, TKE = Transkei), from Port Nolloth in the west to the eastern boundary of the Transkei. Results are plotted in geographical order from west to east. Cross-hatches represent competition angling, and stippled samples represent research angling

In general, in areas where surveys have been conducted over extended or multiple periods, such as False Bay and the De Hoop, Tsitsikamma and Goukamma MPAs, the results provide evidence of declining CPUE of white steenbras over time. White steenbras CPUE recorded along the entire south east coast (Brouwer and Buxton 2002) and Goukamma coastline (Pradervand and Hiseman 2006) were similar to that recorded in the heavily exploited study area within the De Hoop MPA prior to proclamation (Bennett and Attwood 1991). This suggests that white steenbras along the south east coast and much of the south west coast has been severely overexploited, as a result of the high levels of angling effort.

For the South African coastline (excluding the former Transkei and Ciskei coastlines), Brouwer *et al*. (1997) estimated total shore-angling effort of 3 238 921 angler days per year, for the period 1994 to 1996. The greatest proportion of this effort was expended along the KwaZulu-Natal shoreline, which falls outside the core distribution of white steenbras and was not considered in the current analysis. Recreational shore-angling effort in False Bay alone, over the years 1991 and 1992, was estimated at 987 690 angler days per year (at 6 hours per angler day) (Lamberth *et al*. 1994). This highlights the large contribution of the False Bay recreational shore fishery (by effort and catch) to that at the national level. Similarly, Brouwer and Buxton (2002) estimated annual recreational shore-angling effort at 903 186 angler days per year, from 1994 to 1996, along the south east coast shoreline. Brouwer *et al*. (1997) also estimated a total annual shore catch in excess of 4.5 million fish (almost 3 000 mt), by 1996, of which the contribution of white steenbras was low. Based on data available at the time, Bennett (1993a) inferred a total recreational (including competition) shore angling catch of white steenbras by the late 1980s, across its distributional range, of approximately 28 000 fish annually (which equates to 0.62% of the estimated total annual shore angling catch). From 1994 to 1996, Lamberth (1996) estimated a total recreational shore catch for the south west coast alone of 39 000 white steenbras at 86 mt annually. The results highlight the impact that the recreational shore fishery has on white steenbras, and its contribution to the demise of the species.

Is there evidence for stock recovery?

In contrast to the results presented above, Figure 8.7 presents the comparative estimates of CPUE, recorded during some of the surveys previously described and those of an ongoing roving creel recreational shore fishery observer programme, started in 2010, along selected regions of the coast (Anchor Environmental Consultants, unpublished data). The data for the observer programme were not included in the original analysis, due to the short duration of data collection in most areas; however, the programme provides some new results and a useful comparison with previous surveys.

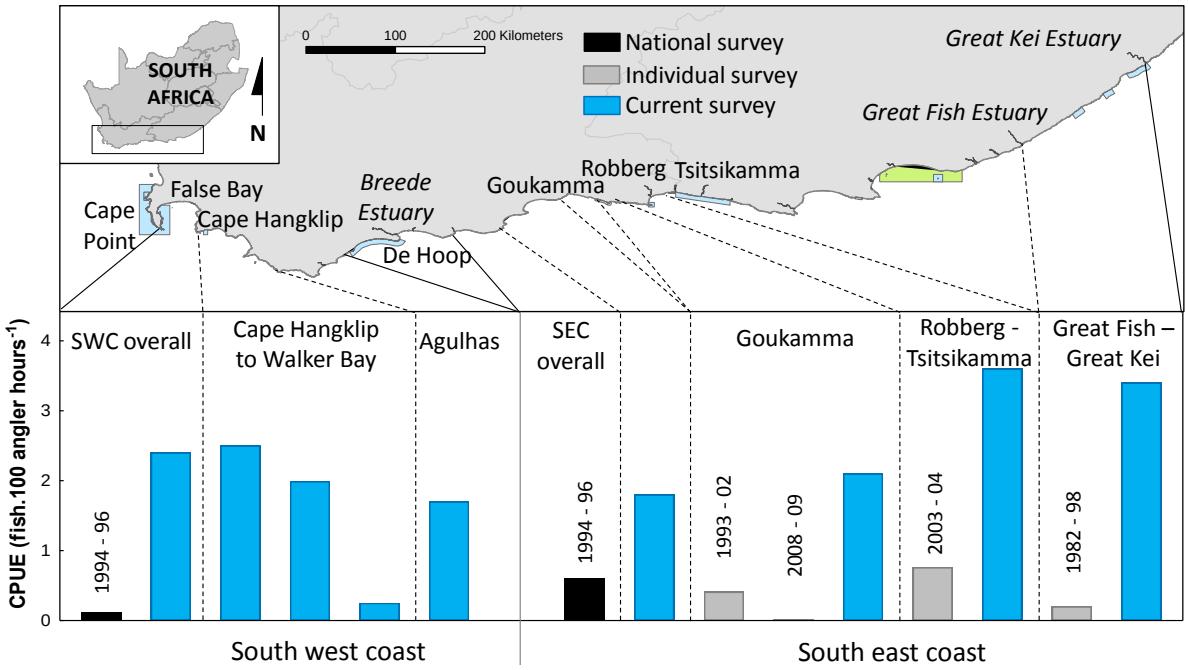

Figure 8.7: CPUE for white steenbras from the national shore fishery surveys for the south west and south east coasts (black bars) and other dedicated roving creel surveys (grey bars), compared with the recent (2010/2011) roving creel observer programme (blue bars; Anchor Environmental Consultants, unpublished data), and map showing the associated sections of shoreline surveyed

Lamberth (1996) estimated white steenbras CPUE at 0.12 fish.100 angler hours^{-1} along the south west coast. The 2010/2011 survey of sections of the south west coast recorded considerably higher CPUE, with an overall white steenbras CPUE of 2.4 fish.100 angler hours^{-1} from Cape Hangklip to Cape Agulhas (Anchor Environmental Consultants, unpublished data). Along the south east coast, Brouwer and Buxton (2002) estimated white steenbras CPUE at 0.6 fish.100 angler hours^{-1}, while CPUE from four areas in the 2010/2011 survey ranged from 1.8 to 3.6 fish.100 angler hours^{-1} (Figure 8.7). The 2010/2011 survey also recorded considerably higher CPUE than those recorded in the Goukamma MPA (Pradervand and Hiseman 2006, van Zyl 2011), from Robberg to Tsitsikamma MPA (King 2005), and between the Great Fish and Great Kei estuaries (Pradervand and Govender 2003).

The increased CPUE values recorded for 2010 and 2011, in all areas surveyed, provide evidence of increased abundance of white steenbras, since earlier surveys, particularly the national survey from 1994 to 1996. The fisheries for white steenbras have undergone considerable changes over the past two decades, the greatest of which was the total ban on commercial exploitation in 2001. Most (80 %) of the white steenbras recorded in this recent observer programme were juveniles, suggesting that the elevated CPUE resulted from improved recruitment. It is possible that the commercial ban in 1995 and the withdrawal of the 20 mt exemption in 2001 relieved sufficient exploitation pressure

on adult white steenbras, allowing for improved spawning success and consequently improved recruitment. While the overwhelming evidence from the last 100 years indicates severe white steenbras population declines, the above evidence together with high CPUE values in the proposed GAENP MPA are suggestive of some stock recovery. This positive trend appears to have resulted mainly from the ban on commercial harvesting, and the national ban on the use of vehicles in the coastal zone, which decreased accessibility to many coastal areas. Factors such as the minimum size increase to 60 cm TL, increased public awareness and favourable environmental conditions for spawning and recruitment may also have contributed (SJ Lamberth, DAFF, pers. comm.).

8.3.2 Commercial net fisheries

Commercial beach-seine fishery

Historically, white steenbras formed an important component of the commercial beach-seine (including the sinking "Russman" seine), purse seine, and gill-net fisheries in South Africa (Penney 1991, Bennett 1993b, Lamberth *et al*. 1997). White steenbras was traditionally one of three species, along with yellowtail *Seriola lalandi* and southern mullet ("harder") *Liza richardsonii*, targeted by the commercial beach-seine fishery, along the west, south west and south east coasts (Lamberth *et al*. 1994). Commercial beach-seine operations were permitted at 35 coastal sites, from Walvis Bay in Namibia to Port Elizabeth on the south east coast (Figure 8.8).

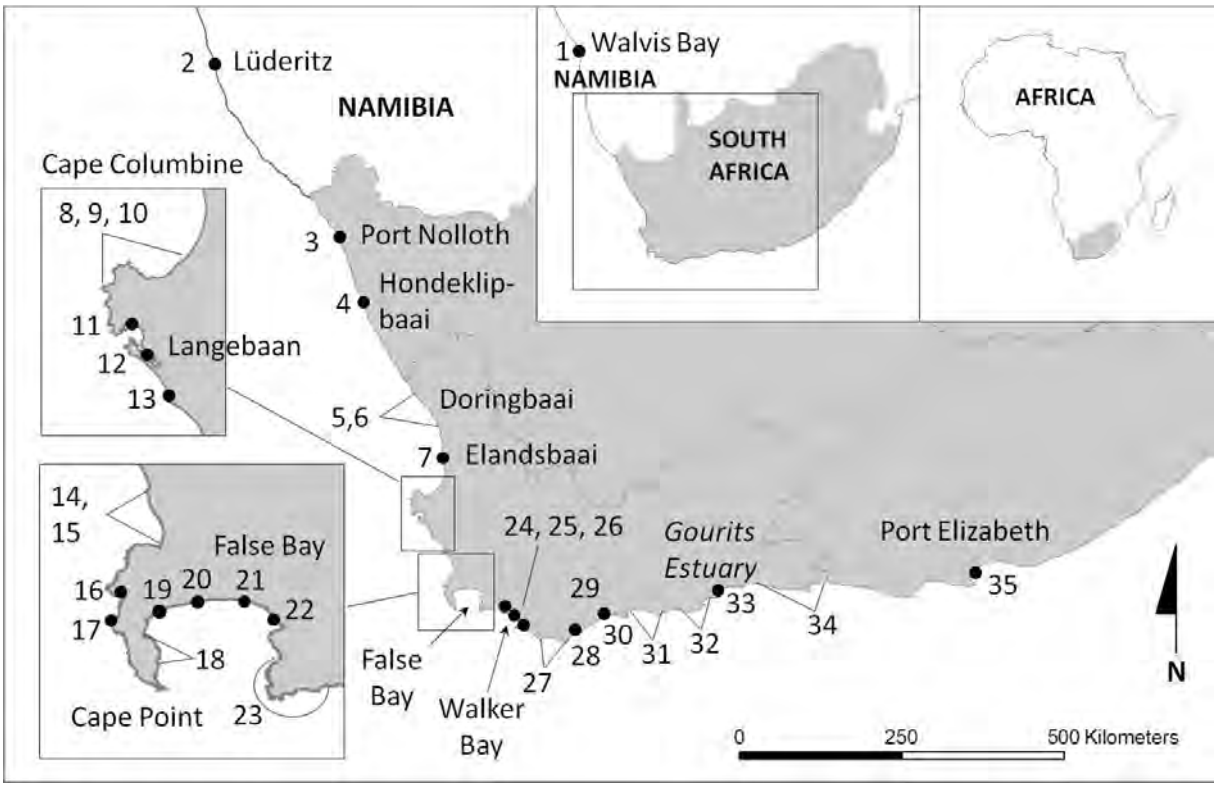

Figure 8.8: Map indicating the 35 coastal areas designated for commercial beach-seine operations

Prior to 1960, the beach-seine fishery was responsible for the majority of the annual white steenbras harvest made along the South African coastline (Bennett 1993a). Although the contribution made by the recreational shore fishery to the total annual catch of white steenbras increased after 1960, the relative contribution of white steenbras to total beach-seine catches remained high. White steenbras was the third most dominant species captured in this fishery from 1977 to 1992 (Lamberth and Bennett 1993), and fourth most dominant in the early 1990s (Clark *et al*. 1994).

Until 1982, the commercial beach-seine fishery was permitted to catch "angling" or "line" species, which included white steenbras, and annual catches of white steenbras averaged about 20 mt, with record catches reaching 40 to 50 mt and almost 100 mt in some years (Penney 1991, Bennett 1993a). However, a ban was imposed on the catch of all angling species in the commercial beach-seine fishery operating in all areas other than False Bay and Walker Bay, after 1982. This management intervention resulted in a marked decrease in the overall catch of white steenbras in this fishery, with annual white steenbras catches of about 3.4 mt after 1984 (Penney 1991).

Prior to 1990, the commercial beach-seine fishery was responsible for approximately 25% of the total annual white steenbras catch by number, and about 50% by mass, along the South African coastline, with the remainder of the catch predominantly taken by recreational shore anglers (Bennett 1993a). Within False Bay, between 1985 and 1992, the beach-seine fishery was responsible for approximately 40% of the total catch of white steenbras (almost 14 000 fish reported for this period), with the remainder of the catch again largely taken by the recreational shore sector (Lamberth *et al*. 1994).

Owing, largely, to its substantial contribution to the total catch made in the commercial beach-seine fishery, white steenbras abundance has declined over the last century. Mean annual reported catches in this fishery declined by 85% over this period, from 23 061 fish.year^{-1} during the time of Gilchrist (1897 to 1906), to 3 147 fish.year^{-1} during the period 1983 to 1991, with declines observed in all coastal regions (Figure 8.9) (Bennett 1993a). The numerical contribution of white steenbras to total beach-seine catches declined from approximately 3.77% at the turn of the last century, to 0.57% in the period 1951 to 1968, 0.43% by the period 1977 to 1987, and to 0.19% by the period 1983 to 1991 (Bennett 1993a). Declines in white steenbras catch were observed even between 1983 and 1991 along the west coast, the south east coast and parts of False Bay (Bennett 1993a). While these declines in areas outside of False Bay are partly a result of a decrease in the targeting of white steenbras as a consequence of the ban on "angling" species outside of False Bay and Walker Bay,

they are likely exacerbated by the general trend of population decline experienced by the species over this period. It is evident that the commercial beach-seine fishery contributed substantially to the overall demise of the white steenbras stock (Bennett 1993b, Lamberth *et al*. 1994).

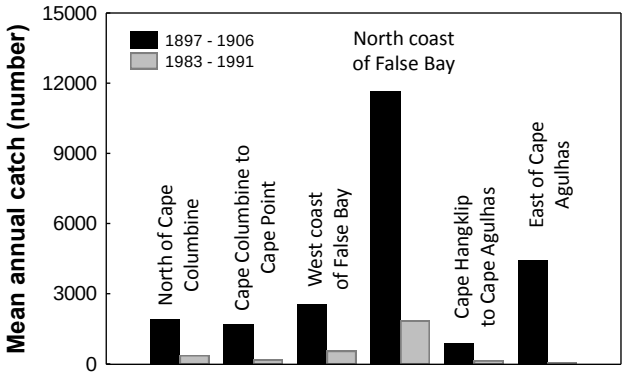

Figure 8.9: Mean annual commercial beach-seine catches for the periods 1897 to 1906 (recorded by Gilchrist) for six regions of the South African coastline and respective catches for the same areas submitted in mandatory catch returns from 1983 to 1991 (after Bennett 1993a)

Since 1974, it has been compulsory for the commercial beach-seine permit holders to submit monthly catch returns to the authorities (Penney 1991). This has made it easier to identify trends in harvesting of the different species in the commercial sector, than in recreational shore catches, which are limited to assessment by few dedicated surveys. The overall decline in the catches of white steenbras over the past five decades is illustrated in the series of Figures 8.10 to 8.13, representing beach-seine catches of white steenbras over different time periods. It appears that the overall decline can be partitioned into a number of phases, with different periods of decline associated with altered patterns of exploitation over the years, in the different sectors. Figure 8.10 depicts the catch and CPUE of white steenbras, as well as the netting effort, exerted by a commercial operator along the northern shore of False Bay, as recorded in a personal catch log from 1950 to 1968 (SJ Lamberth, unpublished data). The data show an increasing trend in the catch and CPUE (fish.haul^{-1}) of white steenbras over the 1950s, but after 1963 annual catches declined rapidly. While the decline in total annual harvest may be a result of the reduced numbers of seine hauls in the later years (Figure 8.10b), this does not explain the decline in CPUE. However, this period coincided with the spatial expansion of shore angler distribution in False Bay more towards sandy shorelines, and the consequent rapid increase in shore angler catches of white steenbras.

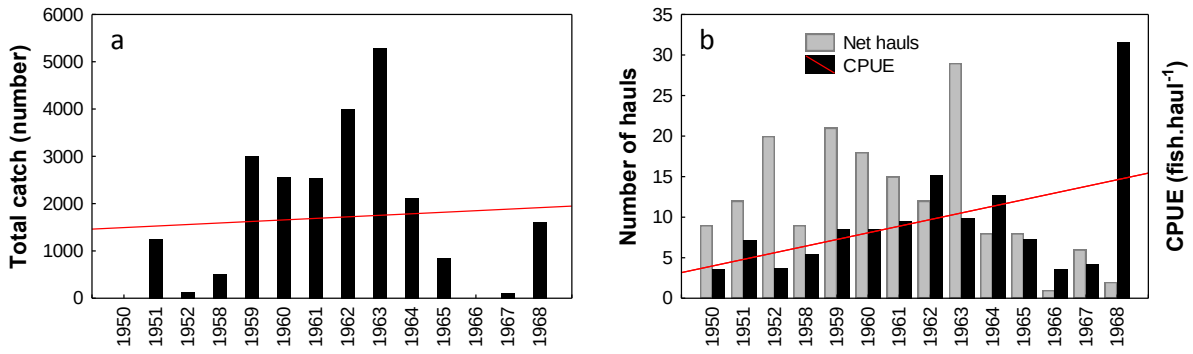

Figure 8.10: Summary of 170 beach-seine hauls, including a) annual catch and b) both the CPUE (fish.haul^{-1}) of white steenbras and the annual netting effort, made by a commercial permit holder along the north shore of False Bay from 1950 to 1968 (SJ Lamberth, unpublished data). The red trendlines represent the linear fits to the data (fitted to CPUE in figure b)

The seine netting effort, as well as the frequency distribution of catches, mean monthly catch and total annual catch of white steenbras made by a second beach-seine operator from the north shore of False Bay, for the period 1975 to 1987, are presented in Figure 8.11.

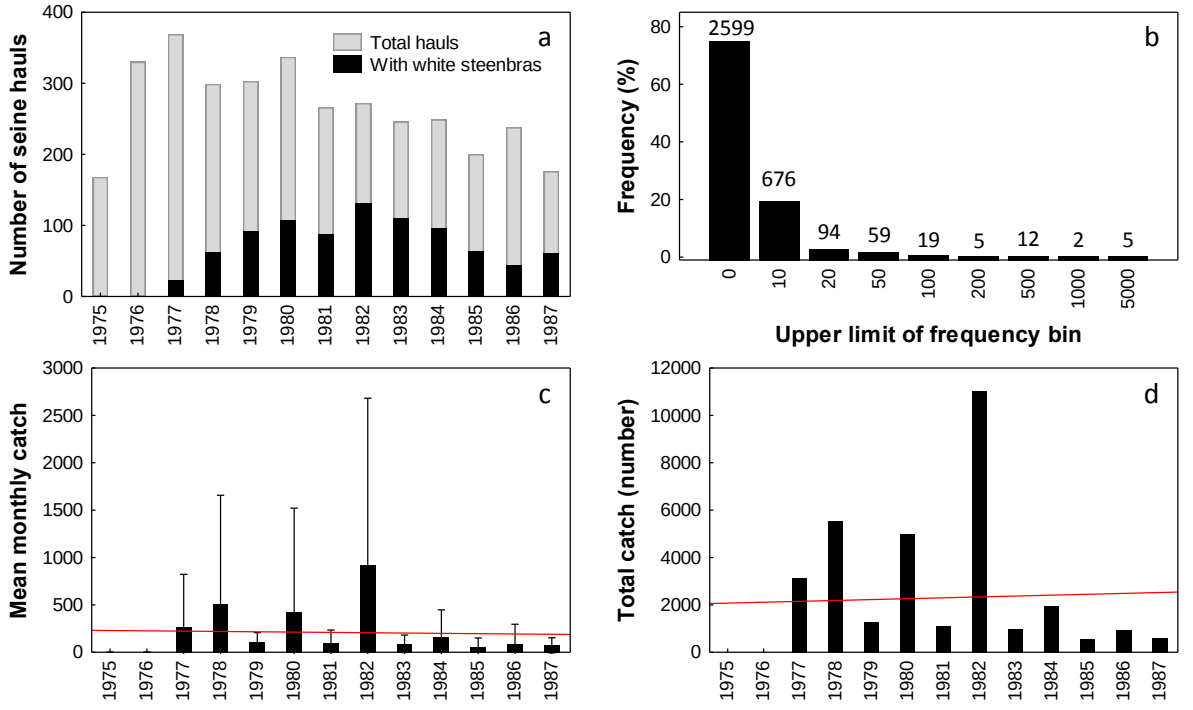

Figure 8.11: Summary of 3 471 beach-seine hauls, including a) the annual number of hauls (with and without white steenbras), b) the frequency distribution of white steenbras catches, c) mean monthly catch (±SD) and d) total annual catch of white steenbras, by a commercial beach-seine operator, from the north shore of False Bay for the period 1975 to 1987. The red trendlines in c and d represent the linear fits to the data

There was a high level of variability in the data, with a large proportion of hauls containing zero white steenbras, although hauls of up to 4 750 individuals were made. There was an initial increasing trend in the annual catch of white steenbras by this operator, which coincided with the period post 1974, when competition shore anglers are suggested to have shifted their effort towards targeting elasmobranchs. It is possible that this shift away from teleost fishes provided some relief for the white steenbras within False Bay, although it is unlikely that this alone accounted for the observed increase in beach-seine catches. This period also coincided with the introduction of the trailable skiboat from KwaZulu-Natal to the south west coast, in the 1970s (Griffiths 2000). Further improvements in fishing equipment, including electronic navigational equipment and echo-sounders, and the building of small-boat harbours, resulted in increased participation in the skiboat fishery around this time (Penney 1991, Griffiths 2000). This change in fisher behaviour may have alleviated pressure on inshore species, such as white steenbras, which are rarely caught off skiboats.

The increased commercial beach-seine catches made over this period may also reflect natural fluctuation in the abundance of white steenbras within False Bay around this time, which led to the peak catches made in 1982 and 1983, in the commercial beach and purse seine fisheries (Penney 1991). The sudden decline after 1982 reflects that of the total commercial beach-seine catch of white steenbras made at the national level, after a peak in 1982 of about 100 mt (Penney 1991). The decline is partly attributable to the vast changes in regulations after 1982, including a closed season, increased minimum size limits, restrictions on net length, a ban on night netting and a ban on the harvest of angling species outside of False Bay and Walker Bay (Bennett 1993a). However, the decline within False Bay is also largely attributable to the excessive hauls of white steenbras made by the purse seine fishery in the late 1970s and early 1980s. Purse seine catches increased in False Bay until the late 1970s, with the total catch exceeding 36 000 mt (Penney 1991), and almost 300 mt of white steenbras landed in 1982 (Bennett 1993a). This suggests that these “good” years had a substantial impact on the stocks of numerous species in False Bay, with purse seine catches contributing substantially to the observed declines in linefish catches in the 1980s.

While the preceding datasets provide an indication of the demographic status of the white steenbras during these periods, they are each taken from a single operator, and are thus subject to potential bias. Data presented in Figure 8.12 were obtained from compulsory catch returns submitted by six permitted commercial beach-seine operators in False Bay, for the period 1983, at the time of the “angling” species ban outside of False Bay and Walker Bay, to 2002, just after the imposition of the commercial ban on the species, in 2001.

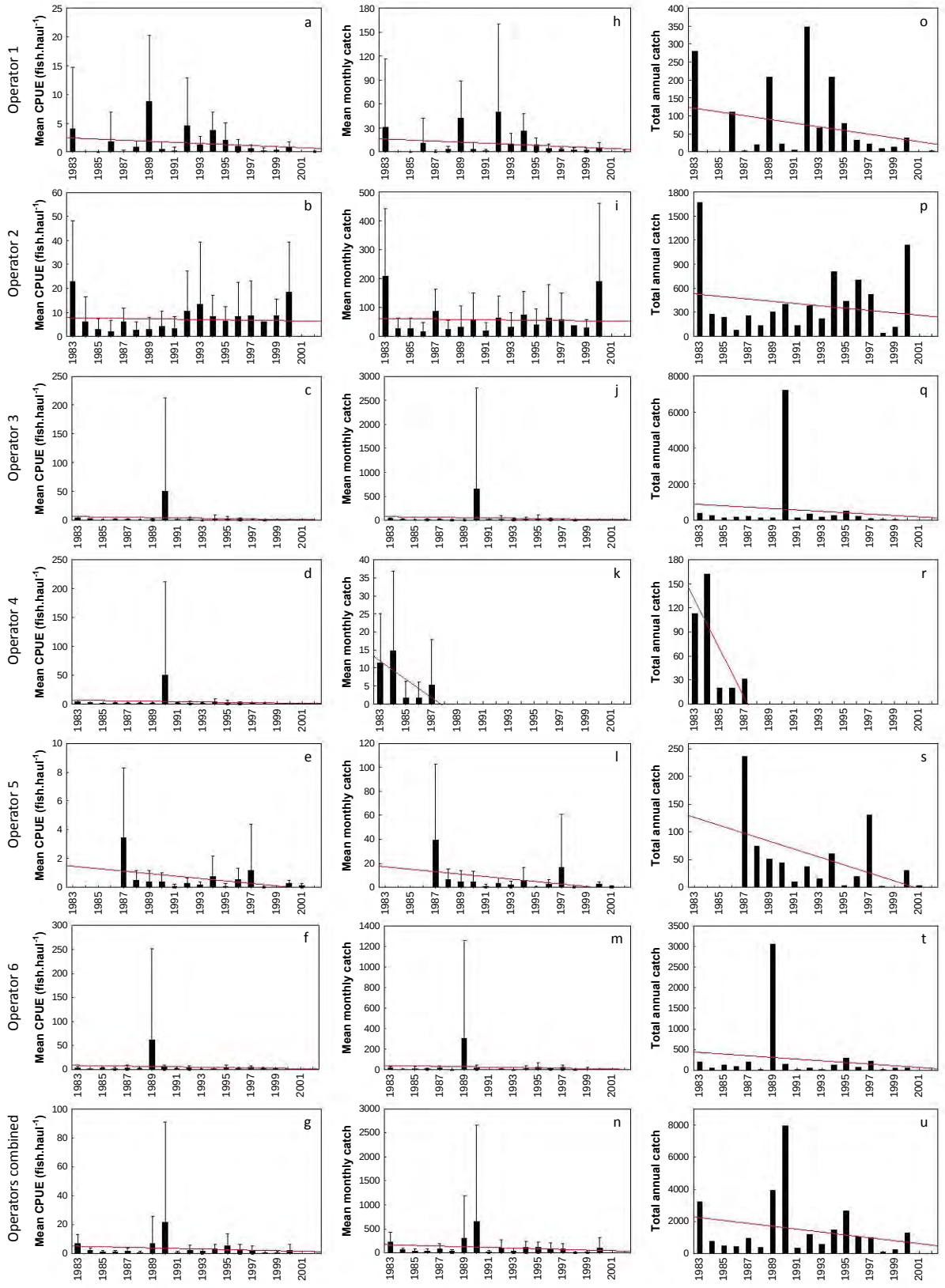

Figure 8.12: Commercial beach-seine catches of white steenbras in False Bay, in terms of mean CPUE (fish.haul^{-1}, a – g), mean monthly catch by number (h – n) and total annual catch by number (o – u), from obligatory catch return data for six licensed operators, and the combined catch for the six operators (g, n, u), from 1983 to 2002. Red lines indicate linear trends in each dataset

There was considerable variability among operators, in terms of mean and total catch, with some operators exhibiting a fairly consistent level of CPUE over the years, and others having short-lived peaks in CPUE and total annual catch. However, most operators recorded peaks in annual catch in the late 1980s and early 1990s, after which catches of most declined relatively sharply, partly as a result of the initial ban, in 1995. Some operators recorded large annual catches after 1995, before the withdrawal of the 20 mt exemption in 2001. Catches of one operator, presented as Operator 2 in Figure 8.12, recorded what could be interpreted as an increasing trend in annual catch over this period, until a decline after 1994, except for a secondary peak in 2000.

