Movement behaviour of three South African inshore sparid species

in rocky intertidal and shallow subtidal habitats

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By

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Abstract

This study investigated the movement behaviour of three inshore South African sparids – blacktail (*Diplodus sargus capensis*), zebra (*Diplodus cervinus hottentotus*) and white musselcracker (*Sparodon durbanensis*), popular inshore fishery species caught in appreciable numbers along much of the South African coast. The first study component examined movements of juveniles in a rocky intertidal nursery area at Schoenmakerskop near Port Elizabeth. Juveniles in a single gully were tagged with Visible Implant Elastomer (VIE) and resighted at the study site on snorkelling gear over a seven-month period. Tagged zebra and musselcracker displayed limited movement between potential low tide refuges, being observed repeatedly in the same gully over the full duration of the study. However, blacktail displayed greater movements and were seen infrequently in the later period of the study, probably having undergone an ontogenetic habitat shift to subtidal areas. There was evidence that blacktail maintain use of their intertidal nursery over high tide, during which the other two species moved into shallower areas adjacent to their low tide refuge.

The results of three national tagging programs were analysed to determine the movement patterns of adolescent and adult fishes. The coast-wide ORI-WWF National Voluntary Tagging Program and two dedicated research programs in marine protected areas (MPAs) at De Hoop MPA and Tsitsikamma National Park (TNP) recorded few large-scale movements of tagged adult blacktail, zebra and juvenile musselcracker. High spatial-resolution data from the TNP suggested movements were usually on scales far smaller than one km. Together with long periods at liberty for many recaptured individuals, this suggests these fishes are long-term residents of small home range areas. However, tagged musselcracker over 600 mm fork-length (adults) were observed to make large-scale movements, including some in excess of 800 km from Eastern Cape to KwaZulu-Natal waters. Predominantly eastward movements of adults recaptured during the spawning season indicate seasonal spawning migrations that occur in different regions of the coast. These enable the use of prevailing oceanographic currents to disperse eggs and larvae to suitable rocky nursery habitat.

The third component of this study made use of high-resolution data on the temporal and spatial distribution of catches by scientific angling in the TNP to examine the daily activity patterns of the study species in relation to diel and tidal cycles, and habitat use. Blacktail capture probability was correlated with the diurnal light cycle, with peaks close to twilight suggesting elevated crepuscular foraging activity. Catches of blacktail, zebra and small musselcracker were correlated with the tidal cycle, foraging peaking over high tide periods. All three species used shallow inshore habitats extensively for foraging, blacktail showing a preference for sandy areas, while zebra and small musselcracker preferred shallow reef. Capture probability of larger musselcracker, however, was unrelated to habitat, possibly evidence of increasing area and habitat use with an ontogenetic change in diet.

The lifetime movement patterns of these three species are discussed in relation to conservation measures and their management in South African fisheries. Restricted movement throughout post-settlement life for blacktail and zebra, and during the juvenile phase for musselcracker, makes local populations vulnerable to overexploitation. At present, MPAs probably play an important role in protecting local blacktail and zebra populations from overexploitation, and limited post-settlement movements mean the degree of larval dispersal between protected and adjacent areas will likely determine the effectiveness of MPAs in enhancing fisheries for these species. By contrast, MPAs likely provide recruits to fisheries for musselcracker during ontogenetic movements and dispersal from MPAs during spawning migrations. MPAs only offer partial protection to adult musselcracker populations in the spawning season, but this could nevertheless be significant under high levels of exploitation.

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Chapter 1 - Introduction

1.1   Fish movement behaviour

Organism abundance changes in space and time with the addition of new individuals through reproduction, loss due to death, and with displacement (movement).   Individual and population movements are thus an important component of their ecology and how they interact with their environment. Fish are generally highly mobile animals capable of a wide range of movement behaviours. They are important members of any aquatic ecosystem, as consumers and/or food sources at all levels of food webs (Power 1990, Polunin & Pinnegar 2002), and agents of environmental change. This can be through physical alteration of their environment (e.g. creation of coral sand by parrotfish (Scaridae; Ogden & Buckman 1973) or through energy transfer between areas or habitats (e.g. ontogenetic shifts between distinct habitats; Nagelkerken & Van Der Velde 2006). Fish movements govern where and when these processes occur.

Fish movements can be described at various levels, ranging from individuals of solitary species, groups of gregarious species to functional groups at the population level that include successive ontogenetic life-history stages, stocks separated on spatial or temporal scales, or entire populations. At a particular level, movements may be characterised in terms of their direction, distance, duration and purpose. These can be on scales ranging from small daily movements within a restricted home range or over successive tidal cycles, to large seasonal inter-ocean migrations or nomadic wandering of individuals. Directed movements of fish are determined by one or more of the following over a range of temporal scales: (i) food availability, (ii) habitat providing suitable shelter, (iii) reproductive activities, (iv) physiologically desirable conditions, (v) evasion of predators or competitors, or (vi) defence of territory. Dingle (1996), describes movement behaviour of organisms in general in his "taxonomy of movement", which dichotomises as three categories, namely (i) home range or resource directed movements (stasis, station keeping and ranging), (ii) movement not directly responsive to home range or resources (migration) and (iii) movement not under control of the organism (accidental displacement).

Knowledge of the movements of exploited fishery resources is essential for effective fisheries management. However, management actions often fail to consider a stock's location both in space and time, and how this may affect its exploitation. Many exploited marine species occupy spatially distinct areas at different stages of their lives (e.g. nursery areas or spawning sites) that may result in greater vulnerability during these periods and require specific management actions. Large movements of highly mobile species may take them successively into areas under separate governance, necessitating transboundary cooperation between nations for their effective management. Conversely, restricted movements of certain species require management on more localised, area-specific scales. Additionally, movements of many fishes impact populations of other species, affecting their physical distribution and abundance and/or recruitment success (Connell 1998, Koster & Mollman 2000), and thus need to be considered in holistic management actions. Knowledge of fish movements is especially important to the use of no-take Marine Protected Areas (MPAs) implemented to conserve ecosystem integrity, populations of particular species or to enhance fisheries (Kramer & Chapman 1999). Fish cannot be adequately protected if they do not spend sufficient time within a MPA, determined by their movement patterns, to reduce their chances of capture. Conversely, movement across a MPA boundary is required for significant enhancement of adjacent exploited populations via larval export, ontogenetic shifts or density-dependent movements from protected populations (Gell & Roberts 2003).

1.2   Management of South African linefisheries

South Africa has a history of overexploitation of populations of marine linefish species targeted in commercial and recreational fisheries. Output (bag- and size-limits) and input (closed seasons) control measures are deemed ineffective because of poor enforcement, or the regulations themselves not being limiting (Griffiths *et al.* 1999). The South African Marine Living Resources Act of 1998 called for long-term management plans for all exploited species, including Operational Management Plans (OMPs) specifying a set of clearly defined decision rules for management action to be taken if necessary upon assessment of the resource. The resultant Linefish Management Protocol (LMP) for each species defines (i) the type of data required to assess the stock, (ii) the quantitative approach to be utilised, (iii) appropriate biological reference points, (iv) long-term goals for the stock and (v) management actions to be taken to achieve these goals (Griffiths *et al.* 1999). Whilst output controls are still important in LMPs, the use of no-take MPAs is viewed as an effective complimentary input management measure.

Currently, MPAs are probably the most effective form of management for long-lived species exposed to intensive pressure by recreational fishermen along the South African coast (Attwood *et al.* 1997a,b). In South Africa, where the rate of human-on-human crime and poverty-alleviation are a major focus of government resource allocation, enforcement of fisheries regulations is under-funded and under-staffed. Prosecution rates in courts already full to capacity and fines for transgressors are insufficient to promote adherence to regulations. Consequently, MPAs may be particularly effective in this situation as it is easier to control fishing activities through area closure than monitoring compliance of individual anglers.

1.3   Study species

Blacktail (*Diplodus sargus capensis*), zebra (*Diplodus cervinus hottentotus*) and white musselcracker (*Sparodon durbanensis*) are three sympatric South African sparid (seabream) species that are major constituents of South Africa's temperate and subtropical inshore marine ichthyofauna. Typical of many South African sparids, the study species are long-lived (maximum age over 20 years), are confined to shallow inshore habitats and exploited throughout their distribution along the South African coast (Buxton & Clarke 1991, Mann & Buxton 1997). While subsistence and recreational fishermen target blacktail and zebra mainly as food, white musselcracker also constitutes an important trophy target due to its large size, particularly among spearfishermen (Mann *et al.* 1997). Although commonly captured in many regions of the South African coast, catches of blacktail and musselcracker have reportedly declined in certain areas (Booth 2000, Mann 2000c, Brouwer & Buxton 2002). Aspects of the basic biology of the three study species and further details on their utilisation in South African fisheries are summarised below.

1.3.1   Blacktail

Blacktail (*Diplodus sargus capensis*) occurs along the entire South African coast and extralimitally to northern Namibia and Mozambique (Heemstra & Heemstra 2004), and is considered a subspecies of *D. sargus*, which occurs as several subspecies from the Mediterranean around Africa to the Red Sea and Middle-East (www.fishbase.org). There appears to be some taxonomic confusion as regards its status, Heemstra & Heemstra (2004) referring to the South African form as *D. capensis* and mentioning possible differentiation into further species at the western and eastern edges of its Southern African distribution.

It seems pertinent to regard the Southern African subspecies (or species) as a population distinct from the other subspecies occurring further north on both African shores and in the Mediterranean. Blacktail attain a maximum size of 450 mm FL, mass of 3 kg and age of over 20 years (Mann & Buxton 1997) and are a ubiquitous species generally found in shallow, inshore marine habitats less than 15 metres deep (Mann 1992), although reportedly occurring to depths of 40 metres (Heemstra & Heemstra 2004). Postflexion larval blacktail recruit into sheltered rocky bays in large numbers (Strydom 2008) and developing juveniles utilise shallow marine environments such as intertidal rockpools and gullies (Beckley 1982, 1985, Smale & Buxton 1989), sandy beach surf zones (Lasiak 1981, Bennett 1989) and the lower reaches of estuaries (Beckley 1983, Ter Morshuisen & Whitfield 1994) as nursery areas. Larger fish occur in loosely aggregated shoals over most rocky bottom habitats, but are also found in sandy areas (Lasiak 1984, Clark *et al.* 1996), particularly along the sand-reef interface (R. Bennett & K. Smith, Department of Ichthyology & Fisheries Science, Rhodes University, pers. comm.). They also enter estuaries and rocky intertidal gullies and are associated with areas exposed to high wave action and turbulence in the breaker-zone, their strong swimming ability allowing negotiation of the rough conditions.

Juvenile blacktail are exclusively carnivorous but a change in dentition with age results in more vegetable matter being ingested (Christensen 1978). Adults consume a variety of invertebrate prey, as well as macrophytes ingested incidentally to epiphytic diatoms (Joubert & Hanekom 1980, Coetzee 1986, Mann & Buxton 1992). Blacktail are partial protandrous hermaphrodites, females developing either directly from the immature phase or alternatively from functional males – but not all male individuals change sex (Mann 1992, Mann & Buxton 1998). Fifty percent of juveniles three years old (approximately 210 mm FL in length) are sexually mature (Mann & Buxton 1998) and the spawning season varies slightly in timing and duration on different sections of the South African coast. Mann & Buxton (1998) reported the spawning season runs from August to March on the Tsitsikamma coast, while Coetzee (1986) suggested it occurs from October to December further east off St Croix Island in Algoa Bay, and Joubert (1981) found spawning from July to September off KwaZulu-Natal. Blacktail is one of the most regularly caught fish species along the South African coast. In most studies of marine recreational shore anglers' catches made in South Africa to date (apart from in northern KwaZulu-Natal) blacktail has occurred in the top five species in terms of abundance (e.g. Coetzee *et al.* 1989, Bennett 1991, Brouwer *et al.* 1997).

It is similarly in the top two species by number caught by scientific shore angling in both the De Hoop Marine Protected Area and Tsitsikamma National Park (Bennett & Attwood 1991, 1993, Cowley *et al.* 2002). Larger individuals are also occasionally shot by spearfishermen (van der Elst 1990).

1.3.2 Zebra

Zebra (*Diplodus cervinus hottentotus*) belongs to the same genus as blacktail, and is in certain respects similar to it. It has a similar Southern African distribution to blacktail and the local subspecies is also regarded as distinct. Elsewhere, other *D. cervinus* subspecies occur from the Mediterranean Sea to north of Southern Africa (www.fishbase.org). Heemstra and Heemstra (2004) refer to the southern African form as *D. hottentotus*, and it could in future be regarded as a separate species. Zebra are found in a number of shallow nearshore marine habitats along the South African coast, although they range to greater depths than blacktail, commonly occuring to a depth of 25 metres (Mann 1992) and reaching depths in excess of 100 metres in certain areas (Heemstra & Heemstra 2004). Adult zebra attain a maximum length of about 590 mm FL, mass of 6 kg and age of 33 years (Mann & Buxton 1997). Juveniles are recorded from shallow *Zostera* (seagrass) beds and other habitat in estuaries, but their major nursery area is intertidal rockpools and gullies (Beckley 1982, 1985, Smale & Buxton 1989). Although subadults regularly enter the lower reaches of estuaries (Whitfield 1998), adults appear confined to rocky reef habitats, where larger individuals are associated with high relief and rugosity (Mann 1992, Smith 2005). Adults are solitary, while subadults and juveniles are commonly found together in small groups or associated with groups of blacktail (Mann 1992).

Juvenile zebra have a carnivorous diet of copepods and other small animals similar to that of juvenile blacktail (Christensen 1978, Mann & Buxton 1992) but with ontogenetic development the diet becomes more specialised and polychaete worms become the dominant prey, especially those found in association with stands of redbait (*Pyura stolonifera*) (Mann 1992). Zebra spawn in summer, with reproductively active individuals recorded from August to December on the Tsitsikamma coast (Mann & Buxton 1998). Unlike blacktail, this species is regarded as a functional gonochorist (rudimentary hermaphrodite capable of developing into either sex from the immature state), and assumed to spawn as pairs matched in size in spawning aggregations over shallow reefs throughout its distribution (Mann 2000b).

Zebra contribute far less to catches of South African recreational fishermen than blacktail, but catches are regular and the species can form a significant proportion of catches in many areas (Bennett & Attwood 1993). It makes good eating and, reaching a larger size than blacktail, is also targeted in some areas by spearfishermen (van der Elst 1990).

1.3.3 White musselcracker

White musselcracker (*Sparodon durbanensis*), hereafter referred to as musselcracker, is an endemic South African species occurring from St Helena Bay to central KwaZulu-Natal (Booth 2000) in shallow inshore habitats. In contrast to the *Diplodus* species, musselcracker can attain a length greater than 1000 mm FL, and mass of 23.5 kg (Buxton & Clarke 1991). Juvenile musselcracker utilise intertidal rockpools (Beckley 1982, 1985, 1988) and gullies (Smale & Buxton 1989) as nursery areas and larger juveniles and subadults are found over shallow reefs (Buxton & Clarke 1991). Juveniles are usually found singly, but may also associate as small conspecific groups (pers. obs.). This appears to be carried through into adult life with adults occurring as single individuals or in small groups for most of the year (Schoeman & Schoeman 1990). Although recorded from the lower reaches of some estuaries, adult fish are usually associated with rocky substrates (Heemstra & Heemstra 2004) where their favoured prey occurs. They are commonly found in exposed areas, even in shallow water in the surf zone, but also occur to depths of at least 30m (Clarke 1988). Juveniles prey on a variety of small intertidal organisms (Buxton & Clarke 1991), but from around 400 mm FL they possess specialised crushing dentition and powerful jaws enabling consumption of a wide variety of larger invertebrate prey such as molluscs, gastropods and the ascidian species redbait (*Pyura stolonifera*).

Like zebra, musselcracker are also rudimentary hermaphrodites. During the spawning season in spring and summer (September to January; Buxton & Clarke 1991) aggregations of mature individuals occur (Clarke 1988, van Rooyen 1988). These aggregations are suggested to be involved in reproductive activity (Schoeman, publishing date unknown), with a spawning migration to KwaZulu-Natal reportedly taking place (Booth 2000). Musselcracker are an important component of South African recreational fisheries, their large size and powerful 'fighting ability' making them a desirable trophy target for shore anglers and spearfishermen alike. Angler surveys have shown musselcracker to be a major target of fishermen in some regions (Mackenzie 2005) and during particular periods (Clarke & Buxton 1989).

Whilst this species is less important numerically than species such as blacktail and galjoen (*Dichistius capensis*), in terms of biomass it contributes disproportionately to overall catches due to its larger size (e.g. Pradervand & Hiseman 2006). There is some evidence to suggest a decline in catches from historical levels in the Port Elizabeth area (Brouwer & Buxton 2002) and historical heavy targeting on breeding aggregations appears to have reduced catches at well-known musselcracker angling localities such as Mossel Bay substantially (Schoeman, publishing date unknown).

1.4   Purpose of the present study

The aim of this study was to describe movement patterns of blacktail, zebra and musselcracker on the South African coast, while its specific objectives were as follows:

i.   Investigate how movement patterns change with ontogeny by quantifying these for juvenile and adult fishes;

ii.   Describe movement patterns of individuals along the South African coast at small (local) and large (regional) spatial scales;

iii.   Examine movements related to daily (diel and tidal foraging/activity patterns) and seasonal (reproductive activity) cycles if apparent;

iv.   Utilise knowledge of post-settlement movement patterns to make recommendations for management of these species and future research directions.

1.5   Thesis outline

Contents of the various chapters in this thesis are outlined below:

- Chapter 1 describes fish movement behaviour in general and its importance from an ecological and fisheries management perspective. The three study species are introduced, their exploitation in South African fisheries discussed and the study aims stated.

- Chapter 2 provides a general introduction to the methods of studying marine fish movement behaviour and describes the study sites relating to the data chapters that follow, including a description of South African nearshore marine environments and general oceanographic patterns.

- Chapter 3 describes movement behaviour of juveniles of the three study species in rocky intertidal nursery habitat at Schoenmakerskop on the Eastern Cape coast. Results are presented for individuals tagged and resighted at the study site over a seven-month period.

- Chapter 4 describes subadult and adult fish movements recorded by long-term tagging studies in two South African MPAs – the Tsitsikamma National Park and De Hoop MPA, as well as from the ORI-WWF National Voluntary Tagging Program. The two MPA studies provide recapture and movement data at a fine- and medium-scale resolution, respectively, whilst the ORI dataset provides information on a coast-wide scale.

- Chapter 5 analyses scientific angling catches from long-term monitoring of protected populations of the study species in the TNP to examine habitat use and associated diel and tidally-related activity patterns.

- Chapter 6 integrates results and conclusions from Chapters 3-5 in terms of the management of the study species from a conservation and fisheries management perspective. Future research related to their movement behaviour and requiring further study is discussed.

Chapter 2 – Methods and study sites

2.1   Methods for the study of fish movement behaviour

Aquatic environments, especially marine habitats, present numerous challenges to the study of fish movement behaviour due to the impracticalities of observing fish underwater. Technological advances (e.g. SCUBA and Remotely Operated Vehicles) have increased potential observation times, but these are still far less than in movement studies on terrestrial animals. Traditionally, knowledge of marine fish movement patterns has been gathered from observations of fish above the sea surface, such as capture localities in fishing activities (e.g. Biden 1948). Movement patterns are inferred from the variation in catches over spatial and temporal scales. Traditional knowledge of these has been transferred between generations of fishermen and forms the basis for successful targeting of many exploited species. To accurately quantify movement patterns, however, numerous scientific studies have been conducted on marine fishes. These generally utilise some method of discriminating between individuals or groups, through the application of identifiable marks (tags) recognisable upon recovery of the fish (e.g. Moran *et al.* 2003, Brouwer *et al.* 2003). Movements of identifiable individuals between successive recoveries are thus revealed; with data on a sufficient number of individuals inferences can be made about movement behaviour at the population level. Simple external tags identifiable above water (i.e. upon capture) are currently the predominant tagging method in fish movement studies, as their application and detection is easy and inexpensive, allowing unique tagging of many individuals.

Numerous forms of external tags exist for fishes (Emery & Wydowski 1987), but normally consist of a subdermally attached tag protruding from the body of the fish and bearing a unique identification code (e.g. plastic 'dart' or 'spaghetti' tags). Because they are by design easily recognisable and interpretable, external tags allow reporting by the fishery and public of tag recoveries, resulting in potentially greater geographical coverage. However, tag loss (Fabrizio *et al.* 1999), potential negative effects on fish health and behaviour (Thorstad *et al.* 2004, Griffiths & Attwood 2005) and high levels of recovery under-reporting (Matlock 1981, Brouwer 1997) may counteract these benefits. Alternatives to classic tag-release-recapture techniques make repeated observations of tagged individuals' positions to study short-term movement patterns. Unique external marks identify individuals to underwater observers, but use is limited by tag loss, practical constraints on observation time and observer-effected fish behaviour (Kulbicki 1998).

Nevertheless, a number of studies have successfully utilised methods such as freeze-branding (Zeller & Russ 2000) and subdermally-placed dyes (Bell & Kramer 2000) or polymers (Visible Implant Elastomer tagging - e.g. Annese & Kingsford 2005) to identify individual fishes in order to study their movements. The latter two methods combine advantages of external tagging methods (ease of detection) with those of internal tagging systems (improved tag retention – see below), as they are placed wholly within the fish's body but remain visible to observers. Internal tags generally have superior tag retention rates to external tags because they are protected from the external environment, but visual tag recognition is usually impossible because the tag is obscured by body tissue. Examples include passive integrated transponder- (Bruyndoncx et al. 2002) and coded wire tags (Buckley 1994), which currently require expensive and/or cumbersome equipment for tag identification.

A number of studies have, however, made use of internal tags in the marine environment to remotely track movements of fish through acoustic telemetry (e.g. Zeller 1997, Eristhee & Oxenford 2001, Kaunda-Arara & Rose 2004). The implanted acoustic tag emits a signal of particular frequency identifying the fish and its position, determined by a hydrophone operated from above or beneath the water surface. Permanent 'listening' stations that detect tagged individuals passing within range can also record positions remotely and arrays of these can be established in particular layouts depending on the location and type of movement behaviour under study (Kerwath et al. 2007b, Childs et al. 2008). However, telemetry is prohibitively expensive for many studies and sea conditions can affect the accuracy of measurements and practicality of data collection, and expose sensitive equipment to environmental damage or destruction. Tag battery life and practical survey area size also limit telemetry studies. Recent technological advances have resulted in the development and use of archival data-storage tags (ADSTs) in movement studies on large marine animals, including some fish species (Domeier et al. 2005, Neuenfeldt et al. 2007). Environmental sensors in ADSTs measure ambient conditions at preset time intervals and write these to tag memory. Recorded temperature, depth and timing of light intensity changes (as a proxy for latitude and longitude) experienced by the fish over time enable its movements to be calculated. Data are obtained either upon recovery of the tag or uploading of stored data from the tag to a satellite when it is exposed above water. This occurs when the fish surfaces, or tags can be programmed to detach and float to the surface after a predetermined period (pop-up satellite tags; Gunn & Block 2001).

Archival systems are presently limited to large-bodied fishes due to tag size, and are expensive, but offer high-quality data for highly mobile fishes over scales beyond the scope of telemetry studies.

2.2 General methods and geographic location of the present study

None of the aforementioned methods is all-encompassing in terms of data collected and practical feasibility, and use of a particular technique is normally a trade-off between data requirements and practical or financial constraints.

Historically, long-term data sets on fish movements have utilised simple external tags, which even under low recovery rates provide data on many individuals because of the sheer numbers tagged and available for recapture. The Oceanographic Research Institute's (ORI) National Voluntary Tagging Program (van der Elst & Bullen 1993) has recorded movements of fishes along the South African coastline since the early 1980's. This project and two subsidiary scientific tagging programs in South African MPAs utilise relatively low-cost tags, applied by volunteers and researchers and recovered over a wide geographic area, to gather data for many fish species, including the three that are the focus of the present study. Recapture data on subadult and adult fishes tagged in the three programs were analysed, and a dedicated tagging study undertaken to examine movements of juvenile fishes in intertidal nursery areas. Below, an introduction to the South African coastal environment as a general background to later discussion, as well as descriptions of the study sites where the various study components were located, is presented. Details on research methods employed for each component are provided in the individual data chapters.

2.2.1 South African coastal marine environments and oceanography

South Africa has a coastline bordered by both the Atlantic and Indian Oceans, extending approximately 3500 km (Figure 2.1). Two major current systems, the Benguela and Agulhas Currents, are located off the west and east coasts, respectively. The Benguela Current flows north along the continental land mass under the control of wind-driven processes (Kamstra 1985) and is characterised by cold, nutrient-rich upwelling that supports high levels of primary production in the nearshore environment (Branch & Branch 1981). In contrast, the Agulhas Current flows southeast along South Africa's east coast from north of the subcontinent, being driven by the Earth's rotation and the associated Coriolis Force as Indian Ocean water meets the continental landmass on the western edge of its basin.

It is thus typical of a Western Boundary Current system (Lutjeharms 2006). It transports warm tropical water southwards, and even though located some distance offshore has a major influence on the nearshore environment of the South African east coast, whose waters are warmer relative to those of similar latitude on the west coast.
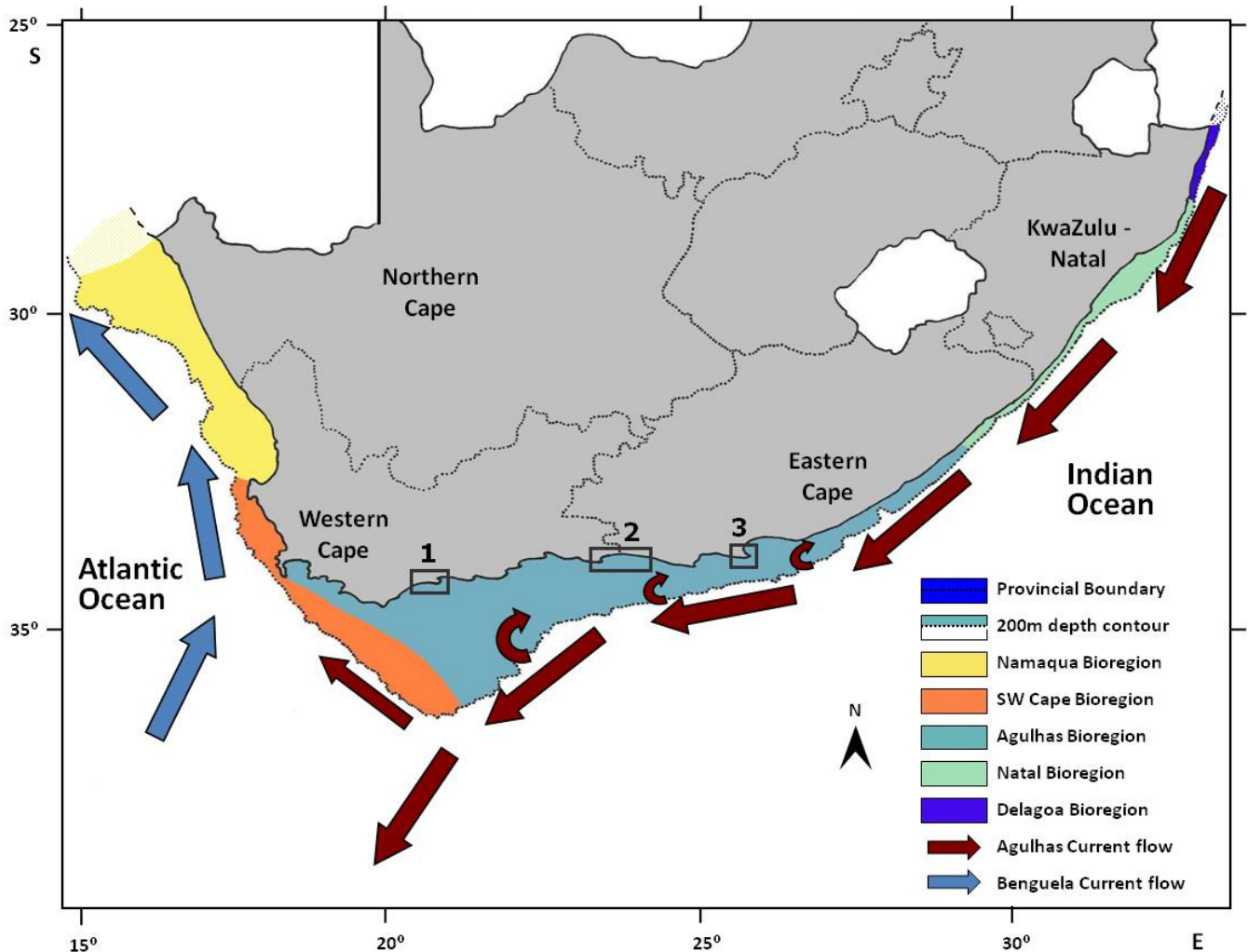
Figure 2.1. Map of South Africa, showing the locations of major current systems and associated inshore bioregions on the continental shelf.

