MOVEMENT PATTERNS OF SPOTTED GRUNTER, *POMADASYS COMMERSONNII* (HAEMULIDAE), IN A HIGHLY TURBID SOUTH AFRICAN ESTUARY

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ABSTRACT

The principal objective of this thesis was to gain an understanding of the movement patterns of spotted grunter *Pomadasys commersonnii*, an estuarine-dependent fishery species, in the turbid, freshwater dominated Great Fish Estuary. Both manual and automated telemetry methods were used to monitor the movements of spotted grunter during two separate studies conducted in summer and spring 2003 and 2004. Acoustic transmitters were surgically implanted into twenty spotted grunter with lengths between 263 and 387 mm TL in the first study and twenty spotted grunter ranging between 362 and 698 mm TL in the second study.

The specific objectives were to gain an understanding of (i) the time spent in the estuarine environment (ii) the space use and home range size, and (iii) the abiotic factors governing the movement patterns of spotted grunter in the estuary.

The nursery function of estuarine environments was highlighted in this study as adolescent spotted grunter spent a significantly larger proportion of their time in the estuary than adult fish ($p < 0.0001$; $R^2 = 0.62$). The increased frequency of sea trips, with the onset of sexual maturity, provided testimony of the end of the estuarine-dependent phase of their life-cycle. Although considered to be predominantly marine, the adult spotted grunter in the Great Fish Estuary utilised the estuary for considerable periods. Adults are thought to frequent estuaries to forage, seek shelter and to possibly rid themselves of parasites. During this study, the number of sea trips made by tagged fish ranged from 0 to 53, and the duration ranged from 6 hours to 28 days. The tidal phase and time of day had a significant effect ($p < 0.05$) on the sea trips undertaken by fish. Most tagged spotted grunter left the estuary during the night (84%) on the outgoing tide, and most returned in the evening (77%) during the incoming tide. Sea temperature ($p < 0.0001$; $R^2 = 0.34$), barometric pressure ($p = 0.004$; $R^2 = 0.19$) and wind ($p = 0.01$) had a significant effect on the number of spotted grunter recorded in the estuary. Spotted grunter were more prone to return to

the estuary after high barometric pressure, when low sea temperatures (upwelling events) prevailed.
There was a significant positive relationship between home range size and fish length ($p = 0.004$; $R^2 = 0.20$). Small spotted grunter (< 450 mm TL) appeared to be highly resident, with a small home range (mean size = 129 167 m^2), that was generally confined to a single core area. Larger individuals (> 450 mm TL) occupied larger home ranges (mean size = 218 435 m^2) with numerous core areas. The home ranges of small and large spotted grunter overlapped considerably yielding evidence of two high use areas, situated 1.2 km and 7 km from the mouth of the Great Fish Estuary.

Tagged spotted grunter were located in a wide range of salinity, turbidity and temperature, but were found to avoid temperatures below 16 °C. The daily change in environmental variables (salinity, temperature and turbidity) had a significant effect on the change in fish position in the estuary ($p < 0.0001$; $R^2 = 0.38$). The distribution of tagged spotted grunter, particularly the larger individuals, in the Great Fish Estuary was influenced by the tidal phase ($p < 0.05$); they moved upriver on the incoming tide and downriver on the outgoing tide.

This study provides an understanding of the movement patterns of spotted grunter in the estuary and between the estuarine and marine environments. Consequently, it provides information that will assist in the design of a management plan to promote sustainability of this important fishery species. The techniques used and developed in this study also have direct application for further studies on other important estuarine-dependent fishery species.

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CHAPTER 1
INTRODUCTION

Spotted grunter, *Pomadasys commersonnii* (Pisces: Haemulidae) (Figure 1.1) is found in inshore coastal regions and estuaries of the Western Indian Ocean (Smith & Heemstra, 2003). In southern Africa, it is most common along the east coast with occasional fish recorded as far west as False Bay during the summer months (Day *et al.,* 1981; Heemstra & Heemstra, 2004). Spotted grunter are fast growing, and attain a length of 12 - 15 mm in their first year (Wallace, 1975a). It has been documented that the length at 50% maturity occurs at 300 mm TL in males (Wallace, 1975b; Webb, 2002) and 360 mm TL in females (Wallace, 1975b). After sexual maturity, spotted grunter increase in weight by 600 - 700g per annum. They attain a maximum size of 870 mm TL and age of approximately 15 years (Wallace & Schleyer, 1979).

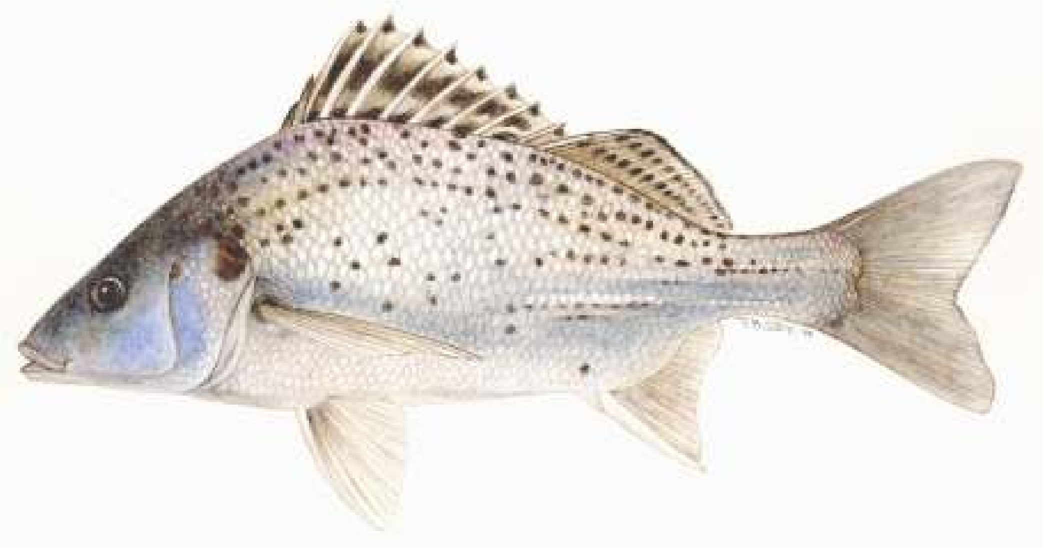


Figure 1.1. Spotted grunter *Pomadasys commersonnii* (Pisces: Haemulidae).

Spotted grunter is a macrobenthivore, with the composition of its diet being dictated by the composition and abundance of the macrobenthos of the particular estuary in which it occurs (Blaber, 1983). In estuaries along the southeastern Cape coast of South Africa, spotted grunter feed mostly on anomurans, namely sand prawn C*allianassa krausii* and the mudprawn *Upogebia africana* (Whitfield, 1980; Hecht &

van der Lingen, 1992). Spotted grunter are euryhaline and have been found to tolerate salinities from 0 to 90 ‰ (Whitfield *et al*., 1981). They can survive in salinities less than 1 ‰ (Blaber & Cyrus, 1981).

Spotted grunter is an estuarine-dependent species, which is defined by Whitfield (1994) as those who would be adversely affected by the loss of estuarine habitats. Juvenile spotted grunter are considered to be wholly dependent on estuaries and their survival in South African waters is determined by the existence of numerous estuaries along the coast (Wallace *et al.,* 1984; Whitfield, 1994c). The South African marine inshore environment is characterised by turbulent wave action, a lack of sheltered shores, and a narrow continental shelf on the east and south-east coasts. In contrast, estuaries are typically calm, sheltered, shallow and despite being subject to a large variation in salinity, temperature and turbidity, are highly productive. As a result, South African estuaries represent a specialised environment, and of the approximately 1 500 fish species found on the continental shelf, less than 100 make use of these systems (Wallace *et al*., 1984). Potter *et al*. (1990) suggested that the rough sea conditions in South Africa encourage juveniles to enter estuarine areas for shelter and protection from predation. Many estuaries along the South African coastline act as nursery areas for juveniles and as feeding grounds for adults from a host of fish species, and are therefore important in the life history of species and in the maintenance of the diversity of coastal fish species (Cyrus, 1991).

Adult spotted grunter are thought to spawn in the KwaZulu-Natal (KZN) inshore coastal zone, on the north-east coast of South Africa, between August and December (Wallace, 1975b; Wallace & van der Elst, 1975; Harris & Cyrus, 1997; Harris & Cyrus, 1999). The eggs and larvae are transported southwards on the edge of the Agulhas Current, and juveniles (20 - 50 mm TL) recruit into the KZN and southeastern Cape estuaries (Wallace & van der Elst, 1975; Whitfield, 1990; Webb, 2002). Recruitment occurs over a prolonged period of 6 - 7 months (Wallace & van der Elst, 1975). Juvenile spotted grunter make use of the nutrient rich estuarine environment where they grow rapidly. Upon attaining sexual maturity (300 - 400 mm

TL, 1 - 3 years), spotted grunter migrate to the marine environment (Wallace, 1975b; Wallace & Schleyer, 1979; Day *et al.,* 1981). Webb (2002) suggested that adult fish from the southeastern Cape migrate to KZN where spawning occurs. To date, there is no evidence to suggest that spawning takes place off the southeastern Cape (Webb, 2002). After spawning, adult fish return to the estuarine environment to feed and regain condition (Wallace, 1975b). The return of post-spawning fish coincides with increased catches by fishers in estuaries and are commonly known as 'grunter runs'. Wallace (1975a) showed that the abundance of spotted grunter in KZN estuaries increases during spring and early summer. Plumstead *et al.* (1989a) found the catch rate of spotted grunter peaked in July and September in the Mbashe Estuary on the Transkei Wild Coast. Webb (2002) also showed an increase in abundance of spotted grunter in the Great Fish Estuary from September to January. He found that 60 % of the catch during these months were adults. Several authors have also observed peaks in the catch rate of spotted grunter between August and February in other southeastern Cape estuaries (Marais & Baird, 1980a; Marais, 1981; Marais, 1983a; Marais, 1983b; Plumstead *et al*., 1985a,b; Pradervand & Baird, 2002). It is thought that adults spend several months in estuaries, and then move back to sea, where they undergo gonadal development and spawn (Wallace, 1975b; Wallace & van der Elst, 1975).

The spotted grunter is one of the most important recreational species along the South African coastline (Fennessy, 2000), dominating the catch of recreational and subsistence fishers in most estuaries in the Eastern Cape and KZN (James *et al*., 2001; Pradervand & Baird, 2002; Mann *et al*., 2002). Since 1992, spotted grunter has been decommercialised and has been classified as a recreational species (i.e. may not be sold). This is primarily because of its inshore distribution and estuarine dependence, which renders it vulnerable to exploitation compared to other purely marine species (Fennessy, 2000). A preliminary stock-assessment conducted in KZN revealed that spotted grunter are currently "slightly" over-exploited (Fennessy, 2000). Lamberth & Turpie (2003) classified spotted grunter as being maximally or optimally exploited, and suggested that the species is likely to be subject to additional fishing pressure in the future. They noted that fishing is a rapidly growing activity and that the catch rate of coastal and estuarine fisheries has declined markedly over the past two decades. Baird *et al*. (1996) and Guastella (1994) observed a decline in spotted grunter catches over a 20 year period. Increases in fishing pressure, particularly in estuaries, is problematic for estuarine-dependent species, such as spotted grunter, as this phase represents a bottleneck for their life history (Lamberth & Turpie, 2003). This emphasizes the importance of estuarine conservation by protecting the habitat and regulating exploitation. At present the fishery regulations for spotted grunter include a minimum size (400 mm TL) and a daily bag limit of 5 per person per day. However, with the declining numbers and general non-compliance to the regulations (Mann *et al*., 2002; Potts *et al*., 2004), alternative management strategies must be sought.

Understanding animal movements in time and space is fundamental to the study of animal ecology and to the design of effective conservation and resource management strategies (Pittman & Mc Alpine, 2001). The estuarine-dependent nature of spotted grunter renders them extremely vulnerable during both their juvenile and post-spawning adult phases. Conservation measures of estuarine-dependent species should therefore be directed at the most vulnerable part of their life cycle (Wallace & van der Elst, 1975). Consequently, an understanding of the spatial and temporal movements of spotted grunter in the estuary is fundamental to the design of management strategies for estuarine-dependent species. While there is some information on the longshore movement patterns of spotted grunter (Sedgewick's/ORI/WWF National Tagging Programme 1984 – present), there has been no research on localised movement patterns within estuarine environments. Moreover, although knowledge exists on the biology of the spotted grunter (Wallace, 1975ab; Webb, 2002), there is a paucity of information regarding the frequency and duration of estuarine residence and the space use patterns within estuaries. Besides having pertinent management implications, quantifying the degree of estuarine use by spotted grunter will greatly enhance our understanding of the ecology of this species.

The Great Fish Estuary was the chosen study site for this study as it has a large population of spotted grunter and hosts a large recreational fishery and a permanent subsistence fishing community. It is situated in a rural area in the Eastern Cape Province of South Africa. This region is economically depressed, resulting in a high dependence on coastal and estuarine fishery resources for food and income. The spotted grunter is the most important fishery species in the Great Fish Estuary, dominating the catch in all studies conducted on the estuary (Ter Morshuizen *et al*., 1996; Pradervand & Baird, 2002; Webb, 2002; Potts *et al*., 2004). Potts *et al*. (2004) showed that fishery resources of the Great Fish Estuary are being placed under increasing fishing pressure. In addition, and although regulated, the Great Fish Estuary is one of the few estuaries in South Africa that has an enhanced freshwater inflow.

The objectives of this thesis are to gain an understanding of the degree of estuarine use of adolescent and adult spotted grunter, an estimate of home range size, space use patterns, movement and distribution of spotted grunter within the Great Fish Estuary, and lastly, understand the abiotic factors governing their movement patterns within the estuary.

Conventional tag and recapture techniques are considered to be cost effective to monitor the movements of fish. Large number of fish can be tagged and this enables one to provide an integrated, population-level view of movements and dispersal patterns. However, a description of small-scale localised movements is not possible as no information on the fish position between release and recapture dates is available. On the contrary, telemetry provides fine-scale temporal and spatial data that is essential for behavioural ecology (Baldwin *et al*., 2002). The objectives of this study could therefore only be achieved through the use of this high resolution sampling technique. Telemetry enables one to track and monitor real-time movements of individual fish by means of transmitters attached to or internally implanted into them. In its broadest sense, telemetry conveys information from one location (the transmitter) to another (the receiver). Radio telemetry involves the conveyance of information via radio signals, while ultrasonic or acoustic telemetry makes use of sound waves. Ultrasonic telemetry is used most often in the marine environment, as the conductivity of salt water hinders the transmission of radio signals. This is because the electromagnetic energy of radio frequencies is rapidly absorbed as it passess through seawater (Pincock & Voegeli, 1992). Therefore, the use of acoustic telemetry in marine environments is the best available technique for monitoring the small-scale movements of marine fishes (Voegeli *et al*., 2001). Ultrasonic telemetry has been frequently used to study localized movements of fish species in estuarine and marine environments, and was accordingly used in this thesis.

Thesis outline

This thesis is divided into six chapters.

Chapter 2 provides a general overview of the study area and the methods and materials used in this study.

Chapter 3 identifies the proportion of time that spotted grunter spend in the estuary and quantifies the dependence of adolescent and adult spotted grunter on the estuarine environment. This chapter also describes the effect of abiotic factors on the movement of spotted grunter between the estuarine and marine environments, and identifies factors influencing these movements.

Chapters 4 and 5 deal with the space use, distribution and movements of spotted grunter in the estuary. Chapter 4 describes the space use of spotted grunter in the estuary and quantifies various home range parameters for each individual fish. This chapter also identifies the different modes of behaviour exhibited by spotted grunter and highlights the factors known to influence the home range of fish. Chapter 5 addresses the abiotic factors governing home range size, movement and distribution of spotted grunter in the estuary, and provides a model to describe the movements and distribution of spotted grunter in response to important abiotic variables.

In Chapter 6, the principal findings of this study are summarized by way of a general discussion. The contribution of this study to the ecology and life history of this species is discussed. The findings are then considered in the context of developing a management strategy for the species. The application of telemetry for research on other estuarine-dependent species and other future research initiatives are discussed.

CHAPTER 2

STUDY AREA AND METHODS AND MATERIALS

Study Area

The Great Fish River is 650 km long, entering the Indian Ocean approximately halfway between Port Elizabeth and East London at 33º 29’ 28’’S, 27º 13’ 06’’ E (Figure 2.1).

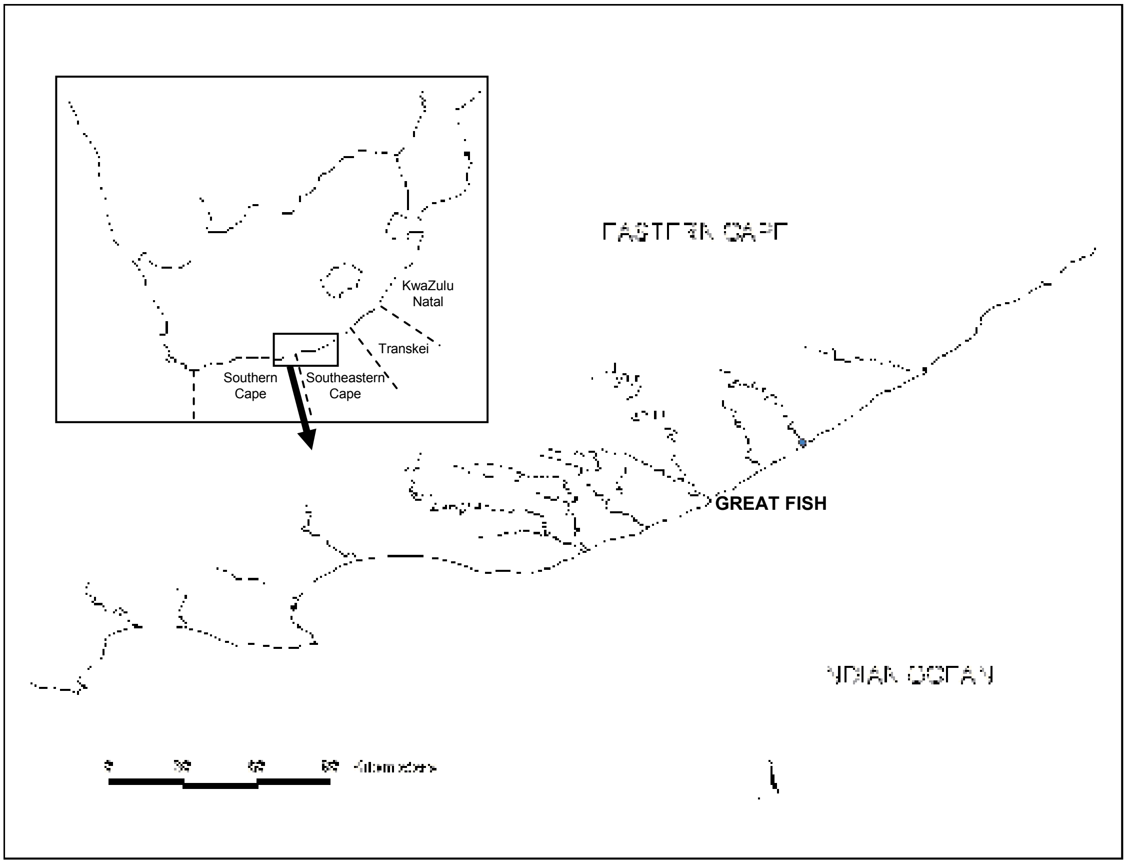


Figure 2.1. The location of South Africa with inset showing the location of the Great Fish River estuary and other estuaries along the Eastern Cape coast.

The estuary is in a rural area and once formed the boundary between the Eastern Cape Province and the former Ciskei. The characteristics of the Great Fish River catchment and estuary are summarised in Table 2.1.

Table 2.1. Characteristics of the Great Fish River catchment and estuary

Characteristics	
Catchment size (km²)	30 366
Mean annual runoff (m^3)	525 x 10^6
Mean annual river discharge (m^3)	224 x 10^6
Estuarine surface area (ha)	192.7
Estuary volume (m^3)	2.25 x 10^6
Estuarine length (km)	12
Mean depth (m) of estuary	1.4
Mean width (m) of estuary	122
Tidal cycle (h)	12.4 (SE ± 0.31)
River Flow per tidal cycle (m^3)	275 x 10^3
Spring tidal prism (m^3)	1.6 x 10^6
Macrophyte cover (ha)	0

Adapted from Allanson & Read (1987), Whitfield (1994), Vorwerk *et al.* (2003)

Livestock ranching and pineapple farming are practiced in the catchment area. Some of the low-lying floodplain areas along the banks of the river and the estuary are cultivated, mostly with maize.

Prior to 1975, the river had a highly variable flow regime. Periods of zero flow frequently occurred and caused the river to form a series of discrete pools, and closure of the estuary mouth (Reddering & Esterhuysen, 1982; O'Keefe & De Moor, 1988). In 1977, the erratic flow of the Great Fish River system was stabilised by the provision of water from the Orange River via an 85 km tunnel. Due to the interbasin transfer system the river was modified from an irregular seasonal flow to a perennial system (Reddering & Esterhuysen, 1982; O'Keefe & De Moor, 1988). The tunnel was designed to supply water, primarily for irrigation, to the Fish River valley. The transfer scheme resulted in a 500-800% increase in runoff in the upper regions of the river. Water abstraction in the lower Great Fish River has resulted in a considerable reduction in flow. The Great Fish

Estuary is presently characterised by large volumes of freshwater derived from the interbasin transfer system, and receives the highest river inflow of any estuary in the Eastern Cape Province (Whitfield, 1994a). This accounts for continuous nutrient inputs and, hence, elevated phytoplankton production, making the Great Fish Estuary a highly productive system.