Variability in CPUE was also high within the catches of each operator, caused by the frequent zero hauls and sporadic large hauls of white steenbras, which complicates the determination of catch trends. Despite this variability, however, the overall trend of declining total catch and declining CPUE are common to most datasets. Overall, for these six operators combined, a peak in catch and CPUE of white steenbras was made in 1990 (Figure 8.12 g, n, u). Subsequently, the total annual catch increased until the ban in 1995, before decreasing until the withdrawal of the 20 mt exemption in 2001; however, CPUE remained low after 1990.

Commercial beach-seine catches at the national level

To illustrate the decline in white steenbras abundance at the national level, the total and mean (±SD) annual catches (by mass) of white steenbras from 197 294 beach-seine hauls conducted by 867 permit holders operating in 34 different coastal areas, for the period 1983 to 2002 (SJ Lamberth, unpublished data), are presented in Figure 8.13. Most of these data were recorded as mass, with a small proportion recorded as numbers. In order to include all records, those including numbers of white steenbras were converted to mass, by multiplying the numbers caught by an estimated mean individual mass of white steenbras in the fishery. A mean mass of 4.0 kg was used (SJ Lamberth, DAFF, pers. comm.), equating to approximately 690 mm TL. While the estimated masses have not been verified, the method is assumed to be accurate, and presented by Lamberth *et al*. (1994) for estimating numbers from data recorded as mass. These data were recorded from 34 coastal areas (Figure 8.8), from Lüderitz in Namibia to Port Elizabeth, on the south east coast. Data for the different permit holders within each area were pooled. Lamberth *et al*. (1994) suggested that the level of under-reporting of the catches of certain species in the catch return data, including white steenbras, was high. Therefore, the values presented here are likely underestimates. However, trends in catch data are fairly robust even when the level of under-reporting is high. It was assumed that the level of under-reporting was consistent both spatially and temporally, within this fishery.

In total, 228 mt of white steenbras were captured from 1983 to 2002. In terms of the spatial distribution of catches, the vast majority was landed in areas 18, 19 and 21, which are all within False Bay (Figure 8.8). A smaller, separate peak in catch was observed at area 8, which effectively includes the area from Cape Columbine northwards for about 60 km, and straddles the mouth of the Berg Estuary (as permit holders in areas 8, 9 and 10 operated in any of the three areas). While the dominance of the False Bay catches is largely a result of the ban on the harvest of angling species in the beach-seine fishery outside of False Bay in 1983, these results illustrate how catches within False Bay represent the majority of white steenbras caught in the beach-seine fishery.

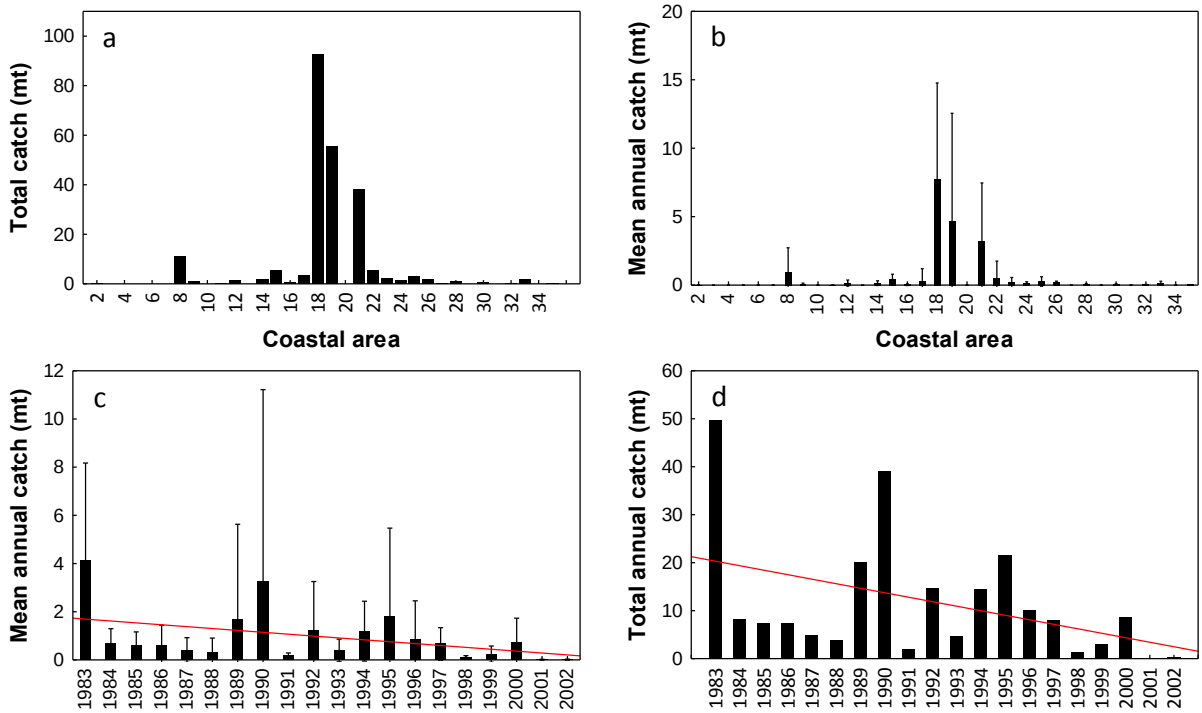

Figure 8.13: Beach-seine catches of white steenbras recorded at 34 permitted areas from Lüderitz (Namibia) to Port Elizabeth (south east coast), showing a) total catch, b) mean (±SD) annual catch by area, c) annual mean (±SD) catch, and d) total annual catch recorded across all areas (in mt), from 197 294 beach-seine hauls conducted by 867 operators. The red trendlines in c and d represent the linear fits to annual mean catch and total annual catch, respectively, over the period 1983 to 2002

White steenbras is believed to be endemic to South Africa (Smith and Smith 1986). Therefore, the negligible catches made at Lüderitz in Namibia (commercial beach-seine area 2) are to be expected, and could be interpreted as stragglers having made nomadic coastal movements further northwards than their endemic distribution would suggest. However, there are reports of white steenbras contributing to catches as far north as Walvis Bay, in Namibia, in permitted beach-seine area 1 (Figure 8.8). This area was not included in the current analysis, as white steenbras recorded in this

area were largely misidentified west coast steenbras (*Lithognathus aureti*). While the majority of these are likely to be west coast steenbras, there is some evidence that white steenbras were historically abundant along the Namibian coastline, possibly as a separate spawning population, but that this stock may have been depleted altogether by severe overexploitation around the end of the 19th century (SJ Lamberth, DAFF, pers. comm.).

Mean and total annual catch pooled across areas showed an overall decline (Figure 8.13 c and d). The peak in total catch in 1983 (49.6 mt) coincided with the high catch made in the purse seine fishery in 1982, and is likely associated with a high abundance of white steenbras in False Bay at the time (Bennett 1993b). The subsequent decline is likely due to the substantial total harvest made in all sectors in the early 1980s. The secondary peak made in 1989 and 1990 followed a period of low catches and CPUE, and may be indicative of a slight recovery in white steenbras numbers since the effects of the harvest in the early 1980s. However, the peak was temporary and in the latter part of the 1990s, the total annual catch reached a 15-year low (0.11 mt), with the stock considered collapsed, and negligible catches of white steenbras recorded after the commercial ban in 2001.

Commercial purse seine fishery

The data for catches made by the commercial purse seine fishery in False Bay were poorly recorded (Bennett 1993a), making assessments of catch and the contribution of the fishery to the total annual catch of each species difficult. This fishery was largely concentrated outside of False Bay, until the collapse of their target species (west coast pilchard *Sardinops sagax* and chub mackerel *Scomber japonicus*) in the late 1960s. These fishers were then attracted to False Bay, due to high availability of pilchard in False Bay at the time (Penney 1991). The purse seine fishery in False Bay was responsible for sporadic catches of white steenbras in the late 1970s and early 1980s. However catch peaked in 1982 with a record catch of almost 300 mt of white steenbras (Bennett 1993a). As these were almost entirely adult white steenbras, these catches are likely to have contributed significantly to the decline of the species (Lamberth and Mann 2000). Purse seine fishing was subsequently banned from False Bay after 1982 (Penney 1991).

Commercial gill-net fishery

White steenbras formed approximately 3% of the bycatch in the combined gill-net and beach-seine fisheries along the south west and south east coasts (Cape Point to East London) prior to 1997 (Lamberth *et al*. 1997). However, in 1998 and 1999, white steenbras were absent from monitored inshore and estuarine gill-net catches along the South African west coast (Hutchings and Lamberth

2002a). Furthermore, Hutchings and Lamberth (2002b) determined, based on surveys, catch returns and processing facility records, that the bycatch of white steenbras in the gill-net fishery along the west and south west coasts in the latter part of the 1990s, was negligible. Considering that the majority of white steenbras captured in the beach-seine fishery is taken within False Bay, and that the mean annual reported catches in the gill-net fishery in False Bay were shown to be only a fraction of those reported for the beach-seine fishery (Lamberth *et al*. 1997), it follows that the contribution by the commercial gill-net fishery to the annual catches of white steenbras was considerably lower than that of the beach-seine fishery.

8.3.3 Boat-based linefisheries (recreational and commercial)

White steenbras is typically an inshore coastal species that features poorly in the catches of recreational and commercial boat-based fisheries. Coetzee and Baird (1981) reported zero white steenbras captured by recreational boat anglers around the St Croix Island in Algoa Bay, from December 1975 to February 1978. White steenbras was the seventh most commonly captured species in the commercial line fishery in False Bay from 1984 to 1992, although this amounted to about 2% of the total catch (Lamberth and Bennett 1993). An assessment of the commercial line (skiboat) fishery from Stilbaai to the Kei Estuary from 1994 to 1996 returned just two white steenbras, at a daily catch rate of 0.002 white steenbras.angler^{-1}.day^{-1} (Brouwer and Buxton 2002), and an assessment of the commercial and recreational boat fisheries in the Transkei from 1995 to 1998 returned a single white steenbras (Fennessy *et al*. 1999). Prior to 2000, recreational and commercial boat-based linefisheries combined produced about 1 mt of white steenbras bycatch annually (Lamberth and Mann 2000), approximately 1.2% of that estimated to have been taken in the recreational shore fishery in 1996 (Lamberth 1996).

8.3.4 Estuaries

The spatial distribution of white steenbras in estuaries was determined as part of a national assessment of ichthyofaunal diversity in estuaries from 1993 to 1999 (Harrison 1998a, b, c, 1999a, b, 2003, James and Harrison 2008, 2009, 2010a, b, 2011). This survey sampled 251 estuaries along the South African coastline, using both seine netting and gill-netting. White steenbras CPUE in the different estuaries, for both seine and gill-netting was highest in the centre of the species core distribution, defined as the area from the Berg Estuary to the Mbashe Estuary (Lamberth and Mann 2000), and decreased towards the edges of this distribution (Figure 8.14). Beyond these boundaries, the catches of white steenbras were negligible.

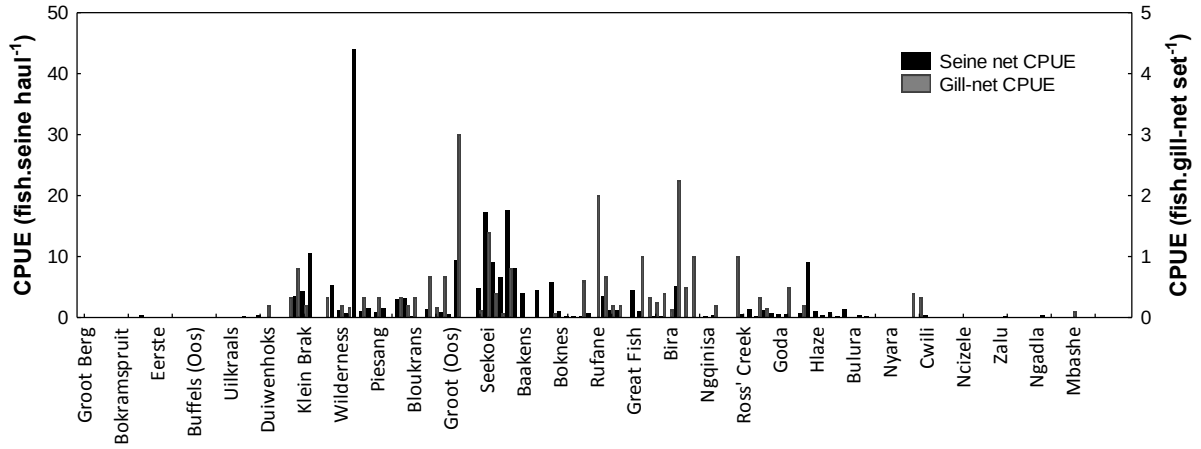

Figure 8.14: Seine net CPUE (fish.haul^{-1}) and gill-net CPUE (fish.gill-net set^{-1}) of white steenbras made in 138 estuaries (names provided for every fifth estuary) within the species core distribution (after Harrison 1998a, b, c, 1999a, b, 2003, James and Harrison 2008, 2009, 2010a, b, 2011)

Estuarine fisheries

Estuarine fisheries constitute a large proportion of recreational and subsistence angling effort at the national level, and the recreational estuarine fishery is of high economic value (Lamberth and Turpie 2003). Angling effort in estuaries has increased in recent years, as a result of the overall increase in fishery participation and the ban on "beach driving", implemented in 2002 (MacKenzie 2005). This increased effort has contributed to further declines in fish stocks. Furthermore, recreational fishing effort is usually concentrated in the lower reaches of estuaries (Baird *et al*. 1996, Potts *et al*. 2005, Cowley *et al*. 2004, 2009), coinciding with the high use area of white steenbras (see Chapter 3).

In the early part of the 20th century, white steenbras was the most abundant "angling" species captured during netting in the Swartkops Estuary, on the south east coast (Gilchrist 1918, in Baird *et al*. 1996). Prior to 1974, netting in this estuary indicated that white steenbras was still the most dominant angling species, although it was only second most common overall by mass, and fourth by number, but contributed more than double the number of another important angling species, spotted grunter *Pomadasys commersonnii*, (Grindley 1974, in Marais and Baird 1980). Over this period, white steenbras was also the dominant angling species in gill-net catches in the Breede and Bot estuaries (Ratte 1977a, b, in Marais and Baird 1980). In 1980, white steenbras CPUE in the Swartkops Estuary was 0.2 fish per 12-hour gill-net set, although by 1992 the species was absent from gill-net catches (Baird *et al*. 1996). In 1995, white steenbras was recorded as the eighth most common species in seine net catches in this estuary, contributing 1.7% by number, and third most common angling species, with just 11% of the catch of spotted grunter (James and Harrison 2010a).

Over the period 1972 to 1978, competition angler catches showed that white steenbras had been reduced to the second most dominant angling species in this estuary after spotted grunter, and comprised only a fraction of the catch of the latter (Marais and Baird 1980). During this period, white steenbras contributed 3.3% to total angler catches in the Swartkops Estuary (Marais and Baird 1980). By the period 1988 to 1993, the contribution of white steenbras to total angler catches had declined to 3.0 % (Baird *et al*. 1996), and to just 2.0% by the period 1996 to 1997, constituting only the fifth most common angling species (Pradervand and Baird 2002).

In the nearby Sundays Estuary, from 1976 to 1979, white steenbras was recorded in gill-net catches as the 15th species overall by number, comprising less than 10% of the spotted grunter catch, at a CPUE of 0.1 fish per 12-hour gill-net set (Marais 1981). By 1980 to 1981, white steenbras had increased to seventh most dominant species in seine net catches in this estuary, and the dominant angling species, with catches exceeding those of spotted grunter (Beckley 1984), and by 1992 to 1993, gill-net CPUE of white steenbras had doubled to 0.2 fish per 12-hour gill-net set (Baird *et al*. 1996). However, by 1995, the species contributed 2.6% to overall seine net catches in the Sundays Estuary, constituting the eighth most common species overall and the third most common angling species, with a catch of approximately 70% of that recorded for spotted grunter (James and Harrison 2010a). By the period 1996 to 1997, white steenbras was only the fifth most dominant angling species in the Sundays Estuary, and contributed just 0.7% of the total angler catch, at a CPUE of 0.14 fish.100 angler hours^{-1} (Pradervand and Baird 2002). More recently, a roving creel survey, from 2007 to 2008, recorded white steenbras as the fifth most common species by number, and third most common angling species, contributing 7.0% to the total angler catch, with a CPUE of 2.0 fish.100 angler hours^{-1} (Cowley *et al*. 2009). Therefore, it appears that the contribution of white steenbras in the Sundays Estuary fishery has fluctuated over the past four decades, increasing initially, but subsequently declining. However, the improved angler catches in the period 2007 to 2008 over those recorded a decade earlier suggest a possible recovery in the abundance of white steenbras in the Sundays Estuary. This may be a result of anomalous catches within this estuary, or the effect of improved recruitment as a result of the ban on the commercial harvest of white steenbras, in 2001.

Gill-netting, seine netting and angler catch data recorded at different times are not directly comparable, due to the variability in selectivity among gears (Marais and Baird 1980). As such, these data are presented simply to illustrate the temporal trends in the catch of white steenbras in the respective estuaries. The following sub-section provides the results of two long-term netting studies conducted in estuaries, to provide insight into the most recent trends in white steenbras abundance.

Long-term monitoring

Long-term netting in two estuaries, the temporarily open/closed East Kleinemonde Estuary on the east coast, and the permanently open Berg Estuary on the west coast, indicate a possible recent increase in white steenbras abundance in estuaries (Figure 8.15). Annual mean CPUE (fish.haul^{-1}), based on a total of 638 seine net hauls made during biannual seine netting in the East Kleinemonde Estuary from 1995 to 2010 (AK Whitfield, PD Cowley, NC James unpublished data) showed a decreasing trend from 1995 until 2002, followed by a general increase (Figure 8.15a). While the initial decreasing trend in CPUE may reflect years in which the estuary mouth remained predominantly closed (Figure 8.15b), the start of the increasing trend from 2002 coincides with the eventual withdrawal of the 20 mt white steenbras commercial catch exemption in False Bay, imposed in 2001. The increasing trend in CPUE likely reflects improved recruitment due to the protection afforded to adult white steenbras after 2001. Figure 8.15c shows the trends in CPUE recorded prior to 2001 and those recorded after 2001.

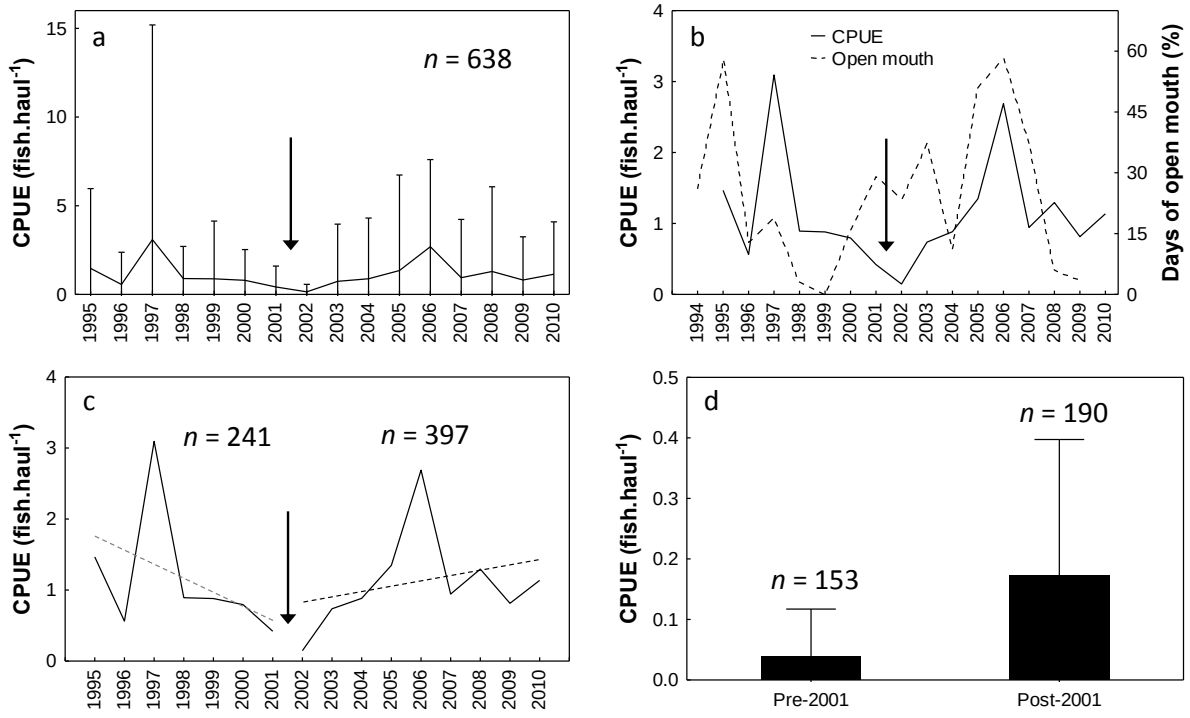

Figure 8.15: Catch trends from a long-term netting study in the East Kleinemonde Estuary from 1995 to 2010, showing a) mean (±SD) annual white steenbras CPUE (fish.haul^{-1}), b) mean CPUE in relation to the percentage of days in each year during which the mouth of the estuary was open to the sea, and c) mean annual CPUE with linear fits to data collected prior to 2002 and those collected from 2002 onwards; arrows indicate the withdrawal of the 20 mt commercial catch exemption. Graph d shows mean (±SD) CPUE (fish.haul^{-1}) of white steenbras in the Berg Estuary for the periods 1992 to 1996 and 2003 to 2007. Samples sizes indicate the number of net hauls (n)

In the Berg Estuary, research seine netting was conducted less regularly than in the East Kleinemonde Estuary, although 153 seine net hauls were made in the estuary from 1992 to 1996, and a further 190 hauls from 2003 to 2007 (K Hutchings, unpublished data). Mean CPUE recorded in the latter period was considerably higher than that recorded in the former (Figure 8.15d). The improved catches resulted from closure of the commercial gill-net fishery in this estuary in 2003 (Hutchings *et al*. 2008). While these data indicate that white steenbras abundance has increased within this estuary, the results are of a preliminary nature, and should be treated as such. A roving creel survey over the period 2002 to 2004 produced just four white steenbras, which constituted approximately 0.1% of the total catch (Hutchings *et al*. 2008).

8.3.5 Spearfishery

There is anecdotal evidence to suggest that white steenbras are regularly targeted in the spearfishery, particularly in areas such as East London to Port Elizabeth, and False Bay; although little data exist for this fishery. A survey of the South African spear fishery from 1984 to 1995 indicated that white steenbras was not an important target species in this fishery (Mann *et al*. 1997). White steenbras also did not feature in a survey of the spearfishery from Cape Hangklip to Walker Bay, from 1995 to 1997 (Attwood and Farquhar 1999). Mann *et al*. (1997) estimated participation in the spearfishery to be approximately 7000 individuals, compared to the 412 000 estimated in the recreational shore fishery (McGrath *et al*. 1997). The number of white steenbras taken annually in the spearfishery is, therefore, likely to be negligible when compared to that taken by the recreational shore and previously the commercial beach-seine fisheries.

8.4 Fisheries management measures

8.4.1 Recreational fisheries

Proclamation of the Tsitsikamma MPA in December 1964 was the first marine regulation to affect the recreational fishery directly, and resulted in decreased effort in the area. The Tsitsikamma MPA was shown to provide protection for white steenbras and numerous other species, with higher CPUE in the protected area than adjacent open areas (Hanekom *et al*. 1997, Cowley 1999).

The linefish management framework introduced in South Africa in 1985 (Government Gazette No. 9543) included the first catch restrictions for numerous linefish species, aimed at providing improved protection for those species showing stock declines (Griffiths 2000). The minimum legal size limit for white steenbras was initially set at 40 cm TL. While this may have decreased the recreational (and commercial) catches of white steenbras slightly, the size is well below the size at 50% sexual

maturity, thereby providing little protection against growth overfishing (Bennett 1993b). As part of the same set of regulations, the maximum daily bag limit was set at 10 per person per day (pppd), for all species (including white steenbras) not listed as "exploitable" or "protected". However, Attwood and Bennett (1995b) estimated that this restriction decreased recreational catches of white steenbras by only 0.1%, as catches in excess of 10 white steenbras pppd were particularly infrequent.

In addition to the linefish management framework, 1985 also saw the proclamation of the De Hoop MPA, for the protection of coastal fishes on the south west coast. Research angling showed significantly improved CPUE of white steenbras after proclamation (Bennett and Attwood 1991), showing that the MPA had contributed to the protection of white steenbras and providing evidence of the potential benefits of MPAs for this species.

As a result of severe stock declines, the maximum daily bag limits for numerous species were revised in 1992, with that for "recreational" species, including white steenbras, being decreased to 5 pppd. However, Attwood and Bennett (1995b) estimated that this would reduce recreational catches of white steenbras by just 1.9%, thereby providing little additional protection for the species.

Once again prompted by stock declines, such as the collapse of the white steenbras stock, minimum legal size limits for certain species were increased in 1996. The increase in the limit to 60 cm TL for white steenbras is likely to have decreased the recreational and commercial catches to a certain degree, particularly within the recreational shore fishery, in which the majority of white steenbras caught were smaller than this size (Bennett 1993b). However, this is still lower than the size at 50% sexual maturity (600 mm FL), meaning that most white steenbras still recruit to the fishery before they are able to spawn.

In 2000, the Dwesa-Cwebe MPA in the Transkei was proclaimed. The location of this MPA in the vicinity of the white steenbras spawning grounds suggests that it would provide considerable protection during the spawning aggregation. However, there is anecdotal evidence to suggest a high level of illegal harvesting within this MPA. If enforcement within this MPA could be improved, this would provide protection for white steenbras at a particularly vulnerable life stage.

The declared state of emergency in the South African linefishery, in 2000 (Government Gazette No. 21949), once again prompted amendments to the regulations governing recreational anglers, with

the maximum daily bag limit for white steenbras being decreased to 1 pppd in 2002 (Sauer *et al*. 2003). However, by this time, most of the "damage" to the stock had already been done, and recreational shore catches suggested that a bag limit of 1 pppd would be exceeded, and therefore come into effect, in just 2% of angler outings (Brouwer *et al*. 1997), thereby providing little protection for the species.

A second, and particularly important, legislation was introduced in 2002, with the ban on the recreational use of vehicles in the coastal zone. This legislation prevented anglers from driving on the beaches, having the effect of limiting access to certain areas of coastline, thereby decreasing shore angler effort in these areas. The result is an increasing trend in white steenbras CPUE in certain 'limited access' areas (PD Cowley, unpublished data). This legislation is, therefore, one of the most effective management measures for white steenbras.

Presently, white steenbras is managed by a maximum daily bag limit of 1 pppd and minimum size limit of 60 cm TL in the recreational and subsistence fisheries, although participation is unrestricted. These fisheries are characterised by poor law enforcement, as well as low compliance by the anglers, exemplified by the high proportions of white steenbras retained in estuarine fisheries that are below the minimum legal size (Bennett *et al*. 1994, Cowley *et al*. 2004, Potts *et al*. 2005). The poor status of the stock and the failed history of management pertaining to the recreational harvest of this species suggest that improved management measures are required, to facilitate stock recovery.