The exact location where the two current systems converge varies, but generally the coast west of Cape Point is regarded as Benguela-dominated and the coast east of Cape Agulhas as Agulhas-dominated, with the area between impacted by both. As water temperature is a major factor in the distribution of marine organisms (e.g. Rogers & Millner 1996), the contrasting temperature regimes of the two currents significantly affect nearshore marine ecosystems, with different species assemblages corresponding to prevailing temperatures in areas under their influence.

As mentioned above, the Benguela current provides cold, nutrient-rich water to the adjacent nearshore environment and this supports highly productive foodwebs off the west coast, characterised by high biomass but relatively few species (Branch & Branch 1981).

Off the northern section of the east coast, the continental shelf is only a few kilometres in width (Lutjeharms 2006) and the adjacent Agulhas Current exerts an overriding influence on the nearshore environment, warm waters allowing the formation of diverse tropical coral reef ecosystems in the northern stretches and subtropical reef systems further south. South of East London (33º2'S, 27º55'E), however, the continental shelf width broadens, reducing the effect of the current on nearshore waters. Here, more temperate ecosystems are found. South and west of Algoa Bay, the continental shelf is wide and shallow in the area known as the Agulhas Banks, the shelf break lying 240 km from shore at its widest extent (Lutjeharms 2006). The Agulhas Current flow tracks the path of the shelf break away from shore and has even less influence on the nearshore environment along this stretch of the coast, here more strongly influenced by coastline topography and resulting features such as localised wind-driven upwelling (Schumann 1999) and coastal trapped waves (Schumann & Brink 1990). This temperate region is characterised by high levels of endemicity for many taxa (Turpie *et al.* 2000).

South African marine areas have been categorised as comprising biogeographic provinces (or bioregions) based on their characteristic faunal communities, which can be seen to generally follow the pattern of influence of the Benguela and Agulhas currents (Sink *et al.* 2004, Figure 2.1). Associated oceanographic conditions not only shape faunal distributions, but also in many cases the reproductive strategies of particular species. The proximity to shore of southward-moving Agulhas Current flow drives inshore current patterns on the east coast, resulting in the early life-history stages of marine organisms (eggs and planktonic larvae) potentially being transported great distances from their origin. This has shaped the reproductive strategies of many coastal species reproducing in this region; spawning takes place 'upstream' of juvenile nursery areas and adult habitat on the east coast, with the southward transport of developing eggs and larvae to these being facilitated by southwesterly inshore currents. Fish species known to make use of this strategy include the geelbek (*Atractoscion aequidens*), red steenbras (*Petrus rupestris*) and white steenbras (*Lithognathus lithognathus*); Hutchings *et al.* 2002).

2.3 Study components and sites

Juvenile movements were examined in a dedicated field study at Schoenmakerskop, near Port Elizabeth in the Eastern Cape (Figure 2.2), while existing long-term tagging datasets were analysed to quantify adult movements. The latter included dedicated tagging programs located in two MPAs on the South African east coast, namely De Hoop MPA and Tsitsikamma National Park (Figure 2.2).
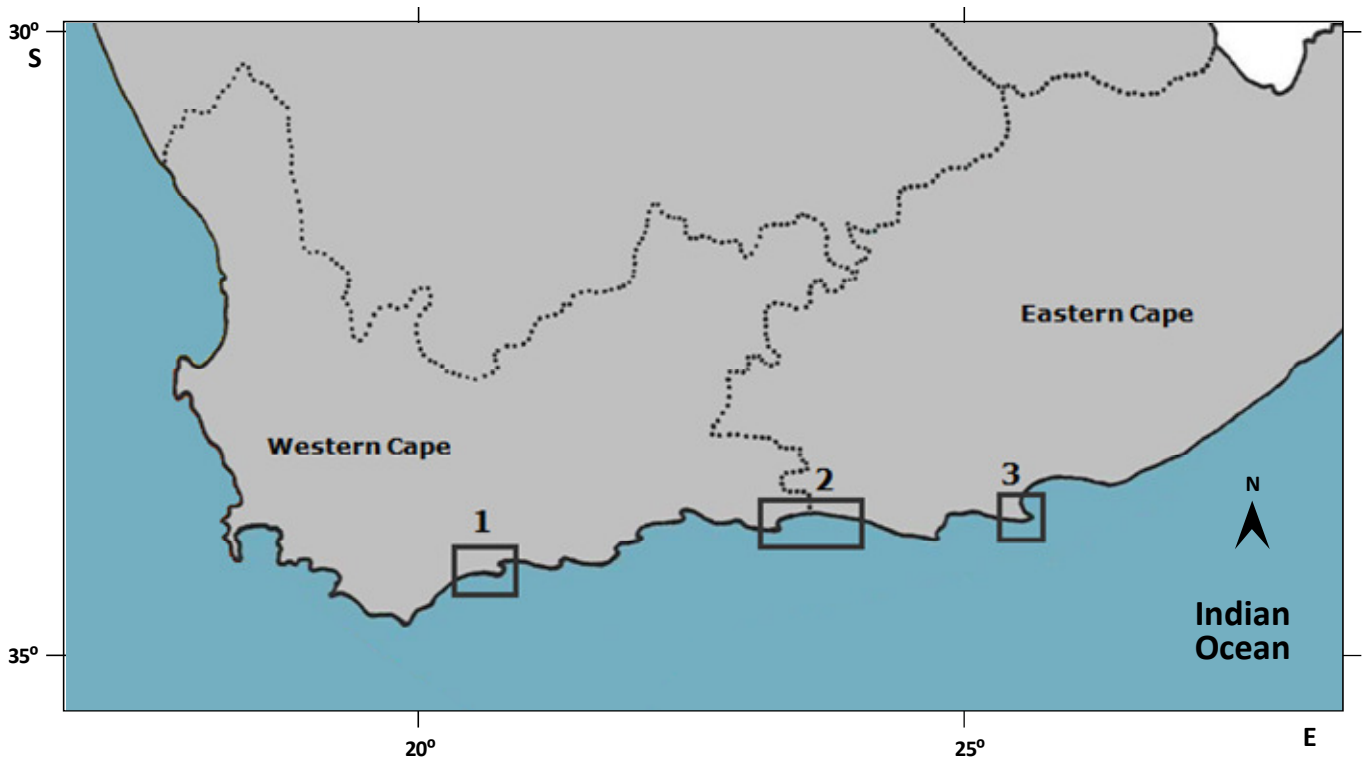
Figure 2.2. Study site locations on the South African coast.

1 – De Hoop MPA; 2 – Tsitsikamma National Park MPA; 3 – Schoenmakerskop.

2.3.1 Movements of juvenile fishes

Rocky intertidal habitats provide unique opportunities to study fish movement behaviour. Rockpools and gullies constituting discrete submerged areas at low tide are readily accessible to researchers and movements are easily quantified. Juveniles of the study species form part of the transient intertidal fish community (Gibson & Yoshiyama 1999), occupying this zone for an extended, but temporary, period as a nursery area (Smale & Buxton 1989). Observations of tagged juveniles in intertidal habitat connected at high tide, but separated as discrete areas at low tide, were made to examine movement between low tide refuges over time.

Study site

The study site comprised an approximately 500m long stretch of rocky coastline situated alongside the village of Schoenmakerskop (34°02'S; 25°33'E), west of Port Elizabeth on the Eastern Cape coast (Area 3 in Figure 2.2) and adjacent to the Sardinia Bay Marine Reserve. The bedrock on this section of the coast consists of parallel fault lines (Smale & Buxton 1989), resulting in the intertidal zone consisting of numerous eroded gullies, coves and shallow areas that contain water even at low tide. Smale & Buxton (1989) studied occurrence of juvenile fishes in intertidal gullies (in their study termed 'subtidal' gullies) in this area. That study and preliminary observations confirmed juveniles of the study species as common in intertidal habitats at the study site. Discrete rockpools were uncommon, but a number of gullies, permanently connected to the sea, were well protected from wave action over low tide and provided areas suitable for observing fish movements. Four intertidal gully areas were chosen in which to quantify movements of tagged fishes (Figure 2.3). Individual areas were adjacent to others but isolated at spring low tide (SLT); although the seaward ends of some gullies were open to the sea they did not connect directly to neighbouring gully areas. The four areas were named (from east to west) Gully 1, Tagging Gully, Channel and Gully 4.
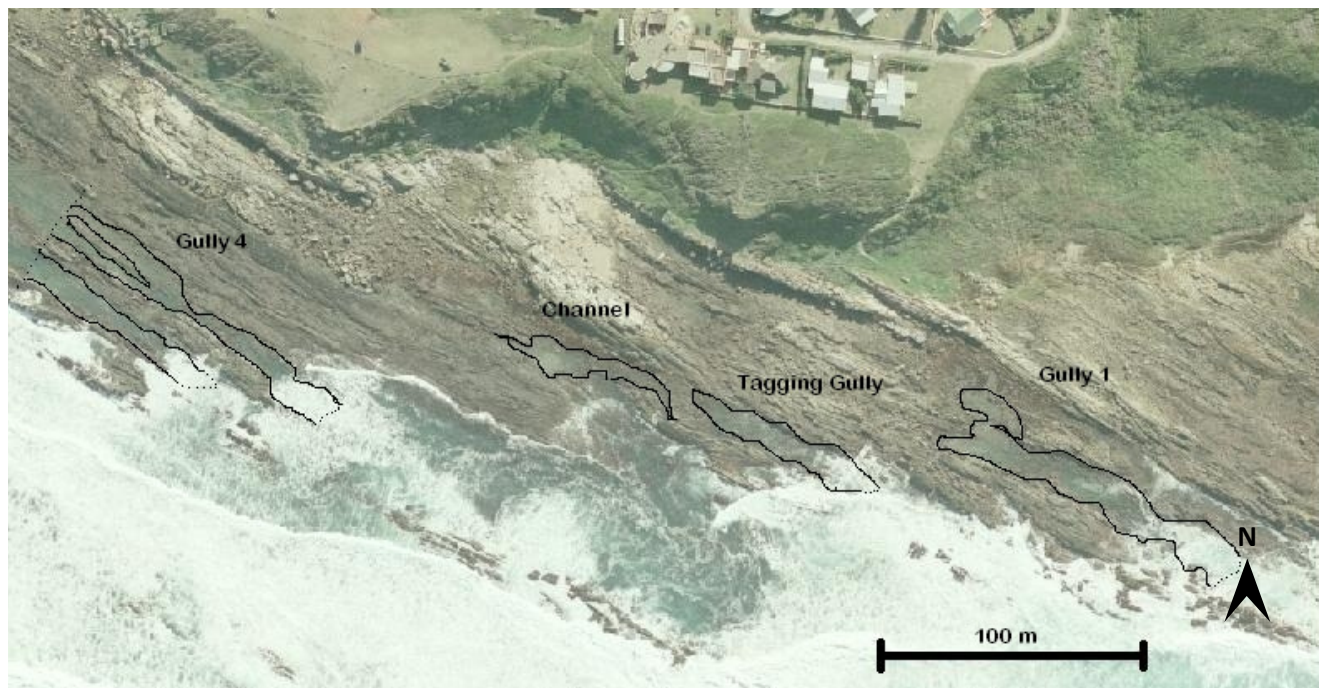

Figure 2.3. Aerial image of the Schoenmakerskop juvenile movement study site taken at low tide (photo courtesy Google Earth®).

Areas differed in their physical characteristics, all having both deep (> 1.5 m) and shallow (< 0.3 m) regions of differing extent at SLT. Gully 1 comprised a large shallow area with coarse sand and mussel shell-covered bottom, connected by a narrow channel to a deep pool-like opening to the sea bordered by rock walls and large boulders; Tagging Gully was relatively deep (up to 2 m), wide (~ 10 m) and straight with a bottom comprising medium-sized boulders (0.5-1 m in diameter) and partially open to the sea at only one end; Channel was separated from Tagging Gully by a narrow rocky ridge that created an overhang (0.7 m deep) on its eastern side. The remainder of Channel comprised a narrow, shallow gully and adjoining broad, shallow area with pebble-covered bottom. Breaks in the rocky wall between the gully and the sea created deeper (~1 m) channels through which water surged; Gully 4 comprised a series of three parallel gullies of varying depth and width approximately 75 metres to the west of Channel. The outermost gully was deep (~2m) and broad (~8 m) with steep rocky walls and sandy bottom, whilst the two inner gullies were shallower (0.4-1 m) and characterised by crevices and overhangs in their rocky walls, and sand bottoms interspersed with small boulders. These two gullies converged in a joint opening to the sea that formed a wide, deep pool with a rocky bottom.

Snorkelling observations suggested the intertidal communities in the four areas were broadly similar, and numerous juveniles of the study species in all four areas suggested that comparably they had similar suitability as nursery habitats. Apart from the study species, the fish community consisted mainly of resident intertidal blennies (Blennidae), klipvisse (Clinidae), gobies (Gobiidae) and the longsnout pipefish (*Syngnathus temminckii*), as well as transient juveniles of subtidal species such as two-tone fingerfin (*Chirodactylus brachydactylus*), mullets (Mullidae) and sparids, including strepie (*Sarpa salpa*), John Brown (*Gymnocratophus curvidens*), Cape stumpnose (*Rhabdosargus holubi*) and white steenbras (*Lithognathus lithognathus*).

2.3.2   Movements of larger fishes

Data on movements of tagged individuals recovered from long-term national tagging programs were analysed to examine subadult and adult movement behaviour. The De Hoop MPA (DH - Bennett & Attwood 1991, 1993) and Tsitsikamma National Park (TNP - Cowley *et al.* 2002) tagging programs complimented the ORI-WWF National Voluntary Tagging Program (ORI), but methodological differences between all three resulted in each being separately analysed.

Whilst ORI mostly utilises volunteer members to tag fishes opportunistically along the entire South African coastline, the MPA programs make use of experienced scientific angling teams (Attwood & Cowley 2005) that visit study sites on dedicated fieldtrips. Table 2.1 summarises attributes of the three programs and brief descriptions of the MPA study sites are given in the sections below (for ORI see section on South African coast above). Further details of angling, tagging and recapture procedures are described in Chapter 4.

Table 2.1. South African tagging programs providing data on movements of the three study species.

Tagging Program	Acronym	Area	Date of inception	Tagging	Basic Information recorded	Biological Information recorded	Recaptures	Spatial resolution of locations
ORI-WWF National Tagging Program	ORI	Entire SA coast	1982	Voluntary & Scientific members	Tag number Date Location	Species Length	Fisheries Public	> 1 km
De Hoop MPA Tagging Program	DH	De Hoop MPA	1987	Scientific personnel	Tag number Date Location Angler effort	Species Length	**MPA site** Scientific personnel	**MPA site** 3.5 km (≤ 1998 100 m (≥ 1999)
							Other areas Fisheries Public	**Other areas** > 1 km
Tsitsikamma National Park Shore-angling Program	TNP	Tsitsikamma National Park MPA	1995	Scientific personnel	Tag number Date Location Angler effort	Species Length Capture time Bait	**MPA site** Scientific personnel	**MPA site** ≥ 5 m
					Water temperature	Tag-scars	**Other areas** Fisheries Public	**Other areas** > 1 km

2.3.3   Study sites

ORI

Tagging of fishes in the ORI program took place opportunistically along the South African coastline in accordance with angling activities of members. Thus tagging effort was excluded from certain protected, private, remote or otherwise inaccessible areas, and higher in some areas with good accessibility (e.g. close to urban centres and popular holiday resorts) than others.

DH

The De Hoop MPA is located in the Western Cape Province within the Agulhas inshore bioregion. Scientific angling took place at two 3.4 km long sites 11 kilometres apart within the MPA, at Koppie Alleen and Lekkerwater (Figure 2.4). The shoreline at both sites is composed of rocky wave-cut platforms extending into the surf-zone, interspersed with stretches of sandy beach (Bennett & Attwood 1991). Subtidal habitats comprise low-relief reefs lying exclusively within the surf-zone at depths less than six metres that periodically become inundated with sand, and thus constitute a highly dynamic environment (Bennett & Attwood 1991).
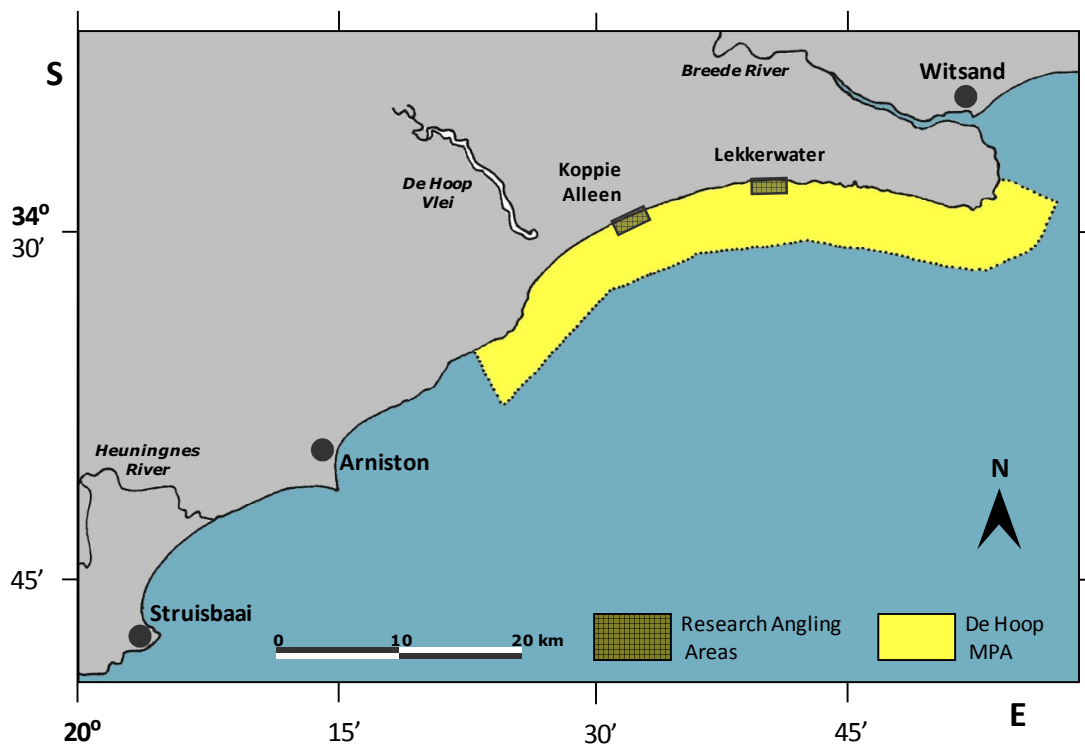

Figure 2.4. De Hoop MPA on the southwestern Cape coast showing locations of research angling areas at Koppie Alleen and Lekkerwater

West of the Koppie Alleen study site the MPA extends a further 18 km, and from the Lekkerwater site 10 km eastwards; in total a 46 km stretch where normal fishing activities were prohibited over most of the study period. However, prior to 1986 and establishment of the MPA, fishing effort was much higher at Koppie Allen than Lekkerwater, which was situated on private land (Bennett & Attwood 1991). Bennett & Attwood (1993) recorded 33 species at the two study sites during scientific angling in the MPA, with galjoen (*Dichistius capensis*) (~57%) and blacktail (~33%) together comprising over 90% of catches.

TNP

Tsitsikamma National Park is Africa's oldest MPA, having been proclaimed in 1964. It straddles the border of the Western and Eastern Cape Provinces (Figure 2.2) and protects a 76 km stretch of coastline between the Groot River (West) (33º59'S, 23º34'E) and Groot River (East) (34º04'S, 24º12'E) (Figure 2.5). The main research angling area comprised an approximately 2.8 km stretch of predominantly rocky coastline close to the western boundary of the MPA between the Klip and Bloukrans Rivers (Figure 2.5).
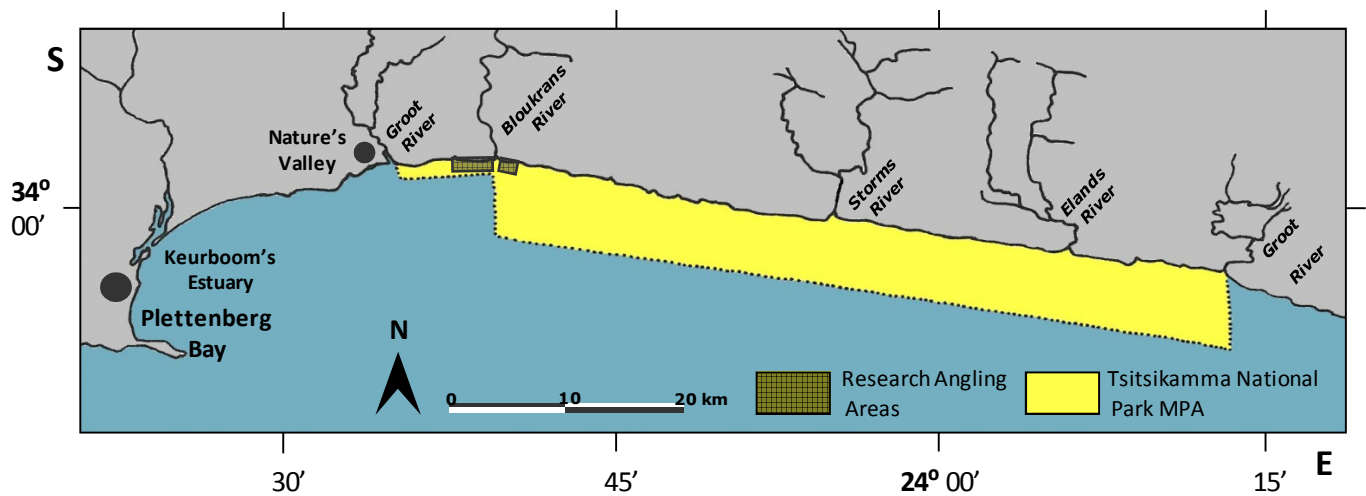
Figure 2.5. Tsitsikamma National Park MPA showing locations of research angling areas. The larger area to the west is the Bloukrans study site, the smaller area the Lottering site.

At the Bloukrans site, steep cliffs rise above rocky promontories and ledges projecting into the sea, resulting in shore topography consisting of deep rocky coves, pebble beaches, sandy bays and areas of scattered rocky outcrops. A number of subtidal habitats exist, with both rocky (including deep, high-profile reef, rocky gullies and shallow, low-profile reef or boulder-beds) and sandy (e.g. banks in vicinity of the river mouths) habitats as well as the transitional habitats between these all lying close to shore.

Research angling and tagging was also undertaken at a second site in the vicinity of the Lottering River Mouth (Lottering Site) from 1998 to 2000. Subtidal habitat here comprised predominantly sandy substrate in the surfzone off the rocky shore. In total 119 marine fish species have been identified from the Tsitsikamma National Park, but research angling only recorded 58 of these (Wood *et al.* 2000). Blacktail (~24%) and galjoen (~11%) were again the two most abundant species recorded.

Chapter 3 - Movement of juveniles between low tide refuges in a rocky intertidal nursery area

3.1   Introduction

Movement studies on small juvenile fishes have presented a problem for researchers due to difficulties in utilising traditional tagging methods. Use of commonly used external tags is usually impossible because the fish is too small to carry the tag. Movement studies on juvenile marine fish are nevertheless important for a number of reasons. Many marine species inhabit specific habitats during the juvenile stages (nursery areas) prior to life in adult habitats. Nursery areas may comprise a limited subset of adult habitats (e.g. shallower areas or microhabitats of subtidal reefs; Henriques & Almada 1998, Tupper 2007) or be spatially distinct areas (e.g. estuaries; Gillanders 2002, Kupschus 2003) providing, *inter alia*, refuge from predation and environmental perturbation, as well as rich food resources (e.g. Kamenos *et al.* 2004). Knowledge of juvenile fishes' use of nursery areas is important from an ecological and management perspective. Within nursery areas juveniles are significant consumers and prey, and important in energy transfer within local foodwebs (Teo & Able 2003). Upon movement to adult habitat or falling prey to transient predators, they also transfer energy to external areas. As they are often located in shallow nearshore habitats (e.g. estuaries, mangrove stands and seagrass beds), nursery areas of many economically important marine species are particularly vulnerable to anthropogenic impacts such as pollution or fishing pressure, which can have serious negative consequences for adult populations and thus certain fisheries (Beck *et al.* 2001).

Blacktail, zebra and musselcracker utilise the intertidal zone of rocky shores as a nursery area (Chapter 1). Numerous studies have examined rocky intertidal fish movements (reviewed by Gibson 1999). However, these almost exclusively involved resident intertidal species for which large-scale movements are uncharacteristic, these fishes possessing morphological (e.g. small, cylindrically-shaped bodies and modified fins for attachment to rocks) and behavioural (e.g. litho-taxis) adaptations to sedentary lifestyles (Gibson & Yoshiyama 1999). Few "transient" (Gibson & Yoshiyama 1999) rocky intertidal species' movement patterns have been reported, but existing studies focused on species that move into the intertidal zone to feed over high tide (van der Veer *et al.* 1992, Rangeley & Kramer 1995). Juvenile sparids are thought to utilise this habitat similarly to resident species, inhabiting them for extended periods during the juvenile phase (Beckley 1982, Smale & Buxton 1989).

The aim of the present study was to examine movement behaviour of juvenile blacktail, zebra and musselcracker in a rocky intertidal nursery area through quantifying use of discrete areas as low tide refuges by tagged individuals, and thus examine movements between adjacent areas in the intertidal zone.

3.2   Methods

3.2.1   Study site

The study took place at Schoenmakerskop near Port Elizabeth on the Eastern Cape coast (see Chapter 2).

3.2.2   Experimental design

Juvenile fishes were marked with unique external tags in a single area of the study site (Tagging Gully – see Chapter 2) over a two-day period. Subsequent observations on their utilisation of discrete low tide areas at the study site were made on bi-weekly fieldtrips between January and August 2006 to quantify long-term movements.

3.2.3   Tagging

Elastomer, widely known by the acronym VIE (Visible Implant Elastomer), was used as the tagging method. VIE is a silicon-based plastic injected in liquid form into the fish's body surface, quickly hardening to form a flexible, solid, biologically inert and highly visible tag (Northwest Marine Technology, Inc. 2008). A range of available colours and suitable tag locations enables VIE tagging to uniquely identify large numbers of small fishes (e.g. Beukers *et al.* 1995, Frederick 1997, Griffiths 2002), including sparids (Doupe *et al.* 2003, Astorga *et al.* 2005). Mortality rates are lower and tag-retention rates equivalent to, or better than, other external tagging methods for small fishes (Malone *et al.* 1999, Brennan *et al.* 2005), studies reporting tag retention rates in excess of 80 percent over periods greater than one year (Catalano *et al.* 2001, Fitzgerald *et al.* 2004). The heavy body scaling of sparids of the size under investigation precluded the use of many body locations (*cf* Astorga *et al.* 2005) for successful tag resighting.

Kerwath *et al.* (2006) placed VIE tags in the caudal fin of adult roman (*Chrysoblephus laticeps*), reporting good *in-situ* tag visibility and high tag-retention rates. After laboratory trials proved successful the caudal fin was selected as the most suitable location for VIE tagging of fishes in the present study. Ultra-light angling tackle, and a baited steel-frame rectangular fish-trap (500 mm x 750 mm with funnel entrances), were used to capture juvenile fishes. Small (size 18-12) debarbed hooks baited with sand-mussel (*Donax serra*) or polychaete worms proved effective and did not cause large mouth-wounds. The trap was baited with pilchard (*Sardinops sagax*). Fishing took place over spring low tide on two successive days in January 2006. Captured individuals were anaesthetised in a 0.4 ml.l^{-1} 2-phenoxyethanol-fresh seawater solution (Kerwath *et al.* 2006) in a bucket, cooled with sealed ice-bags to maintain ambient water temperature, and then placed on a seawater-soaked sponge to minimise body damage during tagging. Because manipulation of the fish was necessary a damp gardening glove was worn during tagging. VIE was injected into the connective tissue along a caudal fin ray with an insulin syringe (0.33 mm/29-guage hypodermic needle) (Figure 3.1).

Figure 3.1. Photograph showing the position of VIE tag along caudal fin ray of a juvenile blacktail.

Tags approximately five millimetres long were applied by inserting the needle as distally as possible alongside a caudal fin ray and threading it along the ray proximal to the caudal pterygiophores. During subsequent needle withdrawal liquid VIE was injected, filling the needle insertion space (Kerwath 2005). Tag injection ended short of the needle entry site to prevent VIE leakage from the fin surface, which increases the chances of tag loss (S. Kerwath, Marine & Coastal Management, pers. comm.). Tags were placed in either one or both of the upper and lower lobes of the caudal fin, were visible from both sides of the fish and from a distance in excess of two metres underwater. Following tagging, fishes were placed in a bucket of cool seawater with air stone circulation and upon complete recovery released back into Tagging Gully. Before tagging of further individuals the hypodermic needle was sterilised in 95% ethanol to minimise the risk of infection.

3.2.4   Movement observations

Tagged individuals were resighted during fifteen-minute underwater surveys of each of four areas in the study site (Chapter 2). These were conducted on standard snorkelling equipment during bi-weekly sampling trips of two to four consecutive days over spring tide periods. During surveys, each area was actively searched for tagged fishes, the presence of which was recorded on a dive-slate. Surveys were initiated in one of the two outer areas (Gully 1 and 4) within one to half an hour before low tide, progressing in turn to each adjacent area in the appropriate direction until all four areas had been surveyed. On successive days initial surveys alternated between Gully 1 and 4 to vary survey direction across the study site during each trip. When conditions allowed, subtidal areas adjoining the intertidal survey areas were also explored for tagged fishes and during particularly calm conditions on the final sampling trip, observations were made in Tagging Gully, Channel and adjoining inshore areas during the incoming tide-phase.