The bathymetry of the Great Fish Estuary is uniform. The estuary channel is narrow (30-100 m wide) and its depth (0.5-3.5 m) is dependent on flooding events (Whitfield *et al.,* 1994). The mouth region is restricted by the presence of extensive sand banks. The estuary is mostly shallow, ranging between 1 m and 2 m (avg. 1.4 m), except for some areas in the lower and upper reaches that are 3 m and 6 m, respectively. The shallow nature of the estuary is a result of the large fluvial sediment load from the catchment (Grange *et al.,* 2000). These sediments are flushed out to sea during episodic floods, but are gradually replaced during periods of low river flow by sand deposits in the upper reaches and mud in the lower reaches (Reddering & Esterhuysen, 1982). The turbid nature of the Great Fish Estuary is also a result of the high levels of suspended sediment carried by catchment run-off, particularly during times of flood.

The water chemistry of the Great Fish River is strongly influenced by underlying rock in the catchment. This has resulted in an increased conductivity. However, the large influx of freshwater derived from the interbasin transfer system dilutes the ions (O'Keefe & De Moor, 1988). The flocculation of sediment, which occurs at the river-estuary interface, decreases the amount of suspended particulate matter in the middle reaches of the estuary. As a result of the net downstream movement of terrestrially-derived sediments, marine sediments are restricted almost entirely to the mouth region of the estuary. Consequently, the lower reaches are mainly marine-dominated, the middle reaches represent the mixing zone between river and sea, and the upper reaches are freshwater dominated (Grange *et al.,* 2000).

Perennial river flow together with tidal exchange ensures a permanently open connection to the sea (Grange *et al.,* 2000). The spring tidal range is between 1 m and 1.5 m in the lower reaches and decreases towards the head (Whitfield *et al.,* 1994). The tidal prism volume exceeds the river water volume by six times during an average tidal cycle. The rapid exchange of water in the estuary, demonstrated by a short flushing time of 0.8 days, is a direct consequence of the magnitude of freshwater discharge into the system (Allanson & Read, 1987).

The estuary is riverine in appearance, with few intertidal mud flats or saltmarshes (Ter Morshuizen, 1996), and few submerged macrophytes. Reeds and sedges occur intermittently along the banks. The eastern shoreline of the lower and middle reaches of the estuary consists mainly of coastal bushveld. The western shoreline between the estuary mouth and the road bridge forms part of the Great Fish Wetlands Reserve, and approximately 50 m above the road bridge, becomes part of the Kap River Reserve, both of which include saltmarshes (Figure 2.2). However, these supratidal saltmarshes occurring in the lower reaches are only inundated during periods of high river discharge and/or exceptionally high spring tides (Whitfield *et al*., 1994). Aquatic macrophyte vegetation is dominated by *Phragmites australis* beds in the upper and middle reaches, with a total lack of submerged estuarine plants such as *Zostera capensis* and *Ruppia cirrhosa* (Whitfield *et al*., 1994).

The Great Fish Estuary supports large subsistence and recreational fisheries. Main access to the estuary can be gained on the eastern and western bank via the coastal road. The R72 coastal road between East London and Port Elizabeth crosses the Great Fish Estuary approximately 1 km from the estuary mouth. Access to the estuary and its fishery resource is gained via four possible routes. The eastern shore of the estuary is accessible both below and above the R72 road bridge (Figure 2.2). Access to the eastern shore between the road bridge and the estuary mouth is controlled by the proprietors of the Fish River Diner. This facility consists of a shop, restaurant and a caravan park. The caravan park is only available to paying visitors (Figure 2.2). This property and facility was previously owned by the Eastern Cape Government, and is run privately through a long-term lease agreement (Potts *et al*., 2004). Access to the eastern shore above the road bridge is obtained by foot from the road bridge or via a rough vehicle track through the privately owned land, and access to the western shore between the road bridge and the estuary mouth is obtained via a gravel road (off the R72 coastal road) that runs through the Great Fish Wetlands Reserve (Figure 2.2). The Great Fish Wetlands Reserve is currently controlled by the Ndlambe Municipality and provides ablution facilities for day visitors and overnight campers. A small residential settlement, within the wetlands, consisting of “holiday shack” homes, is located close to the western bank near the estuary mouth. This settlement is under the control of the Ndlmabe Municipality via a land lease agreement with the homeowners. Access to the western shore above the road bridge can be obtained through the Kap River Reserve where overnight accommodation is only available through booking (Cowley & Daniel, 2001) (Figure 2.2).

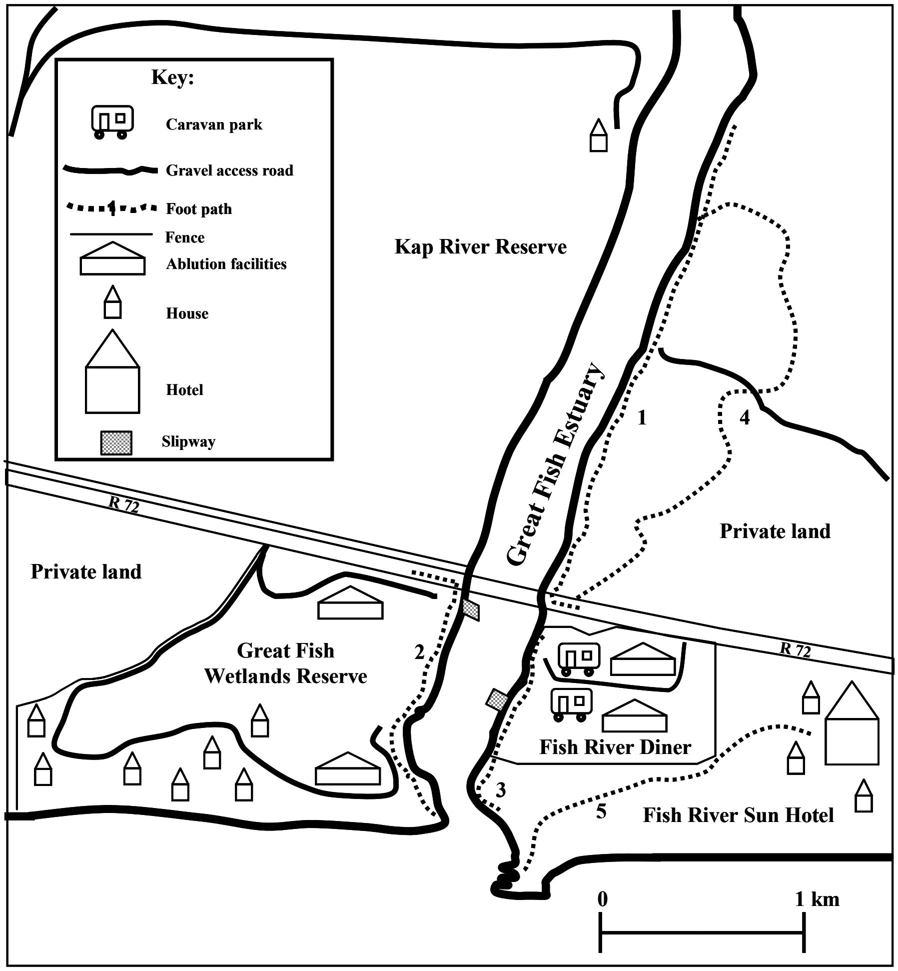


Figure 2.2. Map showing the main access routes to, and human activities around the lower regions of the Great Fish Estuary. 1-5 = footpaths. * Figure adapted from Potts *et al.* (2004)

Abiotic characteristics of the Great Fish Estuary

The abiotic characteristics of the Great Fish Estuary were monitored during two separate telemetry studies, investigating the movement patterns of spotted grunter *Pomadasys commersonnii*. The first study occurred between January and March 2003, and the second study between September 2003 and February 2004. The physico-chemical parameters known to influence fish distribution were monitored at eight fixed stations along the length of the estuary in study 1, and at nine fixed stations in study 2 (Figure 2.3).

Salinity (Atago hand held refractometer), temperature (digital/electronic thermometer), turbidity (Hanna 93703 turbidity meter), current speed and depth were measured at each fixed station. Current speed was calculated from the time that it took a neutrally buoyant object to move 2 meters. Water samples were taken 10 - 15 cm below the surface and ± 30 cm above the bottom. Water sampling took place daily, starting at the lowermost fixed station at approximately 08h00 and proceeding upriver to the uppermost fixed station at approximately 15h00. The sampling regime covered the entire tidal cycle, neap and spring as well as the low and high tide, during both studies.

The mean surface and bottom abiotic variables at each fixed station during both studies are presented in Table 2.2.

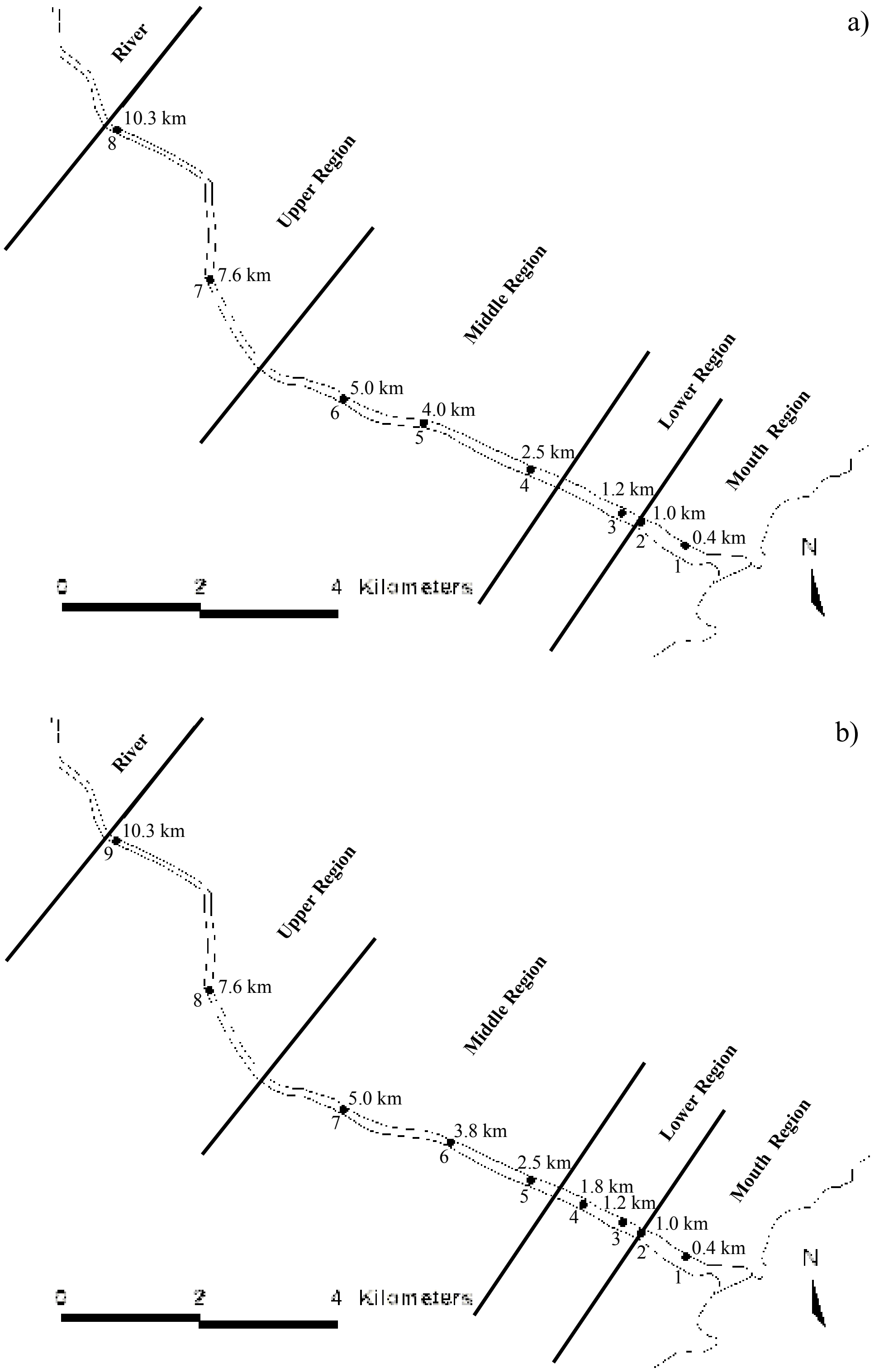


Figure 2.3. The Great Fish Estuary showing the locations of the fixed stations (numbered), their distance from the estuary mouth, and the different regions within the estuary during the a) first study (7 February 2003 - 24 March 2003) and b) second study (29 September 2003 - 15 November 2003).

Table 2.2. Mean (± SD) surface and bottom measurements for each abiotic parameter measured at each fixed station (km from the estuary mouth) along the length of the Great Fish Estuary during the first (7 February 2003 - 24 March 2003) and second study (29 September 2003 - 15 November 2003) studies. S = surface; B = bottom.

STUDY 1

Station	Salinity S (‰)	Salinity B (‰)	Temperature S (ºC)	Temperature B (ºC)	Turbidity S (FTU)	Turbidity B (FTU)	Depth (m)	Current S ($m.s^{-1}$)
1 (0.4 km)	22.7 (± 10.4)	31.5 (± 5.4)	21.7 (± 2.5)	20.3 (± 2.2)	42.9 (± 20.5)	38.1 (± 16.6)	1.6 (± 0.3)	0.3 (± 0.2)
2 (1.0 km)	17.5 (± 10.0)	33.0 (± 3.4)	22.6 (± 2.6)	20.1 (± 2.2)	59.7 (± 28.5)	66.3 (± 40.8)	2.9 (± 0.4)	0.4 (± 0.2)
3 (1.2 km)	12.9 (± 6.6)	30.4 (± 3.6)	23.4 (± 2.6)	20.5 (± 2.5)	71.0 (± 30.6)	71.9 (± 25.5)	1.9 (± 0.3)	0.4 (± 0.2)
4 (2.5 km)	8.8 (± 5.1)	17.0 (± 8.5)	24.6 (± 2.2)	22.9 (± 2.5)	135.1 (± 76.1)	162.7 (± 89.4)	1.0 (± 0.2)	0.4 (± 0.2)
5 (4.0 km)	4.7 (± 3.4)	11.1 (± 8.8)	25.4 (± 2.3)	23.7 (± 2.6)	217.0 (± 99.0)	317.4 (± 135.0)	1.2 (± 0.4)	0.4 (± 0.2)
6 (5.0 km)	3.4 (± 3.3)	10.6 (± 10.2)	25.6 (± 2.2)	24.2 (± 2.8)	227.3 (± 87.2)	310.8 (± 94.0)	1.6 (± 0.3)	0.3 (± 0.1)
7 (7.6 km)	1.1 (± 2.3)	2.7 (± 4.4)	26.1 (± 2.2)	25.5 (± 2.5)	232.6 (± 51.0)	318.4 (± 120.2)	3.8 (± 1.1)	0.2 (± 0.1)
8 (10.3 km)	0.2 (± 0.5)	0.4 (± 0.8)	26.1 (± 2.4)	26.0 (± 2.7)	208.2 (± 42.0)	292.7 (± 113.7)	3.6 (± 0.7)	0.1 (± 0.1)

STUDY 2

Station	Salinity S (‰)	Salinity B (‰)	Temperature S (ºC)	Temperature B (ºC)	Turbidity S (FTU)	Turbidity B (FTU)	Depth (m)	Current S ($m.s^{-1}$)
1 (0.4 km)	23.0 (± 9.2)	30.4 (± 5.8)	18.5 (± 1.6)	17.6 (± 1.1)	18.1 (± 7.2)	18.9 (± 9.0)	1.4 (± 0.3)	0.4 (± 0.2)
2 (1.0 km)	15.9 (± 6.6)	32.7 (± 2.6)	19.6 (± 1.5)	17.7 (± 0.9)	25.8 (± 8.4)	48.1 (± 28.6)	2.8 (± 0.3)	0.4 (± 0.2)
3 (1.2 km)	13.4 (± 5.9)	29.6 (± 5.0)	20.1 (± 1.6)	18.2 (± 1.0)	29.3 (± 9.7)	42.4 (± 18.3)	1.8 (± 0.2)	0.3 (± 0.2)
4 (1.8 km)	10.6 (± 6.3)	25.7 (± 6.5)	20.7 (± 1.5)	18.8 (± 1.4)	36.1 (± 15.5)	47.7 (± 19.7)	1.5 (± 0.2)	0.3 (± 0.2)
5 (2.5 km)	7.9 (± 5.6)	14.5 (± 10.8)	21.2 (± 1.6)	20.2 (± 1.9)	54.3 (± 28.3)	62.5 (± 28.7)	0.9 (± 0.2)	0.3 (± 0.2)
6 (3.8 km)	4.5 (± 3.7)	27.0 (± 7.4)	21.9 (± 1.6)	18.9 (± 1.2)	82.2 (± 48.1)	79.4 (± 49.3)	2.4 (± 0.3)	0.3 (± 0.1)
7 (5.0 km)	2.2 (± 2.6)	10.3 (± 11.7)	22.3 (± 1.5)	21.1 (± 1.9)	105.3 (± 47.5)	132.0 (± 67.4)	1.8 (± 0.3)	0.3 (± 0.1)
8 (7.6 km)	1.7 (± 3.3)	5.8 (± 6.4)	22.6 (± 1.4)	21.7 (± 1.6)	124.6 (± 44.7)	166.9 (± 71.1)	4.3 (± 0.8)	0.2 (± 0.1)
9 (10.3 km)	0.0 (± 0.0)	0.1 (± 0.5)	22.6 (± 1.3)	22.2 (± 1.4)	125.2 (± 30.7)	152.3 (± 34.4)	4.1 (± 0.6)	0.1 (± 0.1)

Strong longitudinal and vertical salinity gradients were observed in the estuary during both studies with a general increase in salinity closer to the mouth and as the depth increased. Salinity stratification was strongly developed with the average bottom salinity at the fixed stations being considerably higher than the average surface salinity. The salinity profile of the estuary reflects high levels of freshwater input as oligohaline (0.5 – 4.9 ‰) conditions often extended into the lower reaches of the estuary. Based on the mean bottom salinities recorded at the fixed stations, the estuary could be divided into four regions according to the Venice System (Whitfield, 1998): euhaline (30.0 – 39.9 ‰), polyhaline (18.0 – 29.9 ‰), mesohaline (5.0 – 17.9 ‰), and oligohaline (0.5 – 4.9 ‰). The euhaline and polyhaline regions were restricted to small areas in the lower reaches of the estuary, while the mesohaline and oligohaline regions occupied most of the middle and upper regions of the estuary (Figure 2.4).

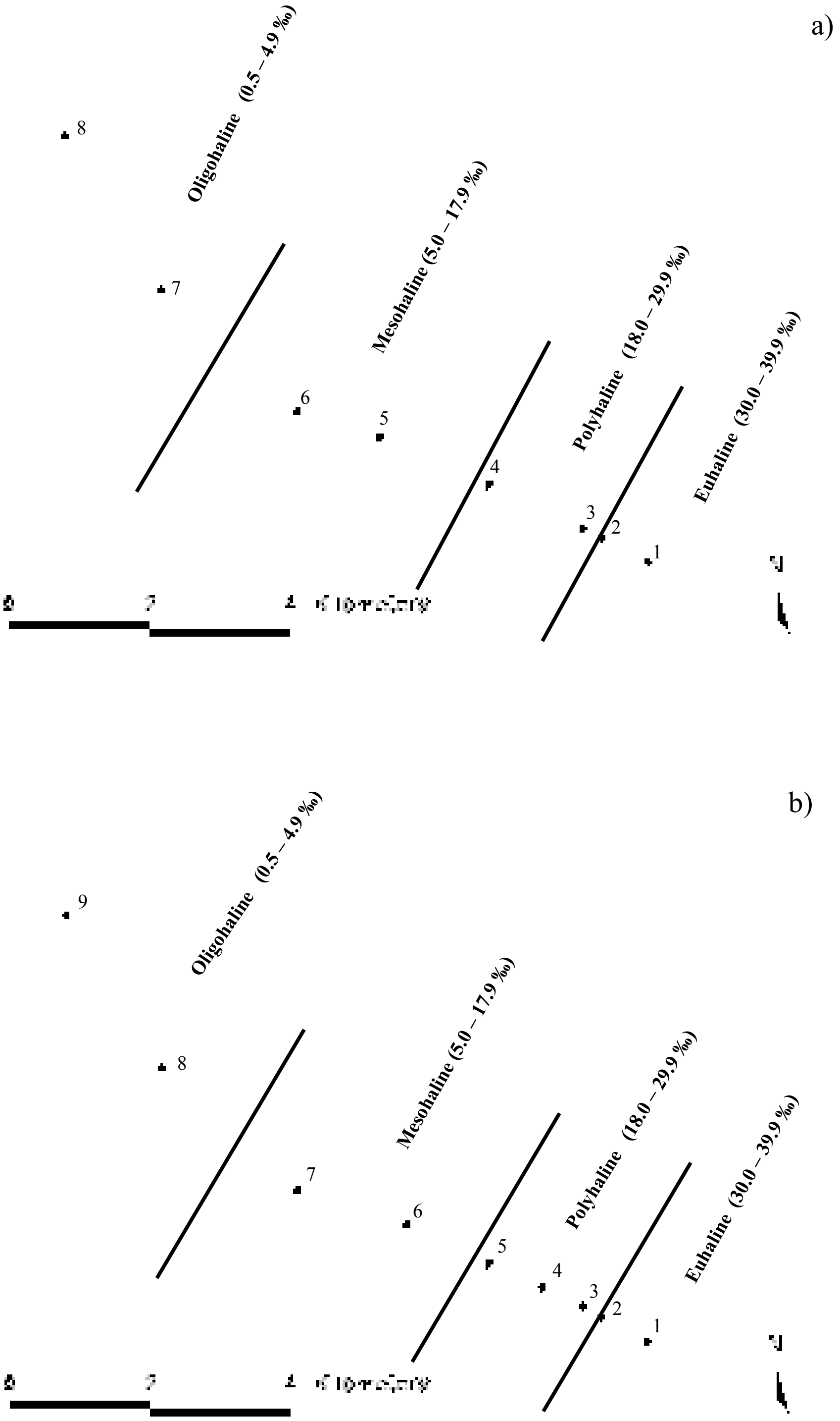


Figure 2.4. The Great Fish Estuary showing the location of the fixed stations (numbered) and the salinity regions according to the Venice system (based on the mean bottom salinity recorded at the fixed stations), during the manual tracking period in a) the first study (7 February 2003 - 24 March 2003) and b) the second study (29 September 2003 - 15 November 2003).