8.4.2 Commercial fisheries

Prior to 1969, the only regulation governing the commercial beach-seine fishery was a minimum mesh size of 44 mm, introduced to protect juvenile fishes (Penney 1991). From 1975 onwards, commercial beach-seine and gill-net operators were required to register their operations and licence their nets (Hutchings *et al*. 2002b). There was a drive at this time to decrease the effort in these fisheries, by limiting the legal area of operation and number of permits allocated (Penney 1991). However, by this time, the catches and CPUE of white steenbras had declined considerably, suggesting that the restrictions had been introduced too late.

The peak catches of white steenbras made in the commercial purse seine and beach-seine fisheries, in the late 1970s and early 1980s, resulted in prohibition of purse seining within False Bay and prohibition of the commercial net harvest of "angling" species outside of False Bay and Walker Bay, after 1982 (Penney 1991). This undoubtedly decreased the effort and potential catch of white

steenbras in the purse seine and beach-seine fisheries, which had been responsible for a large proportion of the catch prior to 1982, and had contributed to the overall decline in the white steenbras stock (Bennett 1993a). However, once again, it is likely that the majority of the "damage" had already been done by this time. In addition to these major fishery regulations, the beach-seine fishery within False Bay was subjected to a number of more specific measures, including a winter closed season, prohibition on beach seining at night, minimum legal size limits for certain species and a considerable decrease in the number of permits allocated (Bennett 1993a). The minimum size limit is likely to have provided some protection for early juvenile white steenbras, although little protection against growth overfishing, as fish were still able to recruit into the fishery two to three years before attaining sexual maturity (Bennett 1993b). Similarly, the closed season was implemented over the winter months, when white steenbras was caught in considerably lower numbers in False Bay, and when adults were believed to undertake spawning migrations to the east coast (Bennett 1993a), thereby causing little reduction in the annual catches of white steenbras. Once again, the newly implemented measures were unlikely to provide a guarantee against growth or recruitment overfishing.

A second suite of additional regulations pertaining to commercial beach-seine operations was implemented from 1988 to 1990 in False Bay. Firstly, certain additional areas within False Bay were closed to commercial netting, including a 1-km stretch of shoreline adjacent to the Eerste Estuary, which Bennett (1992) suggested was likely to have decreased commercial catches of white steenbras from the north shore of False Bay by as much as 75%, thereby providing considerable protection for the species. There was also the complete prohibition of the use of the sinking "Russman" seine net, which had always been restricted to the western shore of False Bay. White steenbras caught using this form of beach-seine net were almost exclusively adult fish, and these operators were responsible for a large proportion of the beach-seine catches of white steenbras over the years (Bennett 1993a). Therefore, the prohibition of these nets in 1990 undoubtedly decreased the fishery pressure on white steenbras, reducing the catches of white steenbras along the western shore of False Bay to almost nothing (Bennett 1992).

The regular beach-seine fishery within False Bay was also subjected to new regulations at this time, with restrictions imposed on the maximum lengths of the nets, as well as the hauling ropes. The number of permits issued was also decreased, which is likely to have decreased effort to a certain degree, although permits that were not reissued were in many cases those of permit holders who had become inactive in the fishery (Penney 1991). Therefore, these measures implemented within

False Bay in 1990 were likely to have provided little additional benefit to white steenbras, considering the magnitude of the other regulations implemented around the same time.

Bennett (1993a) estimated that the SB/R ratio for white steenbras had declined to just 6% of its pristine level, confirming that the stock had collapsed. This was despite the series of increasingly stringent regulations implemented in the different fisheries. Although the commercial net fisheries were still permitted to catch white steenbras after 1993, the poor status of the stock ultimately resulted in a commercial ban on the harvest of white steenbras, and other species, in the commercial net fisheries after 2001. This regulation should have had the effect of completely eliminating white steenbras harvest, other than in the recreational and subsistence fisheries, and therefore has probably contributed considerably to the conservation of the species. However, there is evidence that illegal catches of white steenbras were still made after this regulation, in both the commercial beach-seine and gill-net fisheries (Hutchings *et al*. 2002a). Furthermore, a reduction in total annual white steenbras catch of just 25% (by number) can be inferred from the commercial ban, while participation in the recreational fishery, responsible for the other 75% of the catch, remains unregulated. Despite some evidence of stock recovery, in the East Kleinemonde Estuary and the surf zone of the GAENP MPA, it remains to be seen whether these restrictions were implemented early enough to allow the stock to recover. However, the genetic analyses showed a high level of genetic diversity in white steenbras and a high level of mixing among coastal regions, suggesting a level of resilience within the species, despite the historical and current fisheries mortality.

8.4.3 Additional management considerations

Juvenile white steenbras showed high levels of residency within the study estuaries, with little evidence that these fish spent any time at sea. The results suggest that during the estuarine life stage white steenbras could be effectively protected by means of area closure. Estuarine protected areas would be simpler to enforce than the current daily bag and minimum size limits, and at the same time could protect multiple species. The identification and protection of selected estuaries that act as critical habitats for multiple species would be an effective management option. An Estuarine Management Framework has been established in South Africa, to provide guidelines for the development of estuary-specific management plans and zoning of no-take areas in estuaries.

Sub-adult and adult white steenbras are almost exclusively marine, meaning that the vast majority of white steenbras in estuaries are juveniles, below the minimum legal size limit (60 cm TL). As such, an

alternative to the establishment of a few individual EPAs would be a complete ban on the harvesting of white steenbras within estuaries. If such a measure was enforced, this could protect the juveniles, with little negative impact on compliant estuarine fishers. Such a regulation would be simpler to implement than EPAs in multiple estuaries. However, as with the current minimum size and daily bag limits, such a species-specific measure may prove difficult to enforce.

The high levels of residency exhibited by post-estuarine juveniles and sub-adults in the marine environment suggest that white steenbras could be effectively protected during these two life stages through a network of suitably positioned MPAs that are closed to shore angling (Cowley 1999). By modelling the potential effects of MPAs on the white steenbras stock, Attwood and Bennett (1995a) showed that MPAs would have little effect on yield per recruit (Y/R) but could significantly improve spawner biomass per recruit (SB/R), through the prevention of growth overfishing (Cowley 1999). This was confirmed by the high proportion of individuals recaptured in each tagging programme, within the respective MPA (see Chapter 6), and the improved CPUE of white steenbras in the De Hoop MPA after proclamation (Bennett and Attwood 1991, 1993). The corollary to this, however, is that juveniles and sub-adults are also likely to exhibit residency in areas outside of the protection of MPAs, making them susceptible to localised overexploitation (Lamberth and Prochazka 1994), particularly in stretches of coastline in close proximity to urban areas (Brouwer *et al*. 1997). This highlights the need for improved enforcement of existing regulations.

The larger white steenbras showed a much lower level of residency, undertaking considerable movements, suggesting that adults are unlikely to benefit from MPA protection to the same degree as earlier life stages (Hutchings *et al*. 2002a). However, MPAs for mobile species can be effective if they protect essential habitat, such as spawning grounds (Afonso *et al*. 2009). Bennett (1993a) suggested that the establishment of MPAs in the Transkei area was unnecessary for the protection of white steenbras during the spawning season, as this represented a small proportion of the total annual white steenbras catch. However, individuals aggregating in this area over the spawning season are possibly the only spawning adults, and require protection to ensure that they are allowed to spawn before being captured. Therefore, the establishment of the Dwesa-Cwebe MPA has the potential to contribute considerably to the protection of the species, provided that illegal harvesting within the MPA is prevented.

White steenbras exhibited seasonal catches in different areas, with increased catches in the south Western Cape during the summer months, and in the Transkei area during the winter months

(Bennett 1993a), and showed seasonal variation in the direction of movement between tagging and recapture events, indicative of an annual spawning migration. The predictable nature of this seasonal migration and the spatial concentration in a limited spawning area make these adults vulnerable to overexploitation at this life stage (Bennett 1993b). Marine protected areas are thus likely to offer less protection to migrating adults. A complementary management option at this life stage that takes into account the migratory behaviour is a closed season (Bennett 1993b, Hutchings *et al*. 2002a). Effective closed seasons have been implemented in South Africa for red steenbras, shad *Pomatomus saltatrix* and galjoen *Dichistius capensis*. A closed season was proposed for white steenbras as early as 1993 (Bennett 1993a), yet no such regulation was ever implemented. A strategically designed and well-enforced closed season spanning the known spawning aggregation period in the Transkei, from mid-July to the end of August, to protect adult white steenbras during the spawning season should be considered as a viable management option. In effect, the Dwesa-Cwebe MPA should act as a seasonal closure for white steenbras, as they spawn in this area in late winter; although a closed season would also provide protection for individuals spawning outside of the MPA. It is envisaged that the Ocean Tracking Network (OTN) programme will return more detailed information in the forthcoming years, providing an improved understanding of the timing and extent of white steenbras spawning migrations, and the locations and spatial extent of spawning grounds. This information could then be used to modify and improve management regulations, such as extending or shifting the closed season, or identifying and proclaiming new MPAs.

Chapter 9

Conservation status

9.1 Introduction

Van der Elst and Adkin (1991) and Lamberth and Joubert (1999) identified white steenbras as a priority species for research, conservation and management in South Africa. The species was also identified as one of six flagship estuarine species (Endangered Wildlife Trust 2002), and a keystone zoobenthic predator "whose continued well-being is vital as a functional need of a whole community" (Whitfield and Cowley 2010). White steenbras was originally included in the *Threatened and Protected Species List* published in 2007 (Government Gazette No. 29657) under the category of "Protected species" (i.e. "Indigenous species of high conservation value or national importance that require national protection"), as defined in the National Environmental Management Biodiversity Act (NEMBA). Although later removed from the list, on the basis that it was already protected under the Marine Living Resources Act (MLRA), white steenbras meets certain IUCN (International Union for the Conservation of Nature) categories and criteria for threatened species, and remains a priority species for conservation.

The failure of conventional management measures, such as minimum size and daily bag limits, to protect white steenbras and other South African linefish species (Bennett *et al*. 1994, Brouwer *et al*. 1997, Griffiths 2000, Cowley *et al*. 2002) has brought about the need for alternative or complementary management measures to be used in conjunction with conventional measures, and the need to manage marine resources from an ecosystem perspective (Cochrane *et al*. 2004). As a result, fisheries managers in South Africa, and in numerous other countries, have turned to Ecosystem Based Management (EBM) and marine protected areas (MPAs) for the management and protection of fish stocks at the ecosystem level (Roberts and Polunin 1991, DeMartini 1993, Penney *et al*. 1999, Russ 2002). Pajak (2000) describes three broad domains that should be addressed in EBM approaches to resource management, to ensure sustainable resource utilisation; namely environmental (the resource and its environment), social (those using, impacting on or relying on the resource), and institutional (decision-makers, management authorities and associated legislation).

The World Summit on Sustainable Development (WSSD) held in Johannesburg in 2002 encouraged states to implement the Ecosystem Approach to Fisheries (EAF), by 2010 (Turrell 2004). The EAF is a form of fisheries governance framework, which draws from conventional fisheries management and

EBM principles (FAO 2003, Garcia *et al*. 2003). The basis of EAF is the management of fishery resources with specific goals, to allow for the sustainable use of the resources and to meet the needs of the users, while maintaining the ecosystem complexity, interactions and processes necessary for conservation of proper ecosystem functioning (Garcia *et al*. 2003). This is particularly important for the management of fisheries where resource use takes place in fishery sectors at all socio-economic levels (i.e. subsistence, recreational and commercial sectors). In South Africa, a dedicated EAF Working Group oversees EAF progress and related issues (Shannon *et al*. 2006).

Marine protected areas have been advocated by numerous fisheries biologists as a complementary tool to traditional management measures, and an important tool for the protection of coastal and marine resources (Buxton 1993, Roberts 1998, Hilborn *et al*. 2004, Mann *et al*. 2006). One of the main benefits of MPAs is their holistic nature, providing simultaneous protection for a range of fish and invertebrate species (Attwood and Bennett 1995a, Zeller *et al*. 2003). The numerous biological benefits of MPAs may include decreased fishing mortality (Russ 1991), enhancement of stocks within the MPA through direct protection (Bennett and Attwood 1991, Millar and Willis 1999), facilitation of recovery of depleted stocks (Beger *et al*. 2003), spillover of adults to adjacent fished areas (Bennett and Attwood 1991, Zeller *et al*. 2003), seeding of recruits into adjacent fisheries through larval dispersal (Tilney *et al*. 1996), increased biomass and size structure within the reserve (Buxton 1987, Buxton and Smale 1989, Russ 1991, Roberts and Polunin 1991, Willis *et al*. 2000), increased reproductive capacity and protection of habitat (Gell and Roberts 2003). MPAs can also provide control or reference areas, against which exploited areas may be compared to assess the impacts of fishing or protection on population parameters (Griffiths and Wilke 2002, Hilborn *et al*. 2004). MPAs should not, however, be seen as "a panacea for fisheries management problems", but rather as a complementary measure to conventional management tools, which can be used as part of a suite of management measures (Hilborn *et al*. 2004). Even after the establishment of an MPA, conventional management measures should remain in place in the adjacent exploited areas (Russ 2002). This is particularly important in situations where fishing effort becomes concentrated at the edges of an MPA. As such, MPAs and the EAF can provide possible solutions to the failure of conventional fisheries management in South Africa. However, the potential level of protection afforded by MPAs to individual species needs to be determined, and the effectiveness of few MPAs has been quantitatively assessed (Russ 2002, Zeller *et al*. 2003). Cowley *et al*. (2002) assessed the effectiveness of the Tsitsikamma MPA in the management of four coastal fishes in South Africa, and advocated that the role of MPAs in the management of other linefish species be assessed.

The South African Linefish Management Protocol (LMP), developed specifically for assessing the status of linefish stocks, defines a number of management actions to be taken in the event of stocks becoming overexploited or collapsed. These include minimum size and maximum daily bag limits, closed seasons and areas, and commercial and recreational moratoria (Griffiths *et al*. 1999). However, the LMP recommends single species production models and age-based stock assessments, which are not suitable for all species, and for many species suitable data or mortality estimates are lacking (Attwood 2003). Therefore, for certain species, alternative approaches are necessary.

Although area protection (in the form of MPAs) is included as one form of management regulation in the LMP, several new initiatives adopting EBM principles have been developed. The National Spatial Biodiversity Assessment of South Africa 2004 (Turpie 2004) and the South African National Protected Area Expansion Strategy 2008 (NPAES 2008) highlight the need to expand the nation's network of marine and estuarine protected areas. In addition, the National Biodiversity Assessment 2011 (Sink *et al*. 2011, van Niekerk and Turpie 2011) aimed to identify suitable marine and estuarine areas for additional protection, through the identification of critical habitats at the ecosystem level. Fisheries managers are increasingly adopting a habitat management approach in the management of fishery species to ensure the protection of important habitats (Monaco *et al*. 1998). A "habitat suitability index" (HSI) can be employed to assess the quality and suitability of available habitat for a species or community, to provide additional information for management (Brooks 1997, Brown *et al*. 2000).

Following from these studies, this chapter includes a simple assessment at the species level to identify both critical habitats for white steenbras and areas potentially suitable for additional closure (i.e. where new protected areas could be established) for the protection of white steenbras and other estuarine-associated coastal fishes. This was achieved firstly by assessing the distribution of the species relative to existing protected areas, throughout its core distribution, by drawing on available literature and results from previous chapters. This information was then incorporated into a modified estuarine and coastal HSI-type assessment (Brown *et al*. 2000), which was used to identify actual and potential white steenbras hotspots, potential areas for protection and areas where the species is under severe threat. This also provided information on the level of protection offered to white steenbras and its habitat by current management regulations and the existing marine and estuarine protected area network. Secondly, by drawing from the literature and results from previous chapters, the status of the species was classified according to national and global conservation criteria. At the national level, the species was classified according to the NEMBA Act, and at the international level according to the *IUCN Red List Categories and Criteria* (IUCN 2001).

9.2 Protection status of white steenbras

This section considers the spatial distribution of white steenbras, and the availability of suitable habitat (or at least the suitability of available habitat) to white steenbras at all life stages in both the marine and estuarine environments. The overall aim was to identify estuaries and sections of coastline of importance for white steenbras, and that could potentially serve as suitable areas for further legislative protection for the species. Specific objectives were to:

i. Identify estuaries that are important to or suitable for white steenbras,
ii. Determine the status of protection in estuaries within the white steenbras core distribution,
iii. Relate important estuaries for white steenbras to current estuarine protection levels,
iv. Determine the proportions of coastline within the white steenbras core distribution comprising different habitat types,
v. Determine the proportions of coastline comprising different habitat types, which fall under different levels of MPA protection,
vi. Identify sections of the coastline within the white steenbras core distribution that are important to or suitable for white steenbras,
vii. Relate the important coastal sections for white steenbras to the locations and protection levels of different MPAs, and
viii. Use this information to determine the current protection status of white steenbras.

9.2.1 Analysis approach

Data for the habitat suitability assessments were largely drawn from the Coastal Sensitivity Atlas of southern Africa (Jackson and Lipschitz 1984), a synopsis of available information of South African estuaries (Whitfield 2000), the National Spatial Biodiversity Assessment 2004 Marine Component (Lombard *et al*. 2004) and Estuary Component (Turpie 2004), the National Biodiversity Assessment 2011 Marine Component (Sink *et al*. 2011) and Estuary Component (van Niekerk and Turpie 2011), and an assessment of habitat types along the South African coastline (Harris *et al*. 2011).

The core distribution of white steenbras, for the purposes of this analysis, was taken as that described by Lamberth and Mann (2000), from just north of Cape Columbine in the west to the Mbashe Estuary in the east. The analysis focussed on this section of coastline (hereinafter referred to as the "survey area"), and included small buffer zones on either side, stretching north past Cape Columbine to the Berg Estuary, the northern-most estuary within which juvenile white steenbras are commonly found (Bennett 1993b), and eastwards of the Mbashe Estuary to the Mbhanyana Estuary,

at the eastern boundary of the Dwesa-Cwebe MPA (Figure 9.1). The coastal zone off the Mbashe Estuary and the surrounding areas are associated with the spawning grounds of white steenbras (Bennett 1993b, Hutchings *et al*. 2002a), yet competition shore angling catch data showed that white steenbras was uncommon east of this estuary, comprising less than 0.1% of catch by number (Pradervand 2004). This survey area represented a continuous shoreline of 1 870 km, excluding all islands.

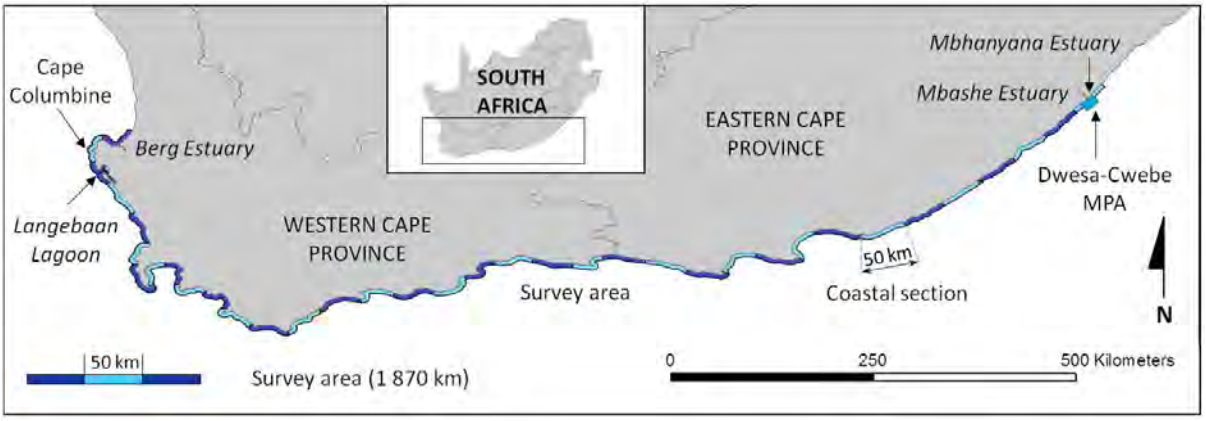

Figure 9.1: Map of the survey area (divided into 50-km coastal sections), spanning 1 870 km from the Berg Estuary in the west to the Mbhanyana Estuary in the east

Estuaries

The first analysis focussed on the estuaries within the survey area, as these ecosystems are essential nursery habitats for juvenile white steenbras (Wallace *et al*. 1984a, also see Chapter 3), and there is evidence that large (adult) white steenbras enter estuaries, although infrequently (Marais 1983, Bennett *et al*. 1985, Bennett 1993b), sometimes as a result of cold marine conditions (Hanekom *et al*. 1989). Proportions of each type of estuary, available surface area and indices of estuary health along this stretch of coastline are presented, as well the levels of protection afforded to the different estuaries.

A scoring system was implemented to rank the suitability of each estuary, from the Berg Estuary in the west to the Mbhanyana Estuary in the east, in terms of its suitability for or potential value to white steenbras. This analysis included all estuaries included in Whitfield's (2000) synopsis of available information on South African estuaries, which fall within the survey area (n = 138). Six criteria that are likely to affect the potential value of each estuary to white steenbras and one direct index of white steenbras density were included in the scoring system, with maximum scores per criterion ranging from 0 to 100 (Table 9.1). Characteristics likely to negatively impact the survival or

success within, or the recruitment into these estuaries were allocated lower scores, while those likely to benefit the species were allocated higher scores. In certain cases scores were allocated subjectively, e.g. fair = 50%, while for other criteria scores represented an index relative to all other estuaries. The aims were two-fold; firstly to determine the current protection status of estuaries most important to white steenbras, and secondly to identify estuaries that should be flagged as potentially suitable candidate estuaries for future protection, for the benefit of white steenbras.

The first criterion was based on Whitfield's (1992) classification of estuary types. Permanently open estuaries and estuarine bays were allocated scores of 100, as they are generally the largest estuaries and can, theoretically, support the largest populations (Maree *et al*. 2003). They are also permanently connected with the sea; thus recruitment into these estuaries can occur at any time. Temporarily open/closed estuaries and estuarine lakes were allocated a score of 75, as they offer important refuges for white steenbras, although the successful recruitment of white steenbras into these systems is dependent on timeous mouth opening (Whitfield and Bruton 1989). River mouth estuaries are permanently open systems, dominated by riverine characteristics, with little marine water penetration, and within the survey area are all small (Whitfield 1992). These systems are likely to be less suitable for white steenbras, although the species has been observed to use such estuaries; therefore, a score of 50 was allocated to river mouth estuaries.

The second criterion was the open water surface area of the estuary (after Colloty 2000). This criterion proved complex to assess, due to large sizes of a handful of systems within the region. As such, the surface area of each system was initially expressed as a percentage of the largest estuary. However, this gave little weight to the smaller systems, and it was felt that transforming the values would be more suitable. Maree *et al*. (2003) suggested that log transformation provided an acceptable alternative. The high number of estuaries with less than one percent of the surface area of the largest estuary resulted in numerous negative log-transformed values. The percentage surface area of each estuary relative to that of the largest estuary was thus multiplied by a scaling factor of 1000, before log-transformation, and each value was again expressed as a percentage of the value of the largest estuary. This provided an acceptable measure, which ranged from >0 to 100.

The third, fourth and fifth criteria considered the health of the ecosystem. Criterion three was the estuarine condition, taken from Whitfield (2000), which represented the level of human disturbance. This was based on four categories; excellent, good, fair and poor, which were allocated scores of 100, 90, 50 and 20, respectively, following Maree *et al*. (2003). Excellent refers to pristine estuaries

with negligible human impact, good refers to estuaries with low impact and no major anthropogenic disturbance, fair indicates degradation within the estuary or catchment with a moderate impact level, and poor reflects estuaries experiencing major ecological degradation (Whitfield 2000). The fourth and fifth criteria were the level of pollution within the estuary and the overall ecosystem threat status, taken from van Niekerk and Turpie (2011). The level of pollution (combining agricultural, domestic and industrial) was rated as low (scoring 100), medium (scoring 50) or high (scoring 20), with scores following a similar scale to estuarine condition. The ecosystem threat status was categorised as least threatened (scoring 100), vulnerable (scoring 75), endangered (scoring 50) or critically endangered (scoring 25). The lower scores allocated for endangered and critically endangered estuaries are due to their likelihood of ecosystem collapse, in which the future contribution to white steenbras (among other species) would be reduced or removed.

The sixth criterion was an estimate of the level of fishing pressure on the estuary, as higher levels of fishing pressure are likely to result in higher levels of harvesting, with greater impact on the population within an estuary. Fishing effort data were taken from van Niekerk and Turpie (2011), and categorised as low, medium, high or very high, which scored 100, 75, 50 and 25, respectively.

The seventh criterion was a direct index of suitability of each system for white steenbras, based on white steenbras abundance recorded in a national netting survey of all functional estuaries in South Africa (Harrison 1998a, b, c, 1999a, b, James and Harrison 2008, 2009, 2010a, b, 2011). The short-term nature of this netting survey is acknowledged, and while it is possible that some values are not representative of long-term trends, this is the most comprehensive ichthyofaunal survey spanning all South African estuaries. The inclusion of white steenbras abundance is not a circular argument, as the analysis was aimed at drawing from all available information to identify actually and potentially suitable estuaries for the species, to determine whether white steenbras “hotspots” are adequately protected under the current levels of protection. Scores for this criterion were subject to a skewed distribution, similar to estuarine surface area (criterion 2), with a few estuaries having exponentially higher scores, and many estuaries having scores of zero or slightly greater than zero. However, unlike surface area, where even the smallest estuary had a positive value, the natural logarithm of a zero catch is mathematically undefined. Therefore, for this criterion, the score was simply taken as the abundance of white steenbras recorded during research netting operations, expressed as a percentage of the maximum recorded in other estuaries within the study region. The criteria and associated scoring system are presented in Table 9.1.

Table 9.1: Criteria for scoring estuaries in terms of potential suitability for white steenbras

Criterion (and source)	Category	Score
1. Estuary type	Permanently open	100
(Whitfield 1992)	Estuarine bay	100
(scoring based on Maree *et al*. 2003)	Temporarily open/closed	75
	Estuarine lake	75
	River mouth	50
2. Estuary open water surface area (Ha)	Natural logarithm of open water surface area of the estuary, relative to that of the largest estuary in the survey area	
(after Colloty 2000)		
(scoring based on Maree *et al*. 2003)		
3. Estuarine condition	Excellent	100
(Whitfield 2000)	Good	90
(scoring based on Maree *et al*. 2003)	Fair	50
	Poor	20
4. Pollution level	Low	100
(van Niekerk and Turpie 2011)	Medium	50
	High	20
5. Ecosystem threat status	Least threatened	100
(van Niekerk and Turpie 2011)	Vulnerable	75
	Endangered	50
	Critically endangered	25
6. Fishing effort	Low	100
(van Niekerk and Turpie 2011)	Medium	75
	High	50
	Very high	25
7. Catch data for white steenbras	Catches of white steenbras in the estuary relative to that in the estuary with the highest catch	
Harrison 1998a, b, c, 1999a, b		
James and Harrison 2008, 2009, 2010a, b, 2011		

After scores had been allocated to each estuary for each criterion, the different criterion scores were subjected to different weighting, based subjectively on their importance to white steenbras and weighted scores were summed across all criteria for each estuary. Weights for all criteria totalled 1.0. Greater weighting was applied to estuarine surface area, fishing effort and white steenbras catch data (as these represent direct indices of available habitat, threat of removal and abundance), such that these each had double the weighting (0.2) of the other four criteria (0.1), which are likely to affect the species indirectly. Individual criteria were then sequentially removed from the analysis, to determine whether the overall observed variability (sum of squared differences between each estuarine score and the mean score) would increase with their removal. However, the removal of no individual criterion provided greater variability, therefore all criteria were included.

Coastal zone

The second analysis involved quantitatively assessing the suitability of the coastal habitat within the white steenbras core distribution, as well as the proportions of coastline and different habitat type falling within different levels of marine living resource protection.