3.2.5   Water temperature

Underwater Temperature Loggers (Vemco®) were placed in two areas (Gully 4 and Tagging Gully) to monitor water temperature over the study period. The instruments were placed under large boulders in the gullies and were between 0.5 and 1.0 m below the water surface.

3.3 Results

3.3.1 Capture and tagging of fishes

A total of 12 blacktail, 12 zebra and 6 musselcracker of lengths 82-172 mm FL were captured, tagged and returned to Tagging Gully on 16 and 17 January 2006 (Table 3.1).

Table 3.1. Juvenile sparids tagged with VIE at the Schoenmakerskop study site

Species	Number tagged	Average length (mm FL)	Length range (mm FL)
Blacktail	12	105.3	82 - 123
Zebra	12	128.5	106 - 172
Musselcracker	6	112.5	90 - 137

Two juvenile musselcracker were the only fish caught in the baited fish trap; all others were caught on baited hooks. A further two blacktail, three zebra and one musselcracker were tagged but died from effects of the anaesthetic on the first day of tagging.

3.3.2 Survey effort

A total of 13 survey trips were made to the study site over spring tide periods from 21 January to 25 August 2006, a total of 37 days. No surveys were undertaken between 12 July and 23 August due to rough water conditions.

3.3.3 Water temperatures at the study site

Average daily temperatures recorded by the two temperature loggers were similar over the study period (average difference between readings of 0.4 ± 0.1°C). Average daily water temperature was 17.4 ± 2.2 °C, but temperatures ranged from 9.96 °C to 22.86 °C. There was a slight decrease in average daily temperatures and diurnal temperature range with seasonal progression to autumn and then winter. However, sudden drops in water temperature (from ~20 to 10-13 °C) occurred frequently during the first two months of the study period, but only on one survey date (17 February – Figure 3.2).
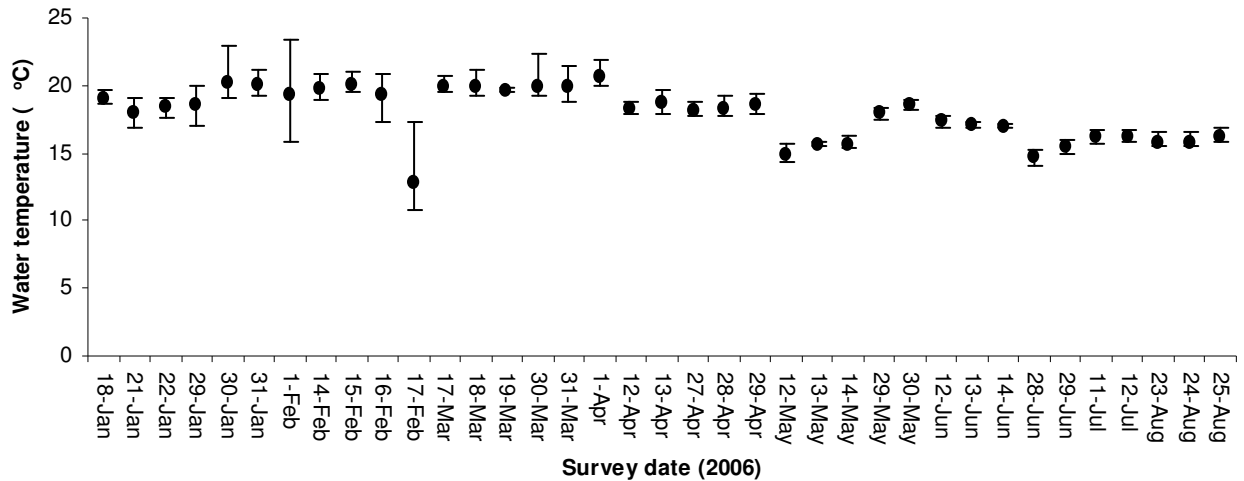
Figure 3.2. Daily average water temperature and range (depicted by error bars) at the Schoenmakerskop study site on survey dates.

3.3.4 Observations of tagged fishes

Tagged individuals of all three species showed high initial frequency of observations at the study site (up to two months post-tagging), but this translated into long-term regular observations for zebra and musselcracker only, with only a single tagged blacktail regularly observed after a period of three months (Table 3.2). Only two tagged fishes (both blacktail) were not observed at least once post-tagging. By the end of the seven-month study period a high proportion of tagged zebra (67%) and musselcracker (50%), but not blacktail (8%) were still observed in the study area. Tagged blacktail were only regularly observed in the first two months of the study, after which few were seen (Figure 3.3). By contrast, the proportion of tagged zebra and musselcracker observed remained high for a longer period, with many still observed upon termination of the seven-month study (Figure 3.3), although this was more pronounced for zebra. Little movement between areas was detected for most tagged fishes, but blacktail displayed a greater inclination to move than the other two species. Only one tagged blacktail (#1) was regularly observed but showed strong fidelity to Tagging Gully, while four of the other nine moved to one of the other gullies and one was observed in both neighbouring gullies (Table 3.3). None were observed to move to the area furthest from Tagging Gully (Gully 4) and only two to Gully 1, but movements between the Tagging Gully and Channel areas were comparatively frequent.

Table 3.2. Numbers of tagged juvenile sparids resighted at Schoenmakerskop study site at monthly intervals post-tagging.

Months post-tagging	Blacktail	Zebra	Musselcracker
0	10	12	6
1	9	11	5
2	5	11	5
3	2	11	5
4	1	11	5
5	1	11	4
7*	1	8	3

*No data for 6 month post-tagging period due to no surveys between 12 July and 23 August due to poor weather conditions
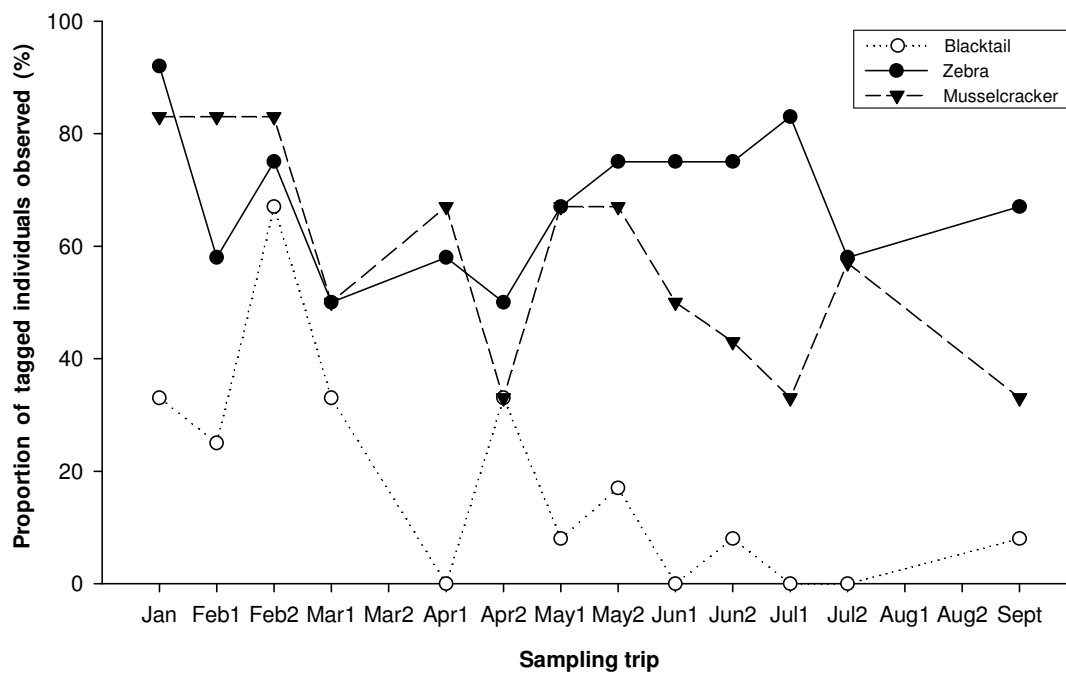

Figure 3.3. Proportion of tagged juveniles of the three study species recorded during each sampling trip.

Table 3.3. Tagged blacktail resighted in different areas at low tide at the study site.
TG – Tagging Gully, Ch – Channel, G – Gully 1. Superscripts refer to the number of observations in the particular area if fish was observed in more than one.

Fish #	FL (mm)	Tagging date	Number of days observed	Observation period (days)	Areas observed
1	113	16 Jan 06	12	222	TG^{11}; Ch^1
2	110	16 Jan 06	0	-	-
3	105	16 Jan 06	2	61	TG
4	111	16 Jan 06	4	63	TG
5	82	16 Jan 06	4	119	TG^2; Ch^1; G^1
6	89	16 Jan 06	2	32	G^1
7	116	16 Jan 06	6	87	TG^3; Ch^3
8	105	16 Jan 06	3	32	TG
9	95	16 Jan 06	2	87	TG
10	111	16 Jan 06	0	-	-
11	104	17 Jan 06	2	14	Ch
12	123	17 Jan 06	4	60	Ch^3; TG^1

Large numbers of juvenile blacktail accumulated in extremely shallow rockpools on one survey date that coincided with a sudden drop in water temperature (i.e. 17 February, during Sampling trip Feb2 in Figure 3.2). Eight of the twelve tagged blacktail were observed in pools directly inshore of the survey areas, after having been largely absent in previous surveys. Observed frequency of movements of juvenile zebra and musselcracker between survey areas were lower than for blacktail, tagged individuals generally being observed more frequently and over a greater proportion of the study period (Tables 3.4 & 3.5). One zebra (#9) moved to Channel early in the study, where it remained for the remainder of the study period, and one musselcracker (#3) was only seen once, in Channel. Apart from these fishes, all tagged individuals were observed over low tide in Tagging Gully. However, some were infrequently observed but nevertheless still alive (confirmed by sporadic observations after long periods of absence). Low resighting rate appeared to be related to fish size, as three of the four zebra with lowest resighting rates were the largest individuals tagged (Table 3.4). Unfortunately the significance of this could not be assessed with much statistical power due to low sample size. One of these fish was observed in subtidal habitat outside of Tagging Gully.

Table 3.4. Tagged zebra resighted in different areas at low tide at the study site.
TG – Tagging Gully, Ch – Channel, G1 – Gully. Superscripts refer to the number of observations in the particular area if fish was observed in more than one.

Fish #	FL (mm)	Tagging date	Number of days observed	Observation period (days)	Areas observed
1	136	16 Jan 06	30	178	TG^{29}; Ch^1
2	128	16 Jan 06	21	221	TG
3	140	16 Jan 06	2	164	TG
4	123	16 Jan 06	3	5	TG
5	115	16 Jan 06	15	222	TG
6	106	16 Jan 06	27	222	TG
7	122	16 Jan 06	30	222	TG^{29}; Ch^1
8	115	16 Jan 06	30	222	TG
9	125	17 Jan 06	32	221	Ch^{31}; TG^1
10	119	17 Jan 06	33	221	TG
11	141	17 Jan 06	12	221	TG
12	172	17 Jan 06	1	163	TG

Table 3.5. Tagged musselcracker resighted in different areas at low tide at the study site.
TG – Tagging Gully, Ch – Channel, G1 – Gully. Superscripts refer to the number of observations in the particular area if fish was observed in more than one.

Fish #	FL (mm)	Tagging date	Number of days observed	Observation period (days)	Areas observed
1	137	16 Jan 06	15	149	TG
2	96	16 Jan 06	6	178	TG
3	102	17 Jan 06	1	13	Ch
4	132	17 Jan 06	23	221	TG
5	118	17 Jan 06	22	221	TG
6	90	17 Jan 06	9	177	TG

Opportunistic observations made during the incoming tide, between 23 and 25 August at the end of the study period, revealed use of both Tagging Gully and Channel during this period (Table 3.6). These mostly comprised individuals recorded over low tide that also made use of shallower regions inshore of the two gullies as these became inundated with water. However, a further two blacktail unobserved at low tide since early in the study were also observed over this high water period.

Table 3.6. Numbers of tagged juveniles observed over the incoming tide at the end of the study period. Superscript indicates the individuals sighted; gul – normal observation gully, sh – shallow area inshore of observation gully.

Sampling date	23 Aug 06				24 Aug 06				25 Aug 06			
	Tagging Gully		Channel		Tagging Gully		Channel		Tagging Gully		Channel	
Area	gul	sh	gul	sh	gul	sh	gul	sh	gul	sh	gul	sh
Region												
Blacktail	2[#1,5]	-	1[#10]	-	-	-	1[#5]	-	1[#1]	-	1[#5]	-
Zebra	3[#5,6,7]	2[#10,11]	-	-	1[#5]	2[#7,11]	-	-	2[#6,7]	2[#8,11]	-	-
Musselcracker	-	1[#3]	-	-	1[#4]	-	-	-	-	-	1[#3]	-

3.4   Discussion

An important requirement of tagging studies is that the tag does not cause unnatural behaviour in the individuals under study, as this limits interpretability of results at a general population level. Tagged fishes were observed swimming naturally soon after tagging, and one tagged white musselcracker was recaptured three times within two days of being tagged. This suggests tagging-induced effects on behaviour were negligible. The high numbers of tagged individuals observed over the remainder of the study also suggests tagging-induced mortality following release did not occur. An important observation for future studies however, was the death of some fishes during tagging. It is likely that elevated temperature of the anaesthetic solution due to hot weather was the cause of mortalities (Weyl *et al.* 1996), as the tagging procedure was identical to that practised successfully in prior laboratory and field trials. After cooling the anaesthetic solution with sealed ice bags no further mortalities occurred. While no formal study was undertaken on VIE tag-loss rates over the study period, it is a widely used method that has shown generally high tag-retention rates in small fishes (see Methods).

Over repeated sampling trips tag condition was subjectively assessed, and only one fish was observed to acquire partial tag damage, which did not progress to full tag loss. For these reasons tag-loss was not considered a potential explanation for absence of individuals in surveys. Results showed long-term association of tagged individuals to restricted areas within the intertidal zone. Tagged blacktail showed the greatest propensity for movement and appeared to cease use of the intertidal zone over low tide from early in the study period. This was likely due to an ontogenetic shift to nearby subtidal habitat with growth, which is supported by data from previous studies. In this study, only three individuals less than 100 mm (total length) were tagged, but Christensen (1978) found juveniles departed the intertidal zone at a size similar to this (90 mm SL) and previous studies in rockpools collected blacktail primarily smaller than this (Beckley 1985, 2000, Bennett 1987, Burger 1990). Although Smale & Buxton (1989) recorded larger blacktail in gullies, juveniles over 100 mm were uncommonly collected in their study in this area. Juvenile blacktail 100-150 mm TL are, however, common on shallow subtidal reefs (Burger 1990, Mann 1992, Fennessy & Chater 1998). The present study thus tagged individuals likely approaching the size at which ontogenetic movement to subtidal reefs occurs. The influx of blacktail in the 'tag-size' cohort into the intertidal zone on one study date appeared driven by a sudden drop in water temperature linked to cold-water upwelling. The resighting of most tagged individuals during this event suggests they remained in subtidal areas in close proximity to the study site and were thus able to return to familiar areas that were utilised as smaller juveniles.

In contrast to blacktail, most tagged zebra and musselcracker showed long-term fidelity to specific areas used over low tide. While no tagged fishes were observed on all survey dates, for most regularly-sited individuals this was likely due to being occasionally overlooked on surveys rather than absence from survey areas (see later discussion on irregularly observed individuals). Visual census methods may be biased by observer-mediated behaviour of particular species or individuals (Kulbicki 1998), although this was not noted and most individuals seemed unconcerned by observer presence. It is possible, however, that certain individuals were generally less active over low tide and thus less conspicuous, although the survey areas were thoroughly searched. Occupation of small, stable home ranges over low tide is a feature of resident intertidal taxa (Gibson 1999, Griffiths 2003a,b) and strong site fidelity within nursery areas has been recorded for juveniles of several marine fish species (Ross & Lancaster 2002, Watson *et al.* 2002, Burrows *et al.* 2004).

Use of specific areas can be mediated by the tidal cycle (Pottoff & Allen 2003, Teo & Able 2003, Dorenbosch *et al.* 2004) and tagged fishes were theoretically able to move between several different low tide refuges during high tide. The observed use of a single low tide refuge suggests either stasis within it over high tide, or active return to it from adjoining areas used during high tide. The limited observations at high tide suggested both of these behaviours may occur; use of shallower areas over flood tide was noted for some individuals (Table 3.6), while other individuals continued to utilise the low tide refuge during this time and perhaps over the full tidal cycle. The restricted low tide refuge area thus probably constitutes the "core" area (Kramer & Chapman 1999) of a larger home range incorporating adjoining areas sometimes utilised during high water periods (e.g. during the large tidal amplitudes associated with spring tides). This would allow the use of similar depth throughout the tidal cycle and an associated reduction in predation risk and exposure to turbulent conditions over high tide. Many resident intertidal fishes make such tidally-related movements (Green 1971, Gibson 1984, 1999), the magnitude of these being constrained by the need to remain within the vicinity of the low tide refuge to allow an easy return to it as the tide drops (Green 1971).

Individual juvenile zebra and musselcracker thus appear to utilise only a fraction of available nursery habitat. Familiarity with a restricted area of the intertidal zone probably facilitates quick escape from aerial and aquatic predators (Gibson 1999), as well as knowledge of the location of food resources (Kramer & Chapman 1999). Familiarity with the 'layout' of their immediate surroundings is probably also advantageous for expedient retreat to shelter (e.g. shallower areas) during rougher water conditions associated with high tide or storm events. Aggressive interactions between conspecifics or with other species were not observed during the present study and it did not appear that territories were established, as has been observed in juveniles of other species (Kudoh & Yamaoka 1998, Bell & Kramer 2000). The patchy distribution of suitable rocky intertidal nursery areas along the South African coast may have lead to the evolution of non-agonistic behaviour during the juvenile phase, facilitating maximum use of this potentially limiting resource. Christensen (1978) found limited resource competition between juvenile blacktail and zebra in the intertidal zone resulting from different temporal utilisation of this habitat (blacktail leaving at smaller size) and utilisation of different food resources, the degree of dietary overlap decreasing with growth.

The sporadic observations of most blacktail and certain zebra and musselcracker were considered unlikely to be due to general overlooking of these individuals. As already discussed for blacktail, it is probable that rare observations were instead the result of a habitat shift linked to growth. Under this hypothesis, rare observations in the low tide refuge were indicative of a maintained association with it during the ontogenetic shift. Observations of blacktail returning to the survey areas over the incoming tide, as well as the observation of a rarely-resighted zebra individual in adjacent subtidal areas during low tide provides evidence for this. It also provides evidence that for these fishes the ontogenetic shift to adult habitat occurs via a 'stepping-stone' process. A gradual (subtidal) extension of the juvenile home range and concomitant reduction in use of the (intertidal) nursery area leads to final establishment of the adult home range separate from the nursery area (Appeldoorn *et al.* 1997). From a core area within the intertidal zone (the low tide refuge), opportunistic exploration of subtidal areas during suitable conditions could initiate this process. These most likely occur over low tide, in temporal opposition to the high tide influx of predators in shallow nearshore areas (e.g. Rangely & Kramer 1995) and when sea conditions are generally calmer than during high tide, and would then have also coincided with low tide intertidal surveys. Such a process allows the fish a well-known refuge to return to during the potentially dangerous transition to subtidal life, but with increasing familiarity with subtidal areas, use of the intertidal zone concomitantly decreases and the core area of the home range eventually shifts permanently to the subtidal.

A similar gradual shift to adult home range through increased temporary excursions away from the nursery area has been suggested by a study on estuarine-dependent spotted grunter (*Pomadasys commersonnii*), with the frequency and duration of excursions to adult marine habitats increasing upon sexual maturity (Childs 2005, Childs *et al.* 2008). Some adult *P.commersonnii* also maintain an association with their nursery area into adult life. Subadults and adults of all three study species are known to utilise extremely shallow areas during high tide (Biden 1948, Christensen 1978, Clarke 1988, Mann 1992) and some individuals therefore probably maintain an association with their intertidal nursery areas throughout life. Future study therefore needs to quantify typical dispersal distances for juveniles to adult habitat. The observed smaller size at which blacktail leave the intertidal zone has possibly evolved due to their greater abundance and shoaling behaviour conferring protection against predation in subtidal habitats. Alternatively, their greater abundance in the intertidal zone may necessitate earlier dispersal due to intraspecific competition.

Although the rocky intertidal zone appears to form their predominant nursery habitat, juveniles of all three species are also found in other habitats (see Chapter 1). The relative importance of these to adult populations should be estimated by future studies. The rocky intertidal zone may represent a critical habitat (Beck *et al.* 2001) that contributes disproportionately to recruitment to adult populations. This can occur through increased juvenile survival during occupation of the nursery area (e.g. reduced predation), as well as upon movement to adult habitat (enhanced growth in critical habitat leading to better individual condition and survival). As proximity of nursery areas and adult habitat influences the scale of ontogenetic movement (Appeldoorn *et al.* 1997) this may also be an important factor determining the importance of particular nursery areas to adult populations. In regions where nurseries and adult habitat are widely separated, the gradual ontogenetic shift could be replaced by directed movements of greater magnitude between these, or alternatively result in shift to closer, but less productive habitats. Both of these would be expected to result in lower survival rates and proportionally less contribution to adult populations.

The development of biochemical techniques discriminating past nursery environments of individuals (e.g. elemental fingerprinting of otoliths (Kerr *et al.* 2007, Fodrie & Levin 2008)) will hopefully enable this in future studies. Due to the proximity of many South African rocky intertidal areas to human coastal developments, they will likely come under increasing pressure from anthropogenic impacts (Crowe *et al.* 2000). Point-source pollution events (e.g. oil (Barber *et al.* 1995) or chemical spills) are a potential threat on local scales and could negatively affect local adult populations that receive recruits from impacted nursery areas. Perhaps a greater threat is that posed by chronic sub-lethal exposure of juveniles to chemical compounds affecting their reproductive development (endocrine-disrupting chemicals: EDCs; Porte *et al.* 2006) and thus having potential knock-on effects in local adult populations. Such chemicals are found in run-off from motor oil and sewage that can accumulate in the intertidal zone (Crowe *et al.* 2000). Establishing the relative importance of different nursery habitats for these species should be undertaken so that adequate protection of critical habitats can be implemented and contingency plans for potential impacts explored.

Chapter 4 - Movement patterns inferred from long-term tagging programs

4.1   Introduction

Studies on fish movement generally take either of two divergent approaches – short-term, intensive studies on a few individuals that allow fine-scale movement patterns to be investigated, often through sophisticated technology such as telemetry; or long-term studies on many individuals utilising less-specialised techniques that yield information which, although limited at the individual level, in combination lead to an understanding of population movements. The latter approach makes use of relatively simple inexpensive technology that is easy to apply, enabling public and commercial entities (e.g. fisheries) to participate in data collection, thereby greatly increasing the geographic extent and volume of data that can be collected to study highly mobile species. Large juveniles and adults of the three study species are potentially highly mobile and live in exposed shallow-water habitats that preclude the use of acoustic telemetry methods and underwater observation to investigate their movements. Therefore, the most suitable methods to assess their movement patterns rely on external marks that are visible upon subsequent recapture.

External plastic dart tags, inserted into the dorsal musculature, have been successfully used to study the movements of several South African coastal fish species (e.g. Buxton & Allen 1989, Attwood & Bennett 1994, Cowley *et al.* 2002, Griffiths & Wilke 2002, Brouwer *et al.* 2003, Kerwath *et al.* 2007a). This tagging method, adopted by the ORI-WWF National Voluntary Tagging program (ORI) and its subsidiary research tagging projects (see Chapter 2), has also been applied on adolescent and adult blacktail, zebra and musselcracker. Some information on the movement behaviour of these species has been published in the scientific literature and indicates high levels of residency and site fidelity for blacktail, zebra and immature musselcracker (Bennett & Attwood 1991, Mann 2000b,c, Booth 2000, Cowley *et al.* 2002), but larger movements for adult musselcracker (Mann 1999, Booth 2000). This study expands on these earlier investigations by describing the movement behaviour of the three study species in relation to (i) changes in age/size, (ii) location on the South African coastline, and iii) seasonal and/or reproductive cycles.   This was achieved through the analysis of mark-recapture data obtained from ORI and two subsidiary research tagging projects in the De Hoop (DH) and Tsitsikamma National Park (TNP) marine protected areas.

4.2   Methods

A description of the South African coastal environment and the study sites, as well as general methods for the respective tagging programs are given in Chapter 2.

4.2.1   Fish tagging and tag recoveries

ORI

The number of active ORI participants varied from approximately 300 to 600 per year (Bullen *et al.* 2008). Anglers did not follow a standardised technique, but recorded the following information on fish that were tagged: angler's name; tag number; date; locality; length and measurement index (e.g. TL or FL). Two types of plastic dart tags (Hallprint™, Australia) were used. Type-A tags (114 mm long x 1.6 mm wide) were generally used only for large fishes (i.e. adult musselcracker) and shorter Type-D tags (85 mm length) for fishes less than 600 mm TL. Tags inscribed with a unique alphanumeric code and the ORI postal address were inserted with a stainless steel applicator into the dorsal musculature and anchored between two inter-neural spines. Tagging localities were recorded on the ORI database as their distance (in kilometres) south of the South African/Mozambique border. Information obtained from fish recaptured by recreational and commercial fishermen, or recovered by other members of the public, was returned via mail to ORI. This included recapture date, locality, fish length (and/or weight) and whether the fish was released or not.

DH

Research teams of 4-6 experienced anglers visited De Hoop MPA on five-day trips to tag and record biological information on the nearshore fish community from one year prior to its proclamation in 1988 (Bennett & Attwood 1991). Initially, monthly trips alternated between two sites (Koppie Alleen and Lekkerwater, see Chapter 2), but from 1994 a two-month interval was established, resulting in three trips made annually to each site. Anglers fished from the shore for extended periods between sunrise and sunset using standard shore-angling gear and varied bait and tackle according to angling-locality characteristics, conditions and personal preferences. To minimise stress, captured fishes were processed swiftly and carefully, using flexible vinyl slings incorporating a rigid central baton and attached measuring tape to land, carry and measure fishes with minimum contact. Fish total length was measured to the nearest millimetre.

Fishes of suitable size (larger than ~250 mm TL) were tagged with the Type-D plastic dart tags (see above) and returned to the sea. Prior to 1999 no site-specific tagging localities were recorded, but from 1999 each site was demarcated with numbered flags partitioning it into one hundred metre stretches (Attwood & Cowley 2005). The capture localities of tagged and recaptured fishes were thereafter recorded as the number of the flag closest to the point of capture. Information on recaptured fishes made at the research sites were recorded as in tagging operations. However, after 1998, no blacktail were tagged, so for this species the only locality information considered was the site of tagging and/or recapture (i.e. Koppie Alleen or Lekkerwater). Tags fouled by epiphyte growth (Figure 4.1) were cleaned and if necessary replaced with a new tag, and all recaptured fish were released. Fish recaptured outside the MPA were reported to ORI by members of the public as described above.

TNP

Scientific shore-angling began at the Bloukrans study site in January 1995, with monthly trips to the study site by a small research angling team (Cowley *et al.* 2002). From 1998 teams of 4-6 anglers, mostly comprising a core group of experienced researchers, visited the site every two months on trips of three to five days. However, from 2004 to 2006 fieldtrips were undertaken quarterly and thereafter biannually (i.e. summer and winter trips). Between 1998 and 2000, research angling also took place at a separate site close to the Lottering River mouth during each trip. Tagging and recapture operations were similar to those at De Hoop, except measurements were expressed as fork length, and additional information on angling activities was recorded (see Table 2.1). All angling localities were named and their position recorded with a GPS (Geographical Positioning System). All the sites in the Bloukrans study area were geo-referenced and incorporated into GIS (Geographical Information System), enabling tagging and recapture positions to be accurately mapped. In the TNP, the presence of characteristic 'tag scars' on (re)captured fishes was also noted (Figure 4.2).

Figure 4.1. Recaptured musselcracker carrying tag fouled by epiphyte growth.

Figure 4.2. Distinctive tag scar on body of recaptured musselcracker.

4.2.2 Movement calculations and analysis

Summary tagging, recapture and movement data on the three study species is provided by ORI in the form of data reports for each species on request (Bullen & Mann 2005a,b,c). However, for this study raw data on all tagged and recovered tagged fishes was obtained from ORI to enable separate analysis of data from the three tagging programs. Movement calculations differed in the case of each particular program, as described below

ORI

Attwood & Cowley (2005) questioned the accuracy (one kilometre precision) of tagging and recapture positions reported to ORI, stating that in some cases these may be out by as much as five kilometres. Therefore, movements (calculated as the distance between reported positions of recapture and tagging) were grouped into five kilometre 'bins', which was felt to be a more appropriate spatial resolution, for analysis. However, maximum and average movements were calculated from the raw distances (i.e. one kilometre scale).