The mean temperature in the Great Fish Estuary was 22.9 ºC (range. 15.2 ºC – 29.5 ºC) in the first study, and 19.6 ºC (range. 15.7 ºC – 25.8 ºC) in the second study. In both studies, there was an increase in the mean surface and bottom water temperature from the mouth to the head of the estuary (Table 2.2). Surface water temperature was on average 1.5 ºC and 1.4 ºC higher than the mean bottom water temperature in the respective studies. The greatest difference between the mean surface and bottom water temperatures was in the lower reaches (Table 2.2). However, owing to the increased depth at station 6 in the second study (see below), this station had the greatest difference in mean surface and bottom temperature. There was a strong seasonal difference in the mean surface and bottom water temperature recorded in the summer months of the first study and the spring months of the second study. Mean bottom water temperature was 20.3 ºC (± 2.2) at station 1 and 26.0 ºC (± 2.7) at station 8 in the first study, while in the second study it was considerably lower, 17.6 ºC (± 1.1) at station 1 and 22.2 ºC (± 1.4) at station 9 (Table 2.2).

During both studies, there was an increase in the mean surface and bottom turbidity from the lowermost to the uppermost fixed stations. The greatest difference between mean surface and bottom turbidity was observed in the upper reaches (Table 2.2). In the first study (summer), mean bottom turbidity was high, 38.1 FTU (± 16.6) at station 1 and 292.7 FTU (± 113.7) at station 9. In the second study (spring), turbidity was lower, 18.9 FTU (± 9.0) at station 1 and 152.3 FTU (± 34.4) at station 9 (Table 2.2)

The depth profile of the estuary during the first study was uniform, ranging between 1 and 2 m, except for a few deep areas in the lower and upper reaches of the estuary. However, the bathymetry of the estuary changed dramatically after a flash flood in May 2003 (149 mm rainfall overnight), creating large scours and holes in the middle (± 4.5 km from the estuary mouth) and upper (± 7 km from the estuary mouth) reaches of the estuary. The most affected area was in the upper reaches of the estuary between 6 and 8 km from the mouth.

The mean surface current speed at the fixed stations decreased gradually from the lower to the upper fixed stations in both studies (Table 2.2).

General methods

Movement patterns and habitat utilisation of spotted grunter in the Great Fish Estuary was recorded using ultrasonic telemetry. Ultrasonic fish telemetry enables one to track and monitor the movement patterns of individual fish by means of acoustic transmitters attached to or internally implanted into the fish. Telemetry allows fish to be tracked for reasonable periods of time (up to one year or longer depending on the transmitter setup). The transmitters used in the study were coded transmitters set to the same frequency, allowing for the simultaneous tracking of many fish.

Coded transmitters have a significantly longer battery life compared with continuous transmitters as they emit acoustic pulse trains that are infrequent and random within a pre-specified time range. Recognition of all pulses associated with a transmitter code is necessary for transmitter identification. The fish tags in the present study transmitted coded signals on a fixed frequency (69 kHz) at random intervals every 5-15 seconds. Transmitted signals can be detected by either a hand-held receiver (hydrophone) or by stationary receivers positioned in the estuary.

During this study, spotted grunter were tagged with V8SC-2L-R256 and V13SC-1L-R256 coded transmitter tags (VEMCO Ltd, Halifax, Canada). The codes for these transmitters consisted of six acoustic pulses. The weight of the transmitters in water did not exceed the recommended maximum of 2% of the mass of any fish (Pincock & Voegeli, 2002), and the dimensions of the gut cavity were also taken into consideration when selecting the minimum size of fish suitable for tagging.

Research Approach

Two separate telemetry studies were conducted. The first occurred between 7 February 2003 and 24 March 2003, and the second between 29 September 2003 and 12 February

2004. The fish were manually tracked using a motorised boat for 36 days in the first, and 42 days in the second study. An additional 95 days of monitoring in the second study was facilitated by the use of moored automated listening stations (ALSs) positioned along the length of the estuary (Table 2.3). The study area was confined mainly to the estuarine environment of the Great Fish River. However, if all fish were not located during manually tracking the survey area was extended into the riverine environment.

Table 2.3. Summary data of the two telemetry studies undertaken in the Great Fish Estuary during 2003/4.

	Study 1	Study 2
Dates	7 February – 24 March 2003	29 September 2003 – 12 February 2004
Study duration (days)	36	137
Manual Tracking period (days)	36	42
Date of Manual Tracking period	7 February – 24 March 2003	29 September – 15 November 2003
Number ALS deployed	4	8
No fish tagged	20	20 (21*)
Size Range (mm TL)	263 – 387	362 – 698

* = one fish was caught by anglers and replaced by another fish

Tagging of fish

In the first study, twenty spotted grunter (avg. 336 mm TL; range. 263 - 387 mm TL), with estimated ages between 2 and 4 years (Webb, 2002), were tagged with coded acoustic transmitters (Figure 2.5, Table 2.4). Similarly, in the second study, twenty spotted grunter (avg. 478 mm TL; range. 362-698 mm TL), with estimated ages between 5 and 10 years (Webb, 2002) were tagged (Figure 2.5, Table 2.4). During the second study one fish was captured on 10 October 2004 (16 days after release). Another fish was tagged with the same transmitter on 14 October 2004.

Wallace (1975b) documented the length-at-50% maturity of spotted grunter captured in KwaZulu Natal to be 300 mm TL for males and 360 mm TL for females. Webb (2002) found that males in the southeastern Cape obtained 50% maturity at a similar length (305 mm TL), and obtained 100% maturity at 450 mm TL. However, in the southeastern Cape the determination of 50% and 100% maturity for females was not possible (Webb, 2002).

Since the length at 100% maturity is 450 mm TL, it was assumed that spotted grunter > 450 mm TL (large fish) were adults, and spotted grunter < 450 mm TL (small fish) were adolescent fish. All fish from the first study and 10 fish from the second study were adolescent fish. All spotted grunter in the first study, and 4 individuals from the second study were smaller than the minimum legal size limit of 400 mm TL.

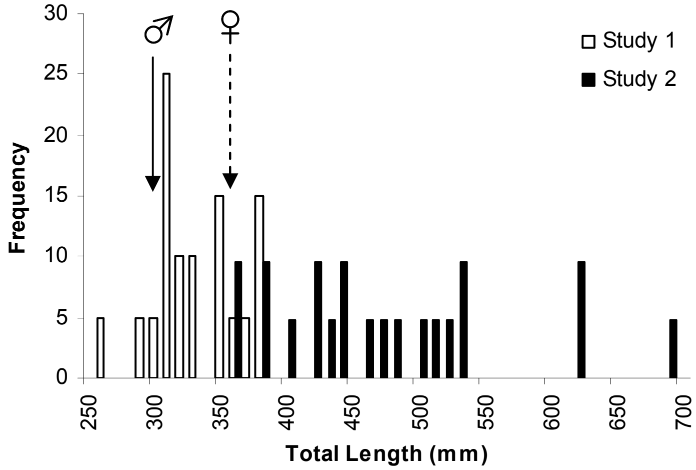


Figure 2.5. Length distribution of the 41 acoustically tagged spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary during the first study (7 February 2003 - 24 March 2003) and second study (29 September 2003 - 12 February 2004). Solid arrow indicates length-at-50% maturity for male spotted grunter in KwaZulu Natal[1] and in the southeastern Cape[2]. Dashed arrow indicated length-at-50% maturity for female spotted grunter in KwaZulu Natal[1]. [1] = Wallace (1975b), [2] = Webb (2002)

Table 2.4. Summary of tagging information for the 41 spotted grunter *Pomadasys commersonnii* tagged with acoustic transmitters in the Great Fish Estuary during the first (7 February 2003 - 24 March 2003) and second (29 September 2003 - 12 February 2004) studies. FL = Fork Length, TL = Total Length.

Fish Code	Study	Tagging date	FL (mm)	TL (mm)	Surgery Duration (min)
20	1	21/01/2003	297	317	0:02:52
21	1	21/01/2003	307	334	0:02:39
22	1	01/02/2003	271	297	0:02:12
23	1	01/02/2003	354	380	0:02:48
24	1	01/02/2003	304	330	0:02:32
25	1	01/02/2003	284	313	0:02:31
26	1	01/02/2003	291	314	0:03:07
27	1	01/02/2003	300	328	0:03:01
28	1	01/02/2003	354	382	0:02:40
29	1	27/01/2003	346	377	0:03:22
30	1	01/02/2003	282	308	0:02:40
31	1	27/01/2003	330	357	0:03:26
32	1	01/02/2003	293	318	0:02:30
33	1	27/01/2003	300	329	0:03:18
34	1	21/01/2003	256	263	0:02:39
35	1	27/01/2003	330	357	0:02:30
36	1	27/01/2003	358	387	0:03:00
37	1	21/01/2003	344	363	0:03:00
38	1	26/01/2003	296	319	0:02:38
39	1	01/02/2003	328	355	0:02:45
50A	2	24/09/2003	415	449	0:02:11
50B	2	14/10/2003	475	515	?
51	2	24/09/2003	432	469	0:02:31
52	2	24/09/2003	354	385	0:02:53
53	2	23/09/2003	390	428	0:02:14
54	2	23/09/2003	576	620	0:02:12
55	2	22/09/2003	390	432	?
56	2	24/09/2003	406	440	0:02:39
57	2	24/09/2003	338	364	0:02:23
58	2	22/09/2003	580	625	0:02:40
59	2	25/09/2003	430	472	0:01:47
60	2	23/09/2003	483	527	0:04:06
61	2	24/09/2003	452	489	0:02:30
62	2	22/09/2003	468	504	?
63	2	23/09/2003	492	534	0:02:13
64	2	24/09/2003	354	387	0:02:28
65	2	22/09/2003	651	698	0:07:52
66	2	22/09/2003	370	403	?
67	2	23/09/2003	395	428	0:02:16
68	2	22/09/2003	495	538	0:02:57
69	2	24/09/2003	332	362	0:02:36

Spotted grunter were caught with barbless hooks on rod and line, using either mud prawn *Upogebia africana* or sand prawn *Callianassa krausii* as bait. Surgery took place *in situ* on the boat. After capture, each fish was immediately placed in an aqueous solution (estuary water) containing 2-phenoxyethanol (approximately 1.0 ml.l^{-1}). This anaesthetic was used as Deacon *et al*. (1997) showed that 2-phenoxyethanol had no significant effect on the growth of juvenile spotted grunter. Once anaesthetized, each fish was measured to the nearest millimeter and placed ventral side up in a wet towel on high density V-shaped foam. During surgery, the fish's gills were continuously flushed with estuarine water. A 1.5 - 2.0 cm incision was made along the ventral surface posterior to the pelvic girdle. The transmitter was carefully inserted into the body cavity and the incision was closed using two independent silk sutures (2/0 Ethicon). The duration of the surgical process averaged 2 min 48 sec in the first study and 2 min 51 sec in the second study (Table 2.4). Following surgery, fish were placed in a recovery bath filled with estuarine water. Once the fish was in a stable upright position and swimming, it was released into the estuary at the catch site. To allow for acclimation the manual tracking of spotted grunter commenced 6 and 4 days after the last fish was released in the first and second study, respectively. During the acclimation period, fish were tracked intermittently to check for any possible tagging effects. None of the fish showed any noticeable abnormal post-tagging behaviour. Laboratory tests conducted on spotted grunter showed no effect of the internally planted transmitter. The spotted grunter tagged with dummy transmitters, which were the exact replicate (size and weight) of the VEMCO transmitters, did not show any post-tagging infection or haemorrhaging and did not exhibit any abnormal post-tagging behaviour and grew over a 100 day trial period (Kerwath *et al.,* in press.). Similar laboratory tests were conducted during this study and similar results were observed. The results suggested that 'aberrant' behaviour and post tag mortality during both studies was unlikely.

Tracking of fish

Two types of receivers were used to detect the position of the tagged fish in the estuary: A VEMCO VR60 receiver linked to a VEMCO VH10 directional hydrophone was used to monitor non-continuous, high resolution spatial data. The VR60 is a general-purpose ultrasonic receiver designed for manual tracking from small boats. The hydrophone was mounted at the base of a stainless steel pipe. The pipe was attached to a bracket on the starboard side of the boat and designed to ensure that the directional hydrophone could be rotated 360 degrees. The hydrophone was positioned approximately 1 m below the water surface, and 20cm below the boat keel.

Stationary automated data-logging listening stations (VEMCO VR2 Receiver) were used to continuously monitor the presence or absence of individual fish within an omni-directional range. The automated listening station (ALS) is a submersible, single channel receiver, which identifies coded transmitters, and is designed to collect and store long-term data. The information collected from the ALSs was retrieved by downloading data *in situ* onto a notebook computer, using VEMCO software, approximately every two weeks.

Manual Tracking

Manual tracking was conducted from a 4.2 m boat equipped with two 25 HP engines. The position of each fish was recorded once a day. Manual tracking sessions began at the river mouth at approximately 08h00. The tracking team then began a slow “zig zag” pattern upriver, with the manual gain control function set a high level (gain 48) until a signal from a transmitter was received. Once a signal was received, the hydrophone was rotated and signal strength monitored to establish the direction of the transmitter (fish). The boat was then steered in the direction of the transmitter, and the gain was adjusted. When the gain was reduced to zero, and the signal strength of the transmitter was the same in all directions, it was assumed that the hydrophone was directly above the transmitter and fish. Once the fish was located, the boat was anchored, the coordinates were recorded using a GPS (Garmin 12) and water chemistry variables were measured. The slow zig zag pattern was continued until all fish were located in the estuary. If all the fish were not recorded in the estuary, the sampling was extended into the riverine environment between 13 and 14 kms upriver. If all the fish were still not recorded, the procedure was repeated on the return trip to the estuary mouth, where the session ended at approximately 18h00.

During the first study period, fish were tracked daily between 7 and 22 February, every third day between 25 February and 6 March, and daily from 9 March to 24 March 2003. During the second study period, fish were tracked daily between the 29 September and 16 October, for eight days between 19 and 28 October, and daily from 31 October to 15 November 2003.

Each study included two 16 consecutive-day sampling sessions that were standardised according to the lunar phase, and tracking was conducted over two semi-lunar cycles. Each session began two days prior to the first quarter (waxing) moon, and the last day of each session was the last quarter (waning) moon.

Automated Listening Stations

During the first study, four automated listening stations were deployed at intervals along the length of the estuary (Figure 2.6a). The dates of deployment for each ALS were: ALS-1 (2003/02/12), ALS-2 (2003/03/08), ALS-3 (2003/01/21) and ALS-4 (2003/01/22). Automated listening stations were removed from the estuary on 16 April 2003.

Prior to the second study, eight ALSs were deployed at intervals along the length of the estuary (Figure 2.6b). They were removed from the estuary on 12 February 2004.

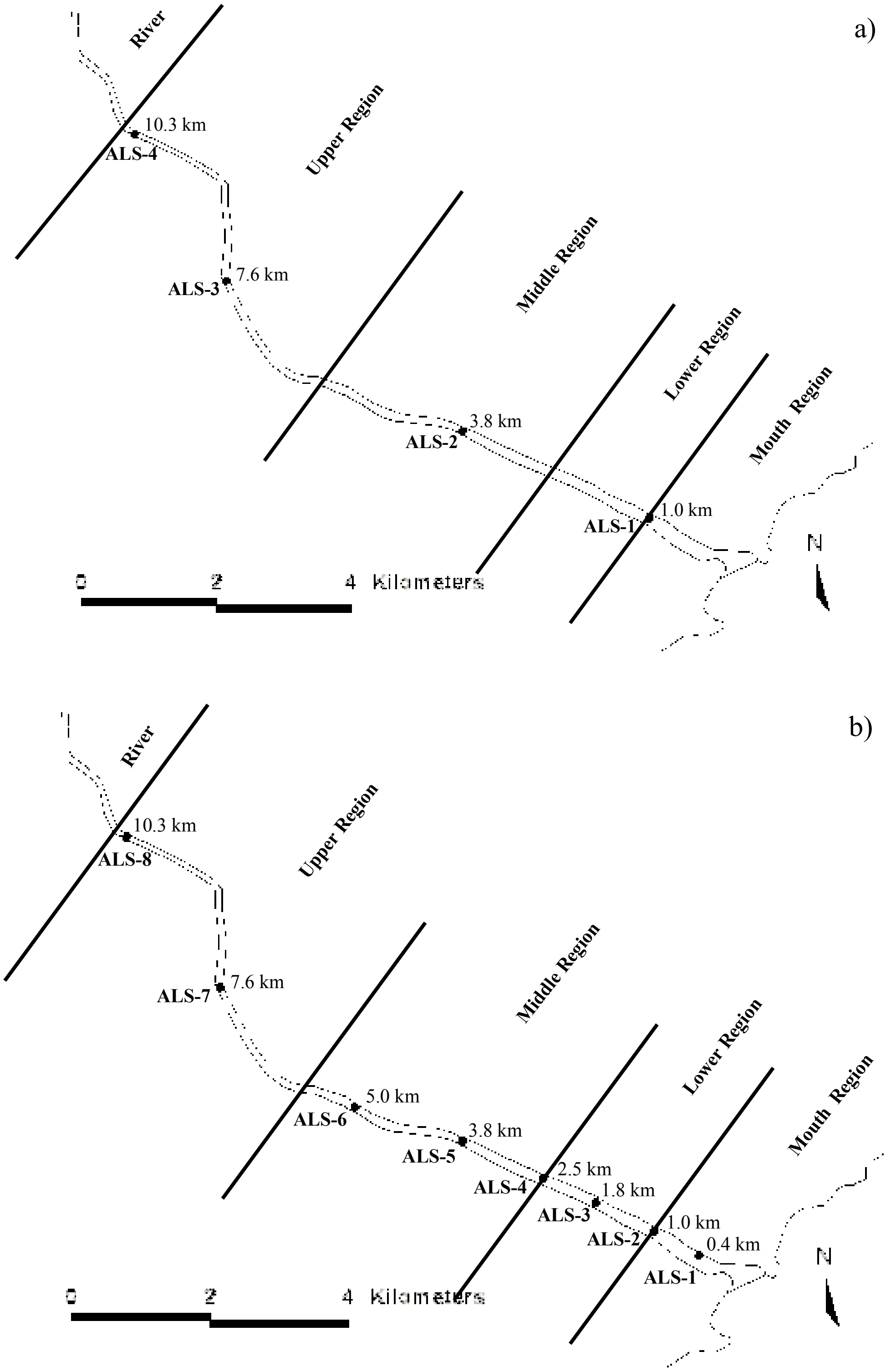


Figure 2.6. Position of the automated listening stations situated along the length of the Great Fish Estuary during a) Study 1 (7 February 2003 – 24 March 2003) and b) Study 2 (29 September 2003 – 12 February 2004).

Code Collisions

Coded transmitters emit a signal every 5 to 15 seconds. Consequently, transmitters often send out signals at the same time. If there were many fish in a particular area the resulting noise could be problematic. The receiver (VR60 and ALS) is only able to detect one coded transmitter at a time, and recognition of all six acoustic pulses of the unique pulse train is required for transmitter identification. If two coded transmitters emit a signal simultaneously at one receiver site, then neither transmitter will be detected. However, due to random pulse transmission the next time the two transmitters emit a signal, the chances are that they will not collide, and both will be detected (Pincock & Voegeli, 2002). However, if many tagged fish are transmitting at the same time in one area, there is a chance (while manual tracking) that an individual fish could not be detected. Although it is unlikely that an individual fish would go undetected on any ALS, it may be possible that if several fish move past an ALS, one or more individuals may pass a receiver without being detected, particularly when reception range is restricted (e.g. under windy turbulent conditions). Furthermore, two individuals transmitting a signal at the same time and location may also result in the mixing of acoustic pulses, termed a “false detection”. False detections occur when one or more pulses from one transmitter combine with those of another transmitter, and both or all are registered. These false detections can often be recognised when the ALS records a transmitter number as a different transmitter that does not exist.

During manual tracking, all false detections were ignored, and if code collisions occurred, the tracking team remained in the area, and adjusted the receiver gain until the codes were deciphered. The ALS data was manually screened for both code collisions and false detections.

Precision and range tests

Precision tests were conducted using the VR60 receiver linked to the handheld VH10 hydrophone. Transmitters were placed at different locations within a 1 km stretch of the estuary and were located by manual tracking. Hidden transmitters were located to the nearest 1 meter. Therefore, the accuracy of the fish's position was limited to the accuracy of the GPS (i.e. approximately 4-5 m).

Range tests were conducted during September 2003 and 2004 and were performed at the ALS locations in the mouth (ALS-1), lower (ALS-2), middle (ALS-4) and upper (ALS-7) regions (see Figure 2.6b). Transmitters were submerged for a fixed period at allocated positions (3 transects) and set distances (every 50 m) from the ALS. The results of the range tests showed considerable variation in the detection capability of the ALSs (Figure 2.7 and 2.8). The detection range of the ALSs ranged from 110 m to 610 m (Figure 2.7 and 2.8). Pincock & Voegeli (1992) stated that the detection range can be reduced through the absorption of acoustic energy by the water. This is affected by silt, air bubbles, and other matter mixed in the water. Parsons *et al*. (2003) also suggested that sea-floor structure and wave-generated noise in the marine environment reduce the strength of acoustic signals. Bradbury *et al*. (1995) noted that the reception range of a fixed hydrophone array tracking system (using 4 omni-directional hydrophones mounted on the sea floor and connected to a multi-channel receiver on shore) decreased during heavy seas and obstructions such as rocks. Matthews (1990) also suggested that underwater vegetation and physical obstructions may reduce the reception of the acoustic signal. The extensive variation in reception range in the Great Fish Estuary may probably be attributed to the influence of tidal phase (altered physico-chemical conditions, particularly salinity and current), wind (increased wave action), bathymetry (silt deposits, flood scours), depth, substrate type (soft mud, hard sand) and physical obstructions (road bridge pylons, sand banks, and large rocks).