White steenbras were shown to exhibit an affinity for sandy shores (see Chapter 8), and are most commonly captured from sandy shores in areas such as False Bay, the Transkei and Algoa Bay (Smith and Smith 1986, Bennett 1993b, PD Cowley unpublished data). Post-estuarine juveniles and sub-adults exhibit residency in the surf zone (see Chapter 6), particularly of sandy beaches and mixed sand and rock shores (Bennett 1991), and are rarely found associated with rocky shores or subtidal reefs (Biden 1948, Bennett 1993b). Therefore, the sections of coastline comprising sandy shores, rocky shores or shores of mixed sand and rock within the white steenbras core distribution were identified, to provide an index of the potential suitability of different coastal sections for white steenbras. Coastal habitats were identified and digitised by Harris *et al*. (2011).

The proportions of the survey area either falling within or outside of MPAs were also determined. As white steenbras has been shown to contribute little to overall catches in the boat-based linefisheries (Brouwer and Buxton 2002), this analysis mainly concerns the prohibition of shore angling. Marine protected areas were, therefore, further divided into sections of coastline in which shore angling is permitted (partial restriction), and those where shore angling is prohibited (full protection).

The South African coastline was divided into 50-km sections (after Lombard *et al*. 2004). Coastal sections of 50 km were deemed suitable for the analysis, as this represents double the maximum displacement observed for juvenile white steenbras (<400 mm FL) and double the mean displacement of older juveniles (400 – 500 mm FL) in the coastal zone (see Chapter 6). The cumulative percentage contributions of sand and mixed sand and rock shores were calculated for each of the 38 50-km sections spanning the survey area (from the Berg Estuary to the eastern boundary of the Dwesa-Cwebe MPA), and these are also presented cartographically.

A scoring system was then applied to the 50-km coastal sections, in a similar manner to that applied to the estuaries. This assessment incorporated four criteria likely to affect the abundance of or suitability for white steenbras in each coastal section. The first criterion was the average of the estuarine scores determined in the previous section, for all estuaries entering each coastal section. This was deemed an important factor, as Bennett *et al*. (1994) suggested that the ongoing

degradation of estuaries is likely a contributing factor to the population decline in white steenbras. The second criterion was coastal habitat type, as described previously, which was calculated as the cumulative proportions of sandy and mixed sand and rock shoreline within each coastal section (after Harris *et al*. 2011).

The two coastal sections associated with the Langebaan Lagoon initially scored poorly, as there are no estuaries entering the sea along this stretch of coastline, and the shoreline of this area was classified as "lagoon" (Harris *et al*. 2011). However, the lagoon itself provides a sheltered, productive environment, similar in certain ways to those provided by estuaries (van Niekerk and Turpie 2011). Therefore, for the coastal scoring analysis, the two coastal sections comprising the Langebaan Lagoon were subjectively allocated estuarine scores of 50 (i.e. half the possible maximum). Similarly, the substrate of the lagoon is predominantly sand and mud (Attwood *et al*. 2007), therefore, the shoreline of each of these two coastal sections was simply allocated a subjective score of 50% sandy and mixed shores combined. This improved the scores within these two coastal sections.

The third criterion was the level of municipal and industrial wastewater discharge in different coastal sections. This was considered an important factor affecting the suitability of coastal habitat for white steenbras (Bennett 1991), as excessive pollution/wastewater discharge can result in severe anoxia within sandy substrate areas (Oelofse *et al*. 2004), which would directly impact macrobenthic invertebrates, such as the white mussel *Donax serra*, sand prawn *Callianassa kraussi* and three-spot swimming crab *Ovalipes trimaculatus* (Bennett 1993b), and thus, indirectly, white steenbras. Pollution could also act directly on white steenbras, either acting as a deterrent, causing physiological stress or infections, or causing mortality. White steenbras suffered mortalities after a raw sewage discharge in the Lourens Estuary, in False Bay (Cliff and Grindley 1982 in Harrison 1998c). There are approximately 67 marine outfalls of municipal and industrial wastewater entering the South African marine and estuarine environments (DWAF 2004), and the volumes of wastewater emanating from these have increased considerably over the last decade (Sink *et al*. 2011). Data for this criterion were obtained from the Department of Water Affairs and Forestry's operational policy for the disposal of terrestrial wastewater (DWAF 2004). Of these 67 outfalls, 36 enter estuaries or the marine environment within the survey area, cumulatively discharging in excess of 250 million m^3 annually (Table 9.2). The estimated cumulative daily volumes of wastewater discharged from each coastal section were determined, and scores were calculated for each as 100 minus the percentage of the maximum daily outfall for any coastal section. The coastal section with the maximum daily outfall volume therefore scored zero, while those with no outfall scored the maximum of 100.

Table 9.2: Estimated daily discharge volumes (m^3) of wastewater from the 36 marine and estuarine outfalls entering the 38 50-km coastal sections from the Berg Estuary to the Dwesa-Cwebe MPA (data taken from DWAF 2004, Sink *et al*. 2011)

	Marine (>2 m deep)		Surf zone		Estuary		Total volume	
Type	Number	Volume	Number	Volume	Number	Volume	Number	Volume
Municipal	4	90 426	11	295 714	5	120 623	20	506 763
Industrial	2	8 254	13	46 994	1	130 000	16	185 248
Total	6	98 680	24	342 708	6	250 623	36	692 011

The fourth criterion was the estimated level of shore-angling effort within each section. Data for this analysis were drawn from Sink *et al*. (2011), which were based on results of shore angling assessments conducted by Brouwer *et al*. (1997) and Mann *et al*. (2003). These data were estimated as the mean angling effort per 50-km coastal section, expressed as the number of anglers.km^{-1}.day^{-1}. As for the wastewater discharge score, the score for angling effort in each coastal section was calculated as 100 minus the percentage of the maximum effort for any coastal section. In this way, the coastal section with the highest score was that with the lowest effort, and vice versa.

Values for each criterion were then weighted and summed across all criteria for each 50-km coastal section. Average estuarine score and habitat type were allocated weights of 0.35, while the levels of total wastewater discharge and fishing effort were allocated weights of 0.15. It was felt that the availability and condition of estuaries and coastal habitat type were likely the most important factors affecting white steenbras distribution or density in the coastal zone. Conversely, although pollution is likely to negatively affect coastal ecosystems, and angling results in direct reductions in density, the level of pollution currently caused by marine outfalls in South Africa is unlikely to cause ecosystem collapse or completely prevent white steenbras from utilising an area, and the level of fishing effort will not prevent new fish from entering an area. Individual criteria were then sequentially removed from the analysis and, as for the estuarine scoring system, the removal of no individual criterion provided greater variability, and all criteria were included.

9.2.2 Analysis outcomes and interpretation

Estuaries

There are 259 estuaries along the South African coastline, although only 138 lie within the 1 870-km stretch of coastline considered in this analysis, from the Berg in west, to the Mbhanyana in the east. The density of estuaries, as well as estuarine condition (Whitfield 2000), showed a general increase from west to east along the coastline (Figure 9.2).

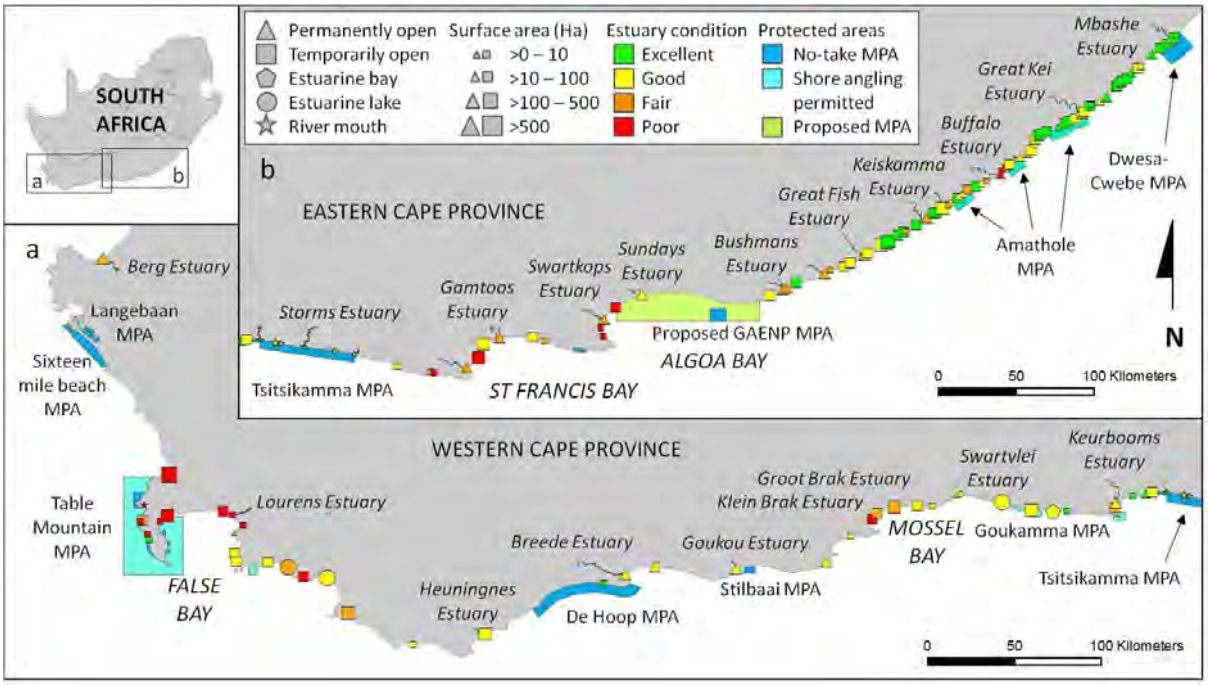

Figure 9.2: Classification of the 138 estuaries from the Berg to the Mbhanyana, in the a) Western Cape Province and b) Eastern Cape Province, in terms of estuary type, open water surface area and estuary health, and their positions along the coast relative to existing and proposed MPAs

The total open water surface area encompassed in these 138 estuaries is approximately 146 km^2, which constitutes 29% of the total estuarine surface area available along the South African coastline. The majority of these estuaries were classified as temporarily open/closed (70.3%) or permanently open estuaries (21.3%), with just 5.1% comprising river mouth estuaries, according to Whitfield's (1992) classification (Table 9.3). The region also includes four estuarine lakes and a single estuarine bay, which together comprise 38.5% of the total open water surface area of estuaries within the survey area. A total of 43 estuaries within the survey area either flow directly into an MPA or form the boundary of an MPA. Fish leaving these estuaries are thus afforded some protection.

Table 9.3: Proportions of different estuary types (after Whitfield 1992) within the survey area of coastline, and those that enter MPAs directly or act as an MPA boundary, from the Berg Estuary in the west to the Mbhanyana Estuary in the east

Estuary classification	Estuaries in survey section		Estuaries associated with MPAs	
	Number	%	Number	%
Permanently open	29	21.0	5	11.6
Estuarine bay	1	0.7	7	16.3
Temporarily open/closed	97	70.3	31	72.1
Estuarine lake	4	2.9	0	0.0
River mouth	7	5.1	0	0.0
Total	138	100.0	43	100.0

In terms of estuaries that are entirely protected through estuarine protected areas (EPAs) or partially protected through formal estuarine or catchment legislation, 35 of the 58 such estuaries in South Africa enter the sea within the white steenbras core distribution (Table 9.4).

Table 9.4: Estuaries (n = 35) that enter the sea within the white steenbras core distribution, which are protected either partially or entirely (including one proposed EPA), through catchment or direct estuarine protection (* indicates estuaries that also enter or form the boundary of an MPA)

Estuary	Protected area	Proportion protected	No-take portion	Source
Diep	Rietvlei NR	Part	Part	1
*Wildevoëlvlei	Table Mountain NP	All		2
*Krom	Table Mountain NP	All	All	2
Sand	Sandvlei NR	<10% (upper reaches)		2
Heuningnes	De Mond NR	Part		1
Breede	Breede River Conservancy	Temporal (night-ban)	All (night only)	3
*Goukou	Stilbaai MPA	Part	Part	4
Wilderness	Wilderness Lakes NP	Part		1
Swartvlei	Wilderness Lakes NP	Part		1
*Goukamma	Goukamma NR	Part		1
Knysna	Knysna NP	Part		2
Keurbooms	Keurbooms River NR	Part (upper reaches)		1
Sout (oos)	De Vasselot NP	All		2
*Groot (wes)	Tsitsikamma NP	All	All	2
*Bloukrans	Tsitsikamma NP	All	All	2
*Lottering	Tsitsikamma NP	All	All	2
*Elandsbos	Tsitsikamma NP	All	All	2
*Storms	Tsitsikamma NP	All	All	2
*Elands	Tsitsikamma NP	All or most	All	1
*Groot (east)	Tsitsikamma NP	All or most	All	1
Tsitsikamma	Huisklip NR	Part (lower reaches)		2
Seekoei	Seekoei River NR	Part (upper reaches)		1
Gamtoos	Gamtoos River Mouth NR	Temporal (night-ban)	(Voluntary)	1
Van Stadens	Van Stadens NR	All		2
*Sundays	GAENP (Proposed)	Part	Part	5
Gqutywa		Most		1
*Nahoon	Nahoon NR	Small part		2
*Nyara	Amathole MPA	Part		1
*Quko	Amathole MPA	All or most		1
*Ngoma	Dwesa-Cwebe MPA	Most		1
*Mendu	Dwesa-Cwebe MPA	Undefined as yet		2
Mendwana	Dwesa-Cwebe MPA	Undefined as yet		2
*Mbashe	Dwesa-Cwebe MPA	Undefined as yet		2
*Ku-Mpenzu	Dwesa-Cwebe MPA	Undefined as yet		2
*Mbhanyana	Dwesa-Cwebe MPA	Undefined as yet		2

NP = National Park, NR = Nature Reserve, MPA = Marine Protected Area

Source: [1]Whitfield and Cowley (2010), [2]van Niekerk and Turpie (2011), [3]Government Gazette No. 34596, [4]Government Gazette No. 31516, [5]Bezuidenhout *et al*. (2011)

Many of these estuaries are small river mouth systems flowing into the Tsitsikamma MPA, or temporarily open/closed estuaries flowing into the Dwesa-Cwebe MPA. Only eight of these estuaries are fully protected (i.e. no-take reserves), constituting a total surface area of 0.56 km^2 (0.4% of the total available estuarine surface area). The Diep and Goukou estuaries are protected in part by no-take zones. The Krom (east) and all seven estuaries flowing into the Tsitsikamma MPA are fully protected from fish harvesting (Whitfield and Cowley 2010, van Niekerk and Turpie 2011), but most occur along rocky shorelines. The Breede (Government Gazettes No. 34596) and Gamtoos estuaries are partially protected through the prohibition and voluntary prevention, respectively, of night-fishing, and part of the Sundays Estuary is proposed to be a no-take zone (Bezuidenhout *et al*. 2011). Therefore, the current level of protection afforded to white steenbras in estuaries is poor.

Estuarine scoring system

Individual estuary scores showed considerable variability, and tended to increase from west to east along the coast (Figure 9.3). The lowest scoring estuaries were generally associated with urban centres. This was particularly obvious at Cape Town (Rietvlei to Sir Lowry's Pass estuaries), Port Elizabeth (Baakens to Coega estuaries) and East London (Buffalo to Nahoon estuaries). Of the 16 estuaries that enter the sea either along the west coast or into False Bay, 12 fell within the lowest 13 ranked estuaries, suggesting that estuaries within this region are considerably less suitable for white steenbras, or are in a particularly poor condition, based on the scoring system applied.

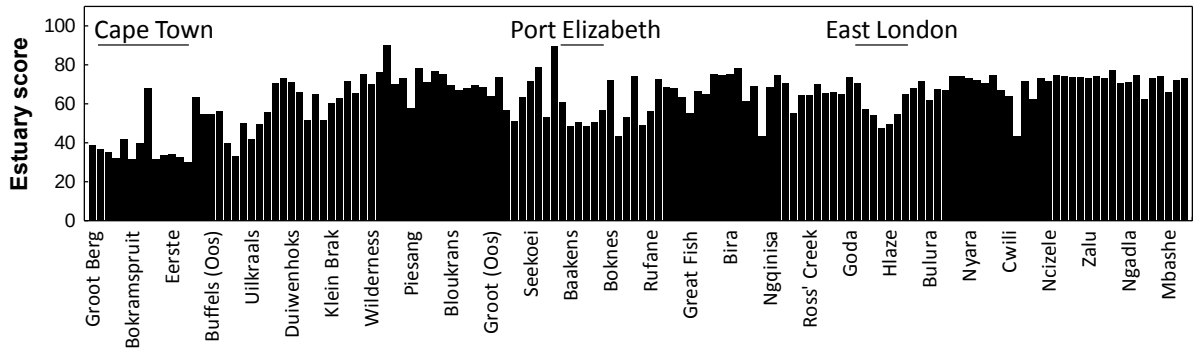

Figure 9.3: Estuary scores for all 138 estuaries (every fifth is labelled) from the Berg to Mbhanyana,

The top 30 scoring estuaries are all situated east of Mossel Bay, and were all classified as least threatened (van Niekerk and Turpie 2011), under the ecosystem threat status criterion (Table 9.5). The surface areas of these estuaries ranged from 6 to 1 697 hectares and most were temporarily open/closed estuaries, with low fishing effort. The relative catch of white steenbras within these estuaries ranged from 0.0% (i.e. no white steenbras recorded) to 100.0% (i.e. the estuary with the greatest white steenbras catch).

Table 9.5: Estuary scores for the top 30 ranked estuaries, based on the estuarine scoring system (TOCE = temporarily open/closed estuary)

Estuary (rank)	Estuary type	Area (ha)	Pollution	Health	Fishing effort	Threat status	Relative catch	Score
1. Goukamma	TOCE	46	L	Good	M	Least	100.0	89.9
2. Van Stadens	TOCE	17	L	Good	L	Least	89.5	89.4
3. Kabeljous	TOCE	72	M	Good	L	Least	54.5	78.7
4. Keurbooms	Perm. open	311	L	Good	L	Least	8.6	78.3
5. Gqutywa	TOCE	42	L	Excellent	L	Least	18.2	77.9
6. Qora	Perm. open	53	L	Excellent	L	Least	0.0	77.0
7. Sout (east)	Perm. open	6	L	Excellent	L	Least	7.3	76.5
8. Swartvlei	Est. lake	1 697	L	Good	L	Least	4.1	76.3
9. Groot (west)	TOCE	29	L	Good	L	Least	15.0	75.0
10. Kaaimans	Perm. open	9	L	Good	L	Least	7.3	74.9
11. Bira	TOCE	74	L	Excellent	L	Least	0.5	74.9
12. Mtati	TOCE	50	L	Excellent	L	Least	1.8	74.8
13. Mgwalana	TOCE	53	L	Excellent	L	Least	1.4	74.8
14.Kobonqaba	Perm. open	37	L	Good	L	Least	0.0	74.7
15.Shixini	Perm. open	25	L	Good	L	Least	0.9	74.5
16. Quko	TOCE	43	L	Excellent	L	Least	0.9	74.5
17.Kiwane	TOCE	34	L	Excellent	L	Least	1.4	74.4
18.Kasuka	TOCE	23	L	Excellent	L	Least	2.7	74.3
19. Kwenxura	TOCE	38	L	Excellent	L	Least	0.0	74.2
20. Nxaxo/Ngqusi	TOCE	31	L	Excellent	L	Least	0.5	74.1
21. Cefane	TOCE	33	L	Excellent	L	Least	0.0	74.1
22. Mendu	TOCE	26	L	Excellent	L	Least	0.0	73.9
23. Ngqwara	TOCE	22	L	Excellent	L	Least	0.5	73.8
24. Cebe	TOCE	22	L	Excellent	L	Least	0.0	73.7
25. Gqunqe	TOCE	22	L	Excellent	L	Least	0.0	73.7
26. Tsitsikamma	TOCE	14	M	Good	L	Least	36.8	73.7
27. Goda	TOCE	14	L	Excellent	L	Least	1.4	73.6
28. Ngoma/Kobule	TOCE	13	L	Excellent	L	Least	0.0	73.3
29. Qolora	TOCE	11	L	Excellent	L	Least	0.0	73.1
30. Nyara	TOCE	11	L	Excellent	L	Least	0.0	73.1

The highest ranked estuary was the Goukamma Estuary, on the south coast. This estuary had low pollution, was in good condition (Whitfield 2000), had moderate fishing pressure (van Niekerk and Turpie 2011) and produced the highest catch of white steenbras of all estuaries in a national survey (James and Harrison 2008). In addition to the Goukamma Estuary, a further five of the top ten ranked estuaries are situated along the south coast, from the Kaaimans Estuary in the west to the Groot (west) estuary at the western boundary of the Tsitsikamma MPA, spanning just 128 km of coastline. Within this region are the Goukamma (ranked 1st), Keurbooms (4th), Sout (east) (7th), Swartvlei (8th), Groot (west) (9th) and Kaaimans (10th) estuaries (Figure 9.4).

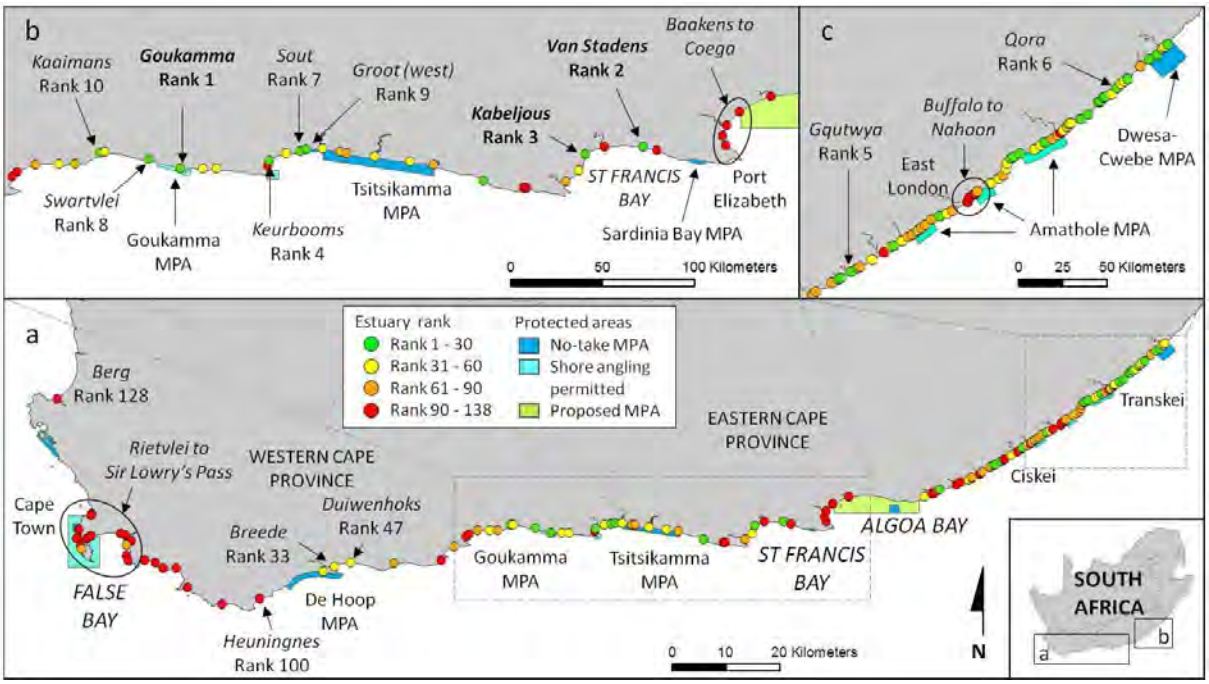

Figure 9.4: Estuary ranks in terms of the estuarine scoring system, for the 138 estuaries from the Berg to the Mbhanyana, showing a) the survey area, b) the south and south east coasts, and c) the former Ciskei and Transkei coasts. Colours represent rank categories, with the 30 highest scoring estuaries presented in green, and the 48 lowest scoring estuaries presented in red

The close proximity of these high-scoring estuaries (Figure 9.4b) suggests that the south coast provides a potentially important refuge for white steenbras. The area also encompasses the Goukamma and Robberg MPAs and borders the Tsitsikamma MPA. The Kaaimans, Groot (west) and Goukamma estuaries also exhibited high densities of white steenbras during a survey of selected South African estuaries (Turpie and Clark 2007) and recent (2011) research netting has confirmed high densities in the Groot (west) Estuary (MKS Smith, South African National Parks, pers. comm.). These estuaries can thus be flagged as important estuaries to white steenbras. The Swartvlei Estuary is particularly important, due to its large size, and should be identified as a priority for the conservation of white steenbras and other estuarine-associated coastal fishes. The Sout (east) Estuary scored highly, but due to its small size is unlikely to support a large community of fishes.

The Kaaimans, Keurbooms and Sout (east) estuaries are not protected, and the Keurbooms Estuary enters the sea at the town of Plettenberg Bay and was recorded to have high recreational angling effort over holiday periods (King 2005). The Swartvlei Estuary falls within the Wilderness Lakes National Park (Whitfield and Cowley 2010); although it remains open to angling. The Goukamma Estuary enters the sea within the Goukamma MPA; however, both the MPA and estuary are open to recreational shore fishing. Consequently, closure of both the Goukamma Estuary and Goukamma

MPA to recreational angling would create a suitable combination of estuarine nursery area and post-estuarine (sub-adult) surf zone refuges, for protection at different life stages.

The second and third ranked estuaries, the Van Stadens and Kabeljous, enter the sea within St Francis Bay (Figure 9.4). These estuaries scored highly, based on the low angling effort and the high catches of white steenbras (van Niekerk and Turpie 2011, James and Harrison 2010a), and can thus be identified as potentially suitable estuaries for the protection of white steenbras, although neither is currently protected with no-take zones. These estuaries are in close proximity to the Gamtoos Estuary. While this estuary scored poorly, there is a drive by local users to prevent fishing in this estuary at night. Therefore, the section of coastline encompassing these three estuaries could potentially contribute to the conservation of white steenbras, if suitable restrictions were imposed on angling in parts of these estuaries, and if compliance with the regulations was improved.

The Gqutywa and Qora estuaries along the east coast were ranked 5th and 6th (Figure 9.4). Both estuaries are small, although the Qora Estuary is permanently open, and both scored highly as a result of their excellent condition, low pollution and low fishing effort. The Gqutywa is one of a number of high-scoring small to medium-sized estuaries situated within the boundaries of the former Ciskei, between the Great Fish and Kei estuaries. Similarly, the Qora Estuary is situated along the coastline of the former Transkei, which also encompasses a number of high-scoring small to medium-sized estuaries. The high number of estuaries and comparatively small sizes (relative to the larger, permanently open systems), suggest that white steenbras, and other estuarine-associated fishes, within these estuaries would benefit more from maintenance of estuarine condition, through estuarine and catchment management, than from an EPA. Thus, local conservation authorities within each area should aim to maintain the high level of estuarine condition within these regions.

The Breede Estuary, ranked just 33rd, is one of only three estuaries (all adjacent) west of Mossel Bay, including the Duiwenhoks and Klipdrifsfontein, which scored within the top 60 estuaries. The Breede Estuary, as well as the nearby Heuningnes Estuary, also produced good catches of white steenbras in a prioritisation survey of selected South African estuaries (Turpie and Clark 2007). The Heuningnes Estuary scored poorly in the estuary scoring system, although it is one of the largest estuaries in the survey area, and therefore likely to support large populations of estuarine-associated fishes. The Klipdrifsfontein Estuary enters the sea within the De Hoop MPA, although it is particularly small, offering little available habitat for fishes. Considering these facts, and their close proximity to the De Hoop MPA, it seems that the Breede, Duiwenhoks and Heuningnes estuaries are likely to be the

western-most estuarine refuges on the south coast contributing appreciably to the overall protection of white steenbras. While the Berg Estuary on the west coast scored poorly in the estuarine scoring system, evidence suggests that white steenbras recruitment into this estuary has improved considerably since the closure of the commercial gill-net fishery in 2003 (Hutchings *et al*. 2008). As such, the management of these four estuaries and their catchments, and the enforcement of regulations within them should be seen as priorities for the relevant authorities.