DH

Movements of all blacktail and other fishes tagged prior to 1999 subsequently recaptured within the MPA were classified either as 'zero displacements', if tagged and recaptured at the same site, or as 11 km (the distance between the two tagging sites) if recaptured at the other site. Fishes tagged and recaptured after 1999 with flag positions at tagging and recapture sites were analysed at a 100 m resolution. Recaptures made outside the MPA and reported via ORI were grouped into five kilometre bins as for ORI data.

TNP

Movements of fishes recaptured at the study site were calculated in ARCVIEW GIS 3.2 (ESRI Ltd) using the measuring tool, and taken as the shortest possible route between the tagging and recapture localities (see Figure 4.3). In the example shown a fish tagged at Sandgatte (SG) was recaptured at Stomp (ST). The thick line indicates the shortest possible route (a distance of ~243 m), while the thin line represents a longer alternative route. Measured distances were expressed to the nearest five metres and grouped into 100 m bins for analysis. Tag recoveries made outside the study site were analysed as in the other two programs.
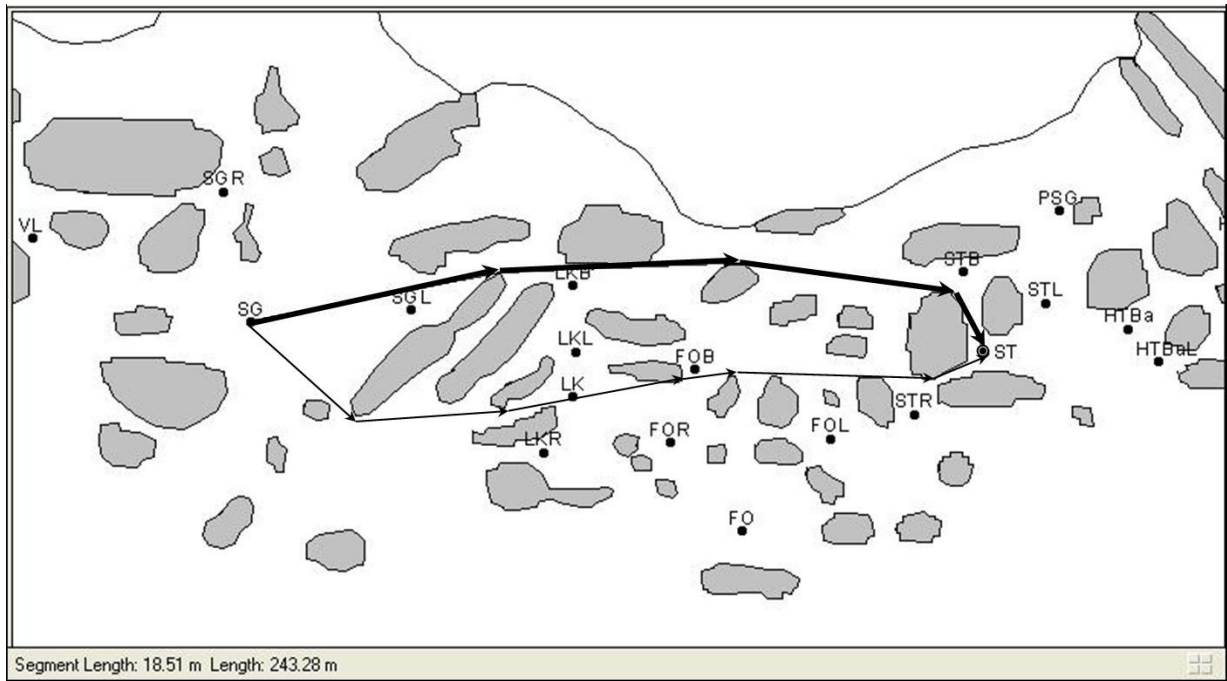
Figure 4.3. Mapped section of the TNP Bloukrans site demonstrating the calculation of the minimum distance moved using the measurement tool in ARCVIEW GIS 3.2.

Analysis of combined data

For TNP and DH total numbers of fish tagged and recaptured were pooled for separate study sites, and recapture rates derived from these. Recapture rates were calculated as the total number of recaptured individuals as a percentage of individuals tagged and released; multiple recaptures of the same individual therefore did not contribute to this value. Movements recorded from all three programs were analysed on a combined scale of five kilometres. Therefore all within-site movements in the MPAs fell within the 0-5 km bin, and between-site movements (DH) in the 10-15 km bin (there were no between site movements in TNP). Unless measured as being larger than 500 m, all MPA within-site movements were recorded as 'zero displacements', as were ORI recaptures recorded at the tagging locality (i.e. as 0 km movement). The effects on movement patterns of time at liberty, fish size, and (for musselcracker) season of recapture were also analysed. Spearman rank correlation was used to investigate the relationship between distance moved and (i) days at liberty, and (ii) fish length. Differences in the proportion and magnitude of movements in an easterly or westerly direction were also assessed. All lengths were analysed as fork length (FL). Lengths reported as total length were converted to FL using conversions given in Mann (2000a,b) and Booth (2000) prior to analysis. Similarly, in cases where size was reported only as weight, published length-weight relationships for each species were used to estimate FL.

In the few cases where no size was reported, estimates of FL at recovery were derived from the species' von Bertalanffy growth equation based on time at liberty and recorded length at tagging.

4.3   Results

4.3.1   Blacktail

A total of 7382 blacktail were tagged in the three programs between 1984 and 2007, with an overall recapture rate of 2.6% (Table 4.2). Recapture rates differed between the three programs, but the only significant difference was a lower rate in TNP compared to DH (two-tailed proportions test, p = 0.002). Recaptured blacktail rarely moved from the tagging locality, with 91% displaying zero displacement at recapture (Table 4.1). Of the individuals that moved, there was no favoured direction of displacement (eight versus nine individuals moved east and west, respectively; Figure 4.4). Both TNP and DH had a single individual that moved more than 100 km (139 and 145 km, respectively), which inflated their average movement values greatly, as well as the overall average (Table 4.1).

Table 4.1. Summary of movement data for blacktail tagged and recaptured along the South African coast, 1984-2007.

Tagging program	Number of fish tagged	Number of fish recaptured {tag-scars}	Recapture rate (%)	Zero displacement (%)	Average & {maximum} movement in km	Average & {maximum} days at liberty
ORI	1883	39	2.07	77.50	1.60 {19}	190 {1028}
DH	3610	122	3.38	94.93	1.47 {139}	283 {2016}
TNP	1889	31 {38}	1.64	87.87	4.27 {145}	365 {2715}
Total	7382	192	2.60	90.57	1.97 {145}	277 {2715}

The high-resolution displacement distances obtained from the TNP for fish recaptured between 0 and 2715 days (average = 365 days) after tagging suggest that movements are generally considerably less than 1 km. A total of 38% were recaptured at the tagging locality, while a cumulative percentage of 68% were recaptured within 100 m, and almost 90% within 500 m, of the tagging locality (Figure 4.5).
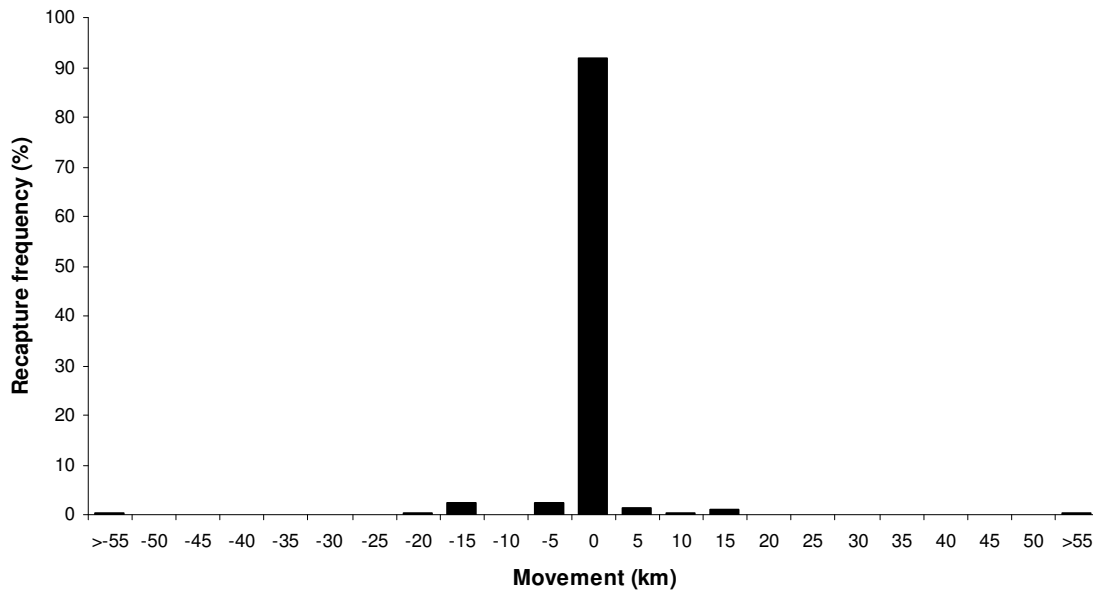
Figure 4.4. Movements of 192 blacktail recaptured along the South African coast (combined programs). Negative values represent displacements in a westerly, and positive values an easterly, direction.

Similar site fidelity for blacktail was recorded at DH. Of 138 recapture events, only two (1.6%) were outside the MPA boundary and only five (4.1%) movements were recorded between the tagging sites within the MPA, located 11 km apart. A further individual was recovered elsewhere in the MPA at least nine kilometres from its tagging site. In total, more than 94% of recorded DH movements were within the two 3.4 km wide tagging sites. Average time at liberty was high in all three tagging programs (Table 4.1) but significantly higher in both MPAs than in the ORI program (Kruskal-Wallis ANOVA, p = 0.0128), individual fish recorded as being resident at TNP and DH for over 7 and 5.5 years, respectively. The distance moved by individuals in the combined programs was not significantly related to time at liberty (Spearman R = 0.088, p = 0.2, Figure 4.6), or to fish size (Spearman R = 0.014, p = 0.839, Figure 4.7). Several individuals (n = 18; 9%) were recaptured twice and one fish on three occasions. Most multiple recaptures (83%) were made at their respective sites in DH and the two recorded from TNP also exhibited limited movements.
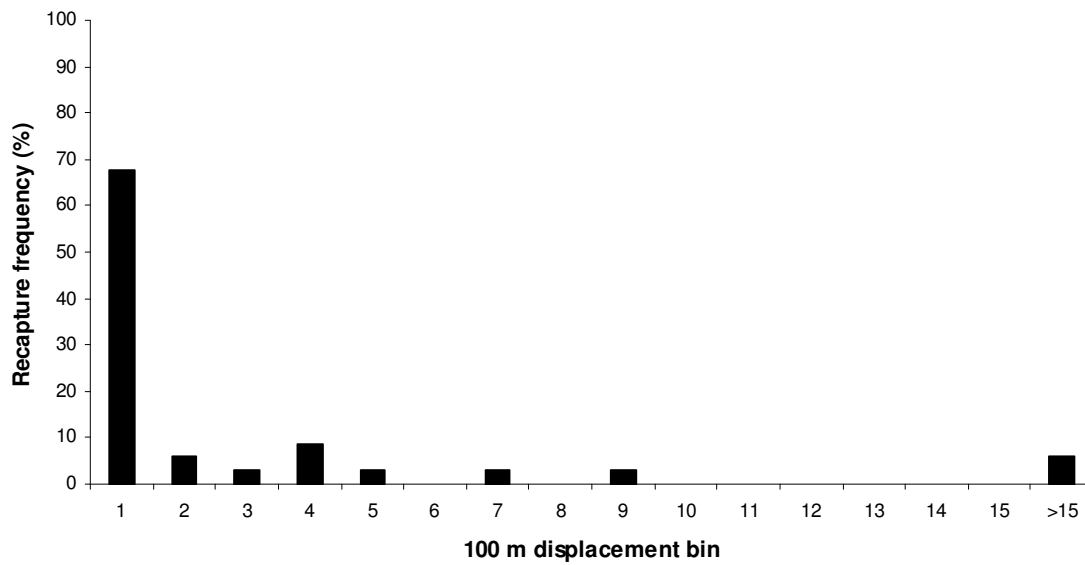
Figure 4.5. Proportion of TNP blacktail movements recorded within 100 m increments from the tagging locality (n = 31).
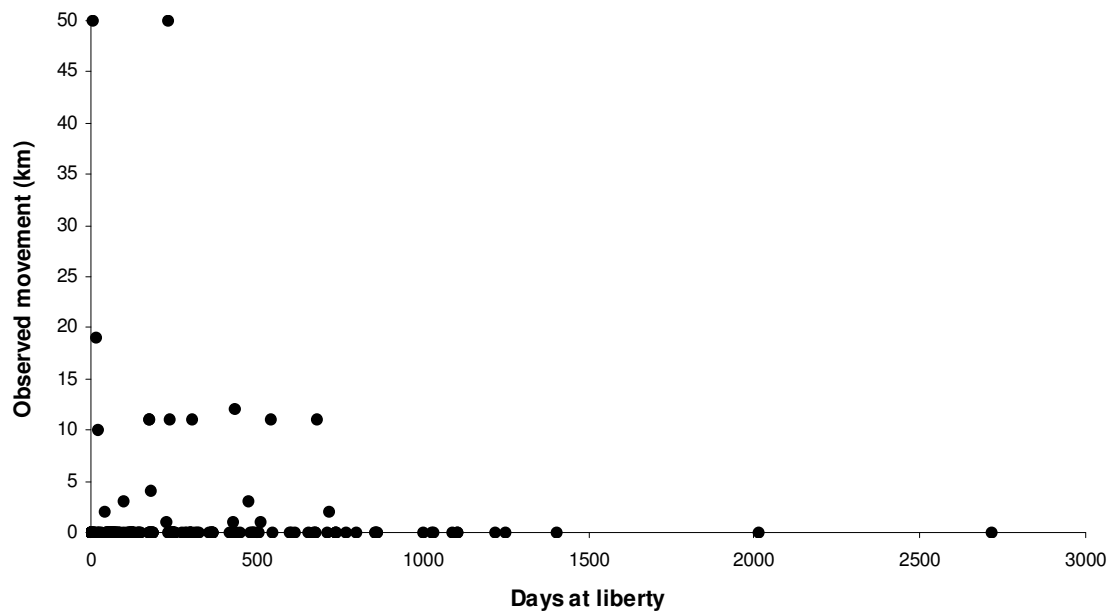

Figure 4.6. Blacktail movements (n = 192) relative to time at liberty
(combined programs; scale not preserved for largest movements - depicted at 50 km).
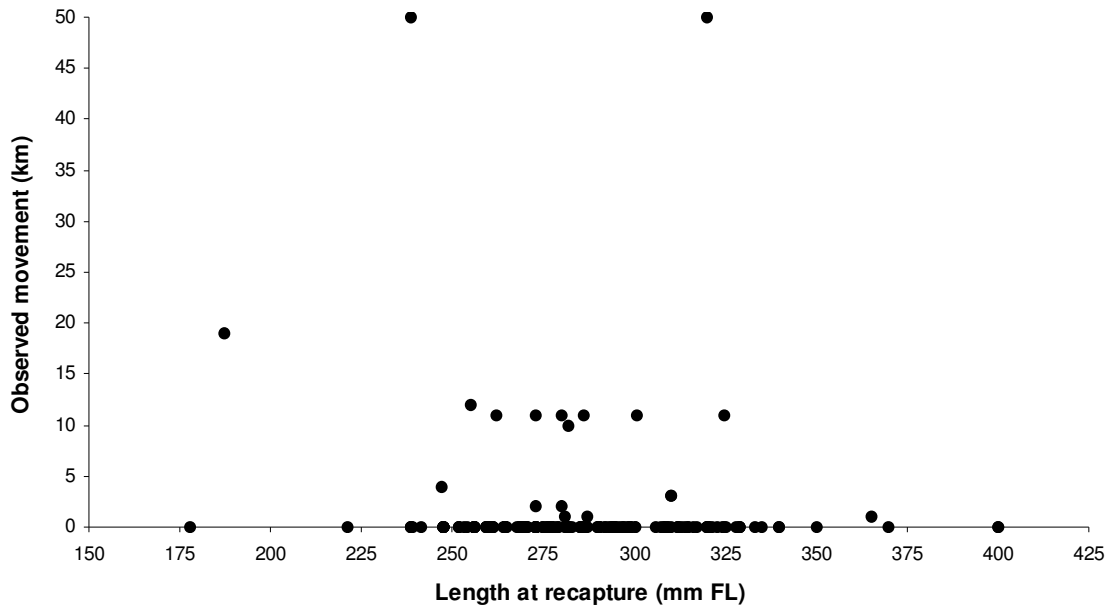
Figure 4.7. Blacktail movements (n = 192) relative to length at recapture (combined programs; scale not preserved for largest movements - depicted at 50 km).

4.3.2 Zebra

Of the 2126 zebra tagged along the South African coastline, 58 were recaptured (Table 4.3). Although TNP had a lower overall recapture rate than both DH and ORI, this difference was not significant at $\alpha = 0.05$ (two-tailed proportions test, p = 0.0504 and 0.057, respectively).

Table 4.2. Summary of movement data for zebra tagged and recaptured along the South African coast, 1984-2007.

Tagging program	Number of fish tagged	Number of fish recaptured {tag-scars}	Recapture rate (%)	Zero displacement (%)	Average & {maximum} movement in km	Average & {maximum} days at liberty
ORI	486	16	3.29	68.75	1.86 {11}	217 {1399}
DH	1195	36	3.01	94.59	1.70 {52}	200 {550}
TNP	445	6 {12}	1.34	85.71	0.14 {1.5}	189 {437}
Total	2126	58	2.73	84.75	1.63 {52}	203 {1399}

Zebra rarely moved from their tagging locality, with 85% of recaptures zero displacements. A few fish recaptured in the ORI program revealed small movements, with a maximum reported distance of 11 km, but over the combined programs only one fish moved further than 15 km. Five of the seven observed 'non-zero' movements were to areas west of the tagging locality (Figure 4.8), but whether this was evidence of a true directional movement pattern was equivocal due to the small sample size.
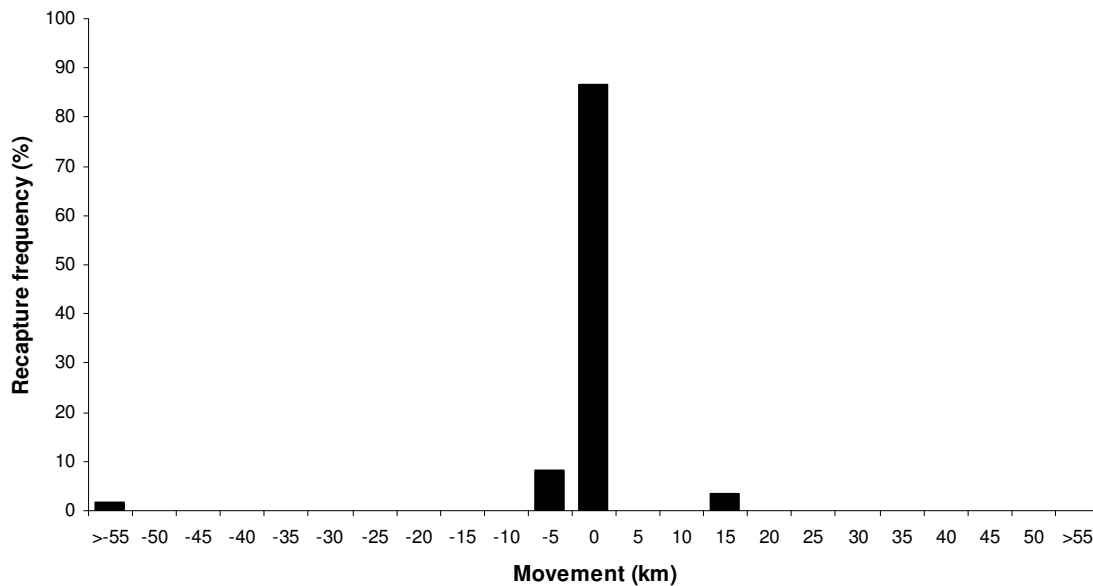

Figure 4.8. Movements of 58 zebra recaptured along the South African coast (combined programs). Negative values represent displacements in a westerly, and positive values an easterly, direction.

At DH, 35 fish (97%) were recaptured within the MPA, of which only one fish moved the 11 km between the two tagging sites. An additional fish moved 52 km west of its tagging site. Eight higher spatial-resolution DH movements recorded after 1998 indicated that zebra movements were generally on a scale smaller than the 3.4 km extent of the DH tagging sites. Six (75%) were recaptured at their tagging locality (i.e. movement $\leq$ 100 m), one at an immediately adjacent locality (i.e. movement $\leq$ 200 m), and the remaining one moved between 2 and 2.2 km. Recaptured zebra from the TNP also exhibited extremely restricted movements, with four of seven (57%) recaptures at the original tagging locality (Figure 4.9).
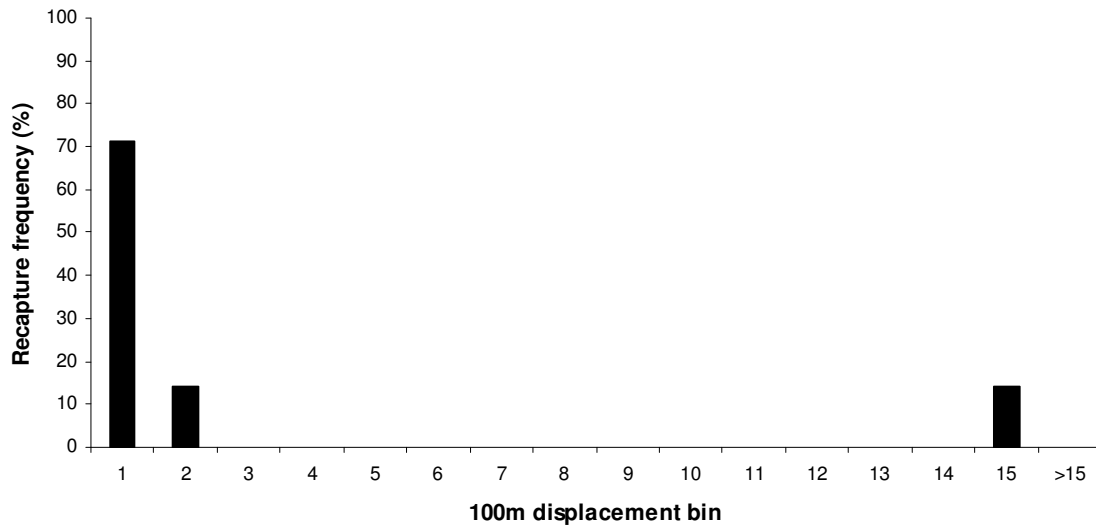
Figure 4.9. Proportion of TNP zebra movements recorded within 100 m increments from the tagging locality (n = 7).

Similar to blacktail, as the majority of recaptures were zero displacements there was no clear trend of zebra movements with either time at liberty or size at recapture (Figures 4.10 and 4.11). There were no significant differences in average time at liberty between programs (Kruskal-Wallis ANOVA, p = 0.268). A fair proportion of recaptures (13.6%) were made over a year after tagging, mostly zero displacements.
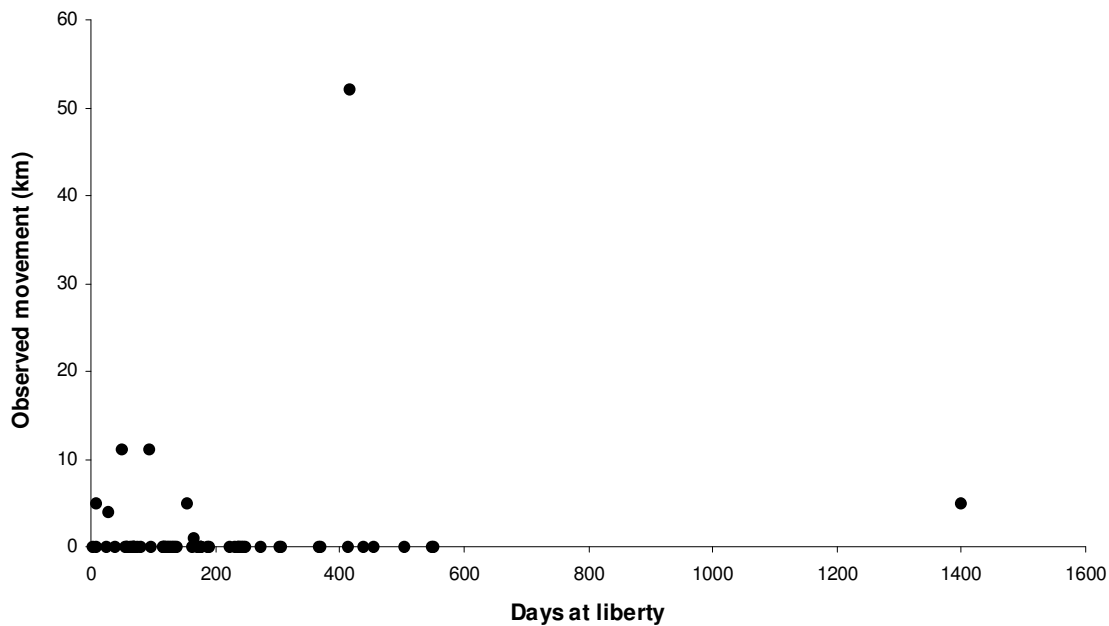

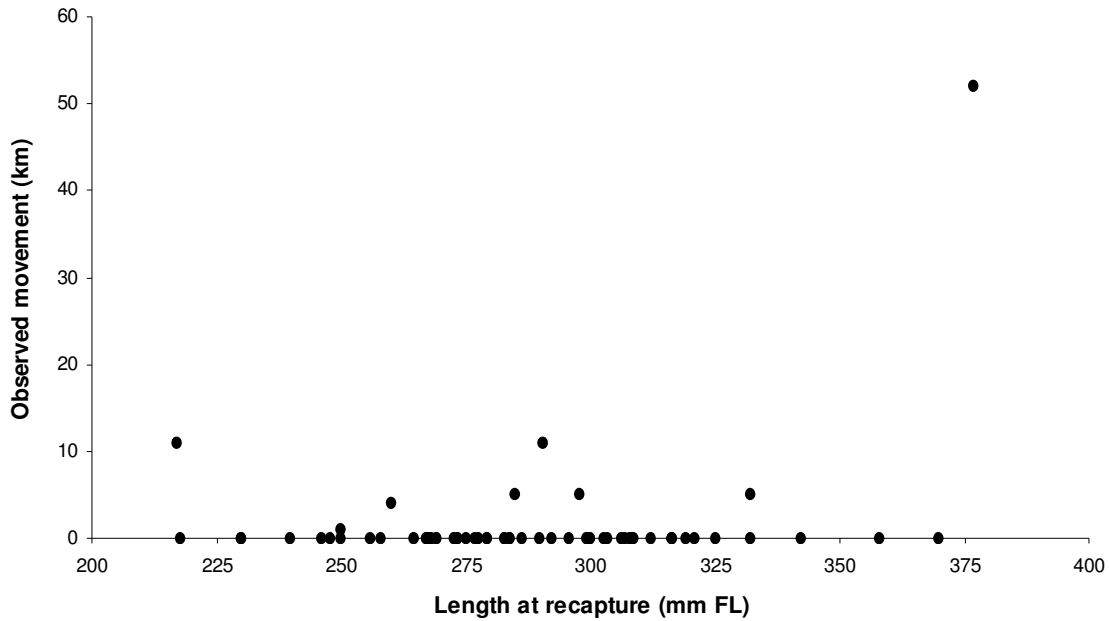Figure 4.10. Observed zebra movements (n = 58) relative to time at liberty (combined programs).

Figure 4.11. Observed zebra movements (n = 58) relative to length at recapture (combined programs).

4.3.3 Musselcracker

Of 1782 musselcracker tagged along the South African coast, 60 were recaptured. DH recapture rates were lower than in both TNP and ORI, although only significantly lower than ORI (Table 4.4; two-tailed proportions test, p = 0.041). Most (66%) recaptured musselcracker revealed limited movements ('zero displacements'), while some (12%) moved between 5 and 25 km either east or west of their tagging locality. Additionally, an even greater proportion (22%) moved distances in excess of 80 km, predominately in an easterly direction (Figure 4.12).

Table 4.3. Summary of movement data for musselcracker tagged and recaptured along the South African coast, 1984-2007.