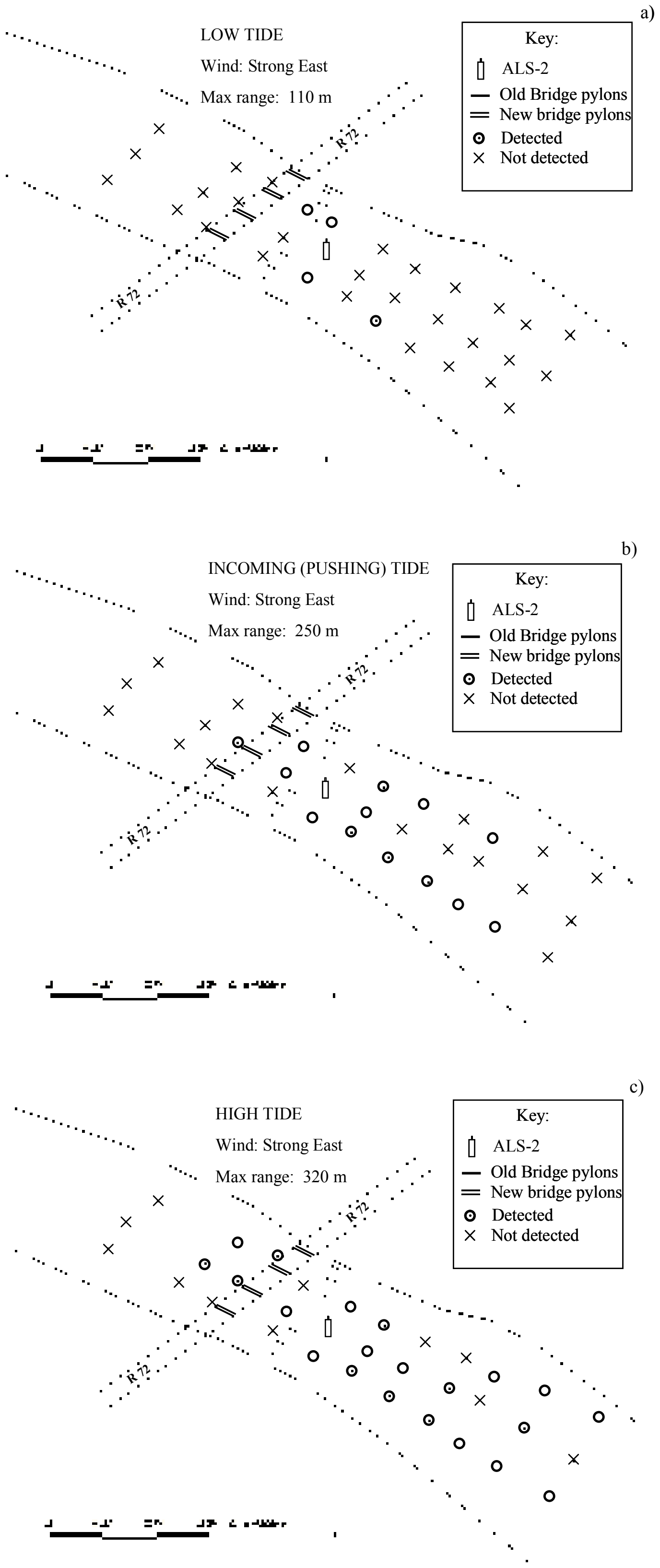


Figure 2.7. Results of range tests conducted in the lower region of the Great Fish Estuary (ALS-2) during the low, incoming and high tides on 13 September 2004.

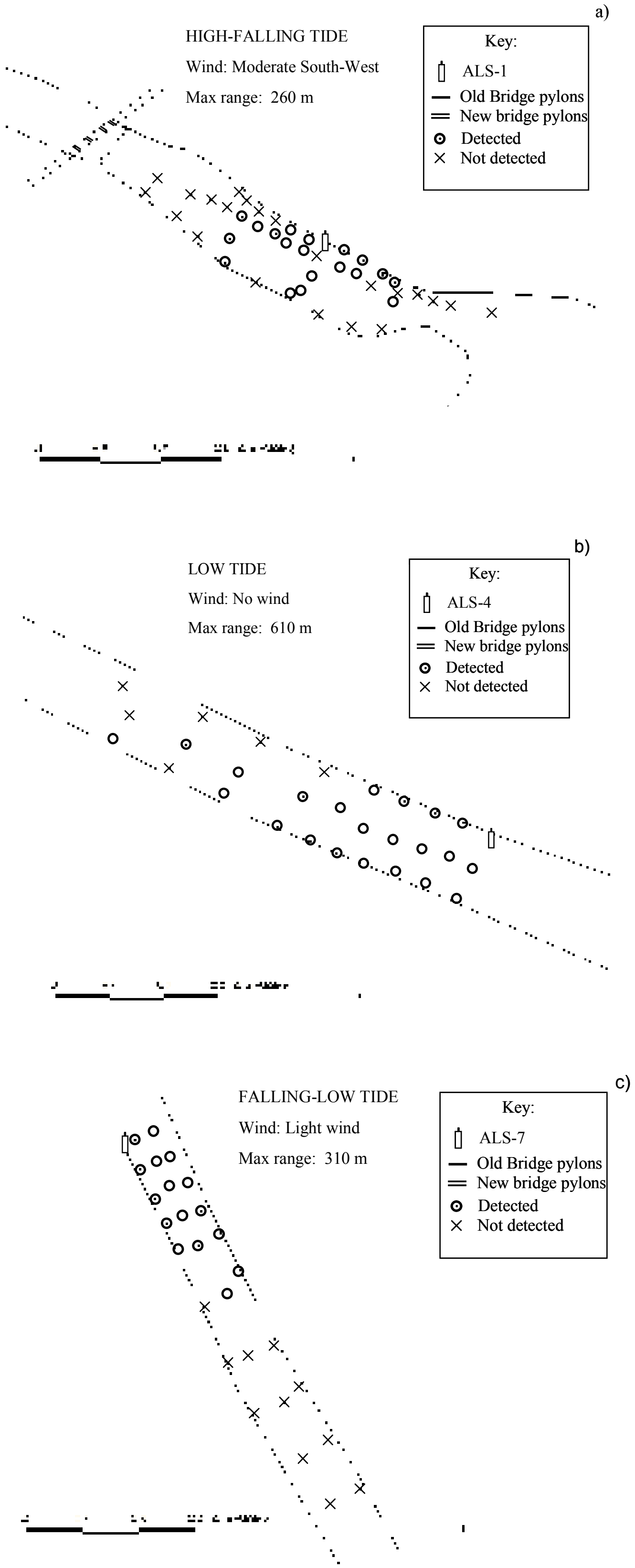


Figure 2.8. Results of range tests conducted in the mouth, middle and upper regions of the Great Fish Estuary during the high, low, and outgoing tides on the 18 and 19 September 2003.

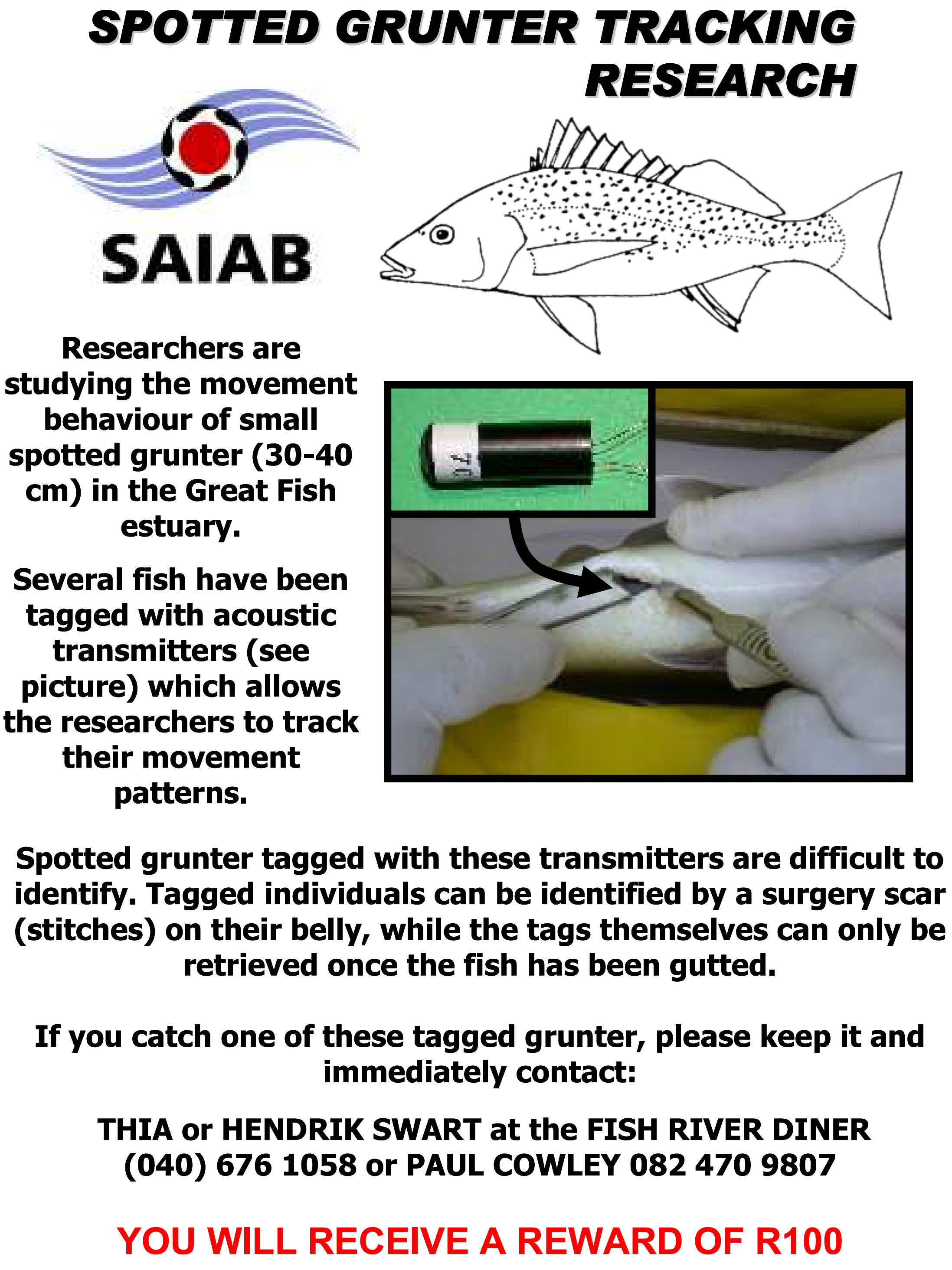
High variation in the detection capability of stationary automated listening stations and portable hand held hydrophones is not uncommon. In the marine environment on the northeastern coast of New Zealand, Egli & Babcock (2004) stated that a functional range of ≤ 500 m was found in range trials conducted with fixed transmitters deployed at set distances from VEMCO VR2 receivers during a 1-week period. However, in the marine environment of Santa Catalina Island, California (USA), Lowe *et al*. (2003) found that the acoustic detection range of VEMCO VR1 receivers was approximately 150 m. Arendt *et al*. (1999) and Arendt *et al*. (2001) found that the detection radius of a VEMCO VR1 receiver was 400 m in Chesapeake Bay, Virginia (USA).

Kerwath *et al*. (in press.) found the maximum detection range of a VEMCO V8 transmitter, received by a VEMCO VR60 receiver to be 400 m in an intermittently open Eastern Cape estuary. In the Mediterranean Sea, Jadot *et al*. (2002) stated the maximum range of a VEMCO VR60 receiver with a VH10 hydrophone was 500m. They suggested that seagrass, rocks and other obstacles reduced the power of the acoustic signal. Arendt (1999) found that the detection range of a VEMCO VR60 receiver attached to an omni-directional and directional hydrophone in the marine-dominated environment of Chesapeake Bay, Virginia (USA), was 300 m and 400 m respectively.

In the Mahurangi Estuary, New Zealand, Hartill *et al.* (2003) indicated that the effective range of the VEMCO VR1 and VR2 receivers was 300m. Taverny *et al.* (2002) found that the reception range of a Lotek SRX-400 receiver and hydrophone in the Gironde Estuary, France, was influenced by the tidal phase, more specifically high turbidity and current speed. They found the mean reception range of 800 m recorded in the lower estuary dropped to < 400 m in the more turbid upper estuary. In Schooner Creek, New Jersey (USA), Szedlmayer & Able (1993) found that the detection range of a stationary directional hydrophone (USR-90, Sonotronics, Tucson) was approximately 130 m.

Public Awareness

A reward system and an awareness campaign was implemented to ensure that fishers returned the transmitter of a tagged fish they had caught. Posters were displayed at every access point on the estuary, as well as at the shop and restaurant (Fish River Diner) situated near the road bridge. The posters described the project, and included a picture of the tag insertion, a reward offer and contact details for people who captured tagged fish (Figure 2.9). The proprietors of the Fish River Diner camping site also informed every fisher residing at their campsite, as well as handled tag returns and rewards. A meeting was also held with the subsistence fishermen explaining the projects purpose. They were shown pictures and the procedures on how to identify and retrieve the acoustic tag as well as the return and reward system. During the sampling periods, the tracking team also informed fishers who they encountered. Concurrent to this study, a survey of the fishery was conducted. The survey clerk informed all fishers of the telemetry research and the reward for returns.



SPOTTED GRUNTER TRACKING RESEARCH

SAIAB

Researchers are studying the movement behaviour of small spotted grunter (30-40 cm) in the Great Fish estuary.

Several fish have been tagged with acoustic transmitters (see picture) which allows the researchers to track their movement patterns.

Spotted grunter tagged with these transmitters are difficult to identify. Tagged individuals can be identified by a surgery scar (stitches) on their belly, while the tags themselves can only be retrieved once the fish has been gutted.

If you catch one of these tagged grunter, please keep it and immediately contact:

THIA or HENDRIK SWART at the FISH RIVER DINER
(040) 676 1058 or PAUL COWLEY 082 470 9807

YOU WILL RECEIVE A REWARD OF R100

Figure 2.9. An example of the reward poster displayed at the Great Fish Estuary during the study periods.

CHAPTER 3

ESTUARINE USE BY SPOTTED GRUNTER

INTRODUCTION

The dependence on estuaries by a large number of fish species worldwide is well documented (Lenanton & Potter, 1987; Blaber *et al.*, 1989; Whitfield, 1990; Hoss & Thayer, 1993; Wallace *et al.*, 1994). Whitfield (1994c) defined an estuary-dependent species as one that would be adversely affected by the loss of estuarine habitat. The main feature of estuarine-dependent fish species is that juveniles are predominantly estuarine and adults are primarily marine. Spawning takes place at sea and juveniles enter estuaries where they remain for a period of between one and three years. The degree of dependence of spotted grunter on estuaries has only been described using information obtained from conventional netting techniques (Wallace & van der Elst, 1975). According to these authors, the early juveniles recruit into estuaries at between 20 to 30 mm TL. Juveniles are dependent on estuaries where some individuals may attain sexual maturity. However, once mature, these fish spend considerably more time at sea. In the case of spotted grunter, the bulk of the adult population is found in the marine environment (Wallace & van der Elst, 1975). However, partially and post-spawned spotted grunter enter estuaries to regain condition after spawning (Webb, 2002). The estuarine phase can last for some months, but terminates before gonad maturation takes place (Wallace, 1975b).

Understanding the degree of estuarine use is of paramount importance if an estuarine species is to be managed, particularly if it is an important fishery resource. While in estuaries, smaller resident spotted grunter and transient adult spotted grunter are highly susceptible to exploitation. Understanding the ontogenetic changes in the degree of temporal estuarine use is imperative to conserve the more vulnerable aspects of their life-cycle (Wallace & van der Elst, 1975).

The technique used in this study formulated the quantification of the extent of estuarine-dependence, the movements between the estuarine and marine environments, and the factors influencing these movements.

The objectives of this chapter were to:

i) determine the proportion of time spotted grunter spend in the estuarine and marine environments;
ii) describe the frequency and duration of movements between the estuarine and marine environments;
iii) describe the effect of tide and time of day on the movements between the estuarine and marine environments;
iv) describe the effect of fish size on the time spent in the estuarine environment;
v) describe the effect of fish size on the frequency of movements between the estuarine and marine environments;
vi) describe the effect of environmental variables on the movements between the estuarine and marine environments.

METHODS AND MATERIALS

The study site and details of the research approach are described in Chapter 2. If a fish was not located in the estuary during manual tracking on a given day, then the data downloaded from the uppermost ALS and the lowermost ALS were checked to establish whether the fish was in the riverine environment, or whether the fish had migrated to sea.

Time spent in the estuary

Study 1

The percent time spent in the estuary by each fish (TIE) was calculated as follows:

$$TIE = \frac{NDL}{NDT} \times 100$$

where NDL is the number of days the fish was located in the estuary, and NDT the total number days tracked.

The average percent time spent in the estuary for all fish (ATIE) was calculated as follows:

$$ATIE = \frac{\sum_{i=1}^{n} NDL_i}{n(NDT)} \times 100$$

where n is the number of fish tracked, NDL_i is the number days located for ith fish, and NDT the total number days tracked.

A fish was considered to be in the estuary if it was recorded during manual tracking. If a fish was not located in the estuary, and was last recorded on ALS-1 (closest to the mouth), it was assumed to be at sea. If a fish was not located by manual tracking on two or more consecutive days, but was later located in the estuary, it was also assumed to have been at sea. The latter assumption was necessary, as reduced reception of the ALS-1 or code collisions (Chapter 2) may have allowed the fish to pass undetected. Such a fish, therefore, either went to sea or was captured in the lower reaches of the estuary, between ALS-1 and ALS-2. The former assumption was confirmed if the fish was later located in the estuary. The probability of the fish being captured and not reported was unlikely due to the public awareness campaign and the reward system offered to local fisherman (see Chapter 2). The positions of three fish (Fish 20, 25 and 31) could not be confirmed for some part of the study and were therefore not included in the calculation. Fish 20 was last recorded during manual tracking on 16 March 2003 in the riverine environment, above ALS-4 and was not recorded again while manually tracking or on any ALS. Fish 25 was last located during manual tracking on 3 March 2003 between ALS-1 and ALS-2 and Fish 31 was last recorded on ALS-2 on 10 March 2003. The subsequent location of these three fish remained unknown, and therefore either left the estuary permanently or were caught and their tags were not returned.

Study 2

The time the fish spent in the estuary in this study was calculated as for study 1. However, due to the extensive coverage of the estuary by the eight listening stations, no assumptions on the fish's position were necessary and the positions of all tagged fish could be confirmed. However, since Fish 50A was caught on 10 October 2003 and replaced by Fish 50B later in the study, they were excluded from the calculation.

To provide higher resolution data, the percent of time (in hours) that each tagged fish spent in the estuarine environment was calculated from the ALS data. The number of hours spent at sea was calculated from the time an individual was last recorded on the lowermost ALS (ALS-1), until the time it re-entered the estuary and was again recorded on ALS-1. This included both day and nighttime data.

Sea trips

In this study, the term 'sea trip' was used when a fish left the estuary for the marine environment. Given the limitations of the first study, the number and duration of sea trips undertaken by each fish could only be determined from the data obtained from the ALSs during the second study.

During the second study, a tagged fish was considered to be at sea if it passed ALS-1 and was only recorded again $\geq$ 6 hours later, without being recorded on any other ALS in the estuary. Furthermore, if the same incidence occurred, but the fish was not last recorded on ALS-1, but on ALS-2, it was also considered a sea trip. This was due to poor reception and/or code collisions on ALS-1 in the mouth region (see Chapter 2).

The effect of the tide and time of day on the sea trips were assessed using circular statistics (Batschelet, 1981). The mean tide and time of day of the sea trips was calculated as theta (Ø), the mean direction of the resultant vector (measured in radians). The Rayleigh test of randomness was used to test whether the sea trips were random or whether they exhibited "directedness/non-randomness" towards a specific time of day and to a specific tidal phase.

Effect of fish length

Nonlinear least squares regression, using an inverse logistic with three free parameters, was used to determine the relationship between fish length and the proportion of time spent in the estuarine environment during the second study.

Effect of environmental variables

The effect of sea temperature, wind direction and atmospheric pressure on the number of tagged fish located in the estuary was determined during the second study period. Wind and barometric pressure data was supplied by the South African Weather Service, while sea temperature was obtained from a temperature logger situated 25 km from the Great Fish Estuary mouth (Marine and Coastal Management, unpubl. data). Sea temperature data was not available from the latter source from 7 November 2003 onwards, and sea temperature was measured daily at the estuary mouth (station 1). Using circular statistics, the mean daily wind direction was calculated as theta (Ø), which is the mean direction of the resultant vector (measured in radians) (Batschelet, 1981).

Multiple linear regression was used to test the effect of each environmental variable (with a 0, 1 and 2-day lag) on the number of tagged fish in the estuary each day during the manual tracking period in the second study. A two-sample t-test was used to test for differences between the number of fish in the estuary during an east and west wind.

Linear regression was also used to determine the combined effect of the abiotic variables. Forward stepwise regression was chosen since both the dependent and independent variables were continuous. The effect of a one-day and two-day lag on the independent variable, barometric pressure, was also considered. The number of fish predicted in the estuary on a given day was modelled as follows:

Number fish in Estuary = β_1 (Sea Temperature) + β_2 (Barometric Pressure) + ε

The residuals of all statistical analyses were analysed for randomness and assessed for departures from normality.