Alignment with national priority estuaries

The Kaaimans, Goukamma, Sout (east), Groot (west) and Gqutywa estuaries were all identified as priorities for full protection (i.e. no-take EPA status), in a study aimed at meeting certain national conservation goals, such as the protection of 40% of the populations of exploited estuarine-associated fish species (van Niekerk and Turpie 2011). Similarly, the Swartvlei, Keurbooms, Van Stadens and Qora estuaries were identified in the same analysis, as priorities for partial protection. The analysis at the national level also identified other estuaries for full protection that were identified in the current study as important for white steenbras, including *inter alia* the Heuningnes and Klipdrifsfontein estuaries. This suggests that the estuaries identified as important conservation estuaries for white steenbras are also important for other taxa, making them particularly suitable for protection. The dominance of smaller estuaries along the coastline, and the fact that most of the high-scoring estuaries were small, highlights the importance of these estuaries to fish populations.

Maree *et al*. (2003) conducted a fish importance rating (FIR) exercise to identify estuaries important for estuarine-associated fishes. The results of the current study were generally not in agreement with those of Maree *et al*. (2003), with only two of the top 10 estuaries identified for white steenbras, Swartvlei (ranked 10th) and Qora (28th), scoring within the top 30 estuaries based on the FIR. The discrepancy is caused by the different criteria used in each study, including ichthyofaunal diversity and species richness in the FIR, which were not included in this single-species prioritisation exercise. Ultimately, single-species assessments are not the optimal mechanism for prioritising areas for protection. However, if priority estuaries can be identified for multiple individual species, it is possible to identify those that will potentially provide the most species with protection.

Coastal zone

Habitat type and level of protection

The South African coastline is approximately 3 330 km, from the Namibian border in the west, to the Mozambique border in the east (Lombard *et al*. 2004), although for the purposes of this analysis only

the portion of coastline encompassing the white steenbras core distribution was considered. This represented approximately 1 870 km from the Berg Estuary to the eastern boundary of the Dwesa-Cwebe MPA. This section of coastline is comprised of approximately 650 km (35%) of sandy beaches, 530 km (28%) of mixed sand and rock and 580 km (31%) of rocky shores (Table 9.6). There is also a natural progression further westwards along the coastline to a greater proportion of rocky shoreline. Langebaan Lagoon is unlike the coastline in the rest of the survey area, and was considered a unique habitat, while the sections of coastline comprising harbour are excluded from subsequent analyses.

Table 9.6: Proportions of different shoreline habitat constituting the 1 870-km stretch of coastline from the Berg Estuary to the eastern boundary of the Dwesa-Cwebe MPA

Shoreline habitat	Length (km)	%
Harbour	10.4	0.6
Lagoon (Langebaan)	101.4	5.4
Mixed shore	529.0	28.3
Rocky shore	577.0	30.9
Sandy shore	652.2	34.9
Total	*1870.0*	*100.0*

Within this stretch of coastline there are 13 existing MPAs and one proposed MPA. These vary considerably in their levels of protection, with certain MPAs governed by strict no-take policies, such as De Hoop MPA, and others allowing varying degrees of resource exploitation, such as Table Mountain MPA. While sandy shores are the dominant type of shoreline overall, when protection in MPAs is considered (at any level of protection), sandy shores become grossly under-represented, constituting only 117 km (6.3 %) of the total 1 870-km stretch of coastline. In contrast, rocky shores contribute less to the total shoreline in this area, but benefit considerably more from MPA protection, with 192 km (10.3%) of rocky shore being protected. In terms of fully protected shoreline (i.e. shore angling prohibited), sandy shores constitute only 65 km in total (roughly 3.5%). While white steenbras in the coastal zone show high levels of residency (see Chapter 6), these 65 km are non-contiguous, and spread across the 14 MPAs, suggesting that even resident individuals are unlikely to be completely protected. Langebaan Lagoon, encompassing the Langebaan MPA, is again an anomaly and while classified as a lagoon is understood to function as a marine bay (Turpie 2004).

The 14 MPAs together encompass an impressive 461 km (almost 25%) of the survey shoreline (Table 9.7), which exceeds the target of 20% suggested at The World Summit on Sustainable Development, in 2002 (Turrell 2004). However, within these MPAs, shore angling is permitted along almost half of the protected shoreline. Proportionately less of the inshore zone associated with this protected

shoreline is open to boat-based angling, although white steenbras is rarely captured outside of the shore fishery (Brouwer and Buxton 2002). This suggests that the MPAs within the white steenbras core distribution are likely to contribute less to the protection of nearshore species, such as white steenbras, than to those species with more offshore distributions.

Table 9.7: Proportions (km and %) of different shoreline habitat included within the boundaries of current MPAs, or outside of MPAs (i.e. open access), along the 1 870-km survey area from the Berg Estuary to the eastern boundary of the Dwesa-Cwebe MPA

Protection status	Lagoon		Sandy shore		Mixed shore		Rocky shore		Total	
	km	%	km	%	km	%	km	%	km	%
Open access	45.5	2.4	535.2	28.8	432.9	23.3	384.8	20.7	1398.4	75.2
Partial protection	17.5	0.9	51.3	2.8	52.4	2.8	79.8	4.3	200.9	10.8
Full protection	38.5	2.1	65.7	3.5	43.7	2.3	112.4	6.0	260.2	14.0
Total	101.4	*5.5*	652.2	*35.1*	529.0	*28.4*	577.0	*31.0*	*1859.6*	100.0

The proportions of coastline within each MPA comprised of sand, mixed sand and rock, and rocky shoreline are presented in Table 9.8, and Figures 9.5 and 9.6, representing the Western Cape and Eastern Cape Provinces, respectively. The shoreline of the proposed Greater Addo Elephant National Park (GAENP) MPA is included to show the additional coastal habitat type that will be protected if the MPA is promulgated, increasing the total shoreline of the survey area within MPAs to 542 km.

Table 9.8: Proportions (km and %) of sand, mixed sand and rock, and rocky shoreline within each MPA in the survey area, from the Berg Estuary to the eastern boundary of the Dwesa-Cwebe MPA

Marine protected area	Lagoon		Sandy shores		Mixed shores		Rocky shores		Total
	km	%	km	%	km	%	km	%	km
Langebaan	55.9	100.0	0.0	0.0	0.0	0.0	0.0	0.0	55.9
Sixteen Mile Beach	0.0	0.0	27.7	85.8	1.4	4.3	3.2	9.9	32.3
Table Mountain	0.0	0.0	16.4	13.7	26.9	22.4	76.7	63.9	120.0
Helderberg	0.0	0.0	5.6	100.0	0.0	0.0	0.0	0.0	5.6
Betty's Bay	0.0	0.0	1.5	15.2	3.4	33.5	5.2	51.3	10.1
De Hoop	0.0	0.0	11.6	23.1	13.6	27.1	25.0	49.8	50.1
Stilbaai	0.0	0.0	6.0	45.1	6.7	50.9	0.5	3.9	13.2
Goukamma	0.0	0.0	18.6	78.6	4.7	19.9	0.4	1.6	23.7
Robberg	0.0	0.0	5.0	38.7	0.1	0.9	7.8	60.4	13.0
Tsitsikamma	0.0	0.0	1.8	3.2	4.1	7.5	48.5	89.3	54.4
Sardinia Bay	0.0	0.0	3.9	36.6	1.9	17.9	4.9	45.5	10.7
GAENP (proposed)	0.0	0.0	63.6	78.4	16.3	20.2	1.2	1.4	81.1
Amathole	0.0	0.0	12.1	23.3	23.2	44.6	16.7	32.1	52.1
Dwesa-Cwebe	0.0	0.0	6.7	33.6	10.0	50.0	3.3	16.4	20.0
Total	*55.9*	*10.3*	*180.6*	*33.3*	*112.4*	*20.7*	*193.3*	*35.7*	*542.2*

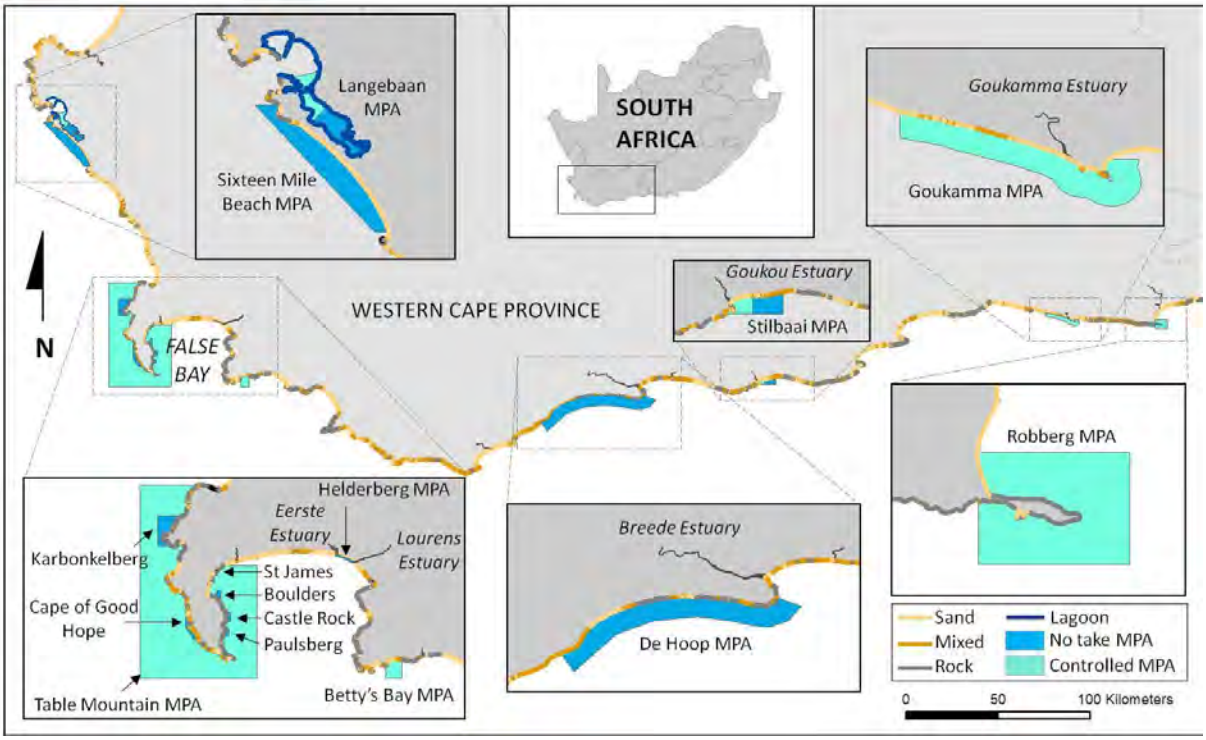

Figure 9.5: Proportions of coastline within the survey section of the Western Cape Province, comprised of sand, rock or mixed sand and rock shoreline (habitat type from Harris *et al*. 2011), as well as the compositions of the shorelines within each of the MPAs along this stretch of coastline

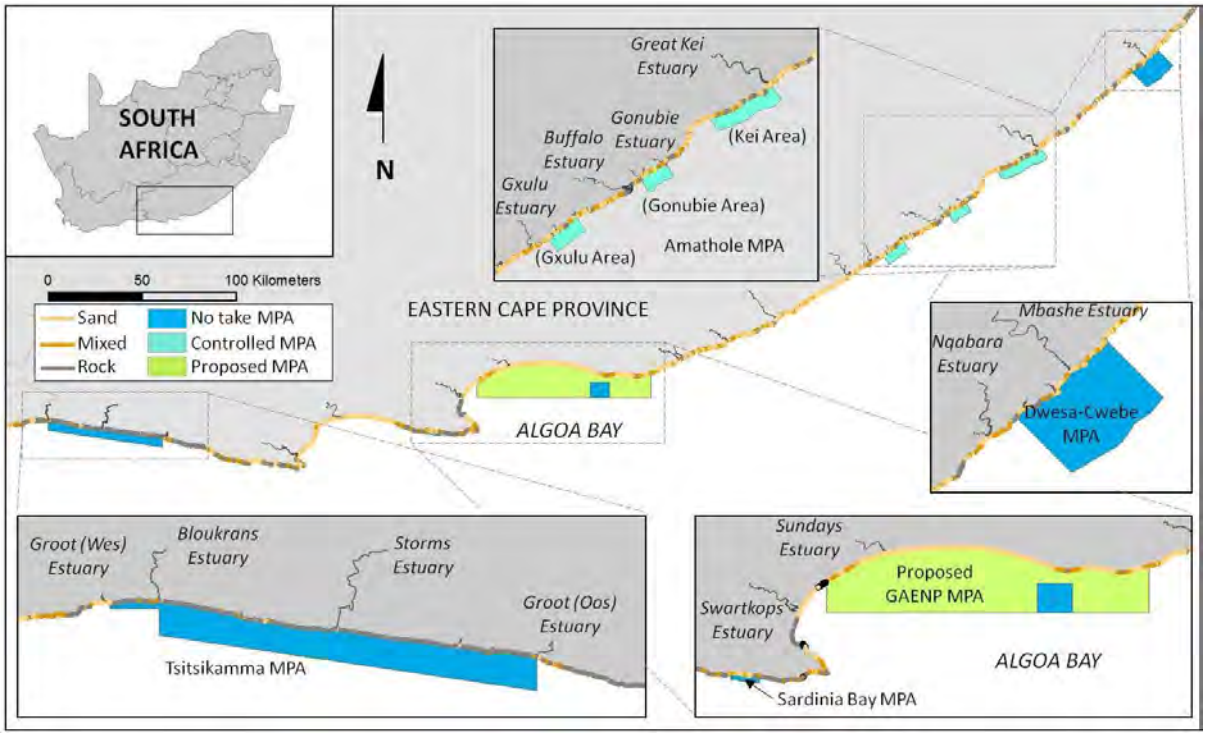

Figure 9.6: Proportions of coastline within the survey section of the Eastern Cape Province, comprised of sand, rock or mixed sand and rock shoreline (habitat type from Harris *et al*. 2011), as well as the compositions of the shorelines within each of the MPAs along this stretch of coastline

Coastal scoring system

When assessing coastal habitat type for the suitability of white steenbras, the proportion of sandy shoreline was first determined. Only four of the 38 50-km coastal sections comprised more than 60% sand. These constituted two short sections of coastline, associated with St Francis Bay and Algoa Bay, and along the west coast (Figure 9.7a). When the proportion of mixed sand and rock was included, a further three sections of coastline were identified; along the former Ciskei coastline, the vicinity of Cape Agulhas/Arniston, and adjacent to the Berg Estuary (Figure 9.7b), in which the proportion of sand and mixed (sand/rock) shore combined was greater than 80%.

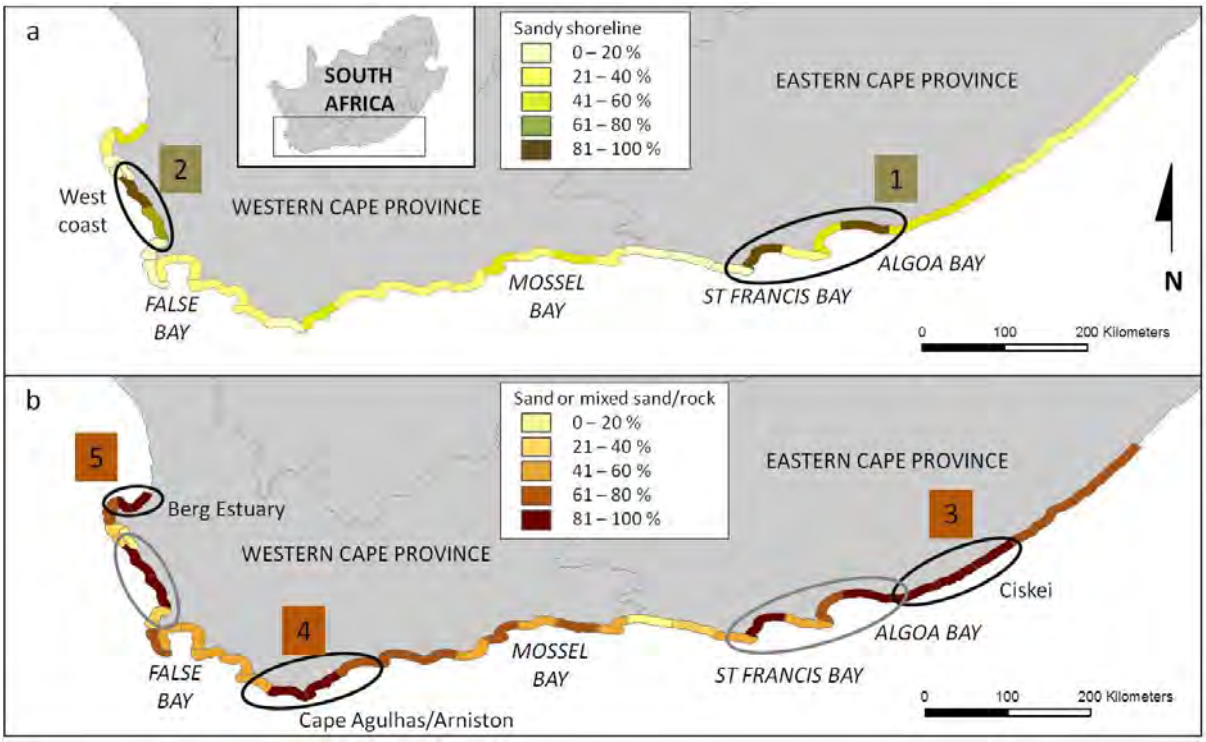

Figure 9.7: Proportions of the 38 50-km coastal sections from the Berg Estuary in the west to the Dwesa-Cwebe MPA in the east, comprising a) sandy shores and b) sandy and mixed shores combined

Mixed shores, such as those found within the De Hoop MPA, are often dynamic in nature, which Bennett and Attwood (1991) suggested maintains invertebrate communities in early successional stages and thus more readily accessible to invertebrate feeders. These mixed shores are considered useful habitat for white steenbras (Bennett 1993b), meaning that overall there is a relatively large proportion of suitable habitat within the white steenbras core distribution, when mixed sand and rock shores are included. However, sandy and mixed sand and rock shores combined that fell within the boundaries of MPAs encompassed a total of 11% of the 1 870-km stretch of coastline, indicating that little potentially favourable habitat for white steenbras within its core distribution is protected.

As with the estuarine scores, the coastal scores showed a general increase from west to east along the coast, from the Berg estuary to the Dwesa-Cwebe MPA (Figure 9.8). Coastal sections with the lowest scores were generally those without estuaries, including six coastal sections along the west coast, as well as a section of the coastline of Algoa Bay, within the proposed GAENP MPA.

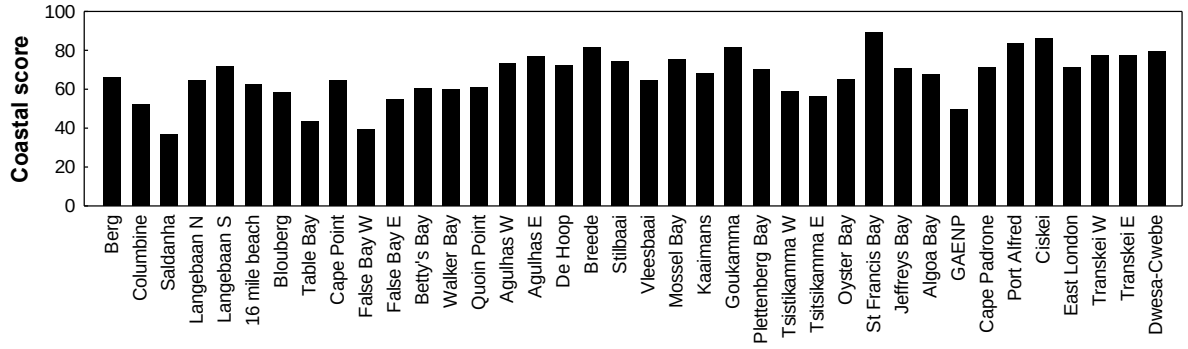

Figure 9.8: Scores for the 50-km coastal sections from the Berg estuary in the west, to Dwesa-Cwebe MPA in the east, based on the coastal scoring system. Labels refer to major landmarks or coastal areas that are associated with each 50-km coastal section

The top 10 scoring coastal sections ranged geographically from Arniston (ranked 9th) in the west to the Dwesa-Cwebe MPA (ranked 6th) in the east (Table 9.9).

Table 9.9: Individual criteria and overall coastal scores for the top 10 ranked 50-km coastal sections

Coastal section rank	Average estuarine score	% Sand or mixed shore	Wastewater discharge ($m^3.day^{-1}$)	Shore angling effort ($anglers.km^{-1}.day^{-1}$)	Coastal score
1. St Francis Bay	71.2	100	0	0.21	89.3
2. Former Ciskei	66.0	97	0	0.28	86.1
3. Port Alfred	64.8	92	0	0.34	83.8
4. Breede Estuary	71.9	77	0	0.16	81.6
5. Goukamma	77.4	77	3 955	0.79	81.2
6. Dwesa-Cwebe	70.1	79	0	0.80	79.6
7. Transkei E	68.0	74	0	0.66	77.6
8. Transkei W	72.5	67	0	0.40	77.6
9. Arniston	55.6	93	0	1.55	77.0
10. Mossel Bay	59.9	76	10 371	0.46	75.5

The highest ranked coastal section was that situated along the shoreline of St Francis Bay, in the Eastern Cape Province (Figure 9.9). This section is comprised entirely of sandy and mixed shores, has low shore angling effort, no wastewater outfall and a high mean estuarine score. This coastal section includes the Van Stadens and Kabeljous estuaries, ranked second and third in the estuary scoring

analysis, and anecdotal evidence indicates that white steenbras are abundant in shore catches in this area. However, the area falls within an almost 600-km stretch of coastline, between the Tsitsikamma and Amathole MPAs, within which just 10 km of shoreline are protected (*viz*. the Sardinia Bay MPA). As the highest ranked coastal section, with two of the top three estuaries, the sandy shores of St Francis Bay, particularly from the Kabeljous to Van Stadens estuaries, represent an important area for white steenbras, and should be identified as a potential area for protection. A combination of estuarine and marine protected areas would create an all-inclusive conservation "unit" that could provide protection for white steenbras from early juvenile to sub-adult life stages.

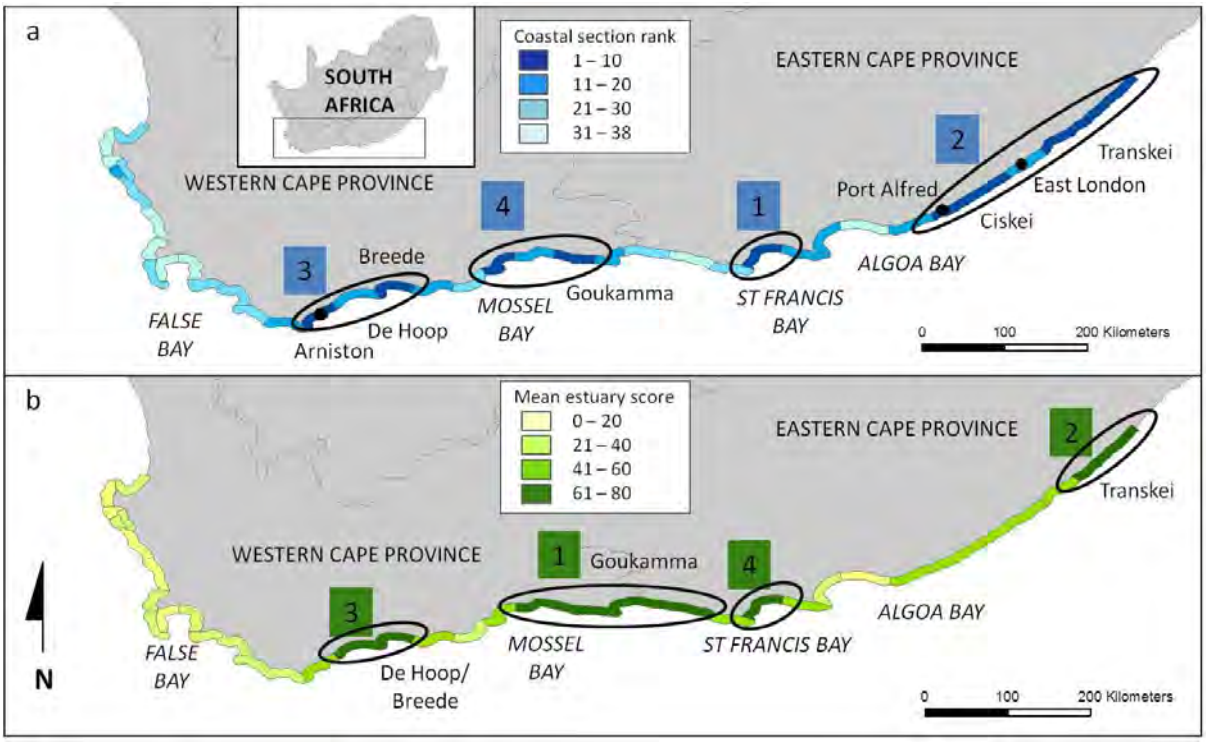

Figure 9.9: Individual scores for the 38 50-km coastal sections from the Berg Estuary in the west to the Dwesa-Cwebe MPA in the east, showing a) the overall coastal score for each section based on the coastal scoring system, and b) average estuarine score per section, based on the estuary scoring system (ellipses indicate areas of high scoring coastline, with numbers indicating their ranks)

Three other high-scoring coastal regions were identified, within which two or more adjacent (or nearby) 50-km coastal sections scored highly (Figure 9.9, indicated by rank numbers and ellipses). A large, high-scoring stretch of coastline was identified to the east of Algoa Bay, encompassing the coastlines of the former Ciskei and Transkei. Within this region, there are six 50-km coastal sections, of which five were ranked within the top 10, including two from Port Alfred along the former Ciskei coast to East London (which itself was ranked 14th), and all three to the east of East London, up to

and including the eastern-most section included in the analysis. This region includes the Dwesa-Cwebe MPA and all three zones of the Amathole MPA, five of the top 10 ranked coastal sections, and 20 of the top 30 ranked estuaries. The area also includes the vicinity off the Mbashe Estuary, which is believed to represent the white steenbras spawning grounds. This area can, therefore, be identified as a second important coastal area for the conservation of white steenbras and should be managed accordingly, including prevention of illegal harvesting within MPAs, enforcement of fishery regulations, and maintenance of estuarine ecosystem functioning.

The coastal sections of the Breede Estuary and Arniston, ranked fourth and ninth, are situated either side of the De Hoop MPA coastal section, which itself was ranked 13th. This area thus forms a third important region, encompassing two of the top 10 coastal sections and the De Hoop MPA, shown to have the second highest shore angling CPUE of white steenbras along the coastline (Bennett and Attwood 1991, and see Chapter 8), as well as the only three estuaries west of Mossel Bay that were ranked in the top 60 estuaries. This region, therefore, represents a third potentially important area for white steenbras, at both the juvenile estuarine and late juvenile/sub-adult surf zone life stages, and what is possibly the western-most section of coastline contributing to the protection of white steenbras at both life stages. This region could constitute a second all-inclusive conservation "unit" for white steenbras and other estuarine-associated coastal fishes, such as the St Francis Bay – Van Stadens – Kabeljous area.

The Mossel Bay and Goukamma MPA coastal sections were also ranked within the top 10, and are separated by the Kaaimans Estuary coastal section, which was ranked 18th. This region, therefore, included two of the top 10 coastal sections, and three of the top 10 scoring estuaries (the Kaaimans, Swartvlei and Goukamma estuaries), as well as the Goukamma MPA. The area can thus be identified as a fourth area of importance for white steenbras, as well as other sandy beach-associated coastal fishes, and the relevant authorities should ensure that this section of coastline is effectively managed, to ensure compliance with fishery regulations. Protection afforded to coastal fishes in this region could be improved through the establishment of a new MPA within the Mossel Bay area, or prohibition of shore angling within the Goukamma MPA and no-take status for the Goukamma Estuary, which was ranked highest in the estuary scoring system. The combination of EPA and MPA would provide a third conservation "unit" for white steenbras, to provide protection at the juvenile estuarine life stage and the late juvenile and sub-adult surf zone life stages.