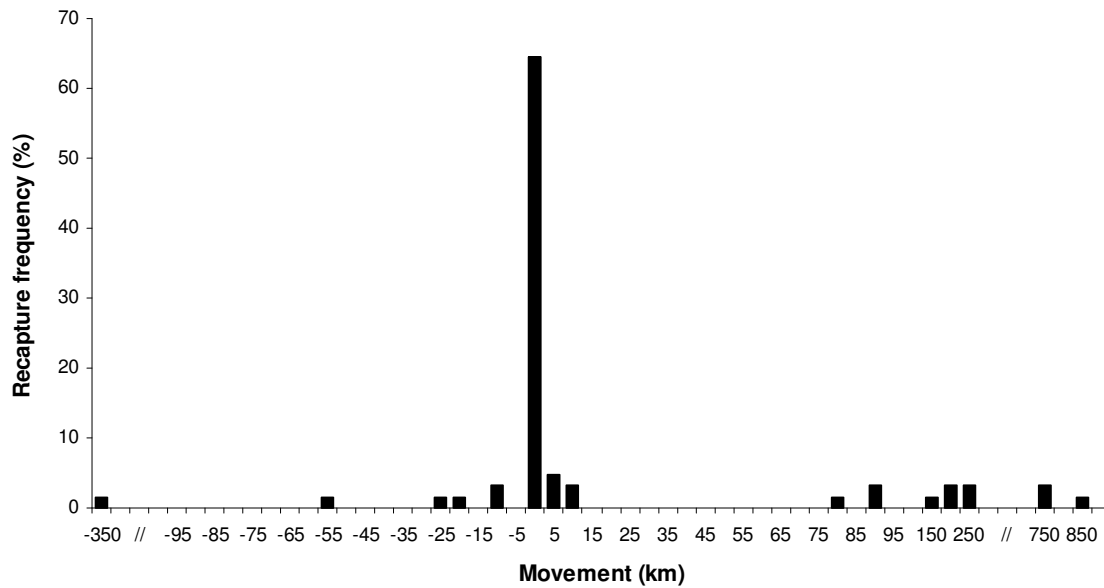| Tagging program	Number of fish tagged	Number of fish recaptured {tag-scars}	Recapture rate (%)	Zero displacement (%)	Average & {maximum} movement in km	Average & {maximum} days at liberty
ORI	821	33	4.02	62.50	96.78 {843}	632 {2313}
DH	393	7	1.78	57.14	50.00 {181}	919 {2409}
TNP	568	20 {10}	3.52	77.27	19.95 {209}	352 {1979}
Total	1782	60	3.37	65.57	63.70 {843}	564 {2409}

Figure 4.12. Movements of 60 musselcracker recaptured along the South African coast (combined programs). Negative values represent displacements in a westerly, and positive values an easterly, direction.

There were considerable changes in observed movements of musselcracker with change in size (Figure 4.13). Juveniles and young subadults (≤ 400 mm FL) showed no movement on a one-kilometre scale (Figure 4.13), and data from the TNP suggested they seldom moved greater than 100 m (Figures 4.14 and 4.15). Approximately half (46%) the recaptures of juveniles in the TNP were made at the tagging locality, with a similar proportion recaptured within 100m of the tagging locality, and the greatest movement recorded for this size-class only 220 m. Larger subadults and adults displayed greater movement. Appreciable movements (≥ 10 km) were only recorded in fish over 550 mm FL. However, the largest individuals recaptured (≥ 750 mm FL) exhibited less movement relative to the 550-750 mm size class (Figure 4.13), although the low sample size precluded a statistical validation of this trend. Increased movement correlated with change in size was exemplified by distances moved by TNP fish of different sizes (Figures 4.14 and 4.15), with 67% (n = 4) of fish > 600mm FL having moved to areas beyond the MPA boundary.
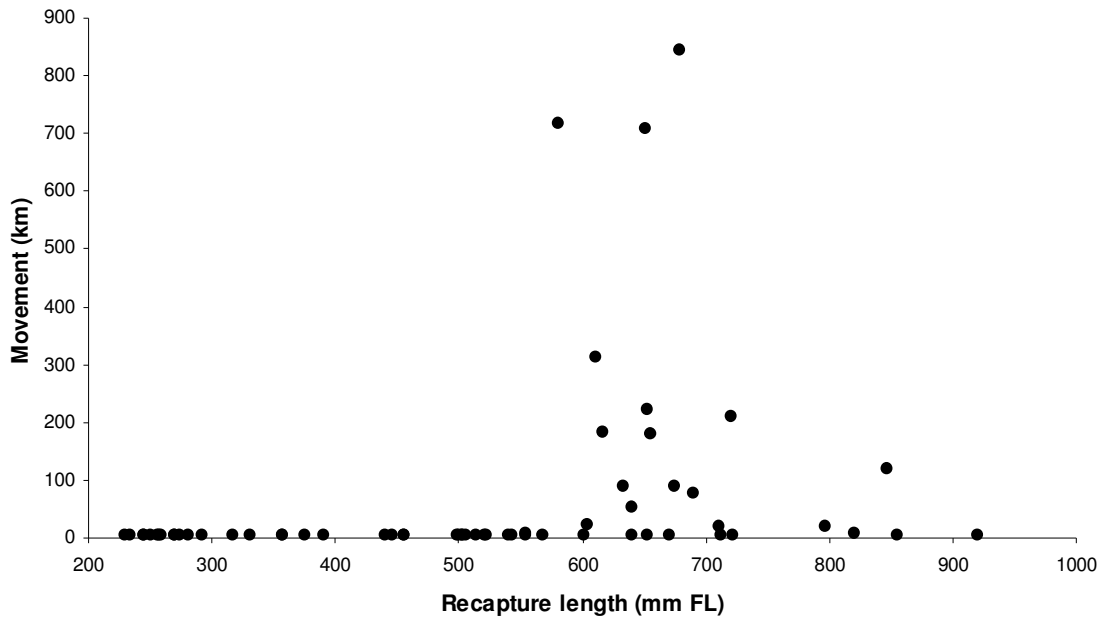
Figure 4.13. Observed musselcracker movements (n = 60) with length at recapture (combined programs).
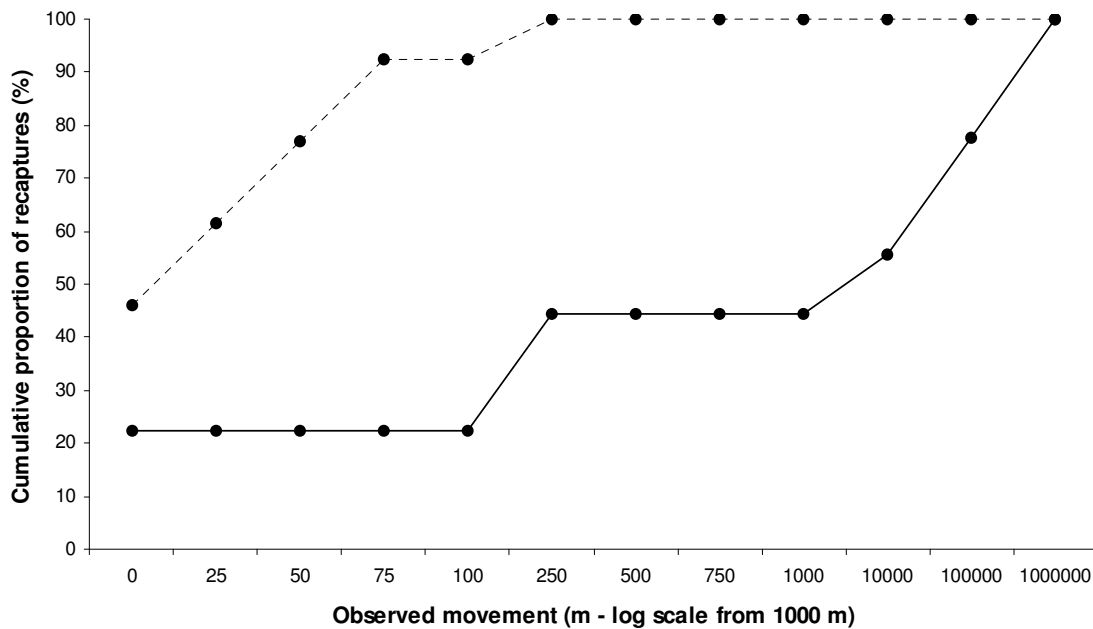

Figure 4.14. Proportion of observed movements of juvenile (---) and adult (—) musselcracker in the TNP that fell within a given distance from the tagging locality (n = 13 (juveniles); 9 (adults), including multiple recaptures). Note non-linearly increasing distance scale.
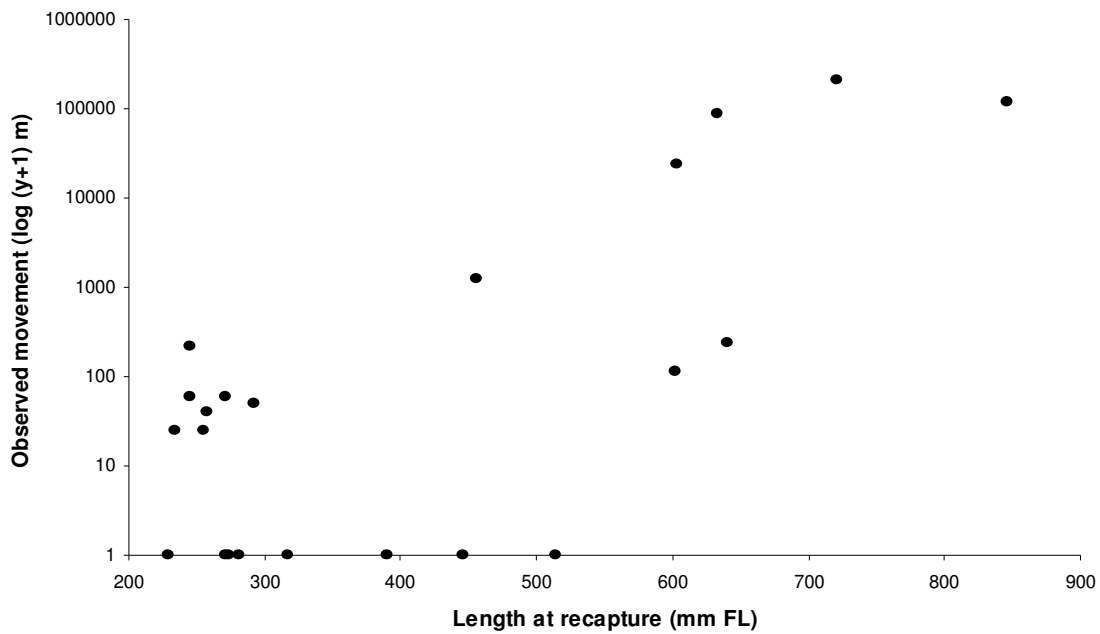
Figure 4.15. Observed musselcracker movements (n = 22, including multiple recaptures) with change in length from the TNP. Note non-linearly increasing distance scale.

Across all three programs nearly 70% (n = 19) of recaptured musselcracker $\geq$ 550 mm FL showed movement from their tagging locality (Figure 4.15), which could be characterised as either (i) limited movements with no trend in direction or seasonality, or (ii) large eastwards movements predominantly during the spring and summer spawning season (August to January; Table 4.4).

Table 4.4. Movements of musselcracker $\geq$ 550 mm FL recaptured along the South African coast (n = 28).

Movement	Number of fish recaptured	Distance moved			FL (mm)			Recaptured in spawning season
	Number {% of total}	Min	Max	Avg.	Min	Max	Avg.	%
Zero	9 {32.14}	n/a	n/a	n/a	554	920	707	77.78
East	13 {46.43}	7	843	265.8	567	840	666.6	84.62
West	6 {21.43}	8	311	71.2	554	820	672.1	50

Based on the magnitude and direction of all movements greater than 10 km, two trends were apparent. Firstly, there was a greater frequency of eastward movements, predominantly recorded during the spawning season and of greater magnitude than westward movements (Figure 4.16). Secondly, recapture areas of fish tagged at different sites along the coast were geographically distinct (Figure 4.16, see discussion). Although a high proportion of eastward movements were observed during the spawning season (August to January - Table 4.4), this was not significantly higher than the proportions of zero displacements and westward movements observed over this period (two-tailed proportions test, p = 0.284).
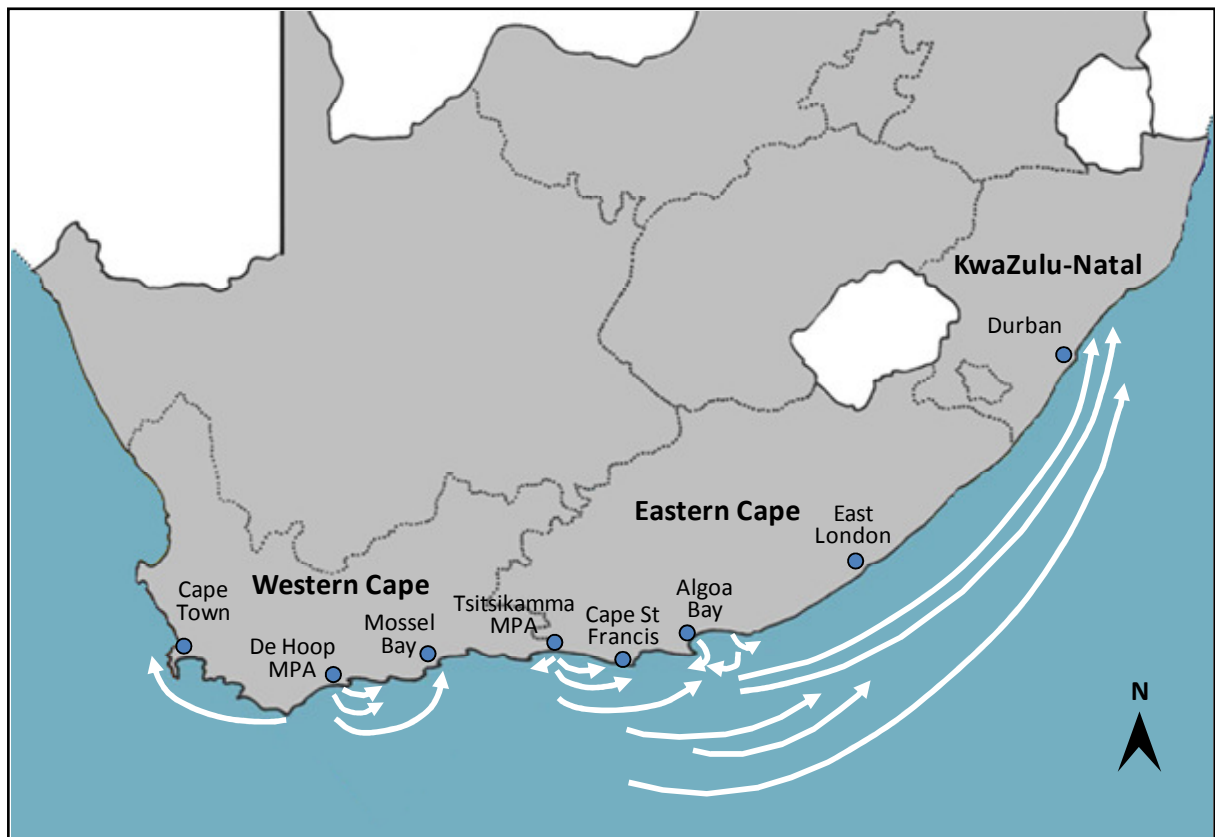

Figure 4.16. Location and magnitude of large-scale movements (> 10 km) recorded for musselcracker along the South African coast. All movement localities are coastal, with their position described by an imaginary line perpendicular to the coastal orientation and meeting the origin (tagging locality) or tip (tag recovery locality) of the respective arrows.

4.4   Discussion

This study made use of movement data, albeit at different spatial resolutions, from three tagging programs that spanned periods exceeding 10 years and covered the entire South African distribution of blacktail, zebra and musselcracker. This allowed for a good appraisal of the movement behaviour and dispersal of these species. Overall recapture rates were low (< 4%), and significantly lower for blacktail tagged in the TNP in comparison to DH. Both of these were highly structured scientific projects with trained scientists applying tags.   The TNP, unlike the DH coastline, is characterised by steep cliffs and a rugged rocky intertidal zone, and it is therefore proposed that higher levels of tag loss, resulting from increased contact with rocks, occurred in the TNP. Additionally, greater amounts of epiphyte growth on tags (Figure 4.1) were recorded on fish from rocky habitats (P. Cowley, South African Institute for Aquatic Biodiversity, pers. comm.). Griffiths & Attwood (2005) suggested fouled tags might alter a fishes' behaviour and/or health, and ultimately result in reduced recapture rates.   High levels of tag loss in the TNP were confirmed by fish bearing characteristic tag scars (Figure 4.2, Tables 4.1, 4.2 and 4.3).   If these individuals were considered normal recaptures, overall recapture rates from the TNP would have been substantially higher and closer to the other programs.   Unfortunately, tag scars were unreported for DH and ORI, making comparisons of tag loss rates impossible.

In contrast to blacktail, white musselcracker in DH had the lowest overall recapture rate. This was likely due to the higher average size of musselcracker tagged in DH than in the other programs. Juvenile (< 400 mm FL) musselcracker were rarely caught at DH relative to larger fish, leading to less of these resident individuals being tagged and recaptured than in other programs. The ORI program utilised predominantly volunteer anglers to tag fishes at varying localities along the South African coastline, whilst the MPA programs (TNP and DH) used experienced scientific personnel (Attwood & Cowley 2005).   The chances of recovering resident fishes (zero displacement) from MPA programs were proportionally higher than the ORI program due to standardised recapture effort and 100% reporting rates. Unquantified levels of 'patchily'-distributed recapture effort and unknown reporting rates outside of the MPA sites thus complicated analysis of coastwide movement patterns. Consequently, the high frequency of zero displacements may need to be considered with caution, as the majority were recorded from the MPA programs, which are characterised by high levels of recovery effort centred on the research site (i.e. zero-displacements) versus outside areas.

However, the DH data allowed for comparison of recapture rates 'within' versus 'between' sites, and together with high spatial-resolution results from the TNP confirmed the predominance of highly restricted movements. Non-reporting of tag-recoveries has been recorded in several South African studies (Attwood & Bennett 1994, Brouwer 1997, Lamberth 1997 cited in Attwood & Cowley 2005, Kerwath 2005) and been ascribed to (i) ignorance and fear of prosecution for illegal fishing activities (e.g. fishing in an MPA), (ii) the desire to keep fishing spots unknown to others, or (iii) simply forgetting to post the tag and recapture information to ORI. Additionally, Brouwer (1997) reported that many fishermen gave recovered tags to angling clubs or fishing tackle shops that subsequently failed to report them to ORI. The vagaries of the South African postal system may also have resulted in the non-recording of tag returns. Recently, tags bearing a mobile phone number have been used in the Addo National Park, enabling fisherman to immediately report recaptures and provide additional data to scientists. Although preliminary, this has proved to be successful (P. Cowley, South African Institute for Aquatic Biodiversity, pers. comm.) and will hopefully result in increased reporting rates in future studies. Movement distances recorded in the ORI database might be in error because localities are sometimes reported as that of the closest town, or as access points to areas with widely-distributed fishing sites. Such errors may significantly influence the results of studies on resident species that display limited movements. If a potential reporting error of 5 km (Attwood & Cowley 2005) were taken into account in this study, more than 50% of blacktail and 80% of zebra movements may have been zero displacements on a one-kilometre scale. Correspondingly, however, certain zero displacements could have misrepresented movements of up to 5 km.

All three species displayed limited movement over long periods. Blacktail and zebra showed extreme residency throughout adolescent and adult life. Similarly, juveniles and young subadult musselcracker were extremely resident, but older individuals displayed both resident and dispersal behaviours, with movements of up to 850 km observed. The limited movement of blacktail, zebra and juvenile musselcracker over relatively long periods was indicative of strong site-fidelity and temporally stable home ranges of limited extent. Although these could not be directly quantified, home ranges are characteristic of numerous reef fish species, both in temperate (Matthews 1990, Lowry & Suthers 1998, Lowe et al. 2003) and tropical areas (Zeller 1997, Eristhee & Oxenford 2001, Meyer et al. 2000, Meyer & Holland 2005), and would be expected for resident blacktail and zebra.

The small-scale movements observed in the TNP suggested home ranges of these fishes spanned alongshore distances of between 10 and 100 m. Kramer & Chapman (1999) provided a prediction of the linear extent of home ranges of resident reef fishes from their length (as a proxy for size). From this, home ranges for average-sized blacktail and zebra (305 and 275 mm FL respectively) recaptured in the TNP were predicted as 123 m and 96 m. Approximately 70% of observed movements fell within this range. Similarly, average-sized musselcracker (281 mm) recaptured in the TNP were predicted to have a home range of 101 m and over 90% of recaptured juveniles were within 75 m of their tagging locality. This is not incongruent with the larger home range prediction as this is based on studies of sometimes widely different species. Individual fish may also have smaller (or larger) home ranges than those characteristic of their species because home range size may be determined by localised environmental characteristics (e.g. habitat features such as reef rugosity).

In addition, it is possible that the recorded angling locality only represented a smaller portion (i.e. a foraging area) of the extended home range of recaptured individuals. Small recapture displacements on a plane parallel to shore may have comprised a smaller component of home ranges that extend in a direction perpendicular to the shore. Individuals with home ranges centred offshore may have made periodic inshore excursions (e.g. during high tide periods) to feed or for other activities (Gibson 2003). Biden (1948) referred to blacktail moving to sandy areas "an hour before high tide" to feed. Similarly, Krull (1999) reported that blacktail move into gullies and similar areas during high tide. The advantages of small, well-established home ranges in the dynamic physical conditions of their nearshore habitats are apparent for these fishes. Knowledge of their home range area enables efficient refuge from predators, foraging, resting, retreat from strong water currents or movement back to these after displacement. Life in shallow water often exposes these fishes to rough water conditions (e.g. in narrow rocky gullies and areas where waves break onto reefs). In this turbulent 'white water' sight alone is unlikely to be successful for navigation, but in combination with sight and the lateral-line system intimate knowledge of the home range area layout probably facilitates efficient obstacle avoidance.

Blacktail and zebra occasionally made comparatively large movements, with approximately 4% of DH blacktail moving at least 11 kilometres between the two tagging sites. Attwood & Cowley (2005) proposed two models of movement for the generally resident galjoen (*Dichistius capensis*), which might be considered applicable to blacktail and zebra. Their "tourist" model predicts fish are resident in a particular area, but make periodic movements to one or more alternative sites along the coast where they reside for varying periods of time before returning to one of the other areas. The alternative "polymorphic" model predicts that the population consists of both resident and nomadic individuals. However, the observed frequency and magnitude of large blacktail and zebra movements was lower than those of galjoen. Lack of movement at second recapture, following initial movement, for one DH and one ORI blacktail suggested permanent establishment of a new home range. There are numerous possible reasons for fishes to abandon their home range, not least of which the stress of capture and tagging resulting in vacation of the thereafter 'unsafe' home range (Thorstad *et al.* 2004). Other potential reasons include ontogenetic migration, displacement by severe sea conditions or competitive processes within an established home range (Kramer & Chapman 1999). There was no relationship between displacement and fish size, so it is likely that the few observed large movements for blacktail and zebra were not linked to ontogenetic factors.

Most of the larger musselcracker (> 550 mm FL) made substantial movements. These fish are powerful swimmers and movements of a few kilometres could easily have been made during the course of normal daily activities. However, many large fish exhibited residency for considerable periods, suggesting that they also had relatively small core home range areas. Following predictions of Kramer & Chapman (1999), a 550 mm FL fish would have a home range close to 500 m in width, while at 800 mm a home range of over 1 km would be expected. Habitat structure (continuity and connectivity) has been shown to influence the distribution (Nanami & Nishihira 2002) as well as the occurrence and scale of daily movements of fishes (Pittman *et al.* 2007, Chateau & Wantiez 2008, Nagelkerken *et al.* 2008). It is probable that in areas where the distribution of reefs supporting sufficient prey is patchy large musselcracker make movements between reefs separated by a few kilometres or more during daily feeding activities, while in areas of continuous reef habitat movements are more restricted. This may have explained movements of intermediate distance, but cannot account for those of larger extent (> 10 km).

Booth (2000) suggested this species undertakes a spawning migration from Southern and Eastern Cape waters to Transkei and KwaZulu-Natal waters. Observed movements of fish tagged from Algoa Bay eastwards recaptured on the central KwaZulu-Natal coastline during the spawning season supported this hypothesis. Such movements were also corroborated by data from shore-angler catch records in KwaZulu-Natal, with musselcracker catches on this section of the coast predominantly occurring between July and November (P. Pradervand, Oceanographic Research Institute, unpublished data). The two tagged fish recaptured between Algoa Bay and KwaZulu-Natal were caught outside this period (late February and April), and were likely fish 'in transit' between these regions. KwaZulu-Natal anglers and spearfishermen refer to an annual musselcracker "run" that begins between late June and August and ends between late November and December, depending on the year (Fishing reports - The Mercury; 2004-2007, Monthly spearfishing reports – www.spearfishingsa.co.za; 2001-2007). Evidently, large numbers of musselcracker undertake a spawning migration to KwaZulu-Natal waters each year. However, during the spawning season musselcracker are also targeted and captured throughout their distributional range, particularly in Mossel Bay (Joubert 1980, van Rooyen 1987, Schoeman, publishing date unknown) and Algoa Bay (Clarke & Buxton 1989, Coetzee & Baird 1981). The KwaZulu-Natal migration must therefore only be undertaken by a proportion of the breeding musselcracker population.

Observed movements of fish tagged at different localities along the coast (Figure 4.16) may represent distinct spawning areas for fish resident in particular regions outside of the spawning season, with (i) fish from Algoa Bay eastwards moving up the Transkei coast to central KwaZulu-Natal, (ii) fish from other Eastern Cape regions moving eastwards towards Algoa Bay, and (iii) Western Cape fish moving eastwards to a locality west of Tsitsikamma (possibly representatives of the well-known Mossel Bay aggregations). Nearshore oceanography supports this hypothesis. Off KwaZulu-Natal and the Transkei the Agulhas Current lies close inshore, and many species have evolved life-histories that utilise southward-moving inshore currents in this area to transport eggs and larvae to nursery areas in the Eastern and Western Cape (Hutchings *et al.* 2002). These species include the white steenbras (*Lithognathus lithognathus*; Bennett 1993), red steenbras (*Petrus rupestris*; Smale 1988) and geelbek (*Atractoscion aequidens*; Griffiths & Hecht 1995). Musselcracker eggs and larvae spawned off central KwaZulu-Natal would be transported southwards and settlement-stage larvae located off the Eastern Cape coast, where large areas of suitable rocky nursery habitat exist.

Lutjeharms *et al.* (1986) reported that recoveries of drift card releases from the South African east coast were highest from those made west of Algoa Bay, these moving in both easterly and westerly directions, while cards released further east off the Eastern Cape coast (e.g. off East London) generally became entrained in the Agulhas current and displaced offshore with its passage along the shelf-break. Similarly, Hutchings *et al.* (2002) suggested that, due to complex water circulation in this region, eggs and larvae spawned here are as likely to be displaced far offshore as southeastwards onto the Agulhas Bank. The region immediately east of Algoa Bay may therefore represent a physical obstruction to successful spawning and consequently necessitate the spawning migration of this species to KwaZulu-Natal waters. While this hypothesis seems counterintuitive to that of larval drift from KwaZulu-Natal to Eastern Cape waters, when they reach this region larvae have probably developed sufficient swimming abilities to avoid offshore displacement, maintaining a nearshore position until settlement.

Similarly, the use of more southerly spawning areas along the Eastern and Western Cape coasts is driven by local oceanographic conditions. West of Algoa Bay the Agulhas current lies a considerable distance offshore, located furthest away in the Agulhas Banks region, and does not affect inshore conditions to the same extent as further east. Drift of eggs and larvae spawned here is more likely to be affected by nearshore oceanography driven by coastline topography and prevailing wind regimes (Schumann 1999, Hutchings *et al.* 2002). Recovered surface drift cards released east of Cape Agulhas on the Agulhas Banks show retention in this region and movement onshore with prevalent southerly summer winds (Shannon & Chapman 1983). In contrast, drift card releases west of Cape Agulhas moved around the Cape Peninsula under prevailing winds and currents and became entrained in the west coast upwelling system (Lutjeharms *et al.* 1986). If pelagic eggs and early larval stages are considered similarly passive particles, spawning in Western and Eastern Cape waters east of Cape Agulhas would lead to retention of eggs and developing larvae in this region, minimising loss to unsuitable Benguela Current waters located west of the Cape Peninsula. It is hypothesised that this would also be a physically less-demanding strategy for fish resident in these waters than to undertake a spawning migration to KwaZulu-Natal.

The eastward migrations of musselcracker and several other coastal fish species to KwaZulu-Natal during the winter months coincide with reduced water temperatures, reduced southward current speeds and increased northeasterly inshore countercurrents (Schumann 1988), thereby providing suitable conditions for the establishment of a seasonal extension of their normal distributional ranges (Garratt 1988, van der Elst 1988b, Beckley & van der Lingen 1999). Observed musselcracker movements to KwaZulu-Natal would certainly fit this hypothesis, and it could be argued that these are therefore not driven by spawning activity *per se*, but rather by physiologically suitable conditions resulting in a seasonal range expansion (Clarke 1988). However, musselcracker arrive in KwaZulu-Natal later than species traditionally regarded as winter migrants and stay well into the summer months during warmer water conditions (P. Pradervand, Oceanographic Research Institute, unpublished data). This would appear to refute the range extension hypothesis, although the seasonal temperature changes on this section of the coast may facilitate the migration process and may have been involved in its evolution.