RESULTS

Time spent in the estuary

Study 1

The number of tagged spotted grunter in the estuary declined over the study period (Figure 3.1).

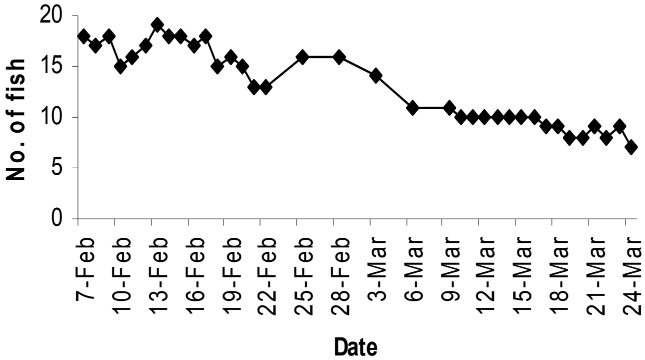


Figure 3.1. Number of tagged spotted grunter *Pomadasys commersonnii* located in the Great Fish Estuary while manual tracking during the first study between 7 February 2003 and 24 March 2003.

Nine of the 20 tagged fish migrated to the marine environment and never returned to the estuary (Table 3.1). The "departure" of an additional two individuals (Fish 25 and

31) were not recorded at ALS-1, but were last recorded at ALS-2. These two fish either migrated to the marine environment or were caught by anglers. There was no evidence of a mass emigration; instead the tagged fish left the estuary randomly over the study period (Table 3.1). Prior to leaving the estuary permanently, six of the nine individuals, and one of the two that were not confirmed at ALS-1, had previously ventured into the marine environment, but for short (one day) sea trips. The other three had never gone to sea before they left the estuary permanently. Six fish remained in the estuary every day during the manual tracking period (Table 3.1). Two fish also remained in the estuary except for one or two short sea trips during the manual tracking period (Table 3.1). However, these two fish left the estuary after the manual tracking period and did not return to the estuary. One individual (Fish 20) spent most of its time in the riverine environment and only ventured into the marine environment for one day.

Throughout the 36-day study period, individual fish were located at an average frequency of 68% (range. 22.2% - 100%) (Table 3.1.).

Table 3.1. Details of the tagged spotted grunter *Pomadasys commersonnii* and the proportion of days (%) each was recorded in the Great Fish Estuary during the 36-day manual tracking period (7 February 2003 – 24 March 2003).

Fish Code	Total Length (mm)	No Positional Fixes	Date last recorded	Days in estuary (%)
20[1]	317	25	16 March 2003	NA
21	334	34	2 April 2003	94.4
22	297	20	7 March 2003	55.6
23	380	36	24 March 2003	100
24	330	18	1 March 2003	50
25[1]	313	19	3 March 2003	NA
26	314	35	13 April 2003	100
27	328	12	19 February 2003	33.3
28	382	34	25 March 2003	97.1
29	377	36	16 April 2003 *	100
30	308	36	16 April 2003 *	100
31[1]	357	12	10 March 2003	NA
32	318	36	16 April 2003 *	100
33	329	13	9 March 2003	37.1
34	263	8	17 February 2003	22.9
35	357	8	18 February 2003	22.2
36	387	15	25 February 2003	42.9
37	363	23	23 March 2003	63.9
38	319	12	23 February 2003	34.3
39	355	36	13 April 2003	100

[1] = Fish that were possibly caught during the study, * = end of study.

Study 2

Most of the tagged spotted grunter remained in the estuary for the first two weeks of the manual tracking period, after which, between five and seventeen fish were recorded daily (Figure 3.2). Fifteen fish were located in the estuary on the last day of the study. Five fish did not go to sea during the manual tracking period (Table 3.2). One fish (Fish 55) migrated to sea during the manual tracking period (10 November

2003), and never returned (Table 3.2). In addition, one fish that left the estuary in December 2003 and two fish in January 2004 also did not return (Table 3.2).

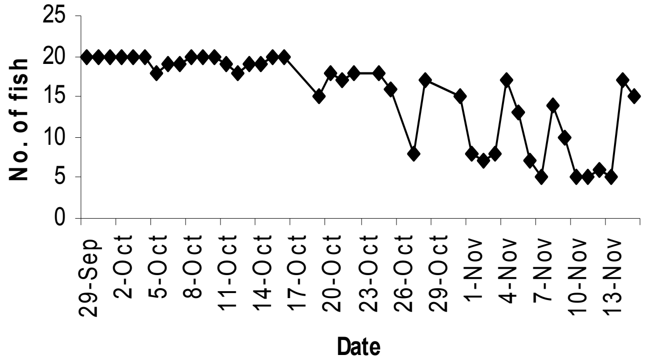


Figure 3.2. Number of tagged spotted grunter *Pomadasys commersonnii* located in the Great Fish Estuary while manual tracking during the second study between 29 September 2003 and 15 November 2004.

Throughout the 42-day manual tracking period, individual fish were located at an average frequency of 77% (range. 48% - 100%) (Table 3.2). However, the ALS data showed that the tagged fish were in the estuary for 67% of the time between 29 September 2003 and 12 February 2004. The ALS data also showed that individual spotted grunter spent between 29% and 100% of their time in the estuary (Table 3.2). Save for two fish (Fish 54 and 63), these values were lower than the proportion of time that each fish spent in the estuary during the manual tracking period (Table 3.2).

Table 3.2. Details of the tagged spotted grunter *Pomadasys commersonnii* and the proportion of time each were recorded in the Great Fish Estuary during the 42-day manual tracking (MT) period (29 September 2003 to 15 November 2003) and during the entire 137-day ALS study period (29 September 2003 to 12 February 2004).

Fish Code	Total Length (mm)	No Positional fixes	Date last recorded	MT days in estuary (%)	ALS hours in estuary (%)
50A[1]	449	12	11 October 2003	NA	NA
50B[2]	515	15	28 January 2004	NA	NA
51	469	32	12 February 2004 *	76	61
52	385	42	12 February 2004 *	100	100
53	428	37	12 February 2004 *	88	73
54	620	22	12 February 2004 *	52	54
55	432	29	10 November 2003	71	26
56	440	42	12 February 2004 *	100	82
57	364	42	12 February 2004 *	100	100
58	625	21	12 February 2004 *	50	44
59	472	28	12 February 2004 *	67	60
60	527	29	12 February 2004 *	69	53
61	489	30	28 January 2004	74	57
62	504	29	12 February 2004 *	69	38
63	534	20	25 December 2003	48	58
64	387	35	12 February 2004 *	86	70
65	698	20	26 January 2004	48	61
66	403	42	12 February 2004 *	100	100
67	428	35	12 February 2004 *	83	65
68	538	32	12 February 2004 *	76	47
69	362	41	12 February 2004 *	100	100

[1] = fish that was caught during study, [2] = fish that was caught and tagged during the study, * = end of study period.

Sea trips

A total of 315 sea trips were made by the 19 tagged fish (excl.50A & 50B) during the second study. The number of sea trips made by each individual ranged from 0 to 53 sea tips (avg. 15.14 ± 13.10 SD) (Table 3.3). One of the five fish that did not leave the estuary began regularly going to sea after the manual tracking period (Table 3.3). The duration of each sea trip for all tagged fish, ranged from 6 hours to 28 days (avg.

2 days 22 hours ± 5 days 6 hours SD) (Table 3.3). Almost half of the sea trips were short (6 - 24 hours), while approximately one third were between 1 and 3 days (Figure 3.3). Only four individuals went to sea for longer than three weeks.

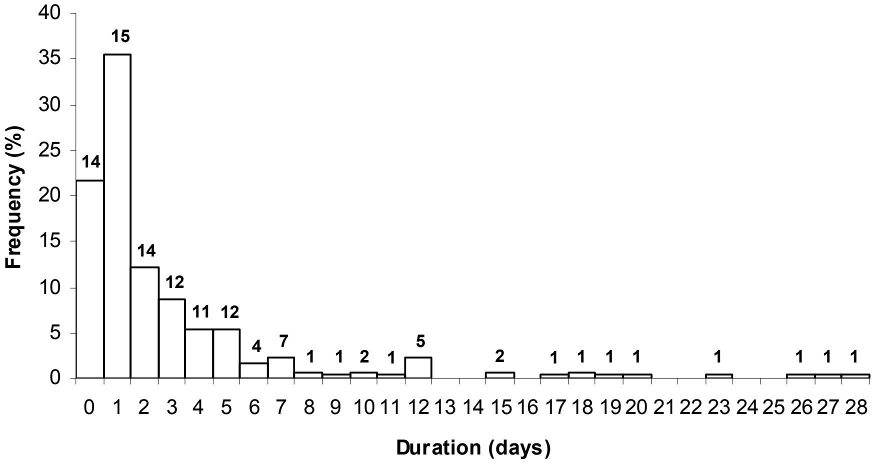


Figure 3.3. The frequency and duration of each sea trip made by the tagged spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary between 29 September 2003 and 12 February 2004 (second study). n = the number of individuals that undertook a sea trip of the given duration.

Table 3.3. Characteristics of the sea trips made by each tagged spotted grunter *Pomadasys commersonnii* during the second study period (29 September 2003 - 12 February 2004).

Fish code	Total Length (mm)	Date of first sea trip	No of sea trips	Duration (average)	Duration (min)	Duration (max)
50A[1]	449	NA	0	0	0	0
50B[2]	515	27/10/03	19	02 23:33:28	00 06:30:19	19 18:14:15
51	469	26/10/03	25	02 13:14:26	00 08:36:32	15 05:43:39
52	385	NA	0	0	0	0
53	428	07/11/03	16	02 07:42:57	00 08:13:44	09 19:22:24
54	620	18/10/03	14	06 17:06:08	00 07:03:16	26 15:20:25
55	432	26/10/03	10 (9 return)	00 19:51:18	00 07:06:41	02 13:02:56
56	440	29/11/03	12	02 00:52:10	00 08:03:00	09 21:27:07
57	364	NA	0	0	0	0
58	625	07/10/03	12	06 08:06:03	00 14:01:23	17 15:02:04
59	472	26/10/03	28	01 23:12:40	00 08:51:03	10 17:21:26
60	527	18/10/03	18	03 20:08:19	00 09:00:57	17 18:23:11
61	489	18/10/03	23	02 13:50:44	00 07:21:37	22 17:55:03
62	504	17/10/03	18	04 17:14:19	00 10:05:27	19 02:40:48
63	534	17/10/03	6	09 13:25:48	01 13:59:02	28 03:29:00
64	387	27/10/03	19	02 03:59:34	00 08:38:35	06 07:56:32
65	698	07/10/03	14	06 01:19:58	00 06:11:16	26 06:27:49
66	403	NA	0	0	0	0
67	428	27/10/03	29	01 15:57:51	00 06:08:56	06 19:30:06
68	538	12/10/03	53	01 08:46:24	00 06:15:45	11 22:46:30
69	362	NA	0	0	0	0

[1] = fish that was caught during study, [2] = fish that was caught and tagged during the study

Significant trends regarding the departure and arrival times of sea trips were observed. Most (84%) departures occurred at night between 17h00 and 05h00, while most (77%) return trips (arrivals) occurred between 12h00 and 00h00. The mean departure and arrival times were at 00h18 ± 04:01 ($p < 0.05$; $r = 0.38$) and 18h04 ± 04:15 ($p < 0.05$; $r = 0.44$), respectively (Figure 3.4).

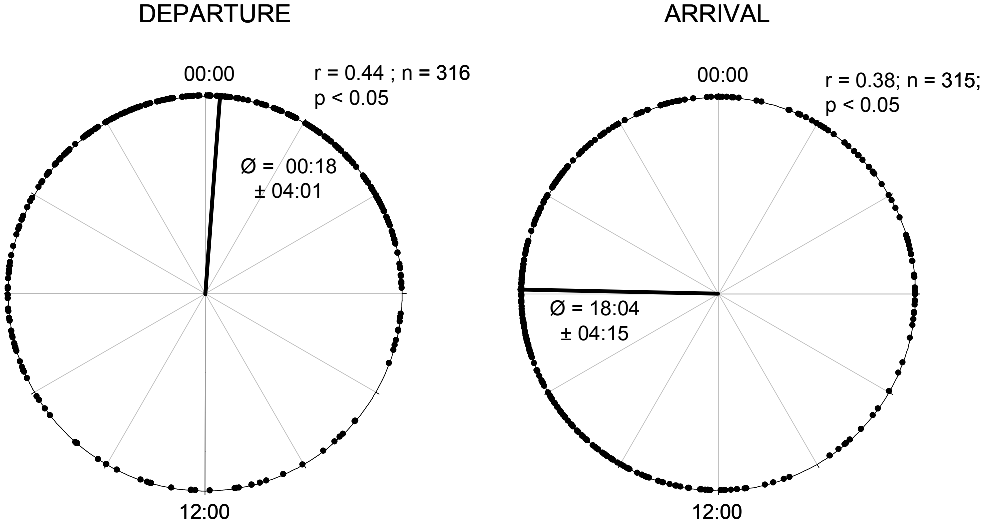


Figure 3.4. The mean (Ø) departure and arrival times tagged spotted grunter *Pomadasys commersonnii* undertook sea trips between 29 September 2003 and 12 February 2004. Theta (Ø) = mean direction of the resultant vector.

There was a significant relationship between the tidal phase and sea trips. Most spotted grunter left the estuary on the outgoing tide (02:59 ± 05:05 after high tide) ($p < 0.05$; $r = 0.11$), while most spotted grunter returned to the estuary during the incoming tide (04:38 ± 04:00 after low tide) ($p < 0.05$; $r = 0.45$) (Figure 3.5).

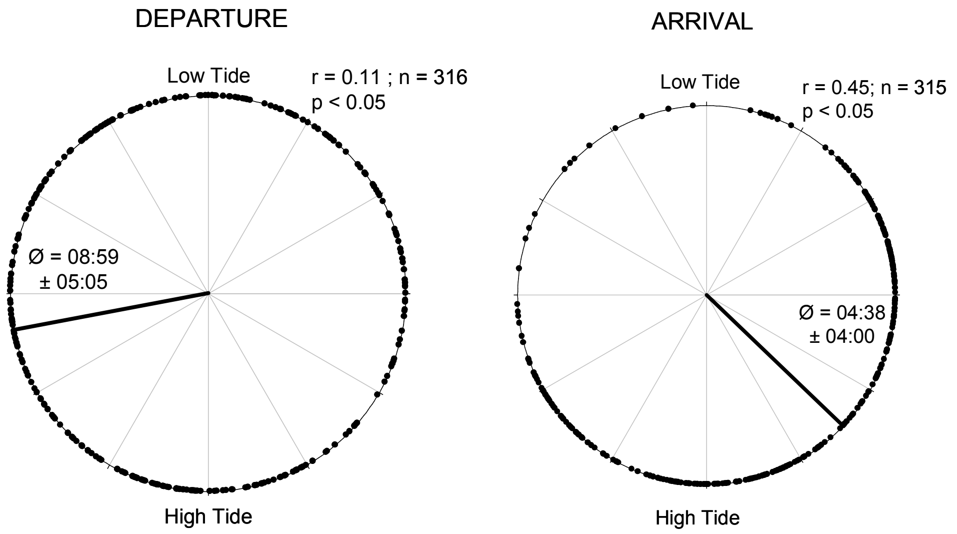


Figure 3.5. The tidal phase and mean time after low tide (Ø) that tagged spotted grunter *Pomadasys commersonnii* undertook sea trips between 29 September 2003 and 12 February 2004. Theta (Ø) = mean direction of the resultant vector.

Effect of fish length

There was a significant relationship between the proportion of time in the estuary and fish size ($p < 0.0001$; $R^2 = 0.62$; F (1, 17) = 44.82. Smaller spotted grunter spent more time in the estuary than larger individuals (Figure 3.6). The model estimated that the minimum time fish spent in the estuary during the study period was 53 %.

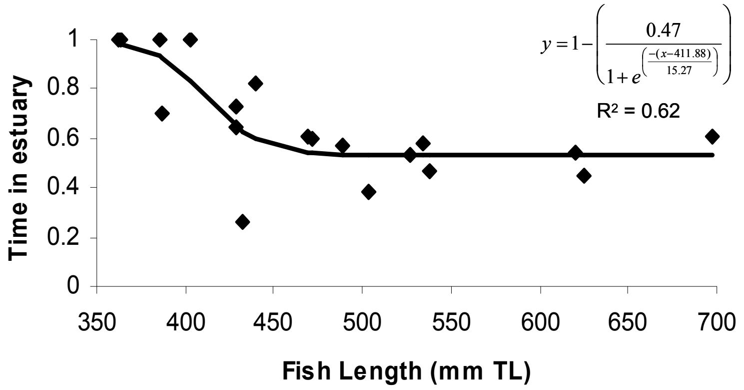


Figure 3.6. Relationship between the proportion of time (hours) spent in the estuary and fish length for tagged spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary between 29 September 2003 and 12 February 2004.

Figure 3.7 shows the relationship between the number of sea trips undertaken by spotted grunter and total length. The effect of fish length on the number of sea trips was mostly evident from four of the five smallest fish which remained resident in the estuary throughout the entire study (29 September 2003 - 12 February 2003) (Figure 3.7). The largest of the five small individuals only began venturing into the marine environment after the manual tracking period (Table 3.3).

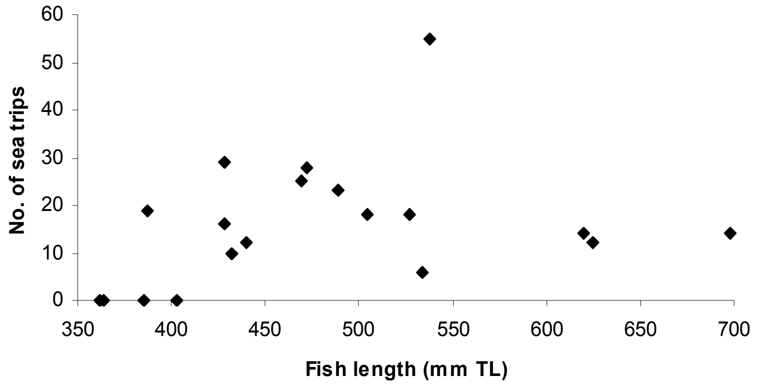


Figure 3.7. Relationship between the number of sea trips and fish length for tagged spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary between 29 September 2003 and 12 February 2004.

Effect of sea temperature, barometric pressure and wind direction

Sea temperature had a significant negative effect on the residency of tagged fish in the estuary ($p < 0.0001$; $R^2 = 0.34$; F (1, 40) = 20.85) (Figure 3.8), showing that fish were more prone to undertaking sea trips at higher temperatures.

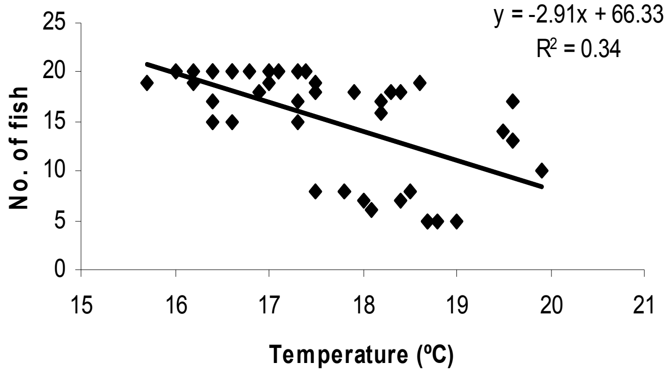


Figure 3.8. Relationship between sea temperature (recorded in the estuary mouth) and the number of tagged spotted grunter *Pomadasys commersonnii* located in the Great Fish Estuary during the second study (29 September 2003 - 15 November 2003).

There was a significant difference between the number of fish in the estuary during east and west winds (p = 0.01; t (1,36) = 2.66). The average number of spotted grunter recorded in the estuary after an easterly wind (18 ± 0.4) was higher than after a westerly wind (13.5 ± 1.3) (Figure 3.9).

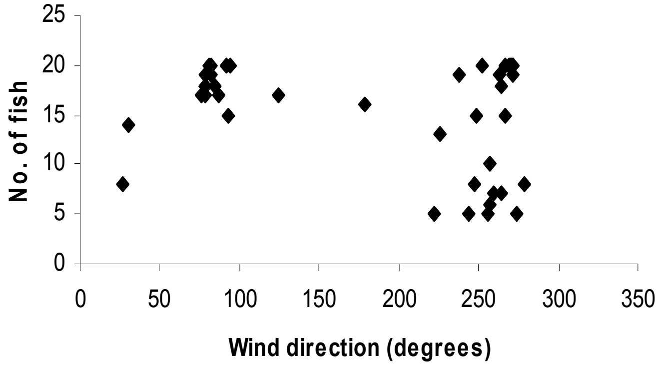


Figure 3.9. Relationship between wind direction (90º = East; 270º = West) and number of tagged spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary during the second study (29 September 2003 - 15 November 2003).

Barometric pressure with a 2-day lag explained the greatest variance in the dependent variable, and was therefore selected over a 1-day lag or no lag. There was a significant positive relationship between the number of tagged fish in the estuary and barometric pressure with a two-day lag ($p = 0.004$; $R^2 = 0.19$; $F(1, 40) = 9.42$) (Figure 3.10), showing that fewer fish undertook sea trips at low barometric pressure.

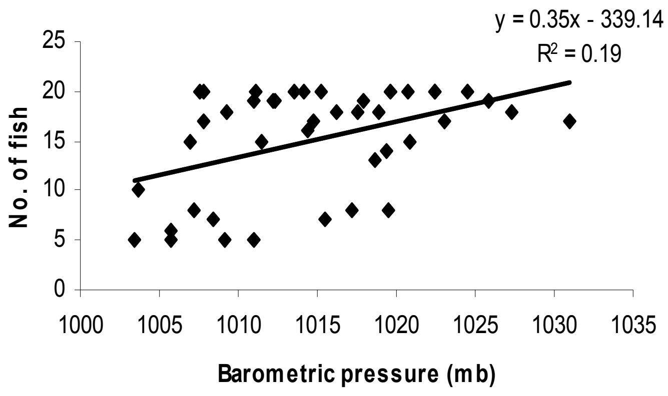


Figure 3.10. Relationship between barometric pressure and the number of tagged spotted grunter *Pomadasys commersonnii* located in the Great Fish Estuary during the second study (29 September 2003 and 15 November 2003).