Alignment with national priority coastal areas

A prioritisation exercise conducted along the coastline between Cape Point and the Dwesa-Cwebe MPA identified 19 priority areas for expansion of the current MPA network (Clark and Lombard 2007). Some of these matched those identified in the current study. Small areas were identified near the mouth of the Duiwenhoks Estuary and between Mossel Bay and the Kaaimans Estuary, as well as the coastline encompassing the Swartvlei Estuary, adjacent to the existing Goukamma MPA, which would be particularly suited to protect white steenbras having used the Swartvlei and Goukamma estuaries as nursery areas. Sites were also identified at the western boundaries of the Tsitsikamma and Sardinia Bay MPAs, which could provide additional protection for fishes having used the high-scoring Groot (west) and Sout (east) estuaries, and Van Stadens Estuary, respectively. Sites were also identified along the Ciskei coast, near the Gqutywa Estuary, and along the Transkei coast between the Amathole and Dwesa-Cwebe MPAs, near the high-scoring Qora Estuary. These sites could all provide additional protection for white steenbras associated with nearby, high-scoring estuaries, if the levels of protection included no-take zones. Clark and Lombard (2007) also identified the sandy shorelines on either side of the Goukamma MPA (encompassing the mouth of the Swartvlei Estuary), and the sandy shoreline of Mossel Bay encompassing the Hartenbos, Klein Brak and Groot Brak estuaries, as being important coastal areas for white steenbras. This agrees with the results of the current study, particularly with the emphasis on the Goukamma MPA as a centre for the protection of white steenbras.

An area of the coastline that was not identified in either the coastal or estuary scoring systems in the current study, but which is known to be an important area for white steenbras, is False Bay (Bennett 1993b). False Bay provides a large area of shallow inshore habitat and sandy and mixed sand and rock shoreline for late juvenile and sub-adult white steenbras, as well as a summer aggregation area for adult white steenbras after their perceived winter spawning migration to Transkei waters (Bennett 1993b). The Bay also offers deeper (15 to 30 m) sandy areas, which harbour dense shoals of large adult white steenbras. False Bay comprised two 50-km coastal sections in the analysis. While these both constituted about 50% sand and mixed sand and rock, the western shore of False Bay scored poorly due to the high level of wastewater discharge (DWAF 2004), and both sections scored poorly due to high levels of shore angling effort (Lamberth 1996, Brouwer *et al*. 1997, Sink *et al*. 2011). The average estuarine scores for the two sections were also low due to poor health (Whitfield 2000), and high levels of pollution, ecosystem threat status and fishing effort (van Niekerk and Turpie 2011). However, despite the low scores, False Bay remains an important aggregation area for white steenbras, and certain estuaries, such as the Zandvlei, act as viable nurseries for the species.

Important habitats for white steenbras

The two scoring systems identified four important coastal regions; Arniston to the Breede Estuary, Mossel Bay to Goukamma, St Francis Bay and the Transkei and Ciskei coastlines (Figure 9.9). These are potentially important areas for white steenbras for two reasons. Firstly, all four areas exhibited high coastal scores and high mean estuarine scores. This resulted from estuarine catches of white steenbras being highest in estuaries adjacent to long sections of sandy and mixed shores. Therefore, each area comprises suitable estuaries, to provide nurseries for early juvenile white steenbras, as well as suitable coastal habitat for post-estuarine juveniles and sub-adults. Managers should seek to ensure the maintenance of the ecosystem health and functioning in each of these areas.

Secondly, most of these areas have high scoring estuaries in close proximity to an MPA. The De Hoop shoreline between Arniston and the Breede Estuary is characterised by the well-established De Hoop MPA, and the Ciskei and Transkei coastlines have the Amathole and Dwesa-Cwebe MPAs, although the Amathole MPA is open to shore angling. Similarly, the Mossel Bay to Goukamma area has the Goukamma MPA, although this is also open to shore angling. The no-take De Hoop and Dwesa-Cwebe MPAs provide protection for white steenbras in the coastal zone, and this could also be achieved in the Goukamma and Amathole MPAs through closure to shore angling. The St Francis Bay shoreline is not afforded coastal protection, although the high estuarine and coastal scores suggest that this area could be of particular importance to both estuarine-phase and surf zone-phase white steenbras. The potential for closure of a section of this shoreline warrants further investigation. Additionally, the protection of certain estuaries within each of these regions would significantly improve the level of protection afforded to white steenbras. Estuarine protected areas with adjacent MPAs would provide valuable protection “units”, providing protection from the time of recruitment through to the onset of sexual maturity, when coastal migrations are initiated (Bennett 1993b).

Juveniles have an obligatory estuarine-dependent nursery phase (Wallace *et al*. 1984a), and rarely use estuaries west of the Berg or east of the Great Kei (Bennett 1993b, Harrison and Whitfield 1995). Assuming that juveniles use only the 138 estuaries from the Berg to the Mbhanyana (as defined for the estuarine scoring system), the total available surface area at this life stage is only approximately 146 km^2. This is further restricted by their resident behaviour and limited area use within estuaries (Chapter 3). Recruitment of estuarine-dependent species into temporarily open/closed estuaries, which dominate the white steenbras core distribution, is reliant on the mouths of these estuaries opening at suitable times. This may be affected by annual periodicity in rainfall, artificial breaching at less suitable times and excess water abstraction (Whitfield and Kok 1992). The same is true for

estuarine lakes, which together with temporarily open/closed estuaries comprise 46% of available estuarine habitat for white steenbras. Failure of these systems to open at suitable times could significantly reduce white steenbras recruitment (Whitfield and Bruton 1989). Late maturity is an evolutionary adaptation that should allow white steenbras to cope with failed recruitment and extended periods of mouth closure. However, when environmental conditions that limit recruitment are compounded with overexploitation, the ecological consequences for such species may be dire.

The distributional range of white steenbras for the purpose of this study was defined as the area from the Orange River in the west to the Mtamvuna Estuary in the east, at the boundary between the former Transkei and KwaZulu-Natal, spanning approximately 2 380 km of coastline. Furthermore, white steenbras are rarely found deeper than 25 m, with post-estuarine juveniles remaining shallower and even closer inshore (<10 m deep) (Bennett 1993b). Therefore, if a conservative maximum depth of 30 m is assumed for the species, the total available habitat within the white steenbras distribution range can be estimated as the area from the coastline to the 30 m depth contour, between the Orange River and the Mtamvuna Estuary, which equates to approximately 6 600 km^2. Furthermore, assuming the core distribution is from the Berg Estuary to the eastern end of the Dwesa-Cwebe MPA (as for the coastal scoring analysis), comprising 1 870 km of coastline, the total available habitat in the white steenbras core distribution from the shore to the 30 m depth contour is 5 050 km^2, highlighting the restricted nature of the white steenbras distribution.

The total surface area of the 14 MPAs (excluding island MPAs) encompassed within the white steenbras core distribution is 2 265 km^2. However, within the region of suitable depth (i.e. between the coastline and the 30 m depth contour), the total surface area included in MPAs is just 820 km^2, which represents 17% of the total habitat available to white steenbras within its core distribution.

White steenbras are believed to migrate to the inshore waters of the Transkei coastline in late winter, where spawning takes place in the vicinity of the fluvial mixed mud and sandbanks deposited by certain estuaries in the region (Bennett 1993b, Hutchings *et al*. 2002b). The inshore area off the Mbashe Estuary is the only confirmed spawning area, and similar catchment and sediment characteristics are limited to the Mtata, Mzimvubu and Great Kei estuaries (van Niekerk and Turpie 2011). The successful spawning of white steenbras in such areas, which may comprise less than 0.5 km^2 in total, is therefore highly vulnerable to both degradation of marine and associated estuarine habitats and overexploitation during aggregation in a limited area. Similarly, the sheltered sand habitat in False Bay offers an important yet restricted summer aggregation area for white steenbras.

9.2.3 Assessment of existing and proposed estuarine and marine protected areas

Estuarine protection

Currently, 35 estuaries within the white steenbras core distribution are protected to some degree, although in most protected estuaries angling is still permitted, offering little protection for fishery species. The fully protected Krom (east) and partially protected Diep estuaries, on the west and east coasts of the Cape Peninsula, respectively, fall outside of the region of estuaries predominantly used by white steenbras and produced zero catches of the species in a national estuarine ichthyofaunal survey (Harrison 1998b). Therefore, these small EPAs contribute little to white steenbras protection.

The Breede Estuary, in close proximity to the De Hoop MPA, offers temporal protection through the prohibition of night-time fishing (Government Gazette No. 34596). There is also a drive to prevent night fishing in the Gamtoos Estuary, which enters the sea in St Francis Bay. While this provides only partial protection, considerable reductions in fishing effort are likely to result in both estuaries, which are potentially important by virtue of proximity to the De Hoop MPA, and abundance of white steenbras (James and Harrison 2010a), respectively. Protection offered by the Breede Estuary can potentially improve recruitment to the shoreline near the De Hoop MPA, meaning that these fish could be protected to some degree for large proportions of their juvenile and sub-adult life stages.

The Goukou Estuary encompasses a no-take EPA and enters the Stilbaai MPA, which also has certain no-take zones. White steenbras was less common in seine net catches in this estuary than other estuaries, but was the third most dominant species, contributing 11.4% to the total catch (Harrison 1999b). Although the no-take zone of the EPA starts 3 km from the mouth, leaving the lower reaches unprotected, white steenbras abundance is highest in the middle reaches of this estuary, which fall within the no-take zone of the EPA (SJ Lamberth, DAFF, unpublished data). As such, the Goukou Estuary and adjacent Stilbaai MPA could offer at least some protection to white steenbras. However, the estuary is small and ranked in the lower half in the estuary scoring analysis.

Seven estuaries, from the Groot (west) to the Groot (east) are protected by virtue of their location within the Tsitsikamma Coastal National Park. Presence of white steenbras in these estuaries suggests that they provide some level of protection, and recent research netting has produced large catches of white steenbras in the Groot (west) Estuary (MKS Smith, SANParks, pers. comm.). However, these are predominantly small river mouths (Whitfield 1992) with little available habitat (0.5 km^2 total) and occur along the rocky shoreline of the Tsitsikamma MPA; therefore, their combined contribution to the overall protection of white steenbras is probably low.

Five estuaries entering the Dwesa-Cwebe MPA, from the Ngoma in the west to the Mbhanyana in the east, are also afforded protection, due their locations within the MPA (Whitfield and Cowley 2010). However, the proportions of each estuary to be protected have not yet been established (van Niekerk and Turpie 2011). As this area forms the spawning grounds for white steenbras (Bennett 1993b), these estuaries are expected to be well-suited for the protection of post-larval white steenbras recruits. However, catches of white steenbras in Transkei estuaries were low (Harrison 2003), suggesting that few white steenbras utilise the estuaries within the Dwesa-Cwebe MPA.

As part of the proposed GAENP, a potential no-take zone has been identified within the Sundays Estuary (Bezuidenhout *et al*. 2011). While the delineation of the no-take area has not yet been established, if suitably positioned, this EPA could provide considerable protection for white steenbras, in an estuary shown to have high catches of the species (James and Harrison 2010a). The estuary scored poorly in the estuary scoring system, due to high levels of pollution and fishing effort and a critical ecosystem threat status (Whitfield 2000, van Niekerk and Turpie 2011). However, if the level of fishing effort can be reduced through the implementation of the EPA, and the levels of pollution and ecosystem threat can be reduced, the proposed Sundays Estuary EPA and adjacent proposed GAENP MPA, could contribute considerably to the protection of white steenbras during its estuarine and surf zone life stages.

Marine protected areas

The recently proclaimed Amathole MPA network in the Eastern Cape Province encompasses a total of approximately 35 km of sandy and mixed shores, spread across the three separate MPA sections. Although a roving creel survey recorded low catches of white steenbras in this region (Brouwer and Buxton 2002), the species was considered the third most targeted by recreational shore anglers in the Eastern Cape Province, and anecdotal evidence suggests that large catches of adult white steenbras are made in the vicinity of the Amathole MPA in late summer, presumably on their return migration from the Transkei coast. However, the combined 52.1 km of coastline spanning the three zones within this MPA are open to shore angling and spear fishing, suggesting that despite its considerable potential to protect white steenbras, in terms of its proximity to the white steenbras spawning grounds and its high proportion of sandy and mixed sand and rock shoreline, the Amathole MPA provides little protection, particularly for spawning or return-migration white steenbras. Within the three MPA zones comprising the Amathole MPA, are the mouths of 17 estuaries, while a further 11 estuaries enter the sea between the different MPA zones. Estuarine netting data from Harrison (2003) showed that white steenbras utilised the estuaries between the Gonubie and Kei sections of

the Amathole MPA, although eastwards of this region the catches of white steenbras were negligible. These estuaries within the Amathole MPA therefore represent the eastern most estuaries of importance to white steenbras, and are likely the first estuaries into which young of the year recruit. As such, the MPA would be particularly suited to the protection of post-estuarine juveniles and adults that have used those 28 estuaries as nurseries. Despite this, none of the estuaries within this region are afforded even partial no-take status. Therefore, the Amathole MPA should be flagged as a potential MPA in which the possibility of upgrading the protection level to full closure should be further investigated, and estuaries (or parts thereof) should be assessed for their possible inclusion into appropriate EPAs.

The Goukamma MPA is characterised mainly by sandy shores, with some mixed sand and rock. The MPA straddles the Goukamma Estuary and is in close proximity to the large Wilderness and Swartvlei estuarine lakes, as well as the Knysna estuarine bay. The nearby estuaries in this stretch of coastline scored highly in the estuarine scoring system. The MPA is therefore particularly well situated to provide protection for post-estuarine white steenbras that have used these estuaries as nursery areas. However, as with the Amathole MPA, recreational shore angling is permitted and effort is high (Pradervand and Hiseman 2006). Consequently, the MPA has been referred to as a "node of exploitation for surf zone fish" (van Zyl 2011), offering little protection for white steenbras. Results of the previous chapter showed that CPUE recorded in this MPA from 1993 to 2002 (Pradervand and Hiseman 2006) was similar to that recorded in the vicinity of the De Hoop MPA prior to proclamation, after which the CPUE of white steenbras increased significantly (Bennett and Attwood 1991). The Goukamma MPA should, therefore, also be flagged as a potentially suitable MPA for which the level of protection could be increased to exclude shore angling, for the protection of sandy shore coastal fishes.

The Langebaan Lagoon and associated MPA offer fishes some of the ecological advantages offered by estuaries, such as a sheltered environment and rich supply of food, although the lagoon functions as an extension of the marine environment and is classified as a marine bay (Whitfield 2005). There are sporadic catches of white steenbras within the lagoon (Anchor unpublished data), which appear to occur as a result of infrequent years of good recruitment (CG Attwood, UCT, pers. comm.), yet white steenbras was absent from two seine net studies of the fish community within the lagoon (Whitfield *et al*. 1989, Clark 2007). There are no estuaries flowing into the lagoon, and none within close proximity along the coastline. As a result, the lagoon itself functions as an important nursery area for certain fishes. Therefore, other than the Berg Estuary, which acts as a nursery for white

steenbras, the Langebaan Lagoon and MPA are likely the only refuge for juvenile white steenbras along the west coast. The MPA includes a no-take zone, which is likely to contribute to the protection of white steenbras in the lagoon in years when white steenbras are present. However, the low present-day catches of white steenbras in the lagoon, despite historical high catches (SJ Lamberth, pers. comm.), suggest that this MPA contributes little to overall white steenbras protection. There is also evidence of non-compliance with regulations (Tunley 2009), and angling effort within the permitted zone of the MPA is high.

The Tsitsikamma MPA is one of the largest and oldest 'no-take' MPAs in South Africa (Cowley *et al*. 2002). Catches of white steenbras were higher in the closed area of this MPA, than the area previously open to recreational shore fishing, suggesting that there is some protection offered to white steenbras (Hanekom *et al*. 1997). However, almost 90% of the coastline of this MPA is comprised of rocky shoreline, which is unfavourable habitat for white steenbras. Therefore, this large MPA is likely to provide less protective benefit for white steenbras, relative to its size, than other MPAs, such as De Hoop.

Sixteen Mile Beach MPA on the west coast has the greatest stretch of sandy shoreline of all the MPAs within the study region (27.7 km). Furthermore, shore angling within this MPA is prohibited, making it well suited to the protection of inshore fish species. Lamberth and Mann (2000) suggested that the majority of the white steenbras stock is found between Cape Columbine and the Mbashe Estuary, although the species featured poorly in shore-angler catches along the west coast (Sauer and Erasmus 1996, Brouwer *et al*. 1997), and Hutchings *et al*. (1999) recorded zero white steenbras in experimental marine and estuarine gill-net catches along the west coast, between Cape Point and the Olifants River Mouth. Furthermore, the ORI tagging programme returned zero recaptures of tagged white steenbras along the west coast (see Chapter 6). The low abundance of white steenbras along the west coast is likely a result of historical overexploitation (SJ Lamberth, DAFF, pers. comm.). As such, Sixteen Mile Beach MPA probably provides little protection for the species.

The close proximity of the Table Mountain MPA, particularly those restricted zones that are situated within False Bay, to the areas of known white steenbras aggregation, such as areas along the False Bay north and north western shores, suggest that this MPA could contribute to the overall protection of the species, particularly for adults during their summer aggregation. Protection within this area is of particular importance as the recreational shore fishery along the south west coast, and within False Bay in particular, contributed considerably to the overall demise of white steenbras

(Lamberth *et al*. 1994). While this MPA protects approximately 13.5 km of sandy and mixed sand and rock shoreline from shore angling, the majority of this protected habitat occurs on the west coast of the Cape Peninsula (i.e. outside of False Bay). Therefore, while it is possible that Table Mountain MPA (proclaimed in 2004) provides a refuge for at least some white steenbras, from the recreational shore fishery, this MPA is probably not contributing largely to the overall protection of this species.

Conversely, closure of a short section of coastline in False Bay encompassing the Eerste Estuary, later incorporated into the Helderberg MPA, was suggested to have considerably reduced the catch of adult white steenbras from the north shore of False Bay (Bennett 1993a). Therefore, despite its small size (5.6 km of which all is sandy shoreline), the Helderberg MPA (proclaimed in 2000) is likely contributing to the protection of white steenbras, particularly in a hypothetical scenario of the commercial ban on white steenbras being lifted.

Sardinia Bay MPA, situated just west of Algoa Bay, forms the only protected section of mainland shoreline between the Amathole and Tsitsikamma MPAs, which spans almost 600 km. The MPA is small, but includes 6 km of fully protected sandy and mixed sand and rock shoreline, along a section of coastline where white steenbras are caught in relatively high numbers (PD Cowley, South African Institute for Aquatic Biodiversity, pers. comm.), and may therefore contribute towards the protection of white steenbras within this area to some degree.

The Stilbaai MPA on the south coast constitutes more than 7 km of fully protected sandy and mixed shoreline, within two no-take zones, situated either side of the mouth of the Goukou Estuary, which itself includes a no-take zone. While the MPA is small, it may contribute to the protection of white steenbras in that area, particularly those that enter the surf zone after having used the Goukou Estuary as a nursery.

The De Hoop MPA is large, with at least 25 km (50%) of its shoreline comprising sandy or mixed shores. The MPA is well-established, with shore angling prohibited. White steenbras was within the top three species in terms of CPUE during research angling in this MPA, and showed a significant increase in CPUE after proclamation (Bennett and Attwood 1991). This MPA also produced the second highest CPUE of white steenbras of any coastal section surveyed (see Chapter 8). The De Hoop MPA is also within close proximity to the large permanently open Breede Estuary, and likely provides a refuge for post-estuarine juvenile white steenbras having used the Breede Estuary as a nursery. The De Hoop MPA thus contributes considerably to the protection of white steenbras.

Almost 17 km of the 20-km shoreline within the Dwesa-Cwebe MPA is comprised of sandy or mixed shores. White steenbras are believed to spawn over the fluvial mudbanks deposited offshore of the Mbashe and other Transkei estuaries (Hutchings *et al*. 2002a). The Dwesa-Cwebe MPA, therefore, plays a vital role in protecting adult white steenbras during the spawning season, where they are particularly vulnerable due to the predictability of their aggregation and their close proximity inshore (Bennett 1993b). As such, this MPA could be flagged as an essential tool for the protection of white steenbras, and should be managed in such a way as to ensure compliance within its boundaries. However, anecdotal evidence suggests a high level of illegal angling within the MPA (Timmermans 2004). Most MPAs along the Transkei coastline (including those outside of the current survey area) are poorly patrolled, offering little protection for inshore fishes (Attwood *et al*. 1997, Mann *et al*. 2003).

The coastline of the proposed GAENP MPA, in Algoa Bay, can be identified as a potentially important area for the protection of white steenbras. The area is characterised by high catches of white steenbras (PD Cowley, unpublished data), and telemetry results suggest that some mature white steenbras may remain within Algoa Bay over the spawning period (see Chapter 6). The area is also located along an almost 600-km stretch of coastline between the Dwesa-Cwebe and Tsitsikamma MPAs, within which shore angling is prohibited for just 10.7 km (Sardinia Bay MPA). The shoreline of the proposed MPA is comprised mainly of sand and mixed shores, and straddles the mouth of the Sundays Estuary, in which James and Harrison (2010a) recorded large seine net hauls of white steenbras, while the nearby Swartkops Estuary supported a large population of white steenbras in the 1900s (Gilchrist 1918, in Baird *et al*. 1996). As such, the proposed GAENP MPA will almost certainly be an important contributor to the future protection of white steenbras, if sufficient coastline within this MPA is closed to shore angling.

Suitability of existing level of protection

The results have shown that the current protected area network is inadequate for the protection of white steenbras. Insufficient estuarine habitat is entirely protected from angling and insufficient suitable marine habitat is included within no-take MPAs, suggesting that the current protected area network is providing less protection for white steenbras than may be hoped. However, combinations of estuarine and marine protected areas, such as those of the Goukamma Estuary and MPA, the Breede Estuary and De Hoop MPA, and possibly the Sundays Estuary and GAENP MPA have the potential to provide considerable protection for estuarine-associated coastal fishes.

Identification of suitable areas for additional protection (for white steenbras) should focus on sections of predominantly sandy and mixed shores, particularly those stretches of coastline in which the proportions of protected area are low, and aim to include areas where white steenbras are known to exist in high densities, preferably within close proximity to, or straddling, one or more estuaries. Such areas that are immediately apparent include 1) the long sandy beaches of St Francis Bay, in the vicinity of the Kabeljous, Gamtoos, Van Stadens and Maitlands estuaries, which showed high catches of white steenbras (James and Harrison 2010a), and 2) the sandy shoreline to the east of Mossel Bay, in the vicinity of the Hartenbos, Klein Brak and Groot Brak estuaries, which also showed considerable catches of white steenbras (James and Harrison 2008). Alternatively, increasing the protection level to prohibit shore angling and spear fishing in some of the more strategically positioned existing MPAs, such as Goukamma and Amathole MPAs, may be a simpler and financially less costly option to implement.

Overall, it seems that De Hoop MPA contributes disproportionately to white steenbras protection, while the Dwesa-Cwebe MPA and potentially the proposed GAENP MPA (if shore angling is prohibited at least in some areas) are well positioned to contribute to the protection of this species. Conversely, MPAs such as Betty's Bay, Goukamma, Robberg and Amathole, where recreational shore fishing and spear fishing are permitted, are currently contributing little to the overall protection of white steenbras, as the species is rarely captured in the boat-based fishery (Brouwer and Buxton 2002). However, the Amathole and Goukamma MPAs are particularly well-suited for the protection of white steenbras, if the level of protection were increased to prevent shore angling.

9.2.4 Additional management considerations

The results indicate that the range of white steenbras is restricted by the availability of suitable habitat. It is possible that the total available area of suitable habitat for spawning adults amounts to no more than 0.5 km^2 (van Niekerk and Turpie 2011). At the juvenile estuarine life stage the available habitat is limited to a maximum of 146 km^2 of estuarine habitat, and at the sub-adult marine life stage the total available habitat within the core distribution is limited to just over 5 000 km^2. The proportion of marine habitat protected is low, while the proportion of estuarine habitat protected is negligible. Ultimately, the species is limited to a narrow belt of inshore habitat, with little protection, within which it is vulnerable to overexploitation and habitat degradation.

The scoring analyses identified a number of potentially important areas for white steenbras, both in estuaries and the inshore marine environment. While much of this important habitat is not currently

protected, areas potentially suitable for the protection of white steenbras, through strategic estuarine and marine protected areas, have been identified. Closure of the Goukamma Estuary and MPA to fishing is likely to increase the abundance of white steenbras along the south coast. Similarly, the closure of the Amathole MPA to shore fishing would considerably improve the level of protection afforded to white steenbras, particularly considering the high number of estuaries in this region and the close proximity to the spawning grounds in the Transkei. The establishment of new no-take MPAs in St Francis Bay, in the vicinity of the high-scoring Van Stadens and Kabeljous estuaries, and in Mossel Bay, in the vicinity of the Hartenbos, Klein Brak and Groot Brak estuaries, which produced large catches of white steenbras (James and Harrison 2008), would also provide protection in areas shown to be important for the species, particularly considering the low levels of protection currently afforded to these areas. Such combinations of estuarine and associated marine protected areas, if carefully designed and suitably enforced, are likely to contribute significantly to the protection and rehabilitation of the overexploited white steenbras stock.

At the same time, this would contribute to the South African National Protected Area Expansion Strategy (NPAES 2008), which aims to increase the proportion of coastline included within no-take MPAs by about 60 km by 2013, and by an additional 350 km by 2028. The latter is further broken down into an additional roughly 60 km of no-take shoreline within the Agulhas Bioregion (between Cape Point and the Mtamvuna Estuary) by 2028. This could be partly achieved through the proclamation of new MPAs, in areas such as St Francis Bay and Mossel Bay, or by increasing the protection level within existing controlled MPAs to no-take status, such as the Goukamma MPA and Amathole MPA, which would considerably improve the protection of white steenbras along the South African coastline.

Ultimately, the level of protection afforded to fishes within estuarine and marine protected areas is dependent on the degree to which the protection prevents harvesting, and the level of enforcement of regulations. As the majority of white steenbras found in estuaries are juvenile fish below the legal size limit of 600 mm TL, these individuals should be protected in estuaries by virtue of their size, without further estuarine protective legislation required; although the low level of compliance in estuarine fisheries suggests that this is not the case (Cowley *et al*. 2004, Potts *et al*. 2005). Furthermore, striving to protect a target percentage of the coastline of a country is of little use, if some of the most threatened components of the fishery are afforded little protection within these protected areas. It is fair to assume that the suitability for and the level of protection offered by the existing MPAs is similar for other estuarine-dependent coastal fishes, such as the leervis *Lichia amia*.