It must be noted that hypothesised musselcracker spawning migration patterns are at present based on very limited recapture data and need to be further examined. This could be achieved by examination of standardised CPUE data; however, at present, only the two widely separated DH and TNP studies provide estimates of effort for reliable abundance estimates from tagging data. Because no effort data is available from the ORI tagging database, the numbers of musselcracker tagged in various regions of the coast at particular times cannot be reliably used for this purpose due to potential spatial and temporal biases (e.g. increased effort in certain areas over holiday seasons). Dynamics of reproductive movements (i.e. exact timing; demographic and social characteristics; relation to potential environmental and biological driving factors; exact localities and frequency of spawning; degree of spawning site fidelity and natal homing; potential stock segregation) could be investigated through genetic studies, otolith microchemistry and/or archival tagging of adults. Given this species' large size, the use of archival data storage tags should be feasible. Natural tags can potentially also be used to uncover temporal patterns in area use of individuals. For example, movement to warmer KwaZulu-Natal waters should be reflected in ^{18}Oxygen stable isotope levels, related to ambient water temperatures (Weidman & Millner 2000, Stephenson *et al.* 2001), deposited in otoliths and possibly scales (allowing non-lethal sampling; Perga & Gerdeux 2001, Kennedy *et al.* 2005) of individual fishes.

Chapter 5 - Foraging activity and habitat-use patterns

inferred from research angling data

5.1   Introduction

The South African shallow inshore marine environment is characterised by dynamic wave action and associated high-energy conditions. The turbulent conditions within these areas make underwater visual census, videography or even remote recording of fish behaviour (e.g. acoustic telemetry) practically impossible. Consequently, studies on the behavioural ecology of resident species within these areas, such as those under investigation here, are extremely difficult. Resident species with relatively small home ranges often have a strong temporal component to their behaviour (Pittman & McAlpine 2003). For example, endogenous circadian rhythms (Boujard & Leatherland 1994) and exogenous environmental factors such as the daily tidal (Gibson 2003) and light cycles (McFarland 1986, Helfman 1993) often influence activity patterns and associated behaviour of many fish species.

Foraging can comprise the dominant behaviour of fish during periods of activity (Matsumoto 2001). The three study species have been described as searchers (Mann 1992, Clarke 1988), whereby they actively seek out prey (Hughes 1980). There is thus a direct link between their foraging behaviour, activity patterns and movements between areas in search of food. Whilst their dietary composition (Buxton & Clarke 1991, Mann & Buxton 1992) and habitat preferences (Clarke 1988, Mann 1992) have previously been described, these did not examine foraging behaviour beyond brief descriptive observations. The use of baited fishing gear to catch fishes has an implicit relationship to their foraging activities. Whilst it may thus be regarded as a biased sampling method for studies on the temporal abundance of fishes, it potentially provides a method of studying their foraging behaviour and activity patterns with respect to temporal rhythms and habitat preferences. Long-term research angling data from the Tsitsikamma National Park (TNP) recorded catches of resident reef fishes at a high spatial and temporal resolution and presented an opportunity to test whether standardised research angling data can be used to infer foraging activity patterns of the study species.

The majority of studies on fish foraging behaviour make direct observations on the animals (e.g. Nanami & Yamada 2008), or spatial and temporal analysis of gut contents (e.g. Bromley *et al.* 1997, Hibino *et al.* 2006). Predominant sea conditions precluded underwater observation of fishes at the study site, and incorporating gut content analysis would have required sacrificing large numbers of resident reef fishes in a MPA proclaimed to conserve their populations, and was not considered. Capture rates (catch per unit effort) on baited sampling gear are often used to infer fish abundance and distribution, but while numerous studies have studied fish behaviour towards baited gear (e.g. Grimes *et al.* 1982, Fernö & Huse 1983, Løkkeborg *et al.* 1989), there have only rarely been reciprocal studies using baited gear to study their foraging behaviour (Hall *et al.* 1990, Løkkeborg 1998). To what extent observed variation in fish capture is attributable to their natural foraging patterns determines the validity of this method. Both ability of fish to detect bait and likelihood of them consuming it may be affected by a number of factors in addition to natural foraging patterns. According to Stoner (2004), these factors include strength and direction of water currents (influencing olfactory detection), water clarity (affecting visual detection and identification of bait and/or angling disturbance), availability of natural prey (trade-offs between preferred food and search time) and fish satiation level (hungry individuals more likely to consume "unnatural" bait). Data collected from research shore-angling in the TNP included time and locality of capture, thereby providing information on the association with diurnal light and tidal cycles as well as specific habitat. This study made use of catch data to infer (i) foraging activity patterns in relation to time of day and/or tidal phase, and (ii) habitat use of the study species, by examining the effects of these factors on probability of capture on baited fishing gear.

5.2 Methods

Details of the Bloukrans study site and research angling activities are described in Chapters 2 and 4. Supplementary information is provided below.

5.2.1 Angling activities

Six years of TNP catch and effort data from late 2001 to the end of 2007 were analysed. All angling localities were named and georeferenced (see Chapter 4). The generally rocky coastline resulted in these being stable in terms of subtidal habitat throughout the study period. Anglers only fished during daylight hours, generally starting within an hour after sunrise and finishing within an hour of sunset.

They were not constrained to fish particular localities, moving between these throughout the day. Periods spent fishing continuously by individual anglers at each locality were recorded and designated unique angling 'stations'. Recorded information included the station locality, start and end times, as well as capture times and fork length (to the nearest millimetre) of all fishes caught. Bait and tackle set-ups, including hook sizes, varied between anglers. The dominant bait species included pilchard (*Sardinops sagax*), redbait (*Pyura stolonifera*), chokka squid (*Loligo vulgaris reynaudii*), octopus (*Octopus vulgaris*), polychaete worms (*Marphysa* spp., *Pseudonereis variegata*), sand mussel (*Donax serra*) and pink prawn (*Haliposoides triarthrus*).

5.2.2 Diurnal and tidal cycles

Angling effort and fish capture times were categorised according to the diurnal (light) and tidal cycles. The daily light cycle was divided into six light-phase categories standardised around times of sunset and sunrise (instead of equal division of the entire day, which varied in length with season), as they are important initiators of activity and behaviour in many diurnal fish species. This resulted in the following six light-phase categories:

1. Dawn (0-2 hrs after sunrise)
2. Morning (2-4 hrs after sunrise)
3. Noon(1) (4 hrs after sunrise to mid-day)
4. Noon(2) (mid-day to 4 hrs before sunset)
5. Afternoon (4-2 hrs before sunset)
6. Dusk (2-0 hrs before sunset)

The tidal cycle was similarly divided into eight categories in relation to high and low tide. 'High' and 'Low' were standardized as one-hour periods between thirty minutes before and after high and low tide, respectively. The remaining tidal period was divided into six equal sections, giving the following ordered tide-phase categories [based on those of Braune & Gaskin (1982)]:

1. High (High)
2. Slow-ebb 1 (SE1)
3. Fast-ebb (FE)
4. Slow-ebb 2 (SE2)
5. Low (Low)
6. Slow-flood 1 (SF1)
7. Fast-flood (FF)
8. Slow-flood 2 (SF2)

5.2.3   Habitat classification

Physical conditions limited the use of traditional quantitative techniques (e.g. underwater transect surveys) to describe habitat at most angling localities.   An indirect two-tiered approach was therefore used to classify these to broad habitat categories – namely sandy, shallow reef and deep reef habitats.   Firstly, experienced research anglers' knowledge of angling localities was utilised to assign them a broad habitat type.   Anglers' knowledge of habitat at particular localities had been acquired during opportunistic above- and below-water observations during exceptionally calm water conditions, and angling activities (e.g. frequency of snagging on reefs versus sand-dominated areas).   Secondly, overall species catch composition at localities functioned as a proxy for habitat and therefore a method of corroborating angler habitat classifications.   All main localities' species compositions were analysed for similarity using cluster analysis (group-averaged Bray & Curtis distances) on square-root transformed relative abundances of individual species.   Occurrence of indicator species, generally restricted to specific habitats, at sites within the resulting clusters identified their habitat type.   Localities that could not satisfactorily be assigned a habitat type using these methods were not included in subsequent capture probability analyses.

5.2.4   Size-classes

All captured individuals of the study species were assigned to a size-class based on their recorded length. Blacktail were classified as small, medium or large, corresponding to fish of length < 250, 250-299 and > 300 mm FL, respectively, zebra either small or large (< 300 mm versus > 300 mm FL), and musselcracker small or medium (< 400 and 400-599 mm FL). Larger musselcracker (> 600 mm FL) were rarely caught during the study period.

5.2.5   Season and water temperature

Months during which sampling took place were assigned the following seasons:

1. Summer (December to February)
2. Autumn (March to May)
3. Winter (June to August)
4. Spring (September to November)

Daily water temperature was recorded by a permanently-moored underwater temperature recorder (depth 20 m) within 30 km of the study site, the temperature anomaly being expressed as 'relative water temperature', defined as the difference from average water temperatures recorded for the corresponding season at the study site over recent years (M. Roberts, Marine and Coastal Management, unpublished data).

5.2.6 Additional data preparation

Each angling station was divided into portions in relation to periods falling within the light- and tide-phase categories. As anglers sometimes fished localities concurrently, the total effort at a particular angling locality during each light- or tide-phase on each day was the sum of all station portions fished concurrently there. All fish caught at each angling locality were similarly assigned to a light- and tide-phase category to quantify capture success or failure for the particular species' length class for each category on each day.

5.2.7 Statistical analysis

For each size class of each species, effects of habitat-type, light-phase, tide-phase, season, relative water temperature and angling effort on probability of capture were analysed with hierarchical logistic regression (Snijders & Bosker 1999, Lee & Nelder 2001). Observed data were the binary outcomes of whether at least one fish was caught during a particular period in a particular locality (1), or not (0). This was expected to follow the single-trial binomial distribution (Bernoulli distribution), and related to a linear combination of the explanatory variables through the logit link function (McCullagh & Nelder 1989). Spatial and temporal coverage of angling effort was highly variable and localities were fished repeatedly over variable categories on the same or different days to others. Unrecorded environmental variables that varied between angling days potentially influenced both angling operations and fish foraging behaviour, and the indirect habitat classification method used also potentially resulted in unquantified small-scale habitat characteristics of particular localities influencing capture probability. Failure to consider the resulting relatedness of data collected on the same day or at the same locality during analyses would constitute (respectively) temporal and spatial pseudoreplication (Hurlbert 1984), potentially bias model parameter estimates and possibly lead to incorrect statistical inference (Millar & Anderson 2004). Hierarchical generalized linear models (HGLMs - Lee & Nelder 2001) were therefore used to account for relatedness of the data.

In HGLMs, random effects incorporate correlation between observations at each level of a nested hierarchy. In this case random effects were included for each angling day and angling locality; the resulting hierarchy consisting of individual observations within each particular angling day and locality. HGLMs compare the residual of each observation to the mean of all observations for its higher levels (i.e. its specific angling day and locality), as well as that of the overall population of observations as in normal regression (Snijders & Bosker 1999). Zero values dominated the observed data set (*ca* 85% of medium-size blacktail observations, the most abundant species caught) and therefore binary capture probability was preferred to capture rate as the measure of foraging activity. As angling trips always coincided with spring tide periods, light- and tide-phases were highly correlated (Figure 5.1) and were only included as explanatory variables in separate analyses.

Selection of final models utilised the Akaike Information Criterion (AIC; Akaike 1981), in comparison of alternative simple logistic models, to arrive at a final model that was then analysed with hierarchical logistic regression. AIC is based on the amount of observed variation explained by a model and its number of parameters, which exert opposing influences on the AIC score, the best-fitting model of the data giving the lowest AIC score. AIC scores were calculated for models containing all main effect combinations as well as first-order interactions of the explanatory variables. As the main variables of interest, light or tide-phase, together with habitat, were always retained in final models. In the final hierarchical analysis, control factors (season and relative water temperature) included by AIC but not significant at α-level 0.1 were dropped from the final model. Significance of all explanatory variables was assessed at α-levels of 0.05 and 0.1 with global Wald tests. Significance at α of 0.05 of differences between predicted means of different categories of significant variables was assessed by comparison of the standard error of the difference between means to their respective 95% confidence intervals (Brandstätter 1999). Because separate analyses were carried out for each size-class, differences between these could not be directly assessed within species. In cases where both light- and tide-phase were significant variables, p-values for other factors presented are from models containing light-phase (in all cases, whether light- or tide-phase constituted the relevant variable did not change overall significance of other variables, except where these were involved in interactions with light- or tide-phase). All statistical analyses were carried out with GenStat (11th edition trial version, VSN International, 2008).
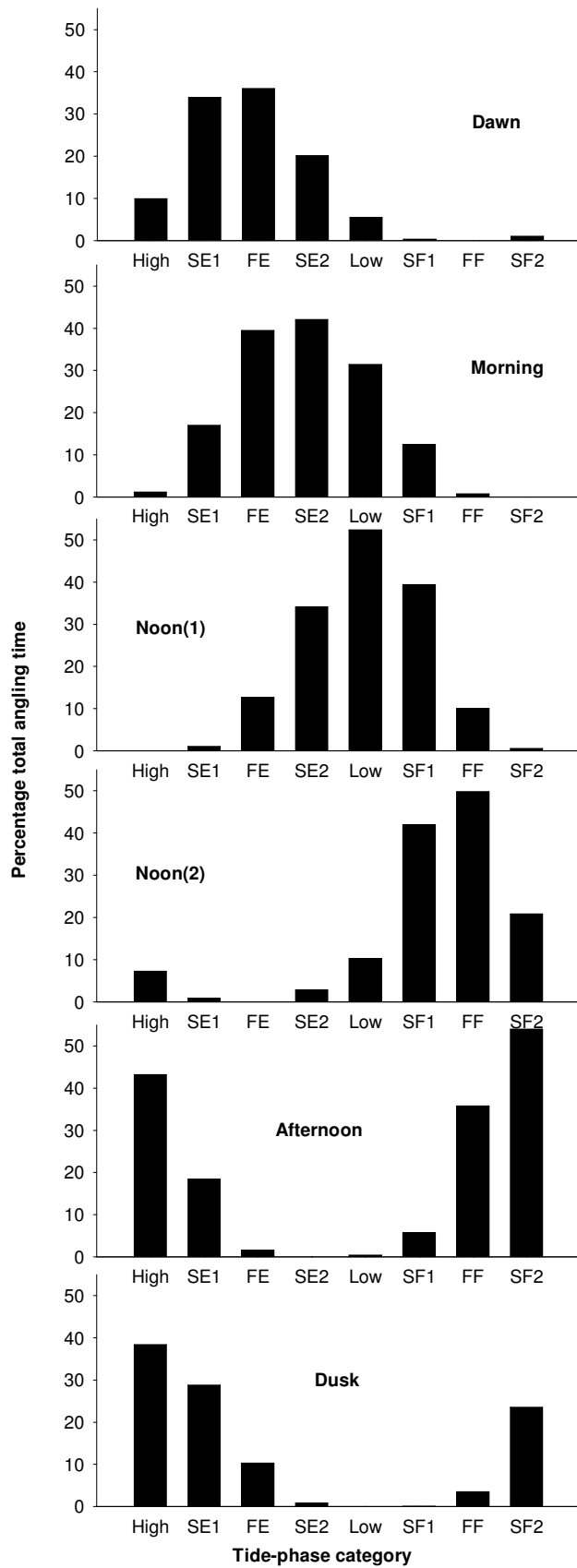
Figure 5.1. Proportion of total angling time in each light-phase category, corresponding to different tide-phase levels, showing the correlation between these two factors.

5.3   Results

5.3.1   Habitat classification

A combination of angler knowledge and species composition analysis (Figures 5.2 and 5.3) resulted in most angling localities being assigned a habitat type. The indicator species chosen as representative of each habitat type were dusky kob (*Argyrosomus japonicus*) and lesser guitarfish (*Rhinobatos annulatus*) for sandy habitats; two-tone fingerfin (*Chirodactylus brachydactylus*) and klipvisse (*Clinus* spp.) for shallow reef habitats; and roman (*Chrysoblephus laticeps*) and *Poroderma* catshark spp. for deep reef habitats (Figure 5.3).
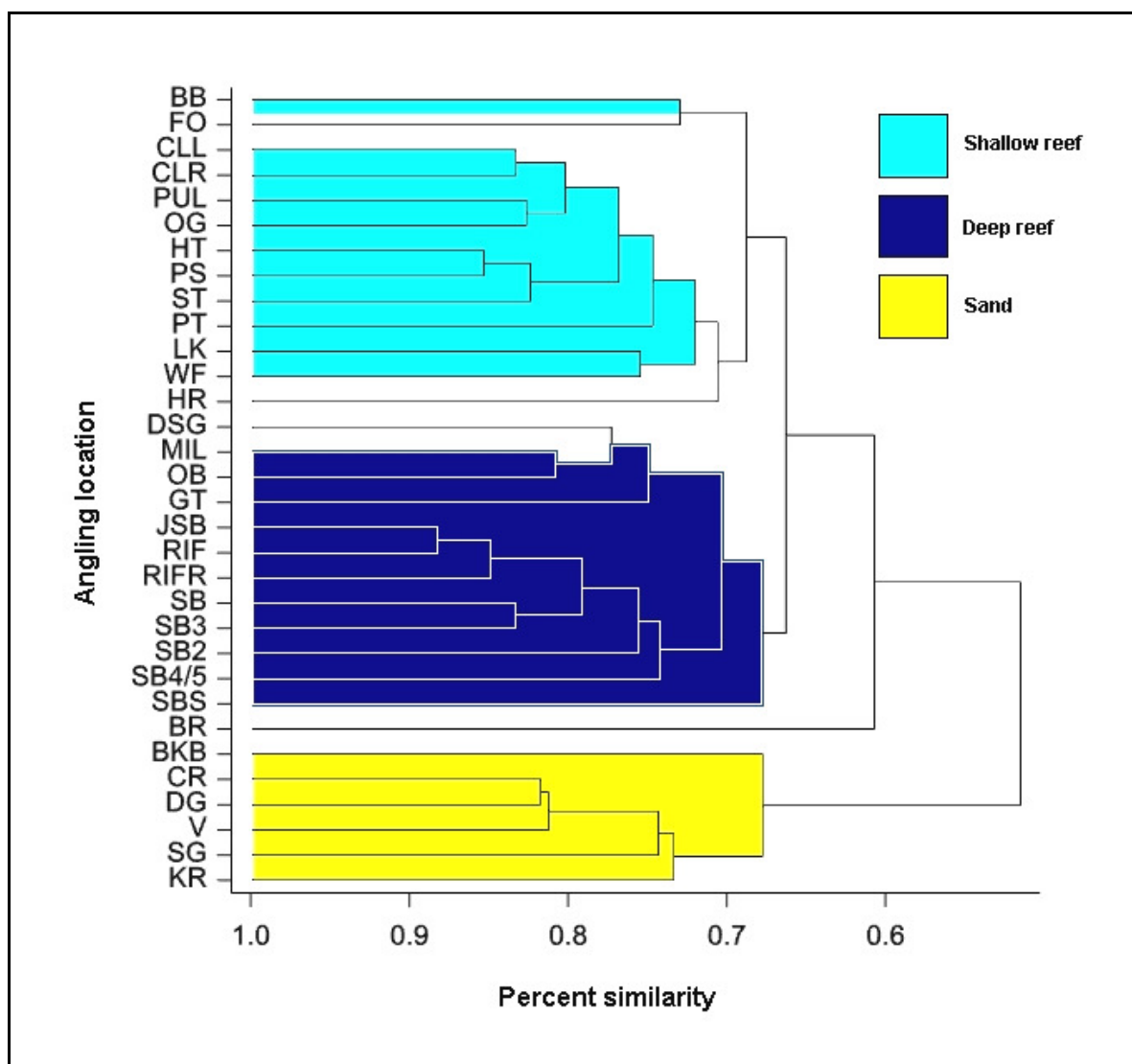
Figure 5.3. Results of the cluster analysis of species composition at Bloukrans angling localities and resulting habitat classification. Codes refer to the name of localities as used by anglers (e.g. BB corresponds to "Boulder Bay", and LK to "Losklippe"; See Appendix 1).

Figure 5.4. Overall catch per unit effort of indicator species in classified habitat types at Bloukrans.

Figure 5.4. Distribution of analysed angling localities and their habitat type at Bloukrans (habitat colours: yellow = sand, light blue = shallow reef, dark blue = deep reef).

5.3.2   Capture probabilities

Data from 132 days, amounting to 4916 hours of angling at the different localities, was analysed with hierarchical logistic regression. Predicted effects of the explanatory variables on mean captur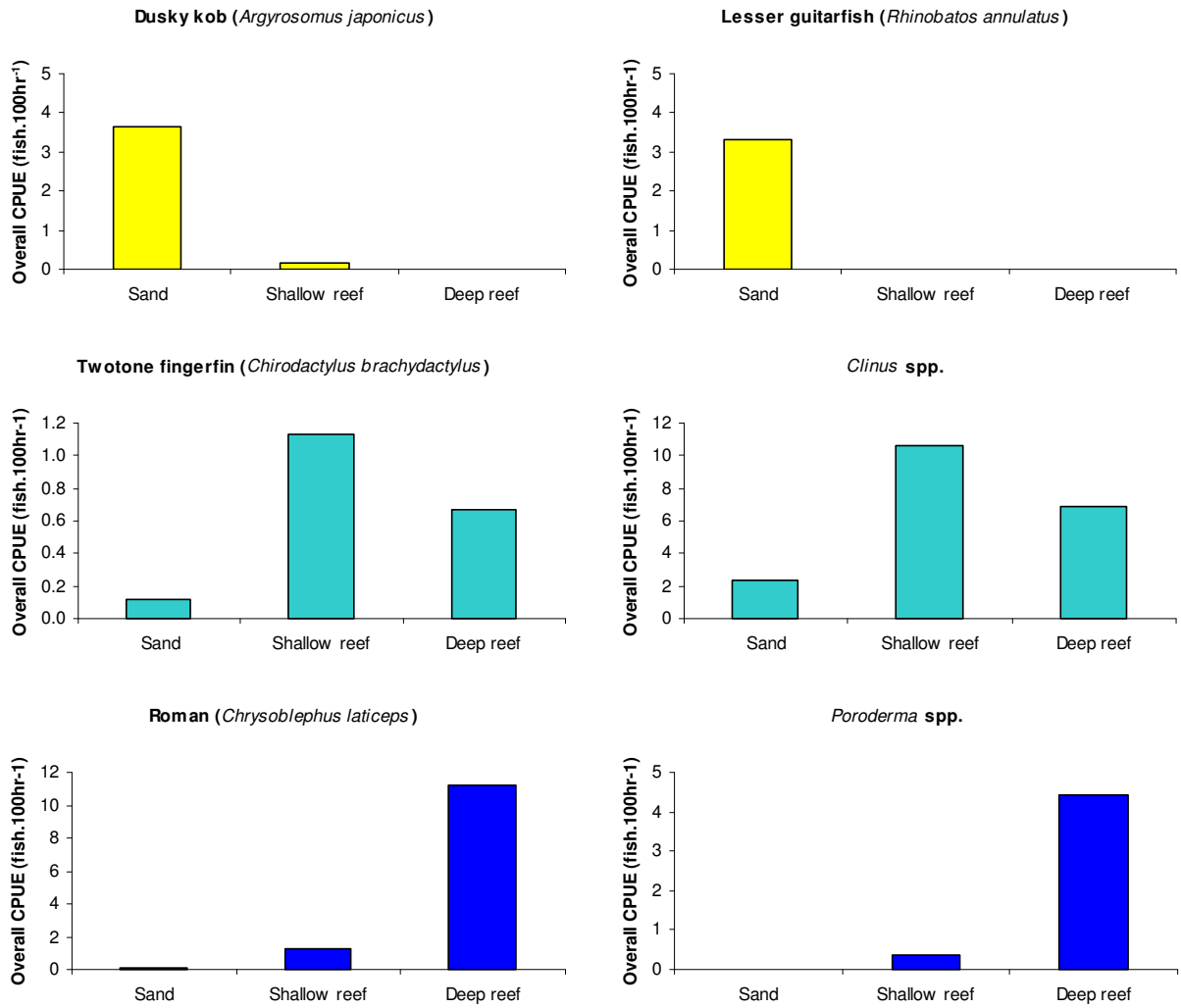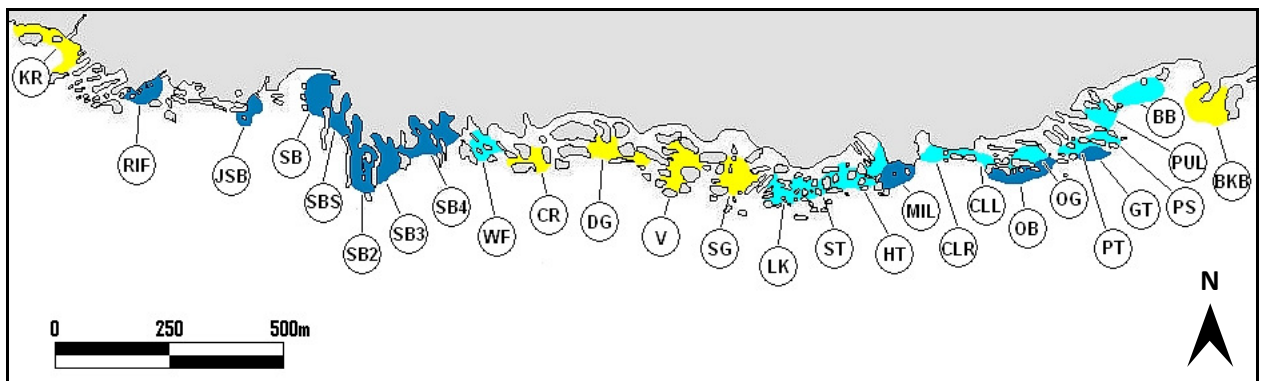e probabilities of different size-classes of each species are presented below. Angling effort was a highly significant factor in all analyses ($p < 0.001$), and is not additionally described. All figures depict the predicted mean probability of capturing at least one individual of the relevant size-class during one hour's angling at different values (or levels) of the explanatory variable at marginal (weighted) levels of other explanatory variables, apart from relative water temperature, which was standardised at 0 in predictions for all other variables.

Blacktail

Main and first-order interactive effects of the explanatory variables on mean capture probabilities of blacktail are summarised in Table 5.1. All size-classes were significantly more likely to be caught over sand than other habitats (Figure 5.5a) and least likely over deep reef, with shallow reef having intermediate capture probabilities. Capture probability was significantly correlated to light-phase (Figure 5.5b), although this was most apparent for medium-sized fish. Blacktail were most likely to be caught in periods closest to twilight (dawn and dusk), although for small individuals morning had similar capture probability to these periods and there was a significant minimum in probability of capture in the afternoon. Analysis of tide-phase effects on capture probability was only significant for large fish (Figure 5.5c), indicating that the less significant dawn and dusk peaks in capture probability for this size-class (Table 5.1) may have been influenced by tidal effects. Large fish were significantly more likely to be caught over high tide-phases (SF2 to SE1) than low and fast-flood categories. There was a significant effect of season for all sizes (Figure 5.5d), with peaks in autumn and lowest capture probabilities in spring and summer. For medium-sized fish this translated into a significant interaction with habitat type, with higher capture probabilities over sand relative to other habitats being driven by differences in summer and autumn (Figure 5.5h). Relative water temperature was also a significant predictor for all size-classes (Figure 5.5e-g), generally having a negative relationship with capture probability. However, for large fish, this relationship was seasonal (Figure 5.5f), being insignificant in summer.

There was also a significant interaction between the effects of relative water temperature and light-phase for large fish (Figure 5.5g), indicating significant increases in capture probability during the dawn and noon(2) phases, but not during dusk or morning, during low relative temperatures.