The number of tagged fish in the estuary was best described as follows:

Number of fish in estuary = -185.64 - 2.5 sea temperature + 0.24 barometric pressure (2-day lag)

Sea temperature explained 34% of the variation ($p = 0.0003$) and barometric pressure with a 2-day lag explained a further 8% ($p = 0.02$).

DISCUSSION

For the purpose of this discussion, short term sea trips are defined as the period when fish left the estuary and returned, while long term sea trips refer to the period when spotted grunter left the estuary and did not return (on the assumption that they were not caught by anglers).

Spotted grunter utilise estuaries as nursery areas and are thought to move from the estuary to the marine environment where they mature (Wallace, 1975a). The results from the first study provide some evidence for this as some of the smaller spotted grunter (< 450 mm TL) began undertaking short sea trips. However, many of these trips may have simply been an expansion of the estuarine environment out of the estuary mouth at low tide.

Evidence for an ontogenetic shift in habitat use was also observed in the second study, where the short term sea trips were more frequent in spotted grunter between 400 mm and 450 mm, and less frequent, but longer in the larger fish (> 450 mm TL). Ontogenetic habitat shifts are common in fishes (Gibson, 1997). Ontogenetic changes allow life stages to respond individually to the different selection pressures experienced in the environment (Ebenman, 1992), and effective use of resources often requires different movement patterns during the life of an individual (Pittman & McAlpine, 2001). Tulevech & Recksiek (1994) noticed a significant behavioural change in the movement patterns of white grunt *Haemulon plumieri* and attributed the change to an ontogenetic shift or a consequence of maturity. Zlokovitz *et al.* (2003) observed a behavioural habitat shift in striped bass *Morone saxatilis* from freshwater to mesohaline, polyhaline or marine habitats after an age of two years. Furthermore, they found that striped bass also exhibited an abrupt ontogenetic habitat shift between freshwater and saltwater environments. Waldman *et al.* (1990) also found that larger striped bass *Morone saxatilis* in the Lower Hudson River and New York City Harbour dispersed greater distances than smaller individuals, and that smaller individuals were recaptured near the estuary while larger fish were caught in coastal habitats further from the estuary. Hartill *et al.* (2003) found that the sea trips exhibited by snapper *Pagrus auratus* in the Maruhangi Estuary, were in part, related to fish length, with larger individuals undergoing more sea trips. The results of this study suggest that there is possibly an ontogenetic shift in spotted grunter behaviour. It appears that on attaining sexual maturity (between 250 and 450 mm TL), spotted grunter begin to utilize the marine environment. This transition possibly represents the beginning of the marine phase of their life history. The most plausible explanations for this habitat shift in spotted grunter are the onset of maturity (Wallace, 1975b), increased spatial requirements (Hartill *et al.*, 2003) and/or the reduced risk of predation in larger individuals (Millinski, 1993). According to Pittman & McAlpine (2001), the most commonly reported ontogenetic changes in movement patterns are associated with refuge function, predation pressure, physiological requirements and diet.

The long term sea trips of the small adolescent spotted grunter may also be attributed to an ontogenetic behavioural change, and may herald the end of their 'resident' estuarine dependent phase. However, since seven of the nine individuals in the first study that did not return to the estuary were greater than the length at 50% maturity for males, and one greater than the length at 50% maturity for females (males: 300 mm TL, females: 360 mm TL, Wallace, 1975b and males: 305 mm TL, Webb, 2002), it is also possible that these individuals left the estuary to initiate a spawning migration. Two of the spotted grunter which migrated to sea (Fish 33 and Fish 36) were caught by anglers in the estuary the following year (3 January and 15 June 2004 respectively). Return migrations (Webb, 2002) or natal homing possibly represents another strategy adapted by spotted grunter and has implications for their management.

The results from both studies showed that smaller spotted grunter spent most of their time in the estuary. Six of the 20 tagged fish remained in the estuary throughout the first study. Three of these fish (whose transmitters were still operating, see Chapter 4) were still located and remained in the estuary for the entire second study period. The four smallest spotted grunter tagged in the second study remained in the estuary throughout the entire 137-day study. This highlights the extent of estuarine dependency exhibited by some adolescent spotted grunter. Tagging reports compiled by Bullen & Mann (2000 & 2004) indicated that spotted grunter tagged with conventional dart tags are largely resident to certain estuaries.

Although fish in the second study were located in the estuary for a large percentage of the 42-day manual tracking period (77%), the ALS data showed that over the entire study period (137 days), the tagged fish spent 67% of their time in the estuary. The minimum time that any of the spotted grunter spent in the estuary during the second study was 53%. Since most of the individuals tagged in the second study were adults, these results are surprising as these fish are considered marine. However, the 137-day sampling period coincided with the time when post-spawning adults are thought to enter estuaries to feed and regain condition (Webb, 2002). Nevertheless, these results highlight the importance of estuaries to adult spotted grunter. Post-spawning, feeding aggregations are often associated with adult fish (Harden Jones, 1968; Pittman & McAlpine, 2001). Cyrus (1991) stated that estuaries along the South African coast act as feeding grounds for adults of a host of fish species. Bok (1988) stated that adult spotted grunter migrate seasonally into estuaries to feed. The high abundance of sand prawn *Callianassa krausii* and mud prawn *Upogebia africana*, the preferred prey item of spotted grunter in the Great Fish Estuary (Hecht & van der Lingen, 1992; Webb, 2002), suggests that this estuary may be an important feeding ground for post-spawning fish of this species.

The frequency (6-55) and duration (6 hrs to 4 weeks) of the sea trips varied between individuals. All but one individual in the second study undertook sea trips of less than 28 days, suggesting that they did not leave the estuary for reproductive activity. One fish (Fish 55) left the estuary and had not returned by the end of the study. This fish may have moved a considerable distance in that time and may have undertaken a spawning migration to KZN. Bullen & Mann (2002 & 2004) showed that adult spotted grunter are capable of considerable long-shore coastal migrations in both north-east and south-westward directions. They suggested that the migrations of even a few individuals could assist in maintaining the genetic diversity of the species over its entire distributional range. A north-eastward spawning migration between August and November has also been observed in another estuarine-dependent species, the dusky kob *Argyrosomous japonicus* (Griffiths, 1996).

Environmental conditions, particularly temperature, appeared to influence the number of tagged fish returning to and/or leaving the estuary during the second study. A higher number of tagged fish were recorded in the estuary during cold sea water temperatures. After periods of high barometric pressure, easterly winds dominate resulting in the upwelling of cold sea water and rapid decline in water temperature

(Schumann, 1998). Warmer sea temperatures, on the other hand, predominate under low atmospheric conditions characterised by westerly winds and the absence of upwelling events. Spotted grunter appear to prefer water temperature between 21 and 23 ºC and avoid water temperature below 16 ºC (see Chapter 5). Therefore, it was not surprising that more tagged spotted grunter were recorded in the estuary following a rise in barometric pressure, strong easterly winds and lower sea temperatures. The combined influence of these variables was explained by the environmental variable model that predicted that the number of tagged fish in the estuary was best predicted by barometric pressure with a 2-day lag and from the real-time sea temperature. Wind also appeared to be a good predictor of number of fish in the estuary. This is most probably since wind speed and direction influences and determines sea temperature (Schumann *et al.*, 1982). The average number of tagged fish in the estuary was higher after easterly winds (cold water) than after westerly winds (warm water). It has been reported that angler catches of ragged tooth shark *Carcharias taurus*, a predator of spotted grunter, are much higher after periods of upwelling (M. Dickens, Bayworld, Personal communication, 2004). It is therefore possible that spotted grunter move into estuaries under low sea temperatures to avoid predation, and hence use the estuarine environment as a refuge area. Stone (1988) suggested that many fish species seek the warmer water of estuaries when the sea is cold.

The movement of spotted grunter between the marine and estuarine environments was facilitated by tidal currents. Most fish left the estuary during the outgoing tide and returned during the incoming tide. Tytler *et al.* (1978) also suggested that it is likely that salmon smolts *Salmo salar* leave the estuary during ebb tides. The use of tidal transport (as mentioned in Chapters 3 and 4) is advantageous as it minimises energy expenditure. The movement of spotted grunter between the estuarine and marine environments was also influenced by the time of day. Most fish (84%) left the estuary between the evening and early morning, and most (76%) returned to the estuary between midday and midnight. The average time that the tagged fish left and returned to the estuary was at midnight (00h18) and during the evening (18h04), respectively. Hartill *et al.* (2003) found that the largest snapper *Pagrus auratus*, tagged in the

Maruhangi Estuary, left the estuary 27 times, exiting the estuary in the early morning and returning in the afternoon. Spotted grunter left the estuary at night and returned from midday onwards. This explains the large proportion of days that the fish were located during the day while manual tracking, and highlights the importance of employing both manual and automated methods, as well as the potential bias in using manual tracking exclusively. Since adult fish use estuaries predominantly for feeding, it appears that they enter the estuary on the incoming tide in the evening and night; feed, and then depart on the outgoing tide. The higher catch rate by fishers in the Great Fish Estuary at night (W.M. Potts, DIFS, Personal communication, 2004) provided further evidence of nocturnal feeding.

The large individual variation in the frequency and duration of sea trips observed between individuals could be a result of individual genetic behaviour or adaptability in response to exploitation. Zlokovitz *et al.* (2003) showed that while most striped bass undertook coastal migrations, some established resident behaviour in the upper estuary of the Hudson River and did not undertake a coastal migration. During this study, approximately half of the small adolescent spotted grunter undertook long term sea trips, while the remaining individuals exhibited higher levels of residency. Spotted grunter are also commonly found in intermittently open estuaries in the southeastern Cape (Whitfield, 1998; Vorwerk, 2002), which may often remain closed for two years, with no connection to the marine environment. This further highlights their ability to adapt a versatile behavioural strategy. The individual behavioural traits of spotted grunter have probably decreased the catchability of these fish and possibly abated the over exploitation of the stock.

The dependency of small spotted grunter to estuaries has implications for their exploitation. Due to the increasing fishing effort in South African estuaries (Lamberth & Turpie, 2003), small spotted grunter, in particular, are susceptible. In recent years, a marked increase in fishing effort has been observed in the Great Fish Estuary (Potts *et al.*, 2004). Furthermore, compliance with regulations pertaining to gazetted bag and size limits is very low, possibly due to the lack of law enforcement

(Potts *et al.*, 2004). Given that small spotted grunter display a considerable degree of site fidelity in the estuary (see Chapter 3), area closure and zoning of consumptive use practices within estuaries may be an effective alternative management option to prevent over-exploitation of adolescent (under-sized) spotted grunter (see Chapter 6).

The results have shown that both adolescent and adult spotted grunter are dependent on the estuarine environment. Their dependence on the estuary is influenced by a number of biotic (fish size, feeding, shelter, and reproduction) and abiotic (sea temperature, barometric pressure, tidal phase and time of day) factors. In addition, there seems to be an ontogenetic behavioural and habitat shift from adolescent to adult fish. Obtaining such high resolution and fundamental information was only possible through the use of telemetry. Although other techniques, namely otolith microchemistry are available to quantify patterns of migration throughout a fish's ontogeny (Secor *et al.*, 1995; Secor, 1999; Zlokovitz *et al.*, 2003), telemetry is the only method that can establish the precise real-time movements of fish between the estuarine and marine environment. Furthermore, given the high resolution data collected using such techniques, it is possible to understand the factors influencing such movements. Few studies have quantified the use of the estuarine and marine environments by fishes (e.g. Hartill *et al.*, 2003; Miller & Sadro, 2003). Tagging and more recently, otolith composition studies have provided information on the migration patterns of striped bass *Marone saxatilis* in the Hudson River (Waldman *et al.*, 1990; Zlokovitz *et al.*, 2003). Hartill *et al.* (2003) documented the use of an estuarine environment, the Maruhangi Estuary in New Zealand, by the marine snapper *Pagrus auratus*, using telemetry, and Miller & Sadro (2003) using telemetry observed residence time and patterns of movement of Coho salmon smolts *Oncorhynchus kisutch* migrating to the ocean, in the Winchester Creek Estuary, Oregon.

CHAPTER 4

SPACE USE AND HOME RANGE

INTRODUCTION

Estimating the home range size of an animal is essential for autecological studies and for developing species specific resource management strategies (Pittman & McAlpine, 2001). Burt (1943) defined the home range of an animal as the area traversed by the individual while gathering food, mating and caring for young. The home range of an animal has been shown to be dependent on its metabolic rate (McNab, 1963), and certain life history characteristics, such as state of maturity or age (Baldwin *et al.*, 2002). Both abiotic (salinity, temperature, turbidity, tidal movements) and biotic (distribution and abundance of food, inter- and intraspecific interactions) characteristics of the environment may influence the home range of an animal (Baldwin *et al.*, 2002; Gibson, 1997; Heupel & Heuter, 2002; Morin *et al.*, 1992; McNab, 1963). Since animals sometimes make exploratory movements outside their "normal" areas of activity, operational definitions sometimes specify that the home range is the area within which some fixed percent (often 95%) of activity occurs (Anderson, 1982). The home range of an animal usually contains a core area, where the majority of normal activity (e.g. foraging and resting) occurs; intermediate areas in which normal activities are undertaken less frequently than in core areas; and outer areas where infrequent exploratory behaviour occurs (Crook, 2004).

The use of telemetry is the most advantageous method to obtain movement data as no other method is able to provide such high resolution data. Furthermore, the incorporation of telemetry data into a geographic information system greatly enhances the usefulness in examining spatial and temporal movement patterns.

Space use and home ranges have been calculated for a wide range of fish species, particularly those that are marine (Matthews, 1990; Morrisey & Gruber, 1993; Holland *et al.* 1993a; Bradbury *et al.*, 1995; Zeller, 1997; Lowry & Suthers, 1998;

Heupel & Heuter, 2002; Jadot *et al.*, 2002), and specifically those inhabiting marine reserves (Holland *et al.*, 1993b & 1996; Zeller & Russ, 1998; Meyer *et al.*, 2000; Eristhee & Oxenford, 2001; Lowe *et al.*, 2003; Parsons *et al.*, 2003; Egli & Babcock, 2004). Studies on the home range and movement of other haemulids have only been conducted on grunts in the marine environment (Burke, 1995; Ogden & Ehrlich, 1977; Helfman & Schultz, 1984; Tulevech & Recksiek, 1994). Despite the large amount of information on space use patterns of fish species in estuarine and riverine environments (Tytler *et al.*, 1978; Helfman *et al.*, 1983; Szedlmayer & Able, 1993; Minns, 1995; Almeida, 1996; Baade & Fredrich, 1998; Bramblett & White, 2001; Baras *et al.*, 2002; Taverny *et al.*, 2002; Hartill *et al.*, 2003), there is a general paucity of information on the home range of fish in estuarine environments.

In southern Africa, no home range studies have been conducted on estuarine-dependent species. Information on the use of space by spotted grunter will improve our understanding of the ecology of this angling species. A sound understanding of the movement patterns of adolescent and adult spotted grunter is imperative to ensure sustainable utilization of this important fishery species.

The aim of this chapter was to describe the home range characteristics of spotted grunter in the Great Fish Estuary. More specifically, the objectives were to:

i) estimate various home range characteristics (size, length, location and number of home range and core areas of use) of spotted grunter;
ii) determine the effect of fish length on the home range characteristics; and
iii) determine long term trends in space use and home range characteristics.

MATERIALS AND METHODS

A detailed description of the study site and research approach is presented in Chapter 2. Two telemetry techniques were used to determine the home range estimates. Data collected by manual tracking and using permanently stationed automated listening stations (ALS). Data collected during the manual tracking period (29 September 2003 to 15 November 2003) was used to determine the home range estimates of each individual, while data recorded on the ALS (29 September 2003 to 12 February 2004) was used to validate the estimates and examine long term trends.

Home range estimates

The GIS software ArcView$^{®}$ GIS 3.2 and the Animal Movement Analysis Extension (AMAE) (Hooge & Eichenlaub, 1997) were used to analyse space use patterns of individual spotted grunter in the Great Fish Estuary.

There is presently no consensus on the effect of autocorrelation on home range estimates. The accuracy of home range estimates is unfortunately biased by time intervals between locations (independence/autocorrelation) (Swihart & Slade, 1985a). Independence between successive observations is an implicit assumption in most statistical analyses of animal movements, and requires that an animal's position in its home range at time $t+k$ is not a function of its position at time t (Swihart & Slade, 1985a). Independence of positional fixes, which excludes the effect of autocorrelation, is often deemed a prerequisite for estimation of home range size and utilization when using telemetry data (Rooney *et al.*, 1998). This is because the lack of independence among observations inflates the degrees of freedom and increases the probability of a Type I error (Legendre, 1993).

Independence is usually achieved in studies characterized by relatively long intervals between observations. However, in studies where there is frequent monitoring of individuals at short time intervals (characteristic of telemetry studies), the validity of the independence assumption is often jeopardized (Dunn & Gipson, 1977). This could result in negatively biased estimates of home range, where home range size is underestimated. To address this issue, a bivariate test of the independent assumptions, first proposed by Schoener (1981) and later further developed by Swihart & Slade (1985a), was used. Swihart & Slade (1985b) developed a method for determining the time at which autocorrelation of sequential data was negligible, and thus statistically independent. They stated that a long time interval between locations is required to meet the assumption of independence. However, although an increased time interval between locations results in a reduction in the degree of autocorrelation, it also reduces the sample size and provides an inaccurate interpretation of the animal's true behaviour, thereby eliminating the biological significance of the analysis.

Many authors (Anderson & Rongstad, 1989; Reynolds & Laundre, 1990; Rooney *et al*., 1998; De Solla *et al*., 1999; Otis & White, 1999) have shown that correcting for independence or autocorrelation can often result in negatively biased estimates of home range and movement patterns. Reynolds & Laundre (1990) showed that estimates of daily movements and home range size of pronghorns *Antilocapra americana* and coyotes *Cants latrans* were underestimated when sampling intervals were based on statistically independent data, and that autocorrelated data provided a better estimate of true home range size than independent data for all sampling intervals. They further stated that restricting sampling effort to intervals exhibiting statistical independence sacrifices biological significance. Rooney *et al*. (1999) showed that correcting for autocorrelation resulted in significant underestimation in range size and rates of movement of Irish mountain hare *Lepus timidus hibernicus* and Bank vole *Clethrionomys glareolus*. De Solla *et al*. (1999) found that kernel densities do not require serial independence of observations when estimating home range. Reynolds & Laundre (1990), Rooney *et al*. (1998) and De Solla *et al*. (1999) recommended that researchers should maximize the number of observations for home range using constant time intervals, to increase the accuracy and precision of the home range size estimates.

Given the above arguments and that by definition, the concept of home range involves autocorrelated movements (Otis & White, 1999), the home range estimates in the present study were not corrected for autocorrelation. Even after increasing the time interval between locations, the data in this study still lacked independence.

Home range estimation

The density of fish observations in this study was calculated using a non-parametric probabilistic kernel smoother. Estimation of the probabilistic density function, also known as the utilisation distribution is of great importance in home range studies (Worton, 1989). The utilisation distribution, hereafter abbreviated as UD, is the probability (usually 95%) of finding an animal at a particular location on a dimensional plane (Anderson, 1982; Worton, 1989), and describes the relative amount of time that an animal spends in that place (Seaman & Powell, 1996).

For the purpose of this study, the area that incorporates 95% of the UD (specified by the 95% density contour) represents the fish's home range i.e. the area within which 95% of activity occurs (Anderson, 1982); while the area that incorporates 50% of the UD (specified by the 50% density contour) is known as the animals 'center' (Dixon & Chapman, 1980) or core area of activity. To summarise:

Home Range = 95% UD
Core Area = 50% UD

The kernel estimates were calculated after Worton (1989). The kernel, *f(x)*, a bivariate probability density function, is placed over each datum and the estimator is constructed by adding *n* components. The kernel estimate has a higher density when many kernels overlap, as there is a concentration of points (fish locations). The resulting estimate is considered to be a true probability density function. Kernel variation at each datum is a function of a smoothing factor (*h*). Therefore, a fixed kernel density estimate is calculated as follows:

$$f_h(x) = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{h^2}K\left(\frac{x - X_i}{h}\right)$$

where *K* is the kernel density (unimodal symmetrical bivariate probability density function), *h* is the smoothing factor that can be varied by the user, X_i is a pair of (x,y) coordinates describing the location of each observation (*X* is a random sample of *n* independent points from the unknown UD), x is the (x,y) coordinates describing the location where function is being evaluated, and n is the number of data points.

Worton (1989) and Seaman & Powell (1996) suggested that the appropriate level of smoothing, or proper selection of h, is an important factor for obtaining accurate home range size estimates. Due to the shape of the study site, the least squares cross validation (LSCV) and the *ad hoc* calculation of the smoothing factor resulted in an unrealistic home range estimate, as most of the area fell outside the boundaries of the estuary. Consequently, the smoothing factor was specified by the user. By trial and error, a 'user input' smoothing factor (h) of 40; provided the best results and was used for all home range calculations. However, while the smoothing factor set at 40 produced a realistic estimate, there were parts of the home range that still fell outside the estuary. Therefore the home range areas were clipped and area recalculated with the polygon of the estuary specified as the boundary. Since only outer areas of the 95% UD were clipped, there was no effect on the kernel estimates themselves.

Due to the longitudinal nature of the estuary, the home range length was also used to describe the space use patterns of spotted grunter. Home range length was calculated from the home range estimates, and was defined as the distance between the two furthermost points of the 95% UD. This was calculated for each individual using the measuring tool in ArcView® GIS 3.2.