9.3 National and international conservation categorisation

A specialist review based on an expert group workshop in November 2004 proposed that white steenbras be included on the "*Threatened and Protected Species"* (TOPS) list[4], as defined in the National Environmental Management Biodiversity Act (NEMBA[5]), under the category of "Protected Species[6]" based on its poor stock status and declines in abundance. The species was categorised as "Protected" in the TOPS list published in 2007, along with other fish species, such as the white shark *Carcharodon carcharias*, seventy-four *Polysteganus undulosus*, brindle bass *Epinephelus lanceolatus,* potato bass *Epinephelus tukula* and the coelacanth *Latimeria chalumnae*, all of which appear in the "Prohibited Species" list for recreational angling. White steenbras was later removed[7] from the TOPS list on the basis that it was "already regulated under the Marine Living Resources Act (MLRA[8])". However, the *Guiding notes for Comments*[9] regarding inclusion or removal of a species from the TOPS list states the following:

> *"Marine mammals have not been included here but will automatically be listed in the CITES schedule. These animals are also protected under the Prince Edwards Islands Act and Marine Living Resource Act. Consideration should be given to the need for listing these animals also in the NEMBA schedules".*

This suggests that a species may be simultaneously protected under the MLRA and the NEMBA schedules. Other fish species included in the TOPS list that are also protected under the MLRA were not delisted. The removal of white steenbras on the basis that it was "already regulated under the MLRA" was, therefore, unfounded. Protection under the MLRA does not negate the white steenbras' need for national protection. Furthermore, the species was identified by the Endangered Wildlife Trust (Endangered Wildlife Trust 2002) as one of six estuarine flagship indicator species, highlighting its ecological importance and 'threatened' status. As a result of its current stock status, and the inclusion and subsequent removal from the NEMBA TOPS list, it was felt that classification of the species against both the NEMBA schedule at the national level, and internationally against the *IUCN Red List Categories and Criteria* (IUCN 2001) would be a worthy exercise.

[4] List of critically endangered, endangered, vulnerable and protected species, published in Government Notice No. R150 of 23 February 2007 (Government Gazette No. 29657)
[5] National Environmental Management: Biodiversity Act, 2004 (Act 10 of 2004)
[6] Indigenous species of high conservation value or national importance that require national protection
[7] Reasons for publication of the amendments made on the National Environmental Management Biodiversity Act (Act 10 of 2004): Threatened and Protected Species Regulations
[8] Marine Living Resources Act, Act No. 18 of 1998
[9] Guiding Notes: Comments on proposed Threatened and Protected Species listings for National Environmental: Biodiversity Act, 2004 (Anon. 2004)

9.3.1 NEMBA listing

The listing of a species as threatened or protected, according to the NEMBA requires "a definite need for protection", based on any one of the following:

"*a) a legal obligation in accordance with CITES; or*
b) that the continued survival of the species is threatened; or
c) the threat to continued survival of the species results from one or more of the restricted activities as defined in NEMBA"

Based on the literature and the results of the previous chapters, there is a definite need for protection of white steenbras, under points b and c above. The criteria met by white steenbras to justify its listing as a threatened or protected species under NEMBA, are based on the following considerations as outlined in the Act:

a) "The need for protection should be demonstrable or at least strongly indicative on firm grounds"
White steenbras catches (both commercial and recreational) have declined drastically over the past three to four decades (see Chapter 8), and particularly so over the period of the 1970s and 1980s (Bennett 1993a). Despite regular revisions of the commercial and recreational regulations governing the harvest of white steenbras, the stock of this species continues to decline. Spawner biomass per recruit (SB/R) of white steenbras was estimated at 6% of pristine by 1993 (Bennett 1993a), and by 2000 the stock was considered collapsed (Lamberth and Mann 2000).

b) "The need for protection should be of national importance and require national scope of application"
The endemic white steenbras is heavily targeted by recreational anglers throughout its distributional range, from the Orange River to the Transkei, and until the commercial ban imposition in 2001, by commercial net fisheries in the Western Cape Province. Genetic data (see Chapter 7) showed that the species is characterised by mixing throughout this distributional range. As such, impacts at one end of the distribution have consequent impacts in other areas. The need for protection and management intervention is, therefore, applicable at the national level. Furthermore, not only is the species threatened by oversubscription in the respective fisheries, but low fine values, low rates of prosecution and practically insignificant consequences for illegal activity result in disregard for legislation (Cowley *et al*. 2004).

c) "Justifiability of the need for protection, based on legal obligation, level and nature of threat or Red Data status"

There is no legal obligation to protect the species based on CITES listings, although trends in catch and CPUE, and the low spawner biomass per recruit (SB/R) ratio (Bennett 1993a), suggest that the continued survival of the species is threatened, and the threat to its continued survival results from one or more of the restricted activities as defined in the NEMBA:

> *""restricted activity" –*
>
> *(a) in relation to a specimen of a listed threatened or protected species, means –*
>
> *(i) hunting, catching, capturing or killing any living specimen of a listed threatened or protected species by any means, method or device whatsoever, including searching, pursuing, driving, lying in wait, luring, alluring, discharging a missile or injuring with intent to hunt, catch, capture or kill any such specimen;"*

d) "Resource value whether financial, cultural or other, coupled with extensive use regimes that may threaten the survival of the species or future value benefits derived from the resource"

White steenbras is one of the most targeted species in the recreational shore fishery (Brouwer *et al*. 1997), which was estimated to contribute ZAR 2 167 million annually to the combined gross geographic product of the coastal provinces of South Africa (McGrath *et al*. 1997). The species is also important in the recreational estuarine fishery (Pradervand and Baird 2002), which has an estimated annual value of ZAR 433 million (Lamberth and Turpie 2003), and is targeted by the recently formalised subsistence sector. As a result, the continued survival of the species is threatened. Already, the effects of overfishing have resulted in a ban on the commercial harvest of white steenbras, and the consequent loss of income from this species.

e) "Listing should lead to a legal regime regulating restricting activities as defined in the act"

Compliance with the minimum legal size limit of 60 cm TL is poor (Cowley *et al*. 2004) (suggesting that there is little protection for juvenile fish). Based on evidence of illegal harvesting activity in the Dwesa-Cwebe MPA (Timmermans 2004), which is geographically suitably positioned to protect the species during its spawning aggregation, adult spawners are not well protected by this area closure. Furthermore, angler catches of more than 1 fish per person per day (pppd) are achieved on only 2% of angler outings (Brouwer *et al*. 1997) (suggesting that the current daily bag limit of 1 pppd provides little protection for adult fish). Based on these findings, and the collapsed status of the species stock, the maximum legislation could include the total exclusion of white steenbras from recreational

harvesting, as has recently been proposed for red steenbras *Petrus rupestris* in South Africa (Government Gazette No. 34596). Based on the existence of a single stock (see Chapter 7), of which the adults aggregate in predictable spawning grounds, the minimum legislation to protect white steenbras should include a closed harvest season for this species spanning the spawning season, and improved enforcement within existing MPAs. Furthermore, recent catches of white steenbras, both in estuaries and the surf zone, provided evidence of increases in white steenbras abundance, which should be considered when formulating management decisions.

f) "Enforcement of listing regulatory regimes should be practicable i.e. be readily interpreted by the general public and be implementable by enforcement agencies"

Removal of white steenbras from the recreational/subsistence list would provide simpler enforcement than minimum legal size, maximum daily bag or area closure limits, as any white steenbras retained, regardless of size or location, would be deemed illegal. A closed season for the species, although more difficult to enforce, would be easily interpretable by the resource user.

9.3.2 IUCN listing

White steenbras was first classified according to *IUCN Red List Categories and Criteria: Version 2.3* (IUCN 1994) as "Lower risk: conservation dependent" (Skelton 1996), and therefore did not meet the criteria for Critically Endangered, Endangered or Vulnerable. However, this assessment is now outdated, new data have since become available and major changes have taken place in the fisheries for white steenbras since this assessment.

For the purposes of the current study, white steenbras was classified according to the *IUCN Red List Categories and Criteria: Version 3.1* (IUCN 2001). The categories of Critically Endangered, Endangered and Vulnerable are assessed by five overall criteria, A to E, as follows:

A) Reductions in population size (recent trends in the number of mature individuals)
B) Geographic range (extent of occurrence and/or area of occupancy)
C) Population size dynamics (current number of mature fish and projected or current decline rate)
D) Population size (minimum threshold number of mature individuals)
E) Probability of extinction (quantitative analysis)

Criteria C to E require estimates of the number of adults in the population, which are not available for white steenbras. The species was, therefore, categorised according to criteria A and B.

A. Reductions in population size

i. Recreational competition angling showed a decline of almost 90% in CPUE, from approximately 6 fish.100h^{-1} in 1968, to approximately 0.7 fish.100h^{-1} in 1990 (Bennett 1993a).

ii. The south west coast shore fishery showed a decline in CPUE from approximately 2.29 fish.100h^{-1} from 1971 - 1984 to approximately 0.9 fish.100h^{-1} from 1994 -1996 (Bennett *et al*. 1994, Lamberth 1996).

iii. White steenbras contributed approximately 30% to annual angler catches by mass along the south west coast shore fishery in the 1960s, approximately 8% in 1990-1991 and as little as 0.6% by 1994-1996 (Lamberth 1996).

iv. The beach-seine fishery showed a decline in mean annual reported catch from 23 061 fish.year^{-1} in 1897- 1906, to 3 147 fish.year^{-1} by 1983 – 1991(Bennett 1993a).

v. The SB/R ratio of white steenbras was estimated at 6% of pristine (Bennett 1993a), as early as 1993. Therefore, according to the LMP, the stock is considered collapsed (Griffiths *et al*. 1999).

The results show that white steenbras stocks have declined significantly over the past 100 to 120 years. In the 1980's the purse-seine fishery in the Western Cape was responsible for annual catches of up to 300 mt. It is suggested that this period was largely responsible for the observed declines. It can, therefore, be assumed that the greatest decline has occurred within the past 30 years (i.e. approximately three "generations" as defined in the IUCN criteria (IUCN 2001). A conservative estimate of population decline could be 70%. As such, white steenbras would meet IUCN criterion A, sub-criterion 2 (b) in the Endangered category, based on the SB/R index of abundance:

> *"2. An observed, estimated, inferred or suspected population size reduction of ≥ 50% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.*
>
> *a. An index of abundance appropriate to the taxon"*

The commercial beach-seine and recreational shore fisheries were each responsible for approximately 50% of the total annual catch of white steenbras by mass (Bennett 1993a). Although the legal commercial exploitation of this species has ceased, recreational exploitation continues.

B. Geographic range

The method for calculating the "extent of occurrence" of a species, as defined in the *IUCN Categories and Criteria* (IUCN 2001), was not suitable for white steenbras, due to its continuous narrow inshore distribution. Therefore, the geographic range was determined as the available habitat within the distribution range of the species, including the area from the coastline to the species theoretical maximum depth of 30 m (Bennett 1993b), as estimated in the previous section. Within this range, between the coastline and the 30 m isobath, is an area of approximately 6 600 km^2, representing the maximum available habitat for white steenbras. Catch data suggest that, in reality, the distribution encompasses considerably less area than the available 6 600 km^2.

In addition, the juvenile distribution (as defined for the estuarine scoring system) was shown to span the area from the Berg Estuary to the Mbhanyana Estuary, encompassing 138 estuaries, with a total available surface area of approximately 146 km^2. The fact that juvenile white steenbras have an obligatory estuarine-dependent nursery phase (Wallace *et al*. 1984a, and see Chapter 3) means that all white steenbras must use these approximately 146 km^2 for at least some part of their lives, highlighting the severe bottleneck during the estuarine nursery phase. The bottleneck becomes further restricting, in that 73% of the 138 estuaries within their distribution are either temporarily open/closed estuaries or estuarine lakes, meaning that the mouths of these estuaries are not always open to allow recruitment of fishes. Based on these results, white steenbras meets IUCN criterion B, sub-criterion 1a, b(v) in the Vulnerable category:

> *"1. Extent of occurrence estimated to be less than 20,000 km^2, and estimates indicating at least two of a-c:*
>
> *a. Severely fragmented or known to exist at no more than 10 locations.*
>
> *b. Continuing decline, observed, inferred or projected, in any of the following:*
>
> *(v) number of mature individuals"*

9.3.3 Summary of classifications

White steenbras meets the considerations for inclusion in the Threatened or Protected Species Lists, under the NEMBA classification, and both the Endangered and Vulnerable categories of IUCN classification, based on different criteria (EN A2b; VU B1ab(v)), providing strong evidence that the species is in need of protection at the National level.

An IUCN assessment previously conducted for white steenbras was submitted to IUCN, although the authors still await a response. The IUCN classification, as presented in the current study, was submitted to the South African National Biodiversity Institute, for inclusion in the National Biodiversity Assessment (Sink *et al*. 2011), and will hopefully be considered in the future management decisions regarding white steenbras.

9.4 Conclusion

NEMBA and IUCN assessments are useful for linefish species, to provide relatively simple, objective and rapid assessments of conservation status, to assist with the prioritisation of species for management and conservation actions. Such assessments for linefish species require information on the species distributional range and area use, availability of suitable habitat, indices of stock status or abundance (e.g. S/BR), estimates of population size or trends in abundance, and estimates of exploitation levels in the different fisheries. Research programmes on other coastal fishes should aim to address these in order that suitable information is obtained on which to base management decisions. NEMBA and IUCN classifications of important linefish species could provide simple, yet valuable means to identify research and conservation priorities.

The results of the previous chapter suggest that there is evidence of improved recruitment of white steenbras into estuaries and abundance appears to be improving in certain coastal areas. However, this should not be seen as a stock recovery, and white steenbras still meets certain criteria under the NEMBA *Threatened and Protected Species List* and the Vulnerable and Endangered categories of the IUCN Red List. As such, the species requires improved conservation and management.

Despite the proclamation of a number of MPAs towards the end of the last century, the current MPA network is insufficient for the effective protection of white steenbras. Only 213 km of sandy and mixed sand and rock shoreline within the white steenbras distribution are included within MPA boundaries, and just 14% of the coastline within the species' core distribution is closed to shore angling. In addition, illegal harvesting of white steenbras is known to occur within the Dwesa-Cwebe MPA, which is otherwise ideally situated for the protection of white steenbras during the spawning season. There is also a paucity of estuarine no-take zones within the species core distribution. Improved management measures for the effective conservation of white steenbras should include prevention of all illegal harvesting within MPAs, closure of additional coastal MPAs to shore angling, identification of suitable sandy shoreline areas for the proclamation of new no-take MPAs, and proclamation of no-take EPAs within the white steenbras core distribution.

Chapter 10

General discussion

Effective management of coastal fishery resources is one of the greatest challenges facing marine conservation in South Africa (Attwood and Farquhar 1999). Management actions to ensure the persistence of exploited species require a comprehensive understanding of their biology, ecology, conservation status, threats and use of essential habitats (Whitfield and Cowley 2010). Furthermore, species associated with estuarine environments require management and conservation efforts in river catchments as well as in estuarine and marine environments (Lamberth and Turpie 2003).

White steenbras has historically been one of South Africa's most targeted coastal linefish species. Stock assessment based on per-recruit models showed that the stock of this species was already overexploited by 1993 (Bennett 1993a), although commercial and recreational harvesting was allowed to continue. White steenbras also has a history of failed management measures, with the stock finally deemed collapsed in 2000. Based on the dire need for improved management of white steenbras, and the lack of necessary ecological information on which to base corrective management decisions, it became obvious that a study addressing these management inefficiencies and gaps in the life history of this overexploited species was crucial. Such a study would require a comprehensive assessment of movements, area use and residency within estuaries, movements within the coastal zone (and between estuaries and the coastal zone), and an assessment of the stock delineation of the species. An updated assessment of the stock status, and the current level of protection afforded to the species, would also be necessary, to ensure that the failures of historical management measures could be identified and rectified. This thesis addressed these needs by adopting a multifaceted approach over multiple spatial and temporal scales.

The primary aim of this thesis was to address the gaps in the current understanding of the white steenbras life history and supplement the knowledge on its ecology. The study incorporated conventional dart tagging and acoustic telemetry to assess movement in estuarine and marine environments, and molecular techniques to assess genetic stock structure. Evidence for the strengths of each method employed is provided by the number of studies having successfully used each technique, and for most techniques by the widespread nature of their use, in terms of different ecological environments. An additional component of the study was the assimilation of available fishery-dependent and fishery-independent catch data, to determine the current status of the stock and to assess the effectiveness of past and current management regulations (as the standard stock

assessment models recommended by the Linefish Management Protocol were not suitable). The study also incorporated a derived "conservation planning-, habitat suitability-type" scoring system to assess the level of protection currently afforded to the species and identify the necessary management actions should protection need to be improved. Finally the species was ranked against national and international conservation criteria to provide an objective standardised assessment of the species' conservation status. By filling the knowledge gaps, the thesis has provided much-needed information upon which to base recommendations for corrective management of white steenbras.

10.1 Movement

Prior to this study, published information on white steenbras movement was limited to that inferred from catch data (Bennett 1993a), a preliminary conventional dart tagging study conducted in the Tsitsikamma MPA (Cowley 1999) and single recapture records from the ORI tagging project. Chapters 3 to 5 provided a comprehensive assessment of juvenile white steenbras movement in a range of estuaries through the use of acoustic telemetry, and Chapter 6 assessed fine scale coastal residency, residency within a coastal embayment, longshore dispersal and movements between marine and estuarine environments, through a combination of conventional dart tagging and acoustic telemetry.

10.1.1 Estuarine movement

Acoustic telemetry has rapidly become a preferred tool for assessing movements of fishes in a range of environments, such as coral reefs (Chateau and Wantiez 2008), coastal embayments (Meyer *et al*. 2000) and rivers (Lyons and Lucas 2002). Telemetry has also been extensively applied in estuaries to determine area use (Able and Grothues 2007b), residency (Abecasis and Erzini 2008), habitat utilization (Cowley *et al*. 2008), cyclical movement patterns (Hartill *et al*. 2003), home range dynamics (Taylor *et al*. 2006) and factors affecting movement (Childs *et al*. 2008b). However, most telemetry studies investigate only one or a few of these parameters. Furthermore, Vasconcelos *et al*. (2010) suggested that ecological studies should focus on multiple estuaries to obtain representative results, yet there are few examples in the literature of studies that have applied acoustic telemetry in multiple estuaries. Able and Grothues (2007b) aimed to provide a comprehensive assessment of the estuarine movements of striped bass *Morone saxatilis*, yet the study was based on a single estuary, despite the authors acknowledging inter-estuary variability in estuarine use in this species.

Passive acoustic tracking is commonly used to assess area use and movement patterns of fishes within estuaries, for example snapper *Pagrus auratus* in the Mahurangi Harbour Estuary, New Zealand (Hartill *et al*. 2003), while manual tracking is used to assess home range size and location, for example mulloway *Argyrosomus japonicus* in the Georges River, Australia (Taylor *et al*. 2006). A

combination of manual and passive tracking is advocated for a more comprehensive result (Lembo *et al*. 2002, Afonso *et al*. 2009), although this is not always considered. Sackett *et al*. (2008) highlighted the lack of comprehensive studies on habitat use of economically or ecologically important fish species in estuaries, and combined manual and passive acoustic telemetry, over a range of temporal scales, to provide a more comprehensive assessment of the movement of summer flounder *Paralichthys dentatus*, although this study still only focussed on a single estuary.

The implementation of acoustic telemetry in a range of estuaries in the current study, varying in estuary type, size and the level of freshwater inflow, allowed a comprehensive assessment of white steenbras movements in estuaries. The combination of manual acoustic tracking in three of the estuaries for short-term high-resolution data, and passive acoustic tracking in all four estuaries for long-term continuous data, in the current study, of more than 50 individuals, provided a more holistic approach and a powerful dataset for the assessment of home range size and location, residency, site fidelity, area use patterns, estuarine dependency, cyclical movement patterns, factors affecting distribution and the identification of essential habitat.

Key findings

Manual tracking revealed that home ranges within these estuaries were small, relative to the size of each estuary. Passive tracking results were consistent with those from manual tracking, with area use restricted to certain areas, mostly in the lower reaches, within which most fish were highly resident, often throughout the duration of the respective study (up to 12 months). This high level of residency within estuaries makes the white steenbras highly susceptible to localised depletion; although simultaneously means that the species could be effectively protected during the juvenile estuarine life stage through suitably positioned and enforced estuarine protected areas (EPAs).

A strong diel movement pattern was identified, present in all individuals, as well as a secondary tidal-associated movement exhibited by fewer individuals. The diel pattern is driven by feeding and predator avoidance, with individuals entering the shallow littoral zone at night to feed, and seeking refuge in the deeper channel areas during the daytime. Shallow littoral sand and mudflats therefore represent critical habitats for the species. Losses to these habitats could pose a significant threat.

Environmental variables recorded during tracking appeared to have little influence on the distribution of juvenile white steenbras within the different estuaries. This distribution is more likely driven by the distribution of benthic macroinvertebrate prey organisms and substrate type.

However, hypersalinity (as a result of low freshwater input and excessive freshwater abstraction) represented an obstruction to the movement of fish into the upper reaches of the Kariega Estuary. Estuaries and catchments need to be managed in such a way as to prevent excessive freshwater abstraction, to ensure that sufficient water reaches the estuary to meet its ecological demands.

These studies confirmed that juveniles are resident in and dependent on estuaries for the first three or four years of their lives. The estuarine nursery phase, therefore, represents an ecological bottleneck in the life history of white steenbras, and estuaries should be considered (and managed) as critical to the persistence of this species.

10.1.2 Coastal movement

After having assessed movement during the estuarine life stage, the scale of the study was expanded to assess movements during the late juvenile, sub-adult and adult life stages, in the marine environment. Again, it was necessary to employ the best methods for answering the key questions. The simplicity and affordability of conventional dart tagging is evidenced by the number of studies that have used this method (e.g. Hilborn 1990, Able and Hales 1997, Cowley *et al*. 2002, Brouwer *et al*. 2003, Griffiths and Attwood 2005). Conventional dart tagging has returned valuable information on the residency and migratory patterns of certain species; for example, identification of discrete stocks of silver kob *Argyrosomus inodorus* in the Eastern Cape and Western Cape provinces of South Africa (Griffiths 1997b), as well as the identification of infrequent, large-scale migrations of the usually resident galjoen *Dichistius capensis* (Attwood and Cowley 2005). However, studies employing this technique have often been based on a single tagging locality, short-term sampling or low numbers of fish tagged/recaptured, for example the recapture of 13 red roman *Chrysoblephus laticeps* and one dageraad *C. cristiceps* in the Tsitsikamma MPA from 1985 to 1986 (Buxton and Allen 1989). An exception to this is the study on the movements of galjoen (Attwood and Cowley 2005), based on long-term tagging data (up to fourteen years) from two MPAs and a private recreational catch log, boasting more than 25 000 tagged fish and more than 2 000 recaptures. Aside from the galjoen study, the tagging data presented in the current study represent one of few comprehensive conventional tagging studies on a single fish species throughout its core distributional range.

The current study drew on data from four ongoing long-term coastal fish tagging programmes for the assessment of white steenbras coastal movements. Three of these studies are based in MPAs, where fishing and data-collection are conducted by researchers and anglers trained to handle, tag and accurately measure fish. The locations of the MPAs along the south west coast, south coast and

south east coast span most of the core distribution of white steenbras. These studies provided long-term (in excess of 25 years in De Hoop), high-resolution, reliable data on residency and dispersal of the species. In addition, the Oceanographic Research Institute's National Tagging Project (ORI project), which spans the entire South African coastline, and thus the entire white steenbras distribution, provided a fourth dataset, spanning 27 years. The long-term and widespread nature of the ORI project has resulted in high numbers of fish being tagged and recaptured. Combined, these programmes provided a robust dataset, with almost 6 000 white steenbras tagged and almost 300 recaptured, at a range of localities, allowing a comprehensive assessment of movement. Few studies have been able to draw on such long-term and widespread datasets. This highlights the value of these long-term tagging programmes and their importance in providing data for studies such as this.

Conventional dart tagging has been used in conjunction with acoustic telemetry to assess the movements of numerous fish species, for example *Diplodus sargus* and *Diplodus vulgaris* in the Ria Formosa Lagoon, Portugal (Abecasis *et al*. 2009), common snook *Centropomus undecimalis* in Charlotte Harbour, Florida, and the Gulf of Mexico (Adams *et al*. 2009) and white trevally *Pseudocaranx dentex* in the Faial Channel, Azores Islands (Afonso *et al*. 2009). The combination of the two techniques in the current study provided a more comprehensive assessment of coastal movements during late juvenile, sub-adult and adult life stages.

Key findings

The infrequent and short-duration visits to estuaries and harbours, recorded on the passive acoustic receivers, confirmed that after leaving the estuarine nursery environment, white steenbras lose their dependence on estuaries. The majority of recaptured fish exhibited residency, although some undertook larger-scale movements. The level of residency and the spatial scale of longshore migrations were dependent on fish size (age). Late juveniles (< 450 mm FL) were predominantly resident, with movements on the scale of hundreds of metres. Sub-adults (450 to 600 mm FL) showed greater magnitude movements, although most remained resident. This was confirmed by acoustic telemetry, which showed long-term residency of sub-adults within a coastal embayment. The high level of juvenile and sub-adult residency within the coastal zone makes white steenbras vulnerable to localised depletion, but simultaneously suggests that during these two life stages white steenbras could be successfully protected by means of nearshore and surf-zone MPAs.

The scale of movements was affected by habitat type, with contiguous areas of open sand allowing small-scale movements (1 to 5 km), whereas movements were restricted to small sandy patches in

areas where non-contiguous patches of sand were scattered amongst rock. Therefore, MPAs for the protection of white steenbras should include considerable proportions of contiguous sandy habitat. Movements were little affected by white steenbras density, coastal region or time at liberty.

The majority of adults (> 600 mm FL) undertook considerably greater movements, up to 600 km, and the level of residency declined substantially, indicative of adults participating in coastal migrations. The level of residency, scale and direction of longshore movements changed seasonally, supporting Bennett's (1993b) notion of a spawning migration. The seasonal nature of the adult migratory behaviour suggests that protection by means of a closed season during the spawning period would be a suitable management measure. Further research using long-term acoustic telemetry will be able to provide information on the timing, duration, and spatial extent of the spawning migration.

The almost complete absence of recorded movements between the Western and Eastern Cape provinces (as observed for silver kob *Argyrosomus inodorus*, Griffiths 1997b) suggested the possibility of multiple stocks. There is anecdotal evidence of historically high abundance and a possible west coast population of white steenbras, which was decimated by overfishing (SJ Lamberth, DAFF, pers. comm.). The limited coastal movement could also have been driven by the oceanography in the region, with the predominant inshore current moving westwards along the south west coast, and the inshore counter current moving predominantly eastwards along the south east coast. However, this was likely a result of the low proportion of adult fish recaptured. The possibility of multiple stocks was subsequently refuted through genetic analyses (Chapter 8).

The life history style displayed by white steenbras conforms to Harden Jones' (1968) classical "triangle" pattern. Spawning takes place in the warmer waters of the Transkei, and eggs and larvae disperse south-westwards along the coastline with the Agulhas Current. Recruitment takes place into estuarine nursery grounds, which provide a good source of food, shelter and protection from predators (Bennett and Branch 1990). Juveniles remain resident in estuaries for up to four years, before entering the surf-zone habitat. This shift may be a form of resource-partitioning as food may become limiting in estuaries for larger juveniles. Juveniles remain in the surf zone, which provides a rich source of epibenthic and infaunal prey items, until reaching sexual maturity, after which they too undertake annual migrations to the spawning grounds (Figure 10.1). This strategy is an ecological adaptation to maximise survival and fitness of the species by enhancing the growth rates of the eggs and larvae (Griffiths and Wilke 2002), and increasing dispersal of propagules to allow widespread recruitment into estuaries along the south east and south coasts (Hutchings *et al*. 2002a).