Table 5.1. Effects of explanatory variables on mean probability of capturing blacktail

* explanatory variable involved in significant interaction (see bottom section of table)

| Size-class	Small		Medium		Large	
Explanatory variable	p {Wald, d.f.}	Differences between pairs ($\alpha = 0.05$)	p {Wald, d.f.}	Differences between pairs ($\alpha = 0.05$)	p {Wald, d.f.}	Differences between pairs ($\alpha = 0.05$)
Habitat	0.001 {14.87, 2}	Sand > Shallow reef > Deep reef	< 0.05*	Sand > Shallow reef Sand > Deep reef	< 0.001 {25.05, 2}	Sand > Shallow reef > Deep reef
Light-phase	0.018 {13.61, 5}	Dawn > Afternoon Dusk > Afternoon Morning > Afternoon	< 0.001 {35.96, 5}	Dawn > Morning to Afternoon Dusk > Morning to Afternoon	< 0.05*	Dawn > Noon(1) Dusk > Noon(1)
Tide-phase	0.688 {4.77, 7}	ns	0.232 {9.30, 7}	ns	0.025 {16.01, 7}	High > FF High > Low SE1 > FF SE1 > Low SF2 > FF SF2 > Low
Season	0.025 {9.36, 3}	Autumn > Summer Autumn > Winter Autumn > Spring	< 0.05*	Autumn > Summer Winter > Summer Winter > Spring	< 0.05*	Autumn > Summer Autumn > Winter Autumn > Spring
Relative water temperature	0.048 {3.92, 1}	n/a	0.048 {3.91, 1}	n/a	< 0.05*	n/a
* Variable interactions	p {Wald, d.f.}	Interaction	p {Wald, d.f.}	Interaction	p {Wald, d.f.}	Interaction
			0.019 {15.15, 6}	Habitat x Season	0.068 {10.68, 5}	Light-phase x Relative water temperature
					0.032 {8.32, 3}	Season x Relative water temperature
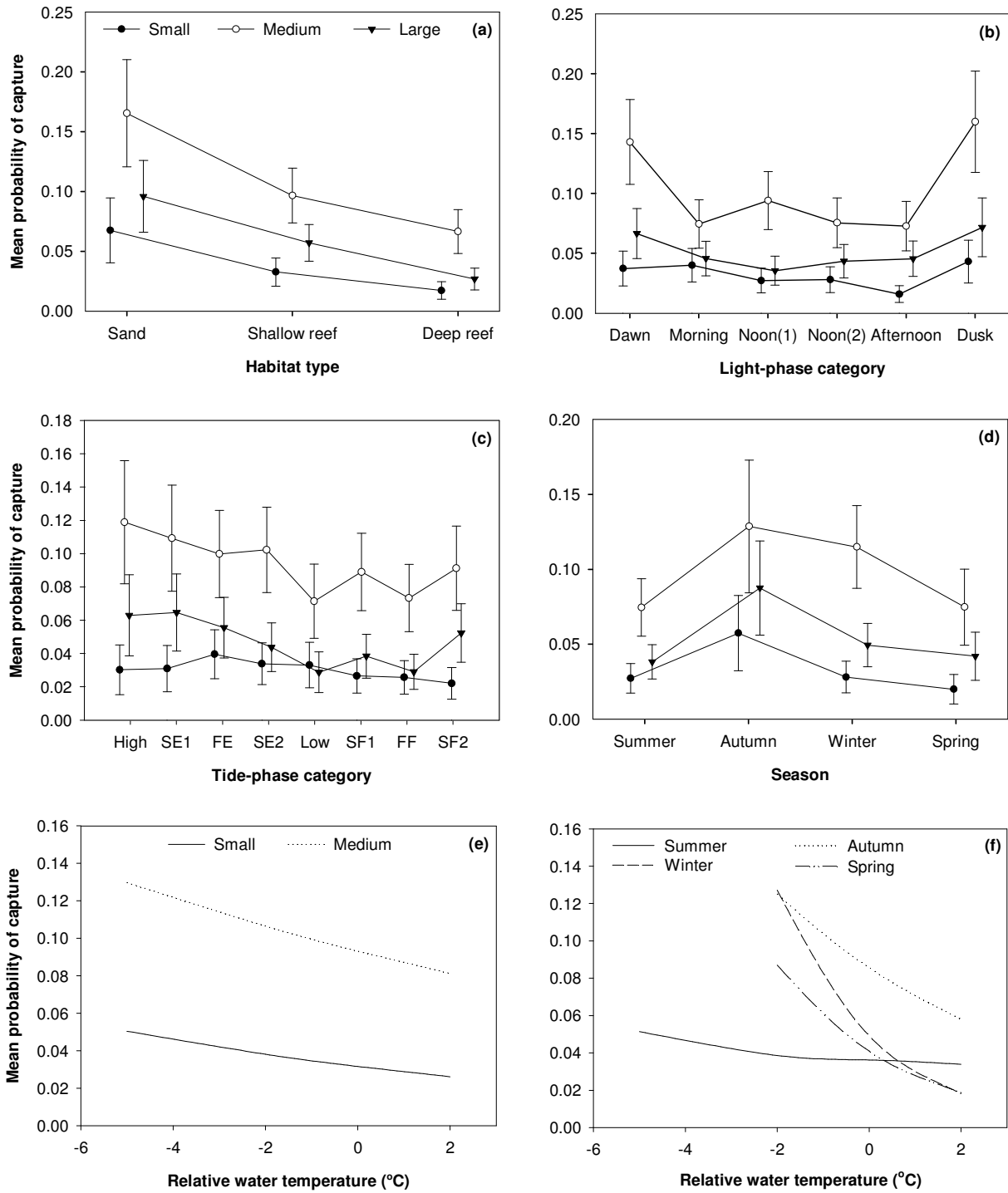
Figure 5.5.a-f. Mean capture probabilities of TNP blacktail predicted by differences in (a) habitat type, (b) light-phase, (c) tide-phase, (d) season and relative water temperature for (e) small and medium size-classes, (f) large fish in different seasons. Error bars represent approximate 95% confidence limits.
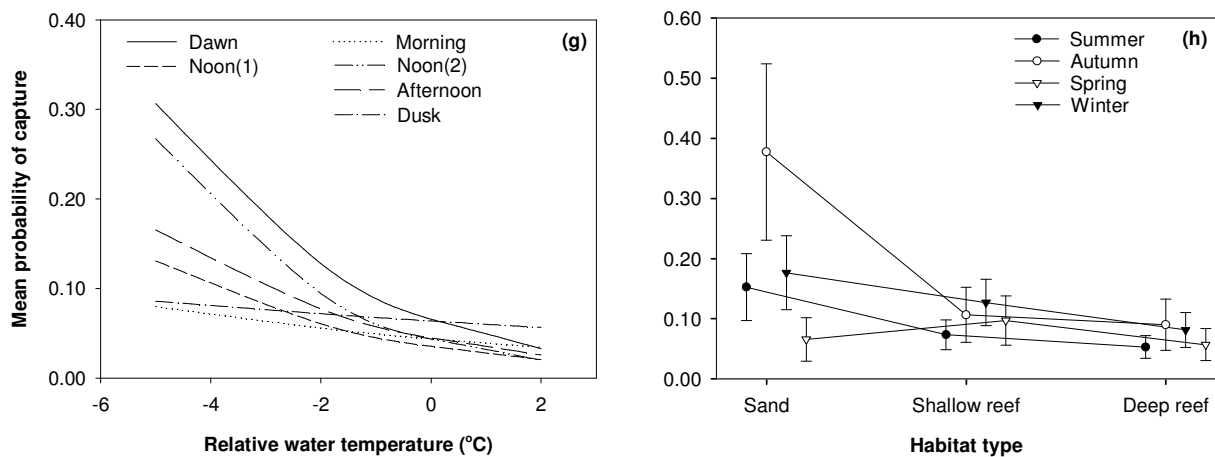
Figure 5.5.g-h. Mean capture probabilities of TNP blacktail predicted by interactions between (f) light-phase and relative water temperature for large fish and (h) habitat and season for medium fish. Error bars represent approximate 95% confidence limits

Zebra

Main effects of the explanatory variables (no interactions were detected) on mean capture probabilities of the two zebra size-classes are summarised in Table 5.2. Mean probability of capturing zebra was significantly lower in deep reef habitat (Figure 5.6a); for small fish only significantly lower than over shallow reef, but for large fish lower than both shallow reef and sandy habitats. Light-phase had different effects for the two size-classes (Figure 5.6b). Small fish capture probability steadily increased from dawn until noon(2), followed by a drop in the afternoon period but a significant peak during dusk. For large fish, although overall effect of light-phase was only significant at α-level of 0.1 (p = 0.6), there was a significant (p < 0.05) minimum capture probability in the afternoon period, followed by a peak during dusk. For both size-classes, capture probability was significantly higher in winter and autumn than spring and summer (Figure 5.6d). Tide-phase had significant effects for large fish only (Figure 5.6c), with peaks during fast-ebb and slow-flood 1 periods compared to the fast-flood and slow–flood 2 periods. Relative water temperature (with a negative relationship) was only significant for large fish.

Table 5.2. Effects of explanatory variables on mean probability of capturing zebra

	Small		Large	
Explanatory variable	p {Wald, d.f.}	Differences between pairs ($\alpha = 0.05$)	p {Wald, d.f.}	Differences between pairs ($\alpha = 0.05$)
Habitat	0.013 {8.72, 2}	Shallow reef > Deep reef	< 0.001 {19.56, 2}	Shallow reef > Deep reef Sand > Deep reef
Light-phase	0.034 {12.05, 5}	Dusk > Dawn Dusk > Morning Dusk > Afternoon Noon(2) > Dawn	< 0.06 {10.60, 5}	Dawn > Afternoon Morning > Afternoon Noon(1) > Afternoon Dusk > Afternoon
Tide-phase	0.544 {4.77, 7}	ns	0.08 {19.70, 7}	FE > FF SE2 > FF SF1 > FF FE > SF2 SE2 > SF2 SF1 > SF2
Season	< 0.001 {16.45, 3}	Winter > Summer Winter > Spring Autumn > Summer	< 0.001 {24.57, 3}	Winter > Summer Winter > Spring Autumn > Summer Autumn > Spring
Relative water temperature	0.147 {2.11, 1}	n/a	< 0.002 {9.98, 1}	n/a
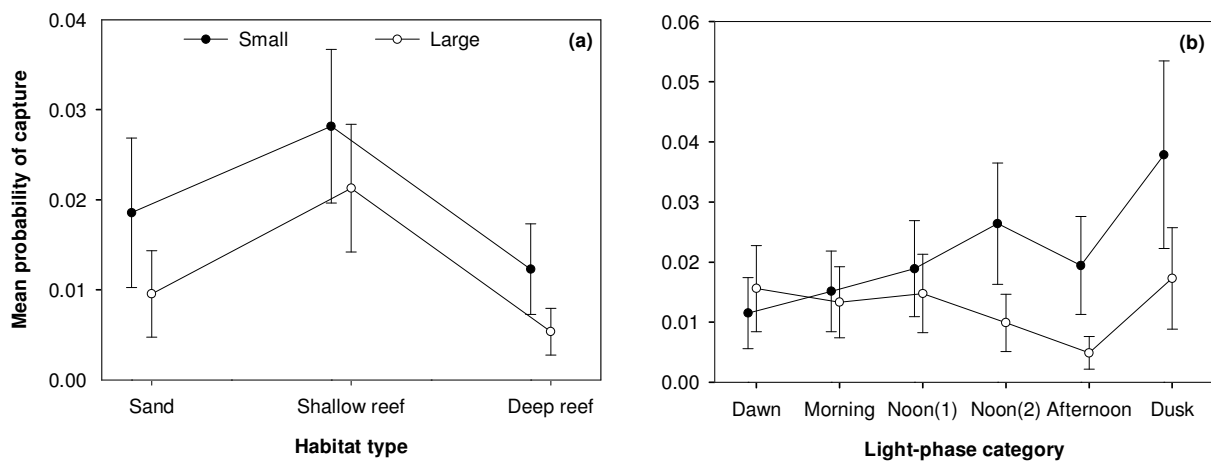
Figure 5.6.a-b. Mean capture probabilities of TNP zebra predicted by differences in (a) habitat type, (b) light-phase
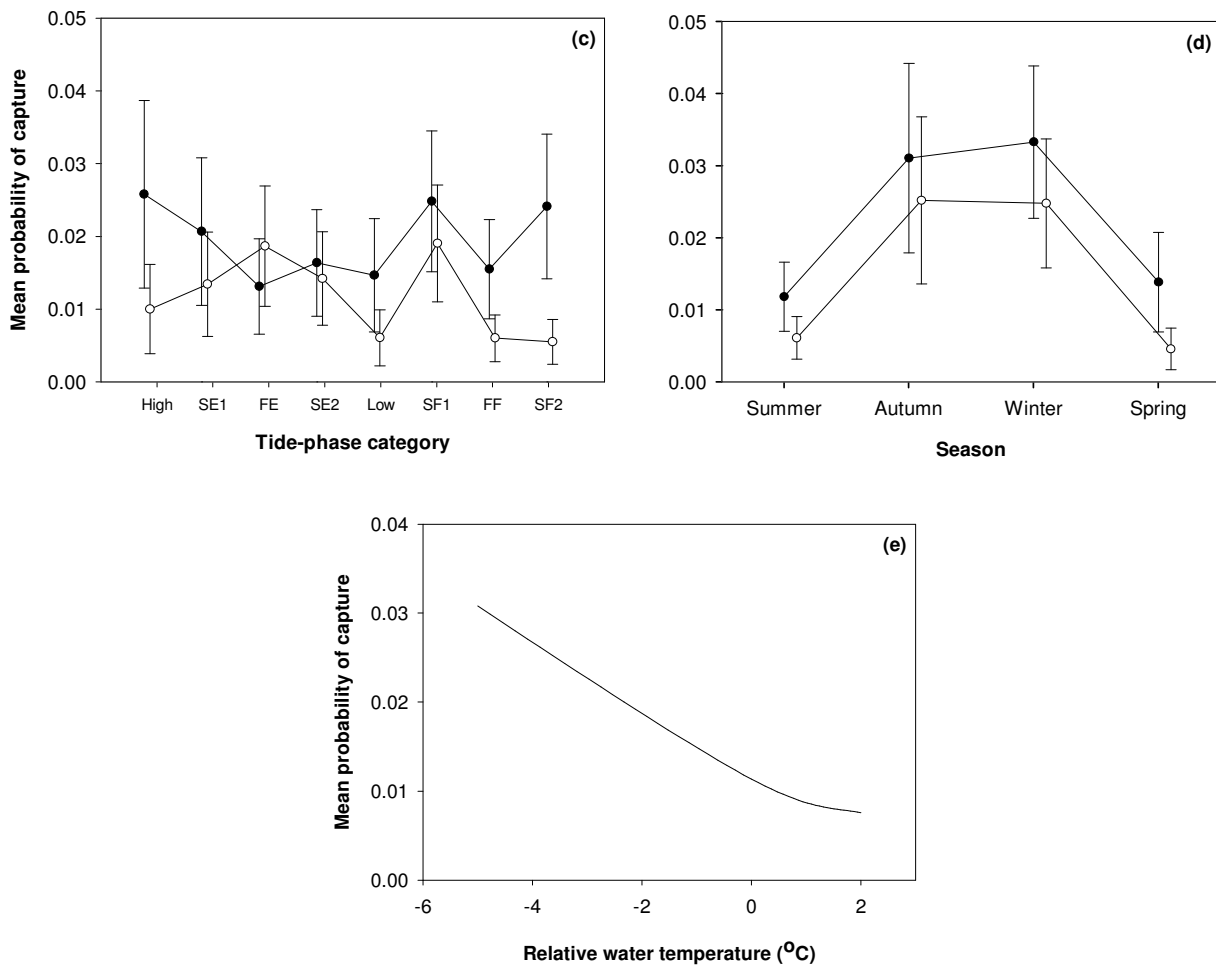
Figure 5.6.c-e. Mean capture probabilities of TNP zebra predicted by differences in (c) tide-phase, (d) season and (e) relative water temperature for fish. Error bars represent approximate 95% confidence limits

Musselcracker

Main and first-order interactive effects of the explanatory variables on mean capture probabilities of the two musselcracker size-classes are summarised in Table 5.3. Habitat only had significant effects on mean capture probability of small fish (Figure 5.7a), being highest over shallow reef, followed by sandy habitat and then deep reef. There were no significant effects of light-phase (Figure 5.7b) or tide-phase (Figure 5.7c). Although the AIC included a significant interaction between habitat type and tide-phase for small fish and this seemed to indicate a trend for higher capture probability over high tide-phases in the predominant shallow reef habitat (Figure 5.7e), this effect was insignificant at an α-level of 0.1 (Table 5.5).

Table 5.3. Effects of explanatory variables on mean probability of capturing musselcracker

* explanatory variable involved in significant interaction (see bottom section of table)

	Small		Medium	
Explanatory variable	**p** **{Wald, d.f.}**	**Differences between pairs** **($\alpha = 0.05$)**	**p** **{Wald, d.f.}**	**Differences between pairs** **($\alpha = 0.05$)**
Habitat	< 0.05*	Shallow reef > Deep reef Shallow reef > Sand Sand > Deep reef	0.278 {2.54, 2}	ns
Light-phase	0.114 {8.87, 5}	ns	0.861 {1.91, 5}	ns
Tide-phase	0.313 {8.23, 7}	ns	0.737 {4.37, 7}	ns
Season	> 0.05*	ns	< 0.001 {21.44, 3}	Autumn > Summer Winter > Summer Winter > Spring
Relative water temperature	< 0.05*	n/a	> 0.05 {2.2, 1}	n/a
* Variable interactions	**p** **{Wald, d.f.}**	**Interaction**	**p** **{Wald, d.f.}**	**Interaction**
	0.049 {7.86, 3}	Season x Relative water temperature		
	0.213 {17.86, 14}	Habitat x Tide		

Capture probability of medium-sized fish was higher in autumn and winter than summer and spring (Figure 5.7d). Seasonal effects interacted with those of relative water temperature for small fish (Figure 5.7f), the positive relationship during other seasons becoming strongly negative during spring.

Figure 5.7. Mean capture probabilities of TNP musselcracker predicted by differences in (a) habitat type, (b) light-phase, (c) tide-phase, (d) seas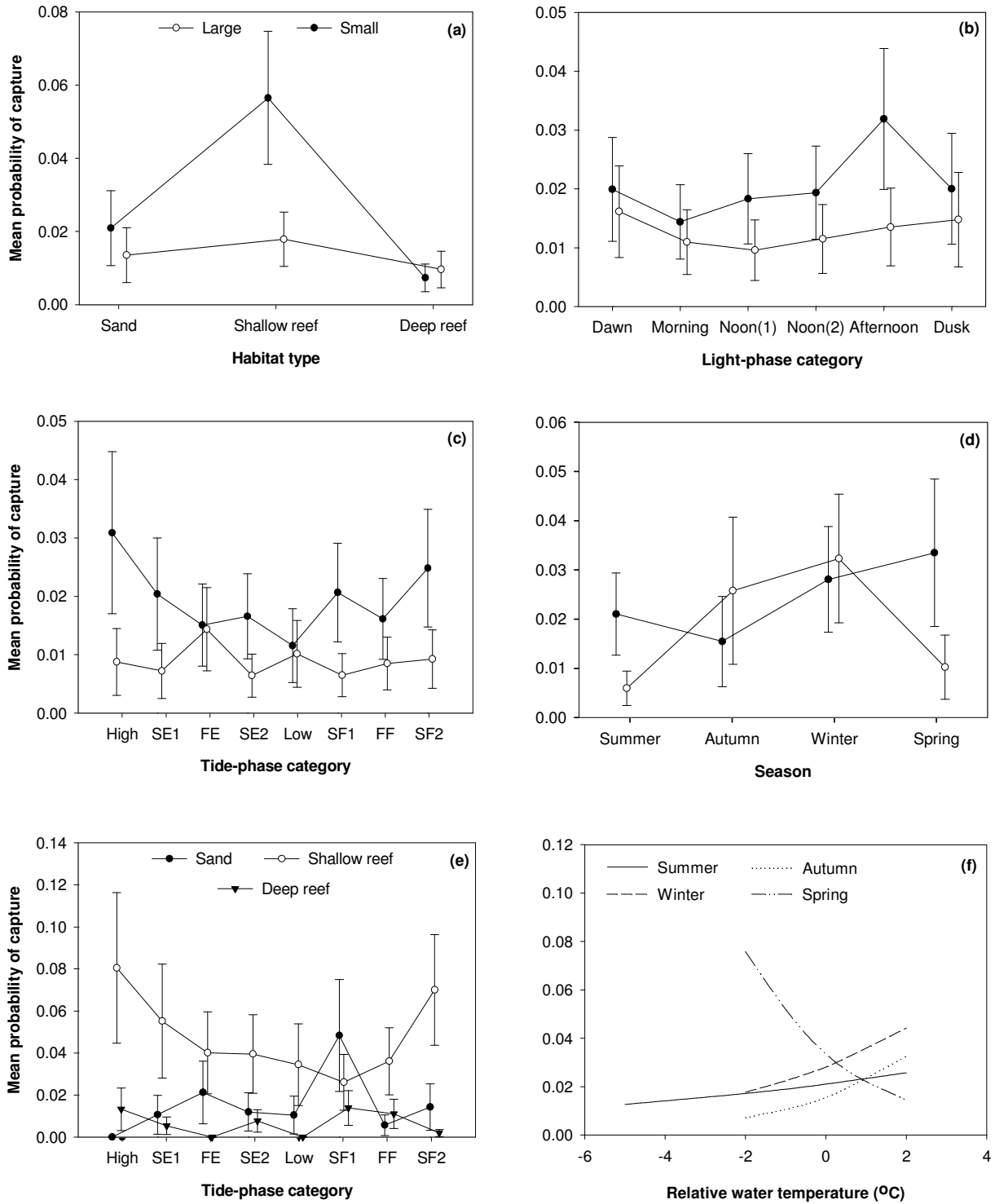on and interactions between (e) habitat and tide-phase, (f) season and relative water temperature for the small size-class. Error bars represent approximate 95% confidence limits.

5.4   Discussion

This study used an indirect method (probability of capturing individuals on baited angling gear) to examine foraging activity of resident fishes in relation to temporal and spatial factors. The large TNP data set spanning several years incorporated data over the full range of environmental conditions affecting angling operations and fish foraging behaviour. However, due to the varying degree of concurrent data collection both spatially and temporally, further attempts to reduce the influence of unquantified factors were necessary. HGLMs are a form of generalized linear mixed model (GLMM). GLMMs have been used in a number of ecological studies (e.g. Legge 2000, Brandão *et al.* 2004, Aukema *et al.* 2005), as well as to standardise catch rates in fisheries science (Millar & Willis 1999, Venables & Dichmont 2004, Helser *et al.* 2004). However, accuracy of standard quasilikelihood estimation methods used in GLMMs to model binary count data have been questioned (Rodriguez & Goldman 2001, Breslow 2005), and in the software used, HGLMs allowed more accurate Laplace approximations in estimation of the mean model (Raudenbush *et al.* 2000) than standard GLMMs.

Effects of three factors potentially affecting performance of baited gear – individual angler experience, hook size and bait species (Attwood 2003), were not analysed and assumed to randomly impact capture probabilities with respect to analysed factors. The majority of angling was undertaken by a core group of experienced research anglers, reducing individual angler effects. The three study species were all readily captured on the full range of baits used in the study and anglers varied their use of bait and hook sizes, and therefore impacts of these were also likely to be minimal. These potential uncertainties notwithstanding, clear trends in the results suggest methods were successful in detecting some natural behaviour patterns of the study species. These potentially arose from changes in both general and foraging activity levels. Within this relatively small study area (*ca* 3 km of coastline), capture probability varied significantly with habitat for all three study species. Effects differed between the species, and sometimes between their size-classes. Tagging studies indicated that few large-scale movements occurred within the study site (see Chapter 4) and appear to discount large-scale daily foraging 'migrations' between different habitats, as have been recorded for numerous marine fish species (Hobson 1973, Meyer & Holland 2005, Unsworth *et al.* 2007). Therefore, observed differences in capture probability were likely to be a function of both the relative abundance of resident individuals living within particular areas and foraging within particular habitats.

Juvenile musselcracker are highly resident and Clarke (1988) found that shallow inshore reefs function as a nursery area after initial use of intertidal areas. If, as suggested earlier (Chapter 3), the ontogenetic shift to subtidal areas occurs via spending progressively more time in areas immediately adjacent to intertidal nurseries, home ranges would initially be established in shallow reef habitat, progressing deeper with increase in age and size. The observed lack of significant habitat differences for larger medium-sized musselcracker, suggests increasing incorporation of deep reef and sandy areas into the home range of older fish, thereby providing further evidence of this ontogenetic habitat shift. Buxton & Clarke (1991) reported differences in preferred prey of musselcracker corresponding in size to the small and medium size-classes studied here, with concomitant development of heavy adult dentition and greater consumption of larger invertebrate prey with increasing size/age. This, together with increased energy requirements of larger individuals, probably necessitates use of a wider variety of habitats during foraging, implying increased home range area and movement with growth, as was found in results from tagging studies (see Chapter 4).

Mann (1992) and Mann & Buxton (1992) examined habitat use and diet of blacktail and zebra in a similar area to this study, finding them abundant in shallow inshore reef environments (less than 10m deep), particularly those exposed to direct wave action. Habitat types categorised in this study all fell within this depth range and, although "deep" reef habitat was generally less exposed to breaking wave action, it is considered all probably fell into the exposed inshore reef category of Mann's study. He, however, made use of underwater counts of abundance and water conditions limited effective estimates in very shallow habitats in the surf zone exposed to heavy wave action - effectively sampled in this study. The present results likely indicate preferential foraging in these shallow habitats and suggests daily activity of these fishes may be greatest in very shallow areas within the shallow inshore zone. Mann (1992) noted the ability of these fishes to enter shallow turbulent waters. Dominant prey items of these fishes are relatively small invertebrates (Mann & Buxton 1992) and such habitats should increase chances of prey being exposed (e.g. through dislodging from shelter in rock crevices, or macroalgae, by water movement) making them desirable foraging areas. Preference for sand habitat by blacktail may be a function of its generalist diet leading it to preferentially forage in disturbed sandy areas for a variety of small invertebrate prey, as has been observed for other species (Hall *et al.* 1996).

Conversely, zebra preferentially consume polychaete worms common in filter-foraging invertebrate colonies attached to rocks in the wave zone (Mann & Buxton 1992), which may explain their peak capture probabilities in shallow reef habitat. It is not clear what drove observed higher capture probabilities of medium-sized blacktail over sand (relative to other habitats) in summer and autumn versus during winter and spring. Although Mann & Buxton (1992) found seasonal differences in diet composition of blacktail, this was mainly for small juveniles and thus an unlikely causative factor. It is hypothesised that reproductive behaviour caused the observed differences. Blacktail reproduction peaks at times corresponding to late winter and spring in this study (Mann & Buxton 1997) and observed differences could thus have been a function of habitat use in relation to social reproductive interactions (e.g. spawning activity over reef habitat versus sandy areas), but further investigation of this was beyond the scope of this study.

The highly dynamic shallow environments favoured by blacktail, zebra and juvenile musselcracker for foraging were unlikely suitable for position maintenance on even a semi-permanent basis, and foraging activities here likely took the form of periodic movement into and out of particular areas with successive wave cycles. Therefore, these fish were not permanently utilising these areas, but selectively for foraging at certain periods, and these were in some cases related to environmental cycles. Light-phase potentially affected foraging activity of the study species through its effects on daily activity rhythms (McFarland 1986, Reebs 2002), and tide-phase through intertidal and shallow inshore areas becoming periodically more accessible for foraging during inundation at high tide. Unfortunately these two factors were temporally correlated (Figure 5.1), limiting discrimination of their respective effects on capture probabilities in analysis, through unmodelled variation from one factor likely reducing confidence around parameter estimates of the other. However, some effects were clearly significant in isolation from the other factor. Peaks during dawn and dusk for medium blacktail were distinct and likely a function of the proximity of these periods to sunrise and sunset. Increased crepuscular activity and foraging have been described for numerous marine fish species in both temperate and tropical environments (Hobson *et al.* 1981, Helfman 1993, Lowry & Suthers 1998, Løkkeborg *et al.* 2000). Significant minimum capture probability for small blacktail during the afternoon is difficult to explain in relation to the light cycle, but this pattern of a distinct drop in afternoon captures followed by significant increases at dusk was also observed in both zebra size-classes.

The large proportion of afternoon angling over periods of maximum onshore tidal flow (fast-flood and slow-flood 2; Figure 5.1) possibly explains this. Strong tidal currents may compound already rough conditions in favoured shallow foraging habitat to create conditions untenable for foraging. Although not always statistically significant, reductions in capture probability during fast-flood compared with phases immediately before and after for medium-sized and large blacktail and small zebra, and minimum capture probability of small blacktail and large zebra during fast-flood and slow-flood 2 (see relevant figures) support this conclusion. Increased capture probabilities over high tide of medium and large blacktail likely incorporates movement into shallow areas inundated at high tide to feed on intertidal food resources (Biden 1948, Mann 1992). Tidally related foraging behaviour has been described for many marine fish species, which either make directed movements into particular areas to feed (Carlisle 1961, Craig 1996, Beyst *et al.* 2002) or display tidally induced activity or behaviour patterns within normally utilised areas (Zeller 2002). Tidal 'migrations' usually described are large-scale shifts in position during particular phases of the tide, whereas any tidally related foraging movements of blacktail are more likely to comprise short excursions into submerged intertidal habitat from slightly deeper areas as conditions allow (e.g. between rough wave sets). In their favoured shallow reef habitat, small musselcracker foraging activity also appeared to increase over high tide, which may also indicate foraging in inundated shallow areas on the high tide for these fishes.

Although not of primary interest, season and relative water temperature were included in analyses to control for their effects on capture probabilities and in most cases were found to have significant effects. A host of factors potentially drove observed seasonal variations in foraging activity, including reproductive activity, prey ecology and water temperature (affecting metabolic rate). Effects of relative water temperature were analysed as this was thought to have relevance to daily variations in capture probability. The generally negative relationship between relative water temperature and capture probabilities of all fishes (apart from small musselcracker) indicated elevated water temperature may have a suppressive effect on foraging activity in these species. The relationship was not found for large blacktail in summer, however, possibly indicating susceptibility to seasonal upwelling and associated sharp declines in water temperature. Upwelling affects resident reef fish behaviour along this stretch of coastline (Hanekom *et al.* 1989, 1997), fish sheltering in crevices and ceasing to feed (Buxton & Smale 1997).

Larger blacktail may be more adversely affected by temperature than smaller individuals, or alternatively be more capable of temporary movement away from the immediate vicinity of small-scale upwelling to escape its effects.