The number of core areas and the number of 95% UD areas were calculated from the home range estimates.

Since the accuracy of home range estimates is biased by sample size, linear regression was used to determine the effect of sample size on the size of the home range (95% UD).

Effect of fish length

Linear regression was used to determine the relationship between fish length and the size of the home range estimates (95% and 50%), and fish length and home range length of each fish from both studies. Linear regression was used to test whether the number of core areas and the number of 95% UD areas were related to fish length.

Long term trends

Since accurate interpretation of a home range relies on observations carried out over both diurnal and seasonal time frames (Lowry & Suthers, 1998), and that shorter monitoring periods can often underestimate the true extent of a fish's movements (Parsons *et al.*, 2003), an assessment of the long term trends on the home range of an animal is required. Long term trends in home range size of spotted grunter was assessed using data collected by the automated listening stations (ALS) and by manually tracking individuals from the first study that were still present in the estuary during the second study. The proportion of the total number of detections, recorded by each ALS, during the manual tracking period (29 September 2003 to 15 November 2003) and during the three month period after the manual tracking period (16 November 2003 to 12 February 2004) was calculated for each individual. The distribution of the proportion of the total number of detections of each individual recorded by the ALSs during the manual tracking period was graphically compared to the total number of detections of each individual recorded by the ALSs for three months after the manual tracking period. In addition, a two sample Kolmogorov-Smirnov goodness of fit test was used to test if the proportion of detections recorded by each ALS during the two periods for each fish were significantly different. The distribution of the proportion of total detections recorded by the ALSs during the manual tracking period, calculated above, was then graphically compared to the location of each fish's home range (95% UD) and core area (50% UD) calculated in AMAE from data collected during the manual tracking period. The home range estimates of three fish (Fish 29, 30, 32), that were tagged in the first study period, and were still present during the second study period (approximately 6 months after the battery expiry date), were calculated and compared during both the first and second studies.

RESULTS

Since one fish (Fish 50A) tagged in the second study was caught on 10 October 2003 (12 days after the beginning of the study), and replaced by another individual (Fish 50B) on 14 October 2004, both were excluded from the home range analyses. Home range analysis using AMAE was therefore computed on a total of 39 individuals (n=20 in the first study and n=19 in the second study).

Home Range Estimates

A total of 41 individuals (263 – 698 mm TL) were tagged and tracked during two study periods. A total of 468 positional fixes were obtained in the first study and 635 in the second study. The number of positional fixes per fish ranged from 8 to 42 (avg. 27.6 ± 10.3 SE). There was no significant linear relationship between the number of positional fixes and home range size ($p = 0.49$). The home range estimates (size, location, number of 50% UD and 95% UD) of the 41 tagged individuals are summarized in Table 4.1. The home range of each tagged fish are graphically presented in Figures 4.1 and 4.2.

Table 4.1. Fish code, total length, number of positional fixes and home range estimates of individual spotted grunter manually tracked in the Great Fish Estuary during two study periods in 2003, study 1 (7 February 2003 - 24 March 2003; Fish 20 to 39) and study 2 (29 September 2003- 15 November 2003; Fish 50A to 69).

Fish code	Length (mm TL)	Number of fixes	Home range (m^2) (95% UD)	Core area (m^2) (50% UD)	Home range length (km)	Number 95% UD	Number 50% UD	Ratio 50:95%
20	317	25	60 434	8 594	9.6	10	1	0.14
21	334	34	232 053	26 065	7.3	10	7	0.11
22	297	20	242 928	19 001	5.7	16	11	0.08
23	380	36	30 639	6 672	3.5	2	1	0.22
24	330	18	194 049	20 029	5.1	9	10	0.10
25	313	19	71 559	9 888	5.9	7	1	0.14
26	314	35	141 466	9 634	5.1	9	1	0.07
27	328	12	104 748	21 728	3.8	6	1	0.21
28	382	34	90 447	6 323	4.5	11	1	0.07
29	377	36	38 994	9 005	0.3	1	1	0.23
30	308	36	45 796	6 712	0.4	2	1	0.15
31	357	12	110 079	5 968	5.1	7	1	0.05
32	318	36	29 324	5 897	0.2	2	1	0.20
33	329	13	28 531	9 566	0.3	1	1	0.34
34	263	8	48 551	6 244	4.6	4	1	0.13
35	357	8	126 407	42 592	4.9	7	7	0.34
36	387	15	67 133	7 970	1.2	12	1	0.12
37	363	23	181 714	4 253	12.1	12	1	0.02
38	319	12	68 668	15 694	1.5	3	1	0.23
39	355	36	75 513	10 683	6.8	11	1	0.14
50A	449	12	67 471	5 809	5.81	6	1	0.09
50B	515	15	176 356	6 648	8.07	11	2	0.04
51	469	32	193 495	6 905	5.5	11	1	0.04
52	385	42	46 521	4 563	6.0	3	1	0.10
53	428	37	142 950	7 478	6.5	11	1	0.05
54	620	22	278 966	11 323	7.4	14	9	0.04
55	432	29	335 577	14 550	10.6	18	7	0.04
56	440	42	83 262	7 020	7.6	11	1	0.08
57	364	42	283 879	11 801	6.8	17	2	0.04
58	625	21	231 752	24 237	8.0	10	10	0.10
59	472	28	135 603	10 250	11.7	15	1	0.08
60	527	29	219 850	14 441	7.5	11	4	0.07
61	489	30	270 759	5 698	13.0	11	2	0.02
62	504	29	234 521	12 590	7.7	12	2	0.05
63	534	20	117 989	6 372	5.5	8	3	0.05
64	387	35	370 660	36 813	7.3	13	10	0.10
65	698	20	190 321	11 430	8.1	11	3	0.06
66	403	42	33 945	6 116	2.9	2	1	0.18
67	428	35	253 071	5 517	6.9	14	1	0.02
68	538	32	311 092	22 928	7.6	14	6	0.07
69	362	41	206 943	7 633	10.0	15	1	0.04

The home range size (95% UD) of spotted grunter was highly variable, ranging from 28 531 m² to 370 660 m² (Table 4.1), with an average of 152 056 m² ± 97 391 SE. The number of 95% UD areas per individual ranged from 1 to 18, with a mean of 9.31 ± 4.75 SE. During the period of this study, 67% of individuals had fragmented home ranges that extended along the length of the estuary (Figures 4.1 and 4.2). However, 26% had home ranges that were confined to specific areas in the lower, 5% in the middle, and 3% in the upper reaches of the estuary (Figures 4.1 and 4.2).

The size of the core areas (50% UD) also varied, ranging from 4 253 m² to 42 592 m², averaging 12 312 m² ± 8 670 SE (Table 4.1). Most fish (62%) had a single core area (avg. 3.0 ± 3.26 SE; range. 1 – 11) (Table 4.1). Eight percent of individuals had two core areas and 31 % had more than two core areas. Fifty-four percent of the fish had their core areas confined to a specific area in the lower reaches of the estuary. The core areas of 13% percent of spotted grunter occurred in the middle reaches and 13% in the upper reaches (Figures 4.1 and 4.2). Twenty-one percent of fish had numerous core areas situated along the length of the estuary (Figures 4.1 and 4.2). These fragmented core areas were not confined to a particular region of the estuary. The extent of overlap of the core areas of individuals was highest in the lower reaches of the estuary, between 1-2 km (59%) and 2-3 km (23%) from the estuary mouth and in a short stretch in the upper reaches (7-8 km) of the estuary (21%). No overlapping core areas occurred from 8 km upstream of the mouth.

The home range length ranged from 0.23 km to 13.02 km (avg. 6.01 km ± 3.24 SE) (Table 4.1). The length of the home ranges of most (67%) fish extended into the upper reaches of the estuary. However, 18% of individuals had a short home range, confined to the lower reaches, and 15% a moderately short home range, extending into the middle reaches.

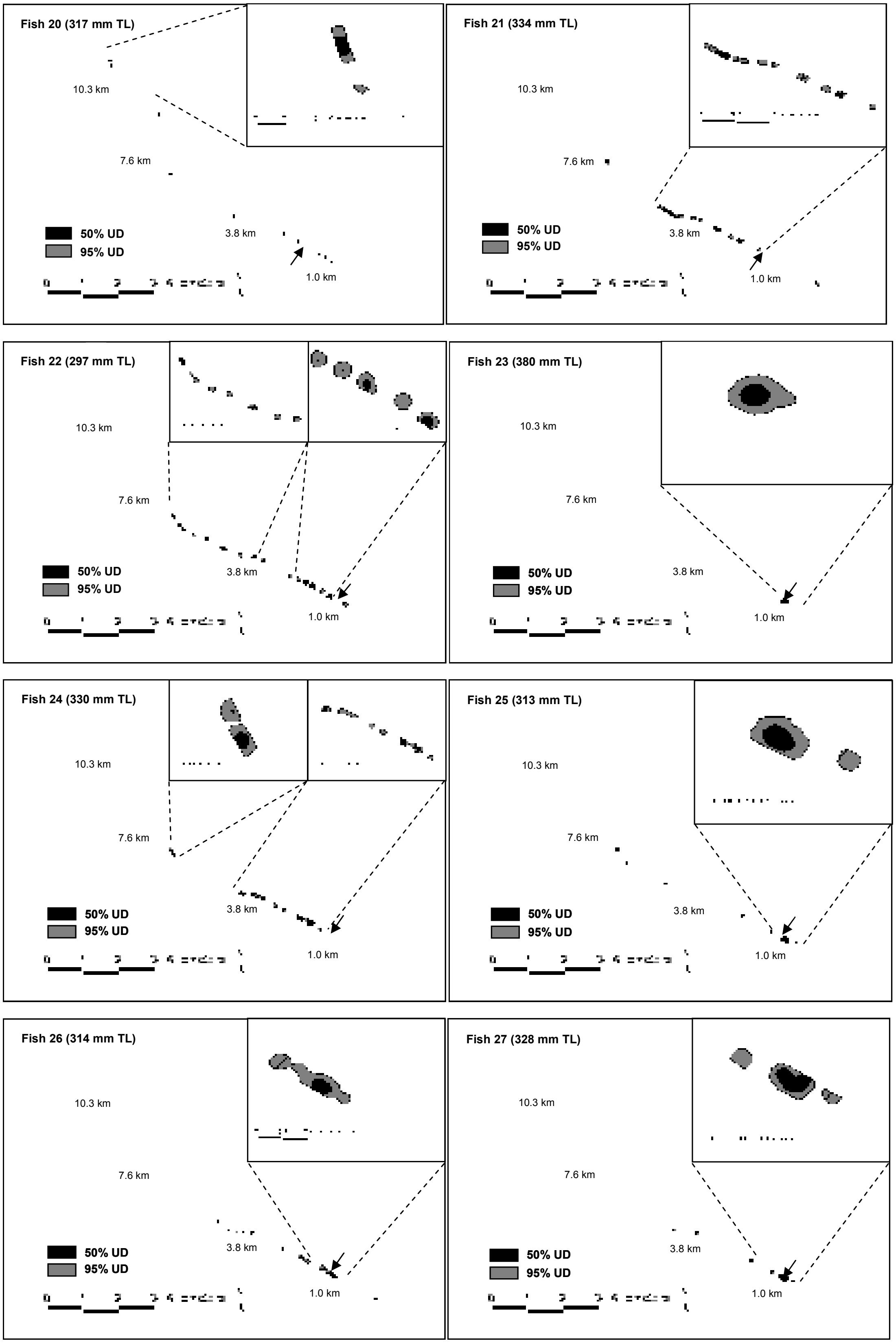
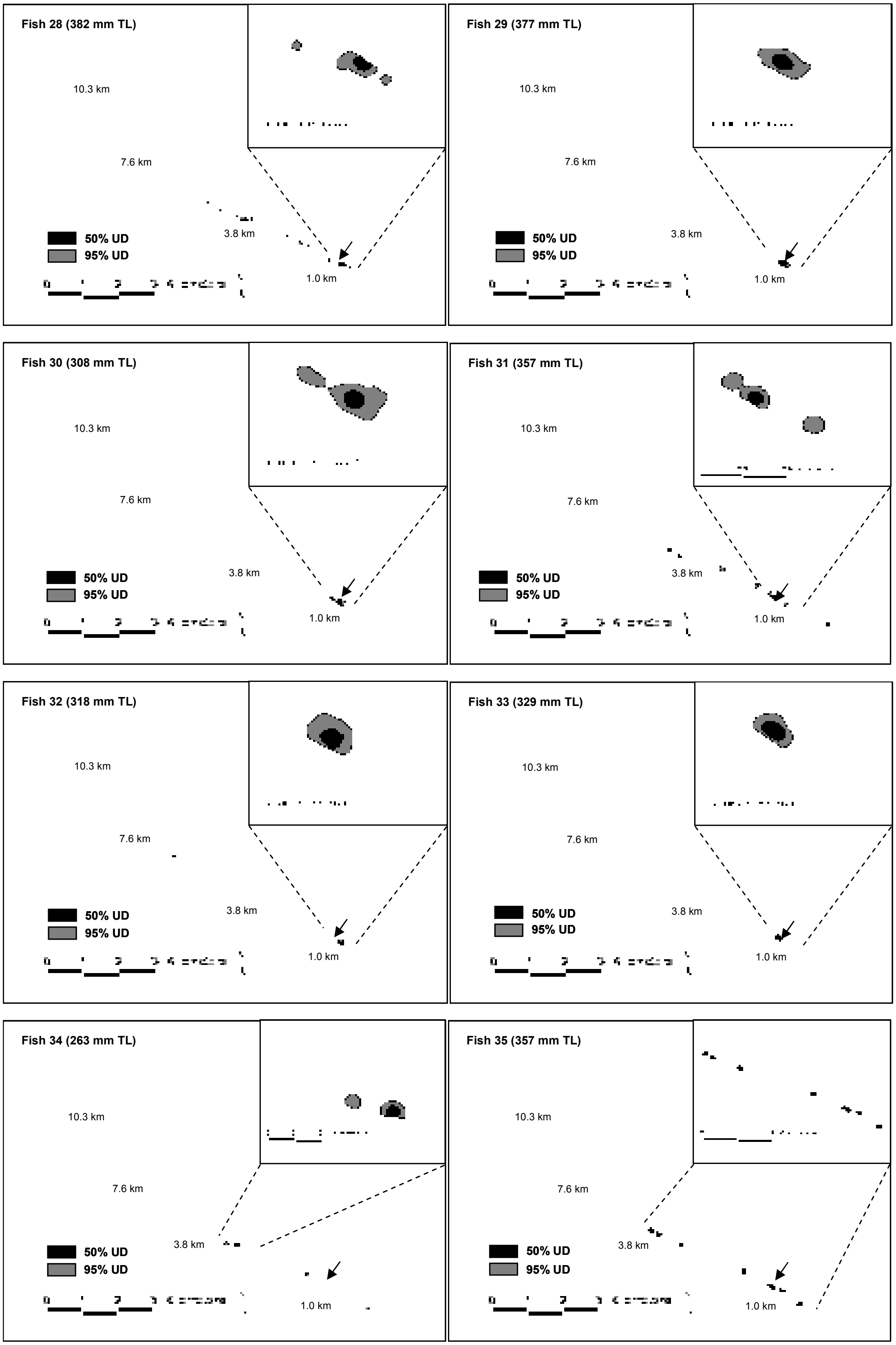


Figure 4.1. Map of the Great Fish Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of spotted grunter *Pomadasys commersonnii* during the first study (7 February 2003 - 24 March 2003). Arrow indicates catch site.


Fish 28 (382 mm TL)

Fish 29 (377 mm TL)

Fish 30 (308 mm TL)

Fish 31 (357 mm TL)

Fish 32 (318 mm TL)

Fish 33 (329 mm TL)

Fish 34 (263 mm TL)

Fish 35 (357 mm TL)

Figure 4.1.cont. Map of the Great Fish Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of spotted grunter *Pomadasys commersonnii* during the first study (7 February 2003 - 24 March 2003). Arrow indicates catch site.

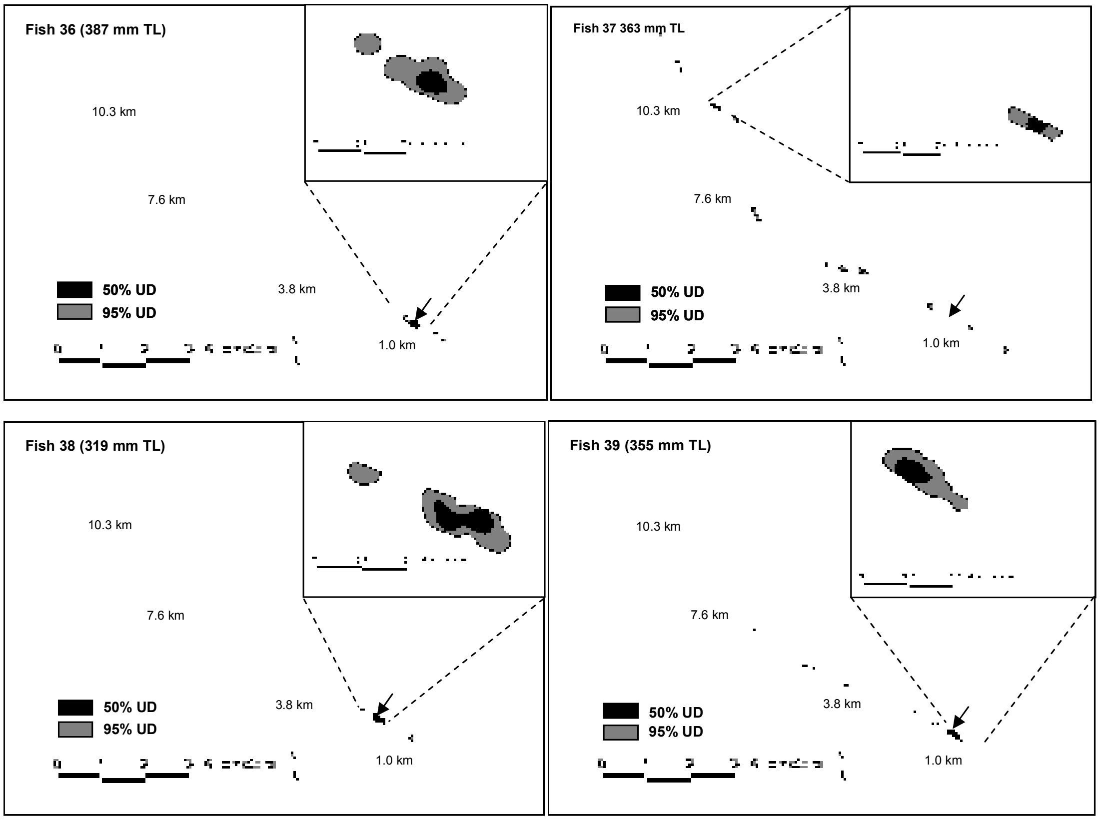


Figure 4.1.cont. Map of the Great Fish Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of spotted grunter *Pomadasys commersonnii* during the first study (7 February 2003 - 24 March 2003). Arrow indicates catch site.

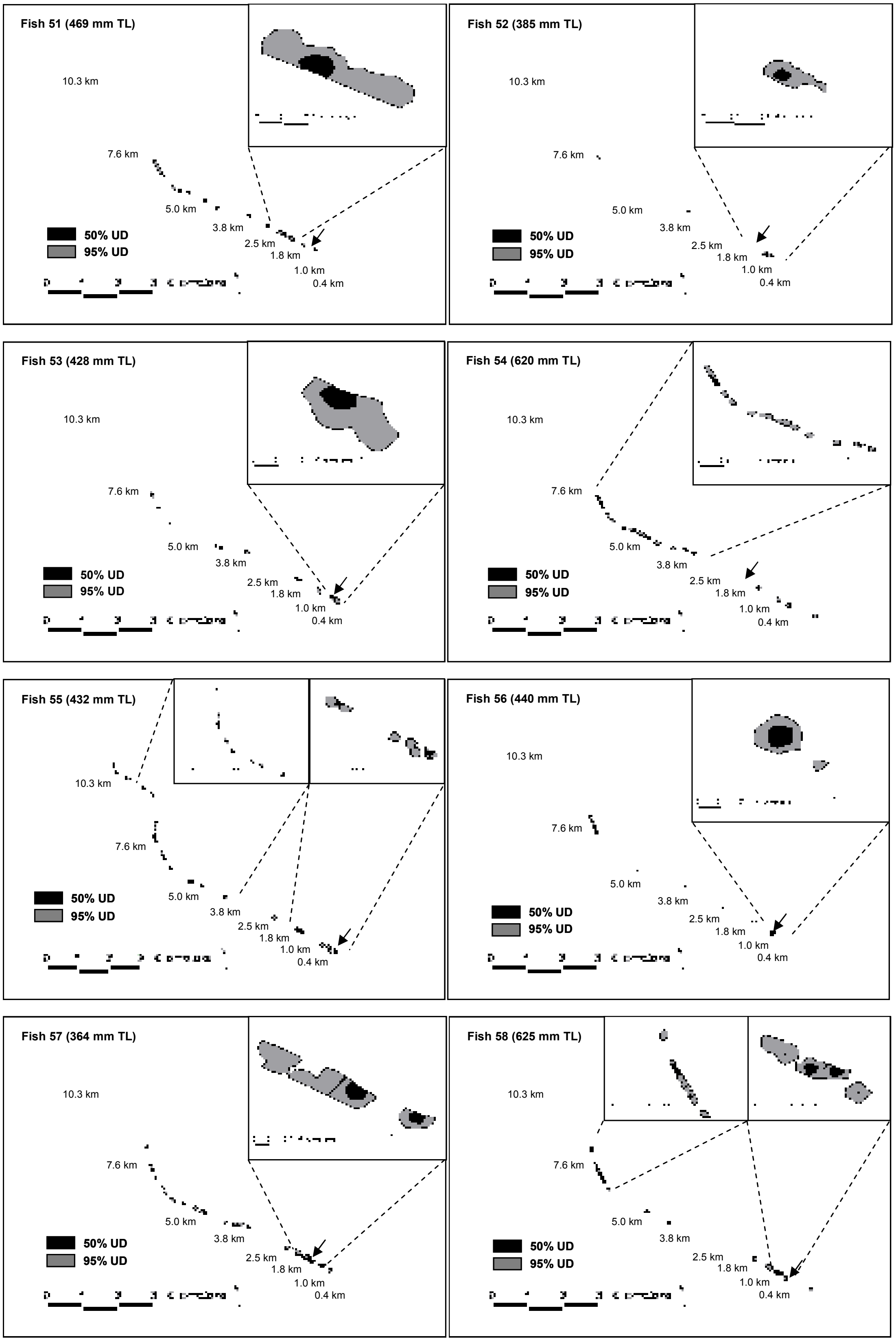


Figure 4.2. Map of the Great Fish Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of spotted grunter during the second study (29 September 2003 – 15 November 2003). Arrow indicates catch site.