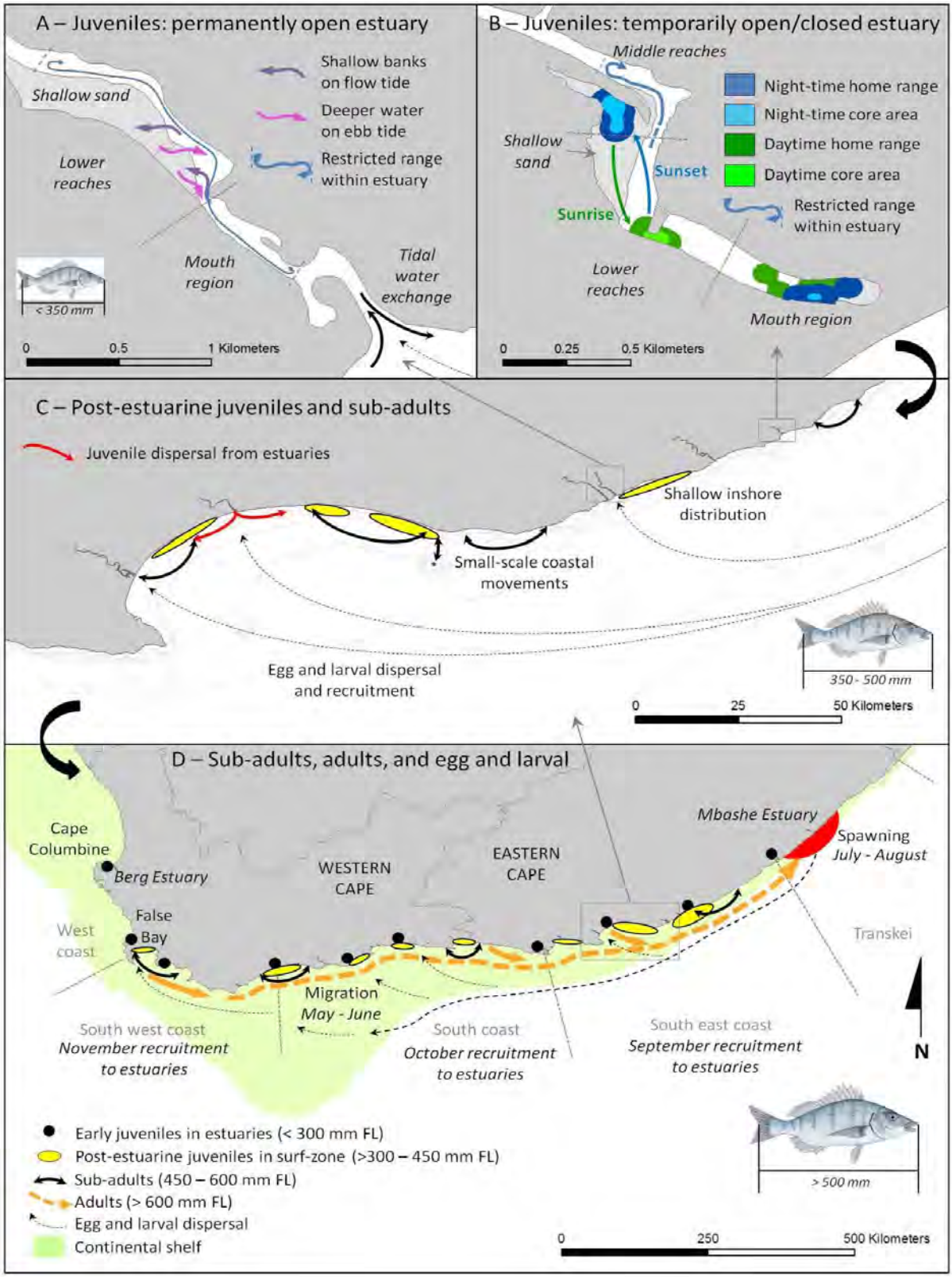

Figure 10.1: Schematic representation of the scale of movement patterns of white steenbras, from the early juvenile estuarine phase in A) open and B) temporarily open/closed estuaries, c) late juvenile and sub-adult surf zone phases, and d) adult migratory phase in the marine environment, assimilated from conventional tagging and acoustic telemetry data and results from the literature

10.2 Genetic stock structure

The combination of four powerful long-term conventional dart tagging datasets and a passive telemetry study contributed significantly towards filling the gaps in the movement at sub-adult and adult life stages. Despite this, however, there was still a lack of empirical evidence connecting the summer aggregation area, along the south west coast, and the spawning grounds in the Transkei. This was addressed at a different scale, which focussed on connectivity among coastal regions at the species level, using genetic analyses.

The ability to detect differentiation at the molecular level that cannot be detected using morphometric, meristic or other stock discrimination techniques, has resulted in a rapid increase in the number of population genetics studies on fishes in recent years. Population genetics studies commonly employ analysis of mitochondrial DNA (mtDNA) or nuclear microsatellites, and numerous studies (which is becoming the norm) have employed both, for example by Teske *et al*. (2011) to assess the genetic stock structure of the red roman, a coastal sparid, in South Africa. Numerous studies have made important genetic discoveries in fishery species, for example, based on mtDNA analysis, significant genetic divergence was identified between South African and Namibian stocks of the deep-water hake *Merluccius paradoxus* (von der Heyden *et al*. 2007), and based on microsatellite analyses, divergence was identified between Baltic Sea and North Sea stocks of turbot *Scophthalmus maximus* (Nielsen *et al*. 2004).

The genetic component of this study represents the first genetic study on white steenbras. Again, it was important to incorporate the best techniques to answer the key questions. The analyses of mitochondrial and microsatellite DNA in conjunction provided the best techniques for detecting large-scale geographic differences or phylogeographic breaks (Teske *et al*. 2011), and subtle population structure (Waples 1998), respectively. Analyses of the genetic material from more than 300 fish, including juveniles and adults, from eight coastal localities spanning the white steenbras core distribution and spanning the major geographic and oceanographic features shown to represent coastal phylogeographic breaks in other species, using mtDNA and 11 polymorphic microsatellite loci, provided a robust assessment.

Key findings

Overall, the observed results and agreement in results between the mitochondrial and nuclear genomes provided robust evidence of a single, well-mixed stock spanning all sample populations, from Langebaan Lagoon to the Transkei. There was no spatial genetic differentiation, no isolation by

distance, and no evidence of localised spawning. There was also no significant genetic differentiation between juvenile and adult samples. Despite evidence of barriers to gene flow in other marine organisms in South Africa, the lack of any clear geographic subdivisions confirms the high level of genetic mixing, indicating that there are few geographic or oceanographic barriers to gene flow in white steenbras. It was concluded that white steenbras exist as a single stock and should be managed as such. Owing to the lack of spatial genetic stock structure, overexploitation or habitat loss in one area could have repercussions throughout the species range, and this should be considered when making management decisions regarding this species.

10.3 Stock, protection and conservation status

The previous stock assessment of white steenbras (Bennett 1993a) is out-dated, and considering the increase in recreational shore fishing effort and other fishery-related changes since its publication it was felt that a reassessment was overdue. However, the standardised stock assessment techniques defined in the South African Linefish Management Protocol (Griffiths *et al*. 1999) are not suited to the available catch data for white steenbras. Therefore, an alternative method for assessing the status of this species was required.

Chapter 8 drew from all sources of available white steenbras catch data, including peer-reviewed and grey literature, long-term and short-term fishery-dependent data for the fisheries targeting white steenbras (roving creel surveys, access point surveys, compulsory commercial catch returns, private catch logs, competition angling data), long-term fishery-independent data (shore-angling research programmes, estuarine netting programmes) and ichthyofaunal surveys, in estuarine and marine environments, conducted throughout the species' core distribution, to elucidate trends in the catch, targeting and CPUE of white steenbras in the different fisheries and protected areas. Few studies have assimilated a dataset from such wide ranging sources, in a benign approach to assess the status of a fish stock. Attwood (2003) adopted a novel approach to assess the impacts of fishing on the stock of galjoen, in South Africa, based on fishery-independent CPUE and conventional tag-recovery data, although this assessment did not include fishery-dependent data. Conversely, other studies have used population modelling or statistical techniques for the analysis of CPUE data from commercial fisheries (e.g. Campbell 2004), although these analyses neglect fishery-independent data and require additional data (such as mortality and catchability estimates) that are not available for many coastal fishery species.

Chapter 9 provided a comprehensive assessment of the protection and conservation status of white steenbras in estuaries and the marine environment, throughout its core distribution. Simpfendorfer *et al*. (2010) assessed the movement patterns and habitat use of smalltooth sawfish *Pristes pectinata* in south west Florida and the Florida Keys, to provide information for improved conservation planning for the species, although this assessment was limited to acoustic telemetry, and only a portion of the species' distribution. The conservation analysis in this thesis drew on the results from the previous chapters, and the approaches of numerous initiatives, such as the National Spatial Biodiversity Assessment 2004 (Lombard *et al*. 2004, Turpie 2004), the National Biodiversity Assessment 2011 (Sink *et al*. 2011, van Niekerk and Turpie 2011), the National Protected Area Expansion Strategy (NPAES 2008) and a number of other studies (e.g. Maree *et al*. 2003, Turpie and Clark 2007), which were aimed at providing information on the status of individual species and habitats, to identify those that are threatened, and to identify suitable areas for protection. This analysis assessed the conservation status of white steenbras, and the availability of and protection afforded to suitable habitats for the species, in estuarine and marine environments, spanning the core distribution of the species, and the geographic range of estuaries used by the juveniles.

Key findings

The analysis of catch data identified severe declines in white steenbras catches made over the latter part of the 20th century, in the recreational and commercial sectors. The results confirmed that both sectors contributed to the overexploitation, with catches made in the recreational shore and commercial beach-seine and purse seine fisheries largely responsible for the stock collapse.

The NEMBA and IUCN classifications provided rapid assessments of the conservation status of white steenbras, highlighting the need for improved management. The IUCN classification, as presented in the current study, was submitted to the South African National Biodiversity Institute, for inclusion in the National Biodiversity Assessment 2011 (Sink *et al*. 2011), and will hopefully be considered in the future management decisions regarding white steenbras. It was determined that white steenbras meets national level criteria for "Threatened or Protected Species", according to criteria defined under the National Environmental Management Biodiversity Act, and the "Endangered" status at the international level, under the criteria of the *IUCN Red List for Threatened Species*.

Traditional management measures, such as minimum sizes and maximum daily bag limits, have failed, largely as a result of a lack of their enforcement (Griffiths 2000). Insufficient sandy shoreline and shoreline of mixed sand and rock within the white steenbras core distribution are protected

within MPAs. Furthermore, insufficient shoreline within existing MPAs is closed to recreational shore angling, and EPAs within the core distribution protect negligible habitat. As such, few MPAs in the existing network provide effective protection for white steenbras. Management regulations governing the harvest of this species should, therefore, be revised, taking into account its "Endangered" status and "Threatened Species" listing. The study identified a number of potentially suitable areas (management units) for additional protection, encompassing coastal sections and associated estuaries that were ranked as having high value to white steenbras.

Despite the failure of traditional management measures and the overexploitation and resultant stock collapse, the analysis of catch data provided some preliminary evidence of improved recruitment of white steenbras into estuaries and abundance appears to be increasing in certain coastal areas. While numerous factors, such as increased awareness and favourable environmental conditions, may have contributed to the recovery, it is most likely due to the series of restrictions pertaining to the commercial harvest of white steenbras during the 1990s, and the ban on the use of vehicles in the coastal zone in 2002. However, this should not be seen as a complete stock recovery.

10.4 Conclusions

The white steenbras is a slow-growing, late-maturing sparid, and thus particularly susceptible to overexploitation, and requires improved management. The different components of this thesis have addressed key ecological questions and contributed substantially towards filling the knowledge gaps in the ecology and life history of this species (Figure 10.2). Estuarine telemetry studies confirmed the high level of dependence on and limited area use within estuaries. Marine movement studies illustrated the high level of residency within the inshore marine environment at the late juvenile and sub-adult life stages as well as large-scale migrations at the adult life stage. Genetic analyses showed a lack of spatial genetic stock structure, and analyses of (and trends in) catch and CPUE highlighted the poor status of the stock. Considering the collapsed state of the stock, it was essential that the thesis address the necessary objectives (including assessment of the stock) in a completely benign manner, thus preventing project-related mortality. The thesis has, therefore, assessed each of Turchin's (1998) functional units, addressing each at appropriate temporal and spatial scales, and reconstructed the life time track, to describe movements throughout the species' life history (Figure 10.2). This information should be used to assist with its management and allow for effective protection and stock rebuilding. Effective management to facilitate the recovery of the white steenbras stock will require a comprehensive management plan that provides appropriate protection throughout the different life stages (Bolden 2000).

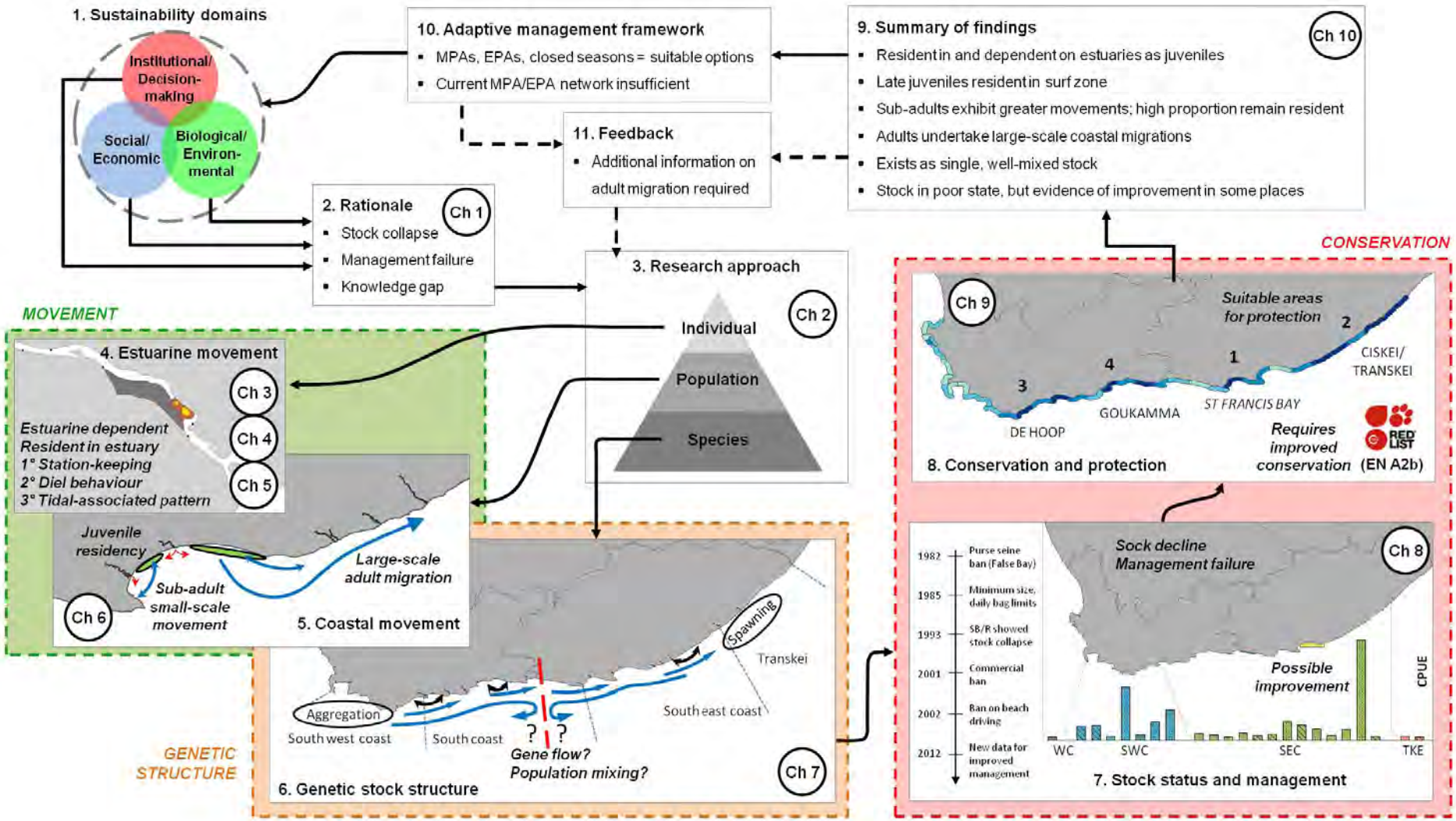

Figure 10.2: Summary flow diagram of the research approach, research themes and key outcomes of the thesis

The highly resident nature of juveniles in estuaries renders them vulnerable to overexploitation in estuaries, making management and conservation of estuaries of paramount importance. Similarly, the tagging data provided evidence of late juvenile and sub-adult residency within the surf zone, highlighting the importance of suitable management to prevent localised depletion in this environment. Therefore, management measures and the design and location of estuarine and marine protected areas in South Africa should be optimised to include the requirements of all life history stages, including estuarine and adjacent coastal environments.

This can be achieved through a combination of well-enforced catch (minimum size and daily bag limits) and effort (area and seasonal closure) restrictions that are realistic for the recreational (and subsistence) anglers (Griffiths 2000). The most suitable management measures appear to be protected area "units", which should encompass EPAs within high-value estuaries and associated MPAs in the adjacent coastline. These would provide protection throughout the juvenile estuarine life stage and the late juvenile and sub-adult surf zone life stages. However, this will require increased proportions of suitable habitat to be protected within EPAs and MPAs, and the prevention of illegal harvesting within protected areas, particularly the Dwesa-Cwebe MPA, in the vicinity of the spawning grounds. A suitably-timed closed season in all areas prior to and during the winter aggregation period (mid-July to the end of August) would provide additional protection for the species, by ensuring that a proportion of adults are allowed to spawn before being captured. Continual monitoring of white steenbras estuarine recruitment and coastal abundance, as well as angler catches, is necessary, to identify trends therein, to assess the effectiveness of contemporary management regulations, such that regulations can be amended accordingly (whether stocks decline further or show improvement).

Despite the information gained through the conventional tagging and acoustic telemetry studies, the migration patterns of adult white steenbras and the exact location and number of spawning grounds remain unknown. The genetic analyses showed that the species exists as a single well-mixed stock, with no localised spawning, which agrees with the sizes and times of estuarine recruitment, confirming that spawning occurs over a single season and likely in a single area, although the migration patterns and extent of the spawning grounds are still not confirmed. Furthermore, whether all mature white steenbras undertake spawning migrations and whether all mature individuals spawn every year also remain unknown. A large-scale acoustic telemetry study has recently been initiated (2011), which will make use of the nationwide array of acoustic receivers that has been deployed as part of the Ocean Tracking Network programme, to provide information on

the spatial extent, timing, route and depth of white steenbras adult migrations, and thus answer some of the final questions regarding the ecology of the species.

The northern boundary of the white steenbras distribution is suggested to be the Orange River (Smith and Smith 1986), which forms the border between South Africa and Namibia, and the genetic analyses in the current study provided strong evidence of a single intermixing population. However, commercial beach-seine data from Namibia include records of white steenbras in the catches. These records may simply be a result of misidentification of the west coast steenbras *L. aureti* or possibly even the sand steenbras *L. mormyrus* (small fish only). Alternatively, the samples could represent an extension of the South African white steenbras *L. lithognathus* stock or a genetically-distinct allopatric *L. lithognathus* stock. Therefore, it is important that samples recorded as white steenbras in Namibia are genetically analysed, to provide information on the genetic stock of origin of these samples, to determine whether the "South African" and "Namibian" stocks need to be managed together, or separately, or whether these simply represent misidentifications.

The failures of historical and current management measures have been identified, and valuable information is provided on which to base decisions for improved management of white steenbras, to facilitate the rehabilitation of the stock of this overexploited, once-prevalent coastal linefish. It is hoped that the results will have application beyond the study species, and that the project provides a framework for similar studies on other estuarine-associated coastal fishes, thereby contributing to the overall improvement of the South African linefish stocks.

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Appendix I

Because time data are of a cyclical nature, it was first necessary to convert times of departure from and arrival at the receiver array to degrees, with a 24-hour cycle being represented as a full circle (360°), and times being presented as angles (i.e. 15° representing 1 hour). Angles (ϕ_i) were calculated from departure and arrival time values (t_i) as follows:

$$\phi_i = \frac{t_i}{24} \times 360 \qquad \text{Eq. 1.}$$

Then, because the arithmetic mean of a set of angles is not applicable, e.g. 270° = -90° (modulo 360°) (Batschelet 1981), angles were converted to vectors (v) with Cartesian coordinates (x, y), where

$$v = \begin{bmatrix} x \\ y \end{bmatrix} = (r, \phi) \qquad \text{Eq. 2,}$$

$$x_i = \cos\phi_i \quad \{i = 1 \ldots n\} \qquad \text{Eq. 3a,}$$

$$y_i = \sin\phi_i \quad \{i = 1 \ldots n\} \qquad \text{Eq. 3b.}$$

and r is vector length, equal to one unit. Because individual time values are un-weighted (i.e. each vector (r, ϕ) represents one time value only), for every individual time value r = 1 (i.e. for time converted to a full circle of 360°). This is termed the unit circle, which has a radius of one unit, and where each r is equal to one unit.

Mean coordinates ($\bar{x}$, $\bar{y}$) for all time values {i = 1... n} were calculated separately for each individual as follows (Batschelet 1981):

$$\bar{x} = \frac{1}{n}\left(\cos\phi_1 + \cos\phi_2 + \ldots + \cos\phi_n\right) \qquad \text{Eq. 4a,}$$

$$\bar{y} = \frac{1}{n}\left(\sin\phi_1 + \sin\phi_2 + \ldots + \sin\phi_n\right) \qquad \text{Eq. 4b.}$$

Mean coordinate values were then converted to a mean angle ($\bar{\phi}$), as follows (Batschelet 1981):

$$\bar{\phi} = \arctan(\bar{y}/\bar{x}) \qquad (\textit{for positive } \bar{x} \textit{ values}) \qquad \text{Eq. 5a,}$$

$$\bar{\phi} = 180° + \arctan(\bar{y}/\bar{x}) \qquad (\textit{for negative } \bar{x} \textit{ values}) \qquad \text{Eq. 5b,}$$

$$\bar{\phi} = 90° \qquad (\text{if } x = 0 \text{ and } y < 0) \qquad \text{Eq. 5c,}$$

$$\bar{\phi} = 270° \qquad (\text{if } x = 0 \text{ and } y > 0) \qquad \text{Eq. 5d,}$$

$$\bar{\phi} = \text{undetermined} \qquad (\text{if } x = 0 \text{ and } y = 0) \qquad \text{Eq. 5e.}$$

When time values are converted to vectors (r, ϕ) and averaged to produce a mean vector ($m = r, \bar{\phi}$), mean vector length (r) represents a measure of the concentration of values around the mean angle (i.e. r no longer has a unit value), and takes a value $0 \leq r \leq 1$ unit), which is calculated as follows (Batschelet 1981):

$$r = \frac{1}{n}\left[\left(\sum \cos\phi_i\right)^2 + \left(\sum \sin\phi_i\right)^2\right] = \left[(\bar{x})^2 + (\bar{y})^2\right]^{1/2} \quad \text{Eq. 6.}$$

The closer the time values (in degrees) are concentrated around the mean angle ($\bar{\phi}$), the closer r will be to 1 (i.e. the full radius of the unit circle), and the more dispersed the values are the more r will tend to 0. Variance around the mean angle ($\bar{\phi}$) is termed angular variance (s^2), or angular deviation (s), and is calculated as follows (Batschelet 1981):

$$s^\circ = \frac{180^\circ}{\pi}\left[2(1-r)\right]^{1/2} \quad \text{Eq. 7.}$$

The Rayleigh test for significance was used to test the null hypothesis that mean angles ($\bar{\phi}$), and thus mean times of departure from and arrival at the array, were not significantly different from random (significance criterion $\alpha = 0.05$). The null hypothesis was rejected where the test statistic $z \geq z_\alpha$, where z is calculated as:

$$z = nr^2 \quad \text{Eq. 8,}$$

where n = sample size, r = mean vector length and z_α was obtained from statistical tables (Batschelet 1981).

Confidence limits around mean estimates were calculated as $\bar{\phi} \pm \delta$, where δ is measured in degrees, and calculated from charts provided in Batschelet (1981). Mean angles ($\bar{\phi}$), angular deviation (s) and confidence limits were then converted from degrees back to time using Eq. 1, by making time (t) the subject of the formula.

Appendix II

DNA extraction

Isolation of genetic material

Genetic material was extracted using the commercially available Wizard® Genomic DNA Purification Kit (Promega, USA), following manufacturer's instructions. A sub-sample was taken from each fish, and dried on a heat block at 55°C for 2 minutes to evaporate the storage ethanol. After drying, 600 µl of a chilled solution containing 120 µl 0.5M EDTA and 500 µl Nuclei Lysis solution® were added, to lyse cells and nuclear membranes. Immediately after adding the EDTA/lysis solution, 15 µl of Proteinase K were added, to denature the DNAses (enzymes) that would otherwise degrade the DNA material, and the reagents were mixed by vortexing. Samples were then incubated on a heat block, for approximately 3 hours at 55°C, during which tubes were mixed by vortexing approximately every 30 minutes. After incubation, 3 µl of RNase solution were added to the solution and the reagents were again mixed by inversion. Samples were further incubated in a water bath for approximately 25 minutes at 37°C, after which they were allowed to cool at room temperature for 7 minutes. Once cooled, 200 µl of Protein Precipitation solution® were added and the samples were vortexed for 20 seconds, and chilled in a freezer at -4°C for 13 minutes.

Removal of cellular debris

Samples were removed from the freezer and centrifuged for 7 minutes at 13 000 rpm, to precipitate the protein. The DNA-containing solution was then carefully pipetted into a 1.5-ml centrifuge tube containing 600 µl of chilled isopropanol, and the DNA material and isopropanol were gently mixed by inversion. The samples were again centrifuged, at 13 000 rpm for 3.5 minutes, and the supernatant was decanted, leaving behind a tight white DNA precipitate.

Elution of purified DNA

DNA was rinsed by adding 600 µl of room-temperature ethanol (70%) to each sample, and the DNA precipitate was gently freed from the sides of tube by inversion. The samples were centrifuged again, at 13 000 rpm for 2.5 minutes, to allow the DNA material to be rinsed with ethanol, which was thereafter aspirated using a pipette. Remaining ethanol was evaporated off, by drying the samples on a heat block at 55°C for 5 minutes with the lids open. DNA material was then rehydrated by adding 100 µl of DNA Rehydration Solution® followed by incubation for 1 hour at 65°C. Extracted products were stored at 4°C until gel electrophoresis or further processing.

Appendix III

MtDNA PCR purification, cycle sequencing and sequencing

PCR Purification

PCR products were purified using the QIAquick PCR Purification Kit (QIAgen). Buffer PB (225 µl) was added to each PCR product (45 µl) and mixed. This solution was then pipetted into a 2-ml QIAquick spin column and centrifuged at 13300 rpm for 60 s, and the flow-through was discarded. Buffer PE (750 µl) was added, the sample was again centrifuged for 60 s and the flow-through discarded, to remove residual ethanol. The QIAqick spin column containing the DNA was placed into a clean 1.5-ml centrifuge tube, 50 µl Buffer EB were added to the QIAquick membrane in the spin column, and the tube was centrifuged for 60 s.

Cycle sequencing

Purified products were cycle sequenced using the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). All reactions were conducted in 20-µl reaction volumes, containing 1 µl DNA template, 0.02mM forward primer (PT), 2 µl BigDye®, 1X buffer-dilution, and made up to volume with distilled water. The cycle sequencing profile consisted of 25 cycles of 96°C for 10 s, 50°C for 5 s, and 60°C for 4 minutes, and hold at 4°C.

Precipitation of cycle-sequenced products

Precipitation of cycle-sequenced products was done using an ethanol/sodium acetate procedure (Sambrook and Russell 2001). Solutions of 1 µl 3M sodium acetate (pH 4.6), 1 µl 0.25M EDTA (pH 8) and 50 µl ethanol (99%) were prepared, to which the cycle sequencing products were added, and mixed thoroughly. Tubes were then vortexed and left at room temperature for 15 minutes, to precipitate the extension products, and subsequently centrifuged at 13 300 rpm for 20 minutes and the supernatant was aspirated and discarded. Pellets were then rinsed with 250 µl ethanol (70%), and vortexed briefly. Tubes were then centrifuged for 13 300 rpm for 5 minutes, and the supernatant was again aspirated and discarded. The precipitated pellet was then dried at 60°C for 5 minutes, and stored in the dark until sequencing.

Sequencing

Samples were sent to a commercial facility (Macrogen Inc., Korea) for sequencing on an ABI 3730 XL Automatic sequencer (Applied Biosystems).