An improved understanding of these fishes' behaviour has important implications for fisheries management. In addition to contributing to a better fundamental understanding of their ecology, these results highlight the need to consider small-scale spatial and temporal effects on capture probabilities when utilising baited gear as a sampling method for studying resident fish species. Surveys using baited gear have been widely used to examine fish abundance, particularly in relation to the protective effects of MPAs (e.g Alcala & Russ 1990, Bennett & Attwood 1991, 1993, Millar & Willis 1999). Studying the unexploited populations within MPAs has also been advocated for assessing natural population parameters and variability for fishery species for more realistic stock assessments. South Africa's Linefish Management Protocols (LMPs – see Chapter 1) require periodic assessment of populations of linefish species in order to gauge the effectiveness of management measures. Long-term monitoring of fishery-independent measures of abundance such as CPUE in scientific surveys is an integral part of such assessments. In the TNP blacktail has also been highlighted as a potential indicator species for long-term monitoring of an inshore ecosystem (Götz *et al.* 2008). The significant variations in capture probability of the study species in relation to the spatial and temporal factors analysed in this study, due to their behaviour, need to be considered when analysing data from fishery independent abundance surveys. Knowledge of natural foraging activity rhythms might also be exploited to design more efficient sampling protocols in multispecies assessments, e.g. targeting specific species during times of the day when they are known to exhibit peak foraging activity.

Chapter 6 – General discussion

In this study blacktail, zebra and musselcracker displayed both similar and divergent patterns of post-settlement movement, depending on the life-history stage under investigation. As juveniles, all three species are resident to restricted areas of rocky intertidal nursery habitat. Although morphologically adapted to undertake large-scale movements within contiguous rocky habitat, they exhibited movement behaviour characteristic of resident intertidal species. The dynamic nature of South Africa's east coast probably necessitates this. The physical stability of rocky shores (*cf.* sandy areas or estuaries that form the main nursery areas of many other inshore species) counters the inherent instability of conditions associated with strong wave and tidal action in this environment. Within structurally stable rocky intertidal habitat, restricted movement and long-term site fidelity afford developing juveniles the best chances of avoiding accidental displacement to hazardous areas such as the subtidal zone, that has high predator abundance, or stranding in upshore areas with inadequate water levels at low tide. High levels of movement over a large area would conceivably decrease individuals' ability to sufficiently familiarise themselves with the physical layout of their environment to take expedient shelter from strong tidal currents and rough seas impinging on the intertidal zone.

The tidal cycle may necessitate some movement perpendicular to the shore in response to the rise and fall of water levels, and this also appears to follow a repetitive, restricted pattern within a small area immediately adjacent to the low tide refuge. Thus, an individual juvenile's home range comprises a core area centred on the low tide refuge but including adjacent areas utilised over high tide. The likely mechanism by which these species accomplish ontogenetic shifts in area and habitat use is similarly facilitated by the tidal cycle. Although not explicitly quantified in the present study, movements of small juveniles are restricted within small intertidal pools on the periphery of gullies during low tide; these likely constituting their core home range areas (pers. obs.). Under this hypothesis, with ontogenetic development (i.e. increased body size and improved swimming capabilities) the home range increasingly incorporates deeper areas immediately adjacent to the low tide refuge, through progressively extended explorations of these at high tide when rockpools become connected to these areas. Such areas with suitable physical characteristics for larger individuals (e.g. deeper water, greater area, increased shelter and greater prey abundance/size) become the low tide refuge that constitutes the core area of their expanded home range.

It follows that use of previously utilised areas is maintained during movement away from the low tide refuge over high tide as previously described. A similar process facilitates the ontogenetic shift to subtidal habitats adjacent to the intertidal zone, these being initially explored on temporary excursions and ultimately replacing the low tide refuge as the core home range area. Use of the (previously-utilised) intertidal home range core area is now restricted to high tide periods. Thus, with ontogenetic development there is a simultaneous expansion and shift in location of the core area of the home range, from small intertidal rock pools to semi-bounded intertidal gullies to subtidal inshore habitats that form the final location of adult home range cores. Juvenile blacktail leave the intertidal zone at smaller size than zebra and musselcracker, probably facilitated by their greater propensity to shoal functioning as an anti-predation mechanism.

Utilisation of restricted home range areas continues in subadult and adult life. Within their home ranges adult blacktail and zebra utilise habitats differentially for foraging, which is linked to both the diurnal and tidal cycles. Both species preferentially forage in shallow habitats along the sea/shore interface, blacktail having a preference for sandy areas close to reefs, whereas zebra preferentially forage in shallow rocky areas. Blacktail foraging activity peaks around twilight periods, and but also follows the tidal cycle, peaking over high tide when these fish are able to enter the intertidal zone. Both blacktail and zebra tend to forage less over periods of maximal onshore tidal flow, however. Foraging within the intertidal zone likely represents continued association with their specific intertidal nursery area for many individuals.

Thus, when considered together with the small size of their long-term adult home ranges, many blacktail and zebra appear likely to remain within an extremely restricted nearshore area throughout their lives. Data gathered in this study at different stages of ontogenetic development suggest that typical post-settlement lifetime movements for these fishes occur within a few hundred metres of where they initially settle. Although large zebra are sometimes found in deeper areas (Mann 1992, Heemstra & Heemstra 2004), this may only be in areas where deep reef habitat is located close to shore (i.e. not necessitating a large-scale ontogenetic shift from intertidal nursery areas). Musselcracker are initially restricted to small areas of shallow reef habitats within the subtidal zone. With maturation, however, they begin to utilise other habitats in daily foraging activities, probably facilitated by the development of heavier dentition enabling the consumption of larger invertebrate prey.

With continued growth, musselcracker exhibit the potential to disperse large distances, including a seasonal long-distance directed migration related to reproductive activity. Seasonal targeting and recorded movements of tagged adult musselcracker suggest different spawning areas along the coast. The location of these has probably evolved to take advantage of prevailing oceanographic currents to maximise transport of eggs and larvae, produced in spawning aggregations, to areas of the coast with suitable rocky intertidal nursery habitat. Spawning in KwaZulu-Natal waters (that this species does not frequent outside the spawning season) probably constitutes the best means of ensuring adequate larval supply to areas east of Algoa Bay, where the nearshore environment is considerably impacted by southwest Agulhas Current flow. This 'up-current' strategy is utilised by several other South African reef fish species. However, the dynamics of musselcracker spawning migrations (e.g. stock segregation, spawning site fidelity of individuals, degree of natal homing, makeup of spawning aggregations in terms of geographic origin of individual fish, aggregation size and frequency and location of spawning events) are unlikely to be fully understood until a range of techniques are utilised for its study.

Our present knowledge of the lifetime movement behaviour of the three study species as described in this study can be graphically depicted in Figure 6.1, showing the location and scale of ontogenetic, daily and (in the case of adult musselcracker) seasonal reproductive movements (Figure 6.2).
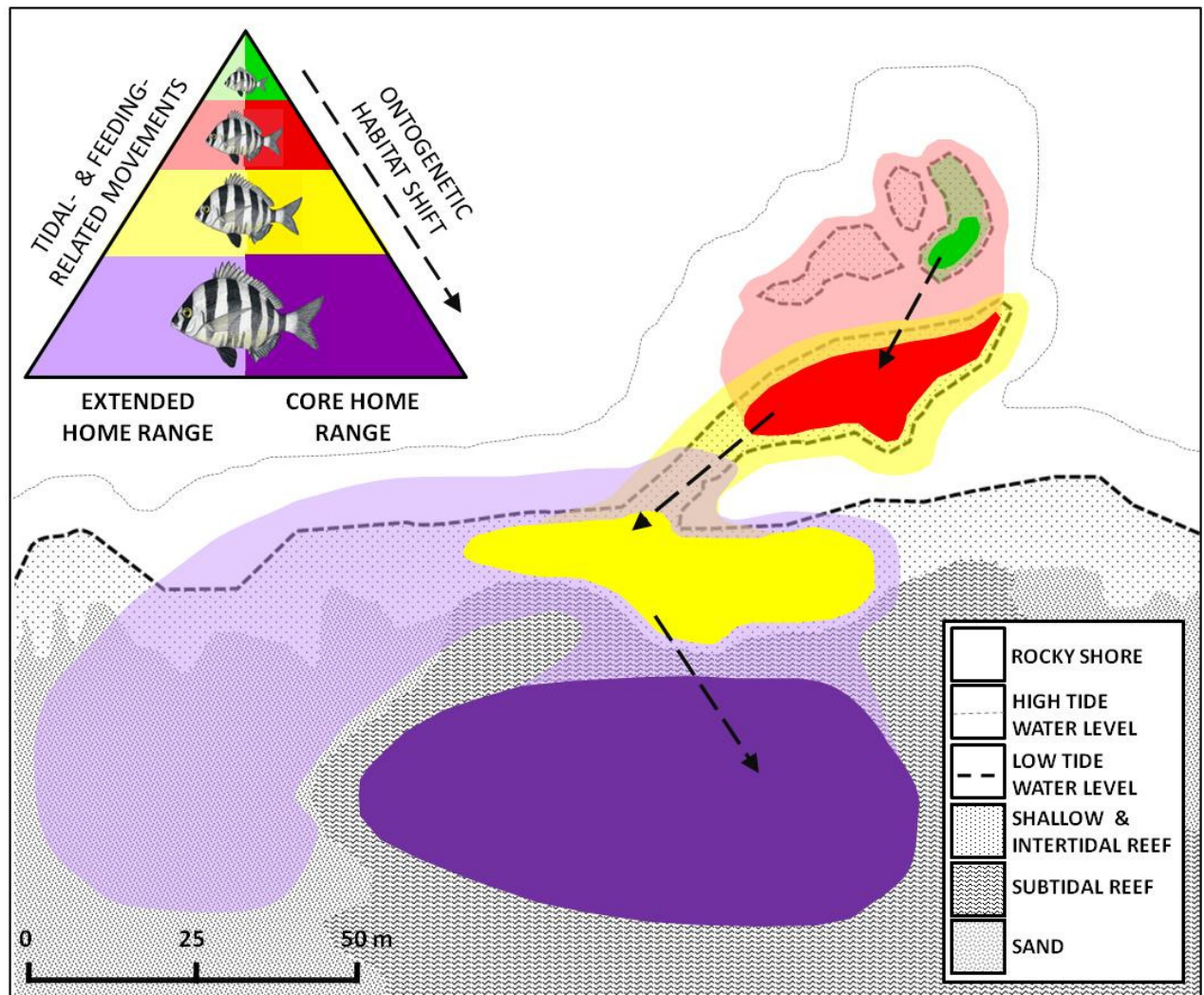
Figure 6.1. Stylised representation of characteristic lifetime movement behaviour for the three study species. Home range area and the number of different habitats utilised increases with age. Ontogenetic habitat is characterised by a gradual progression in the location of the home range core area from intertidal nursery habitats (initially rockpools and later intertidal gullies) to shallow subtidal and slightly deeper inshore reefs. However, mature fish maintain contact with their intertidal nursery during feeding excursions away from their core home range. Seasonal spawning migrations of musselcracker take place on much larger scales, and are depicted in Figure 6.2. (Zebra illustration copyright South African Institute for aquatic Biodiversity and NISC).

Figure 6.2. Representation of hypothesised annual spawning migrations of musselcracker along the South African east coast. Migration paths are generally eastwards, with major spawning grounds 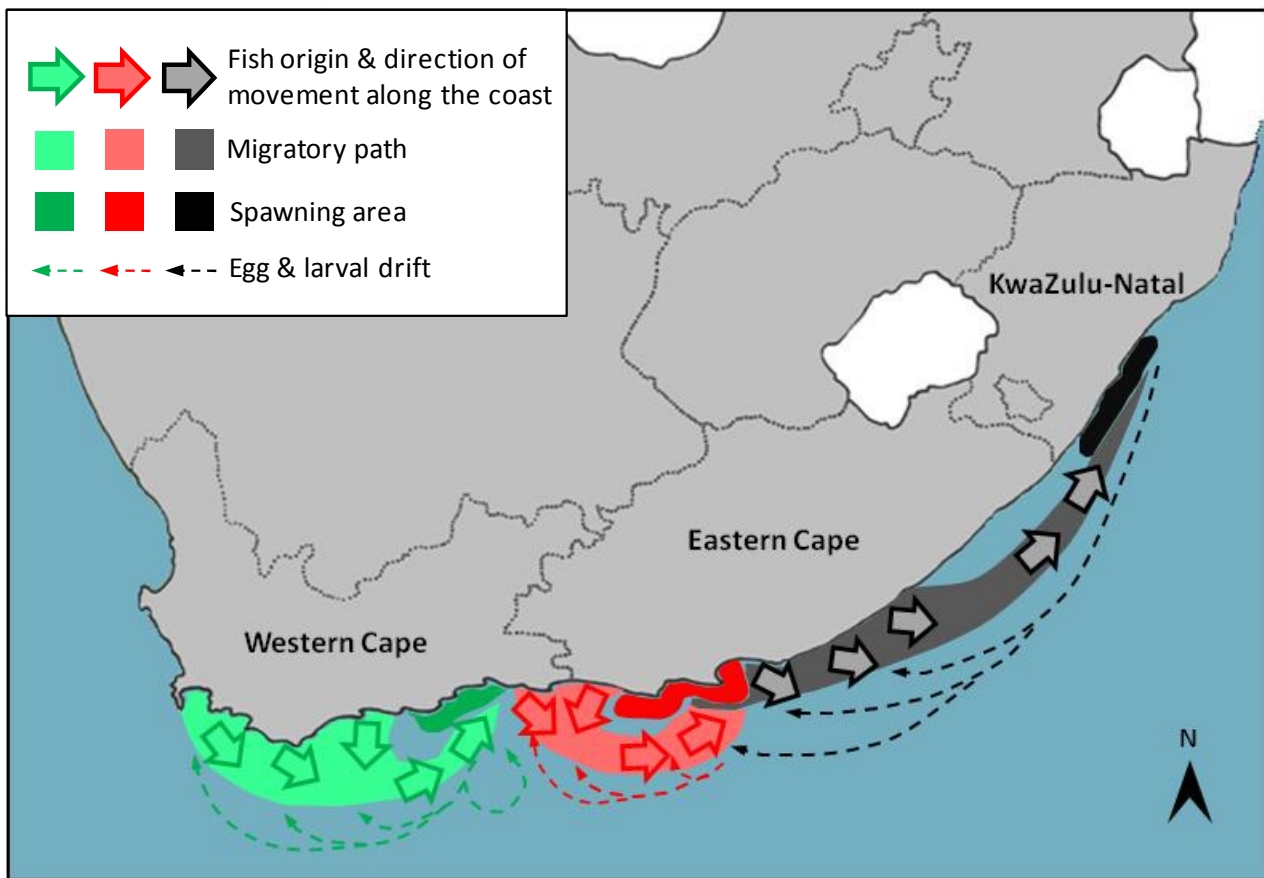in the vicinity of Mossel Bay, Algoa Bay and central KwaZulu-Natal visited by fish resident on different areas of the coast. Prevailing currents disperse eggs and developing larvae to the Eastern and Western Cape where suitable rocky intertidal nursery habitat is present. Note that migration paths are a stylised representation of the general direction of coastal alongshore movements (i.e. not depicting offshore movements).

Implications for management in South African fisheries

Management strategies for conservation and sustainable utilisation of exploited marine species need to recognise dynamics of their movement behaviour (Acosta 1999, Attwood & Cowley 2005). Their location in time and space affects patterns of exploitation of individuals or populations and effectiveness of particular management measures (e.g. Flynn *et al.* 2006). The study species are appreciably exploited in South African shore fisheries and potentially vulnerable to over-exploitation.

This is especially relevant given populations of many other targeted species have been severely depleted (Mann 2000a) and they will be exposed to increasing fishing effort until significant recovery of these stocks, as already recorded by Bennett *et al.* (1994) for blacktail in the southwestern Cape. Under prevailing local and global economic conditions, high poverty levels and associated poor food security of many South African households exacerbates this situation. Consequently, South African coastal fish populations will be exposed to increasing pressure from subsistence fishers (Branch *et al.* 2002, Mann *et al.* 2003).

When resident juveniles, large numbers of all three species are vulnerable to other anthropogenic impacts on the rocky intertidal zone. These could result from either point-source pollution or chronic exposure to compounds affecting growth or future reproductive development. The consequences will become more pervasive with increased coastal development, unless this is properly regulated (Thompson *et al.* 2002). Existing rocky intertidal nurseries may also be affected by anthropogenically-induced climate change. Rising sea levels linked to global warming would be expected to change the characteristics of many rocky intertidal nursery areas on local or regional scales. If this results in a decrease in their extent, detrimental effects on overall juvenile survival would be expected. Climate-induced changes in weather patterns may also result in increased storm activity and/or rough sea events that reduce the suitability of many areas as nurseries through regular 'flushing out' of this habitat. In regard to the above, it is therefore necessary to determine the importance of the rocky intertidal zone as a 'critical habitat' for these species.

Upon entering subtidal habitats larger juveniles and subadults should in theory be exempt from fishing mortality until they reach minimum retainable size, but lack of law enforcement renders this assumption questionable, particularly where coastal resources are primarily exploited for food. Subadult musselcracker could be particularly vulnerable due to their relatively large size constituting a sizeable catch. As adult recruits appear to be derived predominantly from adjacent nursery areas, the above impacts on juveniles potentially have significant knock-on effects on local adult populations, either in recruitment failure or reduced fitness of recruits. As adults, long-term residency of blacktail and zebra to restricted areas increases their vulnerability to localised population depletion (Gunderson *et al.* 2008).

Assuming equal catchability, site-attached species experience higher total mortality in intensely exploited areas than more mobile species that become periodically less vulnerable to exploitation when outside that area. Effects on a resident species' overall population therefore depend on both the distribution and level of exploitation over its range. On localised scales, considerable impacts by even moderate fishing pressure could result from these species' low intrinsic population growth rates. Attwood (2003) theorised that natural refuges from fishing pressure on the South African coast (e.g. privately-owned or otherwise inaccessible areas) may be important for population maintenance in another predominantly resident species (galjoen, *Dichistius capensis*). Similarly, the national ban on off-road vehicles on South African beaches instituted in 2001 has probably created a number of inaccessible areas, thereby reducing fishing pressure on resident populations (P. Cowley, South African Institute for Aquatic Biodiversity, pers. comm.). Such areas remain as pockets of high population density that buffer effects of exploitation in other areas; either through density-dependent movements or supply of recruits in larval dispersal. However, propensity for site-attachment may conceivably counteract density-dependent processes, for example when social benefits of conspecifics presence are important to behaviour (Shumway 1999). In the present study, observed rates of tagged blacktail movement from protected areas (with high population density) to adjacent exploited areas of lower population densities were negligible (Chapter 4), indicating density-dependent processes may not increase this species propensity for movement.

In contrast to the *Diplodus* species, musselcracker reproductive movements confer a pattern of exploitation pressure that differs between the spawning season and other times of the year. Targeting of musselcracker during the spring and summer spawning seasons by both shore-anglers (Clarke & Buxton 1989) and spearfishermen (van Rooyen 1987) is well known. Targeting of fish spawning aggregations can result in severe population declines from increased catchability, due to associated behaviour (e.g. elevated feeding rates) and population concentration (Garratt 1996, Sadovy & Domeier 2005), or disruptive effects on reproductive behaviour (Sadovy 1996). Musselcracker appear more easily caught in the spawning season due to their clumped distribution. Aggregating fish's behaviour also makes them less aware of spearfishermen (van Rooyen 1987). Temporal catch restrictions (i.e. closed seasons) for species with changing seasonal catchability have been used with success in the management of some exploited species.

For example, it appears closed seasons have benefited seasonally migrating South African elf (*Pomatomus saltatrix*) stocks (van der Elst 1988a). A similar restriction for musselcracker, however, would be difficult to implement given that it constitutes a 'compensatory' catch during closed seasons of other species (elf and galjoen) Clarke & Buxton (1989).

South African shore and estuarine fisheries are characterised by poor compliance with regulations and inadequate enforcement levels (Brouwer *et al.* 1997, Hauck & Kroese 2006, Smith *et al.* 2007) and present catch restrictions are likely ineffectual as management measures for these species in many areas of the coast (Cowley *et al.* 2002). Alternative management measures should thus be considered, one of which is the use of no-take marine protected areas. No-take MPAs have been promulgated globally both for conservation of exploited populations and their potential enhancement in adjacent areas (Polunin & Roberts 1993, Russ 2002, Gell & Roberts 2003), and South Africa has highlighted the value of MPAs as a tool in management of its exploited fish populations (Bennett & Attwood 1991, 1993, Attwood *et al.* 1997a,b), including the study species Bennett & Attwood 1991, Cowley *et al.* 2002).

Movements at an individual or population level greatly influence protective and fishery-enhancement effects of MPAs (Kramer & Chapman 1999, Munro 2000). Their high degree of site-fidelity suggests even small, well-protected areas will protect considerable numbers of blacktail and zebra from fishing pressure, as for other sedentary species (Willis *et al.* 2001, 2003, Kerwath *et al.* 2007a,b). Although fisheries enhancement from post-settlement movement to exploited areas through ontogenetic (Appeldoorn *et al.* 1997) or density-dependent (Abesamis & Russ 2005) spillover is therefore probably limited, MPAs may buffer or even enhance adjacent fisheries by supplying recruits via export of pelagic eggs and larvae (Tilney *et al.* 1996, Attwood *et al.* 2002, Domeier 2004). They also function as areas where genetic integrity of the stock is preserved, as intensive exploitation may be expected to lower genetic diversity through the removal of locally-adapted genotypes. To ensure significant enhancement of exploited populations siting of future MPAs should therefore consider local oceanographic currents and larval dispersal dynamics. Under intense outside exploitation levels, MPAs may require significant self-recruitment (Cowen 2002, Swearer *et al.* 2002) for population maintenance (Hastings & Botsford 2006) or the creation of MPA networks located to maximise both dispersal between protected populations and to exploited areas (Palumbi 2003, Leis 2005).

Conversely, if larval export rates are low (Jones *et al.* 1999, 2005) fishery enhancement for highly resident species from single, large MPAs is unlikely to match yield lost to the fishery in closing the area to exploitation (Carr & Reed 1993). However, this may be offset by management benefits of large MPAs valuable to fisheries, such as protection from overall stock collapse, providing biological reference points for fishery assessments (Attwood 2003) and ecosystem-based benefits to other species (Ecosystem Principles Advisory Panel 1999). Adequately enforced no-take MPAs incorporating suitable habitats will protect resident juvenile and subadult musselcracker populations. However, large-scale movements of older fish take them into exploited areas and MPAs therefore only provide temporary protection for adult populations. In contrast to the *Diplodus* species, ontogenetic spillover from MPAs may play an important role in providing recruits to fisheries targeting musselcracker. MPAs protecting large contiguous areas of suitable juvenile nursery habitat, such as the Tsitsikamma National Park, appear most effective for this and are particularly relevant given potential anthropogenic impacts on unprotected nursery areas. Large MPAs probably also protect (and therefore maintain) significant adult populations outside the spawning season more effectively than small (e.g. less than five kilometre wide) MPAs, given these large fish's potential for large-scale movements. However, even small MPAs could also significantly reduce total fishing effort on this species, particularly on migratory aggregations that move through them. If fishing activity significantly affects spawning behaviour, MPAs could also provide areas where spawning can take place undisturbed.

The suitability of no-take MPAs as fisheries management tools has recently been debated (Kaiser 2005, Gardmark *et al.* 2006). However, South Africa's lack of voluntary adherence to fishing regulations and adequate enforcement makes use of MPAs the only viable option for sustainable utilisation of these and other endemic reef species at present. Importantly this should be seen from conservation and ecosystem-based management perspectives in addition to that of fisheries-enhancement (Jones 2007). While populations of the study species are not presently regarded as 'collapsed' or 'threatened', restricted movements of individuals during at least part of their post-settlement life make them vulnerable to localised depletion under even moderate exploitation rates. In many areas exploitation pressure is intense, and as angling participation increases local declines will be further manifested at the population level.

Given the current lack of basic information on larval dispersal and resulting population connectivity and stock segregation, it is pertinent that the important (and varying) roles existing MPAs may currently play in maintenance of exploited stocks of these and other species are upheld. When the overall benefits of MPAs are considered, recent claims to re-open sections of existing MPAs for "restricted access" fishing (Sunde & Isaacs 2008) are not only unjustifiable on any biological basis, but would constitute flagrant disregard for the precautionary approach to fisheries management (FAO 1995). The demonstrated effectiveness of Marine Protected Areas in protecting exploited populations from overfishing and increasing biomass of resident species also offer a prime opportunity for educating fishermen on the merits of adhering to regulations through demonstrating their effects on population and average fish size. With South Africa's under-resourced enforcement capacity it is imperative that effective public education programs are instituted to instil a more sustainable attitude towards the use of coastal resources.

At a broader level, all management decisions should be based upon a sound knowledge on the status of an exploited species in a particular area and how local populations are responding to fishing pressure and present management strategies. Periodic assessments of exploited populations are required in South Africa's Linefish Management Protocols to assess the effectiveness of particular management actions (see Chapter 1), and long-term monitoring of protected and exploited populations is required to provide reference points on which to determine trends. Catch per unit effort (CPUE), based on research angling surveys, is currently used as a method of determining popuation abundance in monitoring studies of shorefishery species (Götz et al. 2008). However, the results presented in Chapter 5 highlight the necessity of ensuring such studies take spatial and temporal factors influencing the foraging behaviour of the study species into account when undertaking such assessments, as they will affect catchability and thus the interpretation of results of population assessments based on CPUE.

Although the maintenance of a well-managed network of MPAs may resolve the long-term conservation needs of the study species, more research is required to fill present knowledge gaps. For example, future studies quantifying the relative contribution distinct nursery habitats make to adult populations, and how these and habitat connectivity affect the timing and magnitude of ontogenetic movements should be undertaken.

A better understanding of musselcracker spawning migrations is also necessary to understand their population dynamics. Recent advances in population genetics (Nielsen *et al.* 2005, Jamandre *et al.* 2007) and the use of chemical signatures, retained in hard tissues such as otoliths and reflecting past environment conditions experienced by individuals, offer potential methods to examine both these questions. A major unresolved area of these species' lifetime movement patterns, as for most marine fishes, is the dispersal dynamics of their pelagic eggs and larvae. Previously-assumed high levels of population connectivity maintained through long-distance passive dispersal of these life-history stages are currently being questioned by results of recent studies on small-scale oceanographic circulation (James *et al.* 2002) and pre-settlement stage larval fish swimming abilities (Leis & Carson-Ewart 1997) and behaviour (Leis 2002). At the functional population level, low post-settlement movement of blacktail and zebra suggests major population connectivity only occurs via larval dispersal. Spawning migration patterns of musselcracker make use of South Africa's east and south coast oceanographic regimes for dispersal and retention of settlement-stage larvae to regions with large areas of rocky intertidal nursery habitat, but the dynamics of larval dispersal from different regions of the coast remain unquantified.

In particular, the possible existence of separate musselcracker stocks, maintained through natal homing in spawning migrations and larval dispersal trajectories, should be investigated. If present these may require different management strategies. The possible stock, or even species, differentiation in southern African blacktail (and possibly zebra) populations (Mann 2000c, Heemstra & Heemstra 2004) also requires investigation. In addition to answering these questions, the rapidly expanding use of genetic analyses involving microsatellite DNA markers (e.g. Curley & Gillings 2009), together with studies utilising natural and artificial biochemical tagging of larval otoliths (Campana 2005, Elsdon *et al.* 2008) will hopefully lead to direct estimates of dispersal and population connectivity for these species in future studies. This will enable better-informed management strategies for their conservation and sustainable human use to be formulated.

Appendix 1 – Tsitsikamma National Park research angling localities

Locality code	Angler locality name	Habitat type
BB	Boulder Bay	Shallow rocky reef
BKB	Bloukrans Bank	Sand-dominated
CLL	Clinton's Rock Left	Shallow rocky reef
CLR	Clinton's Rock Right	Shallow rocky reef
CR	Cormorant Rock	Sand-dominated
DG	Deep Gully	Sand-dominated
DSG	Dogshark Gully	Unclassified
FO	Far Out	Unclassified
GT	Gate	Deep rocky reef
HR	Hut Rock	Unclassified
HT	High Tide Beach & Bank	Shallow rocky reef
JSB	Jan se Bank	Deep rocky reef
KR	Klip River Bank	Sand-dominated
LK	Losklippe	Shallow rocky reef
MIL	Mother-in-Law's	Deep rocky reef
OB	Otter Bank	Deep rocky reef
OG	Otter Gully	Shallow rocky reef
PS	Pigsty	Shallow rocky reef
PT	Point	Shallow rocky reef
PUL	Pulpit	Shallow rocky reef
RIF	Riff	Deep rocky reef
RIFR	Riff Right	Deep rocky reef
SB	Santer Bank	Deep rocky reef
SB2	Santer Bank 2	Deep rocky reef
SB3	Santer Bank 3	Deep rocky reef
SB4/5	Santer Bank 4 & 5	Deep rocky reef
SBS	Santer Bank Sloep	Deep rocky reef
SG	Sandgatte	Sand-dominated
V	Vee	Sand-dominated
WF	Waterfall	Shallow rocky reef

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