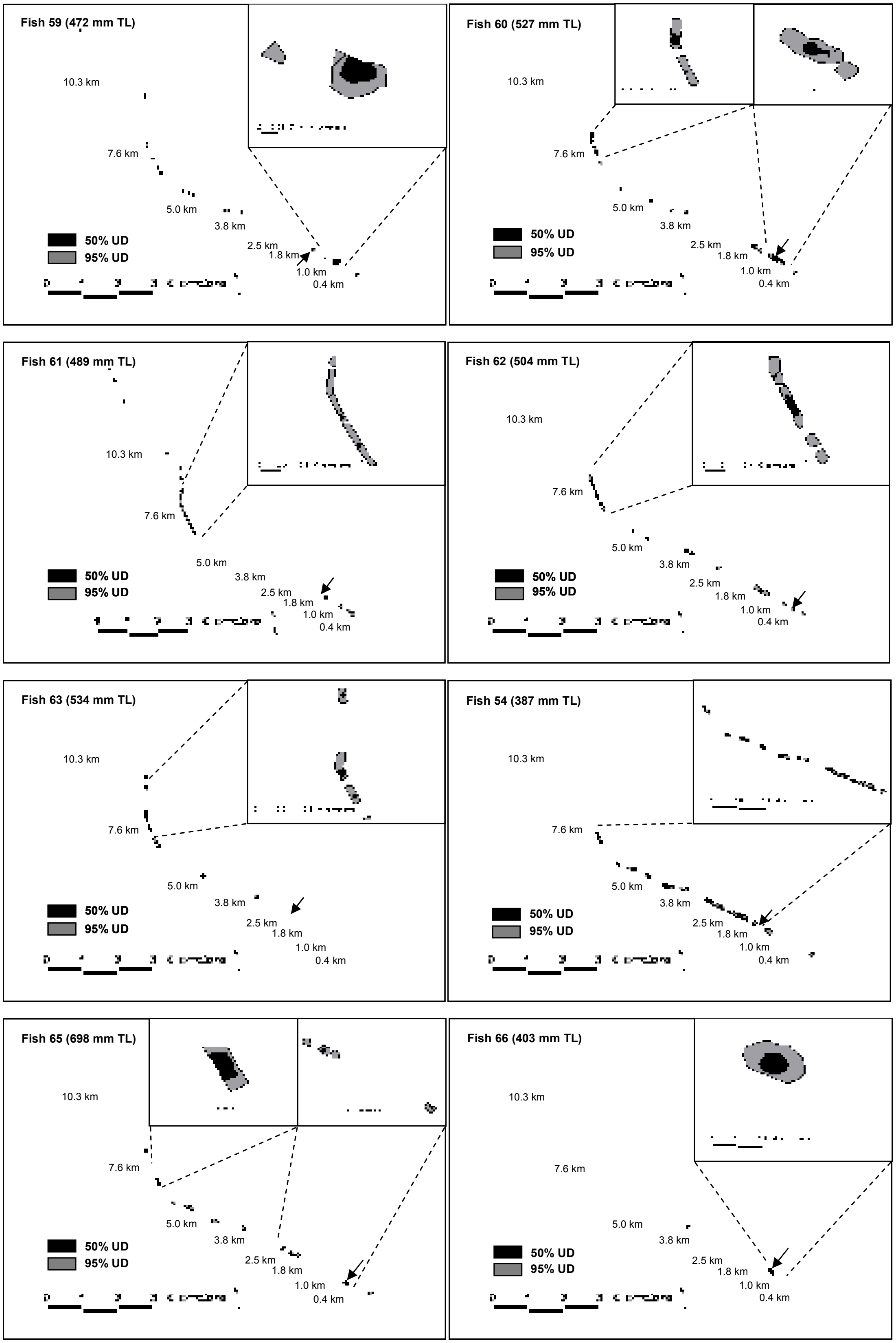


Figure 4.2.cont. Map of the Great Fish Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of spotted grunter *Pomadasys commersonnii* during the second study (29 September 2003 – 15 November 2003). Arrow indicates catch site.

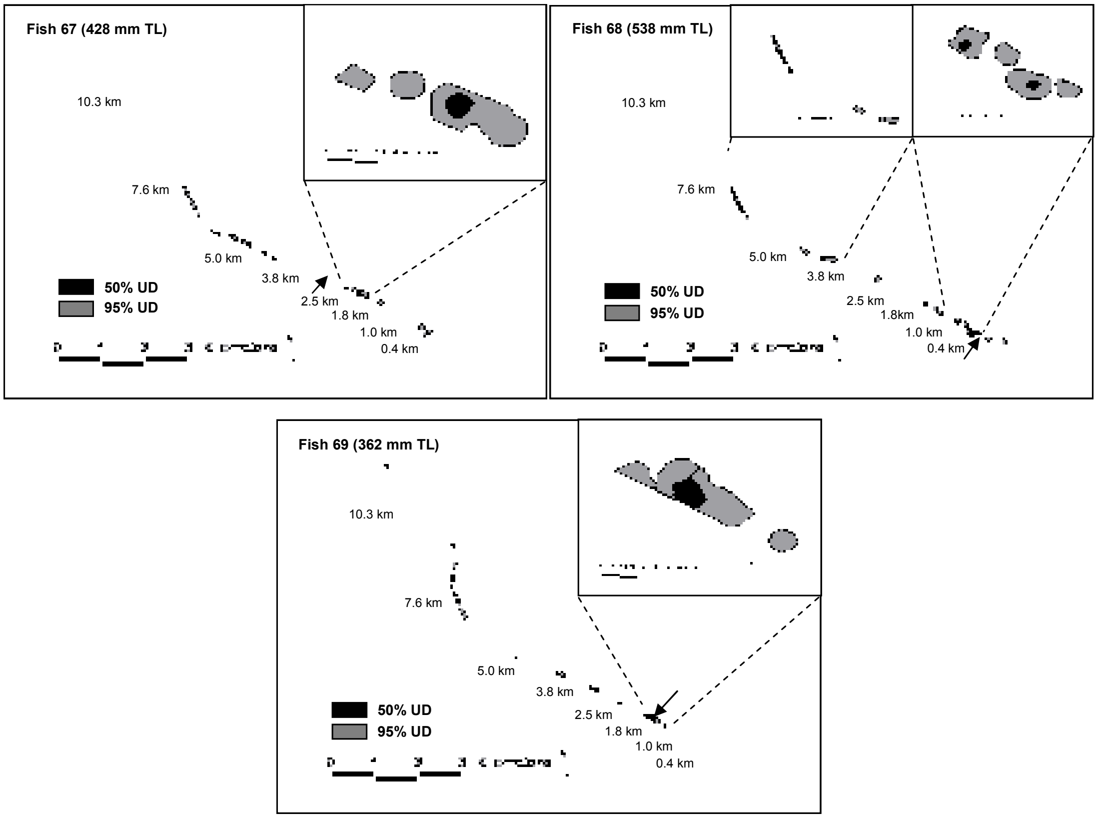


Figure 4.2.cont. Map of the Great Fish Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of spotted grunter *Pomadasys commersonnii* during the second study (29 September 2003 – 15 November 2003). Arrow indicates catch site.

Effect of fish length

The average home range of smaller spotted grunter (< 450 mm TL) was 129 167 m² ± 97 722 SE (range. 28 531 – 370 660 m²), while the larger fish (> 450 mm TL) had a larger home range size, 218 435 m² ± 61 272 SE (range. 117 989 – 311 092 m²). There was a significant positive relationship between home range size and fish length ($p = 0.004$; $R^2 = 0.20$; $F(1, 37) = 9.24$) (Figure 4.3).

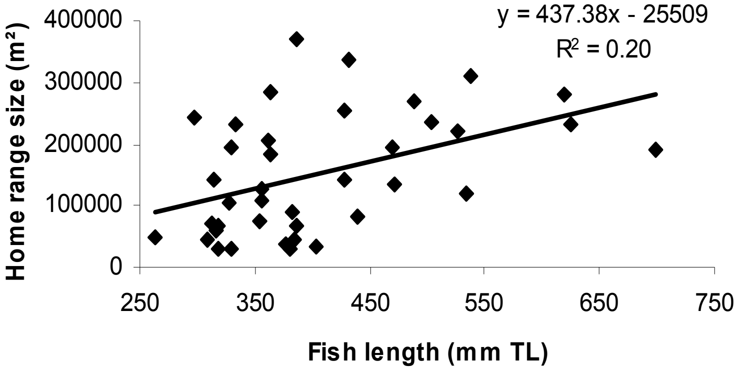


Figure 4.3. Relationship between home range size (m^2) and the length (mm TL) of spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary.

The average number of 95% UD areas of the smaller spotted grunters (avg. 8.48 ± 5.15 SE; range. 1-18) was slightly lower than that observed in the larger group (avg. 11.70 ± 2.11 SE; range. 8-15). Furthermore, there was a weak, though significant, positive relationship between the number of 95% UD areas and fish length ($p = 0.02$; $R^2 = 0.13$; $F(1, 37) = 5.53$) (Figure 4.4).

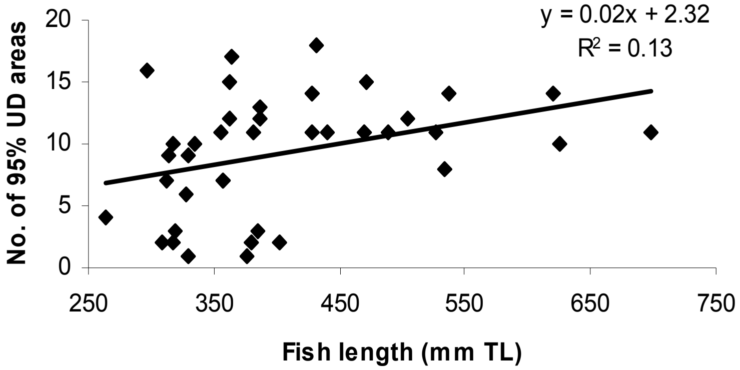


Figure 4.4. Relationship between the number of home range (95% UD) areas and the length of spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary. The smoothing factor, *h*, was pre-specified at 40 and remained constant.

Ninety percent of individuals from the larger group had fragmented home ranges, with 10% having home ranges confined to an area in the upper reaches of the estuary. No individuals from the larger group had their home ranges confined to the lower reaches of the estuary. By contrast, only 62% of the smaller fish had fragmented home ranges, and 34% had their home ranges confined to a specific area in the lower reaches. Although the location of core areas differed between the two size groups, the average core area size of the small and large fish was similar, 12 207 m^2 ± 9 416 (4253 – 42 592 m^2) and 12 617 m^2 ± 6 436 (5 698 – 24 237 m^2), respectively. There was no significant relationship between the size of the core area (log-transformed) and fish length ($p = 0.60$; $R^2 = 0.01$; $F(1, 37) = 0.27$) (Figure 4.5).

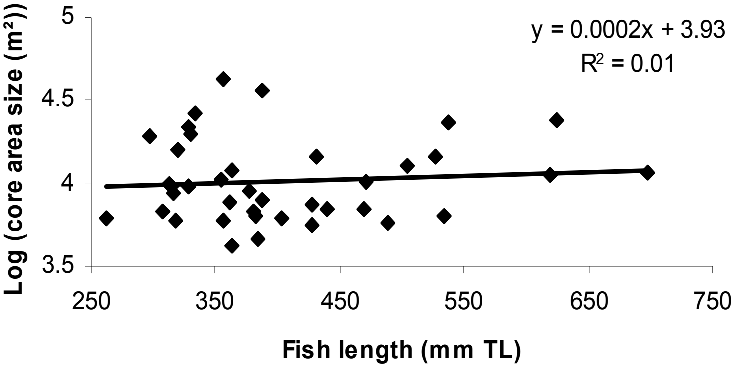


Figure 4.5. Relationship between the size of the core areas (m^2) and the length of spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary.

The number of core areas per fish was slightly lower for the smaller group (avg. 2.62 ± 3.24; range. 1-11) than for the larger group (avg. 4.1 ± 3.21; range. 1-10). Since the data violated the assumptions of normality (after several transformations), a linear regression between the number of 50% UD areas and fish length could not be fitted.

Seventy-six percent of spotted grunter from the smaller group had one core area, 3% had two core areas and 21% had more than two core areas. By contrast, 60% of individuals from the larger group had more than two core areas, with 40% having either one (20%) and two (20%) core areas.

Most (66%) of the fish in the smaller size group had their core areas in the lower reaches of the estuary, with few in the middle (10%) and upper (7%) reaches. Seventeen percent had multiple core areas along the length of the estuary. In contrast, the core areas of 30% of the larger fish were situated in the lower reaches, 20 % in the middle and 30% in the upper reaches. Twenty percent of the large fish had multiple core areas along the length of the estuary.

Seventy-two percent of the small fish had overlapping core areas between 1 and 2 km from the estuary mouth. By contrast, only 20% of the large fish had core areas in this region. Seventy percent of their core areas were in the upper reaches, and only 3% of the smaller fish's core areas overlapped in this area. A greater proportion of the larger fish had overlapping core areas in the mouth region, in comparison to the smaller group, 40 % and 7 % respectively.

The average home range length of individuals from the smaller size group was shorter (avg. 5.26 km ± 3.18 SE) than the larger group (avg. 8.21 km ± 2.41 SE). Furthermore, the minimum home range length recorded in the smaller group (0.23 km) was considerably shorter than the larger group (5.47 km). However, the maximum home length recorded by the small group was only slighter shorter (12.14 km) than that recorded by the larger group (13.02 km). There was a weak, though significant, positive relationship between the home range length and fish length ($p = 0.01$; $R^2 = 0.16$; $F(1, 37) = 7.24$) (Figure 4.6).

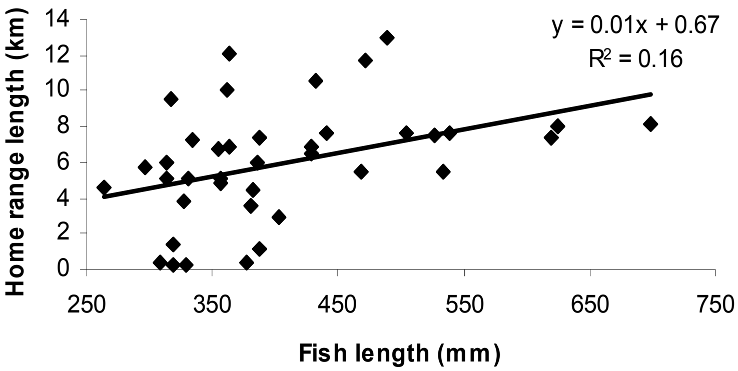


Figure 4.6. Relationship between the home range length (km) and total length of all spotted grunter *Pomadasys commersonnii* recorded in the Great Fish Estuary.

Long term trends

Peaks in the distribution and proportion of total detections at each ALS site corresponded with the home range core areas. Examples are given in Figure 4.7. The distribution and abundance of peaks in total number of detections during the manual tracking period and the three month period after the manual tracking period were similar (Figure 4.7). There was no significant difference between the proportion of detections recorded at each ALS for each fish during the two periods.

The location and size of the core area of the three fish that were manually tracked in both the first and second studies were similar (Table 4.2; Figure 4.8). Each fish remained in the same core area during both studies (Figure 4.8). While the core areas of two of the fish remained similar, Fish 32 had a substantially larger core area during the second study (Table 4.2; Figure 4.8). The home range was much larger and longer during the second study for Fish 29 and Fish 32 (Table 4.2; Figure 4.8). In contrast, the home range size, length and number of 95% UD areas of Fish 30 was smaller in the second study (Table 4.2; Figure 4.8).

SMALL (< 450 mm TL) **LARGE (> 450 mm TL)**

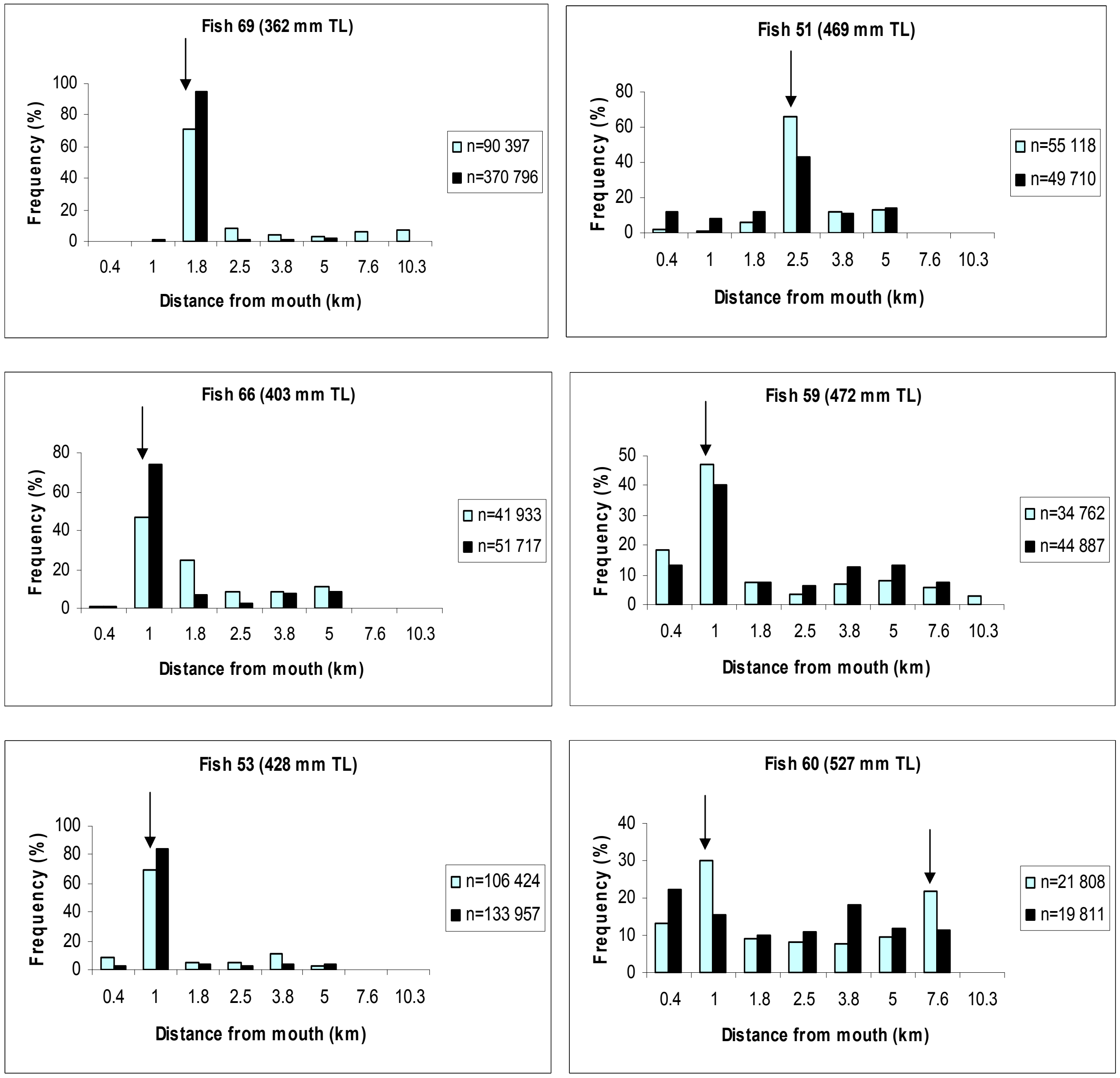


Figure 4.7. Percentage of total number of detections of three small fish (< 450 mm TL) (Fish 53, 66, and 69) and three large fish (> 450 mm TL) (Fish 51, 59, and 60) at each ALS, situated along the length of the Great Fish River Estuary. Light shaded indicate the manual tracking period (29 September 2003 - 15 November 2003) and dark shaded bars, the 3 month period after manual tracking (15 November 2003 - 12 February 2004). Arrows indicate the location of the core areas calculated using AMAE.

Table 4.2. Home range estimates of Fish 29, 30, and 32 manually tracked in the Great Fish River Estuary during both study 1 (7 February - 24 March 2003) and study 2 (29 September 2003 - 15 November 2003).

Fish 29 (377 mm TL)	**Study 1**	**Study 2**
No. positional fixes	36	33
Home range (95 % UD) (m^2)	38 994	61 263
Core area (50% UD) (m^2)	9005	8561
Home range length (km)	0.32	6.33
No. 95 % UD	1	7
No. 50 % UD	1	1

Fish 30 (308 mm TL)		
No. positional fixes	36	25
Home range (95 % UD) (m^2)	45 796	21 244
Core area (50% UD) (m^2)	6712	6359
Home range length (km)	0.44	0.17
Number 95 % UD	2	1
Number 50 % UD	1	1

Fish 32 (318 mm TL)		
No. positional fixes	36	15
Home range (95 % UD) (m^2)	29 324	51 380
Core area (50% UD) (m^2)	5897	8619
Home range length (km)	5.55	5.99
Number 95 % UD	2	4
Number 50 % UD	1	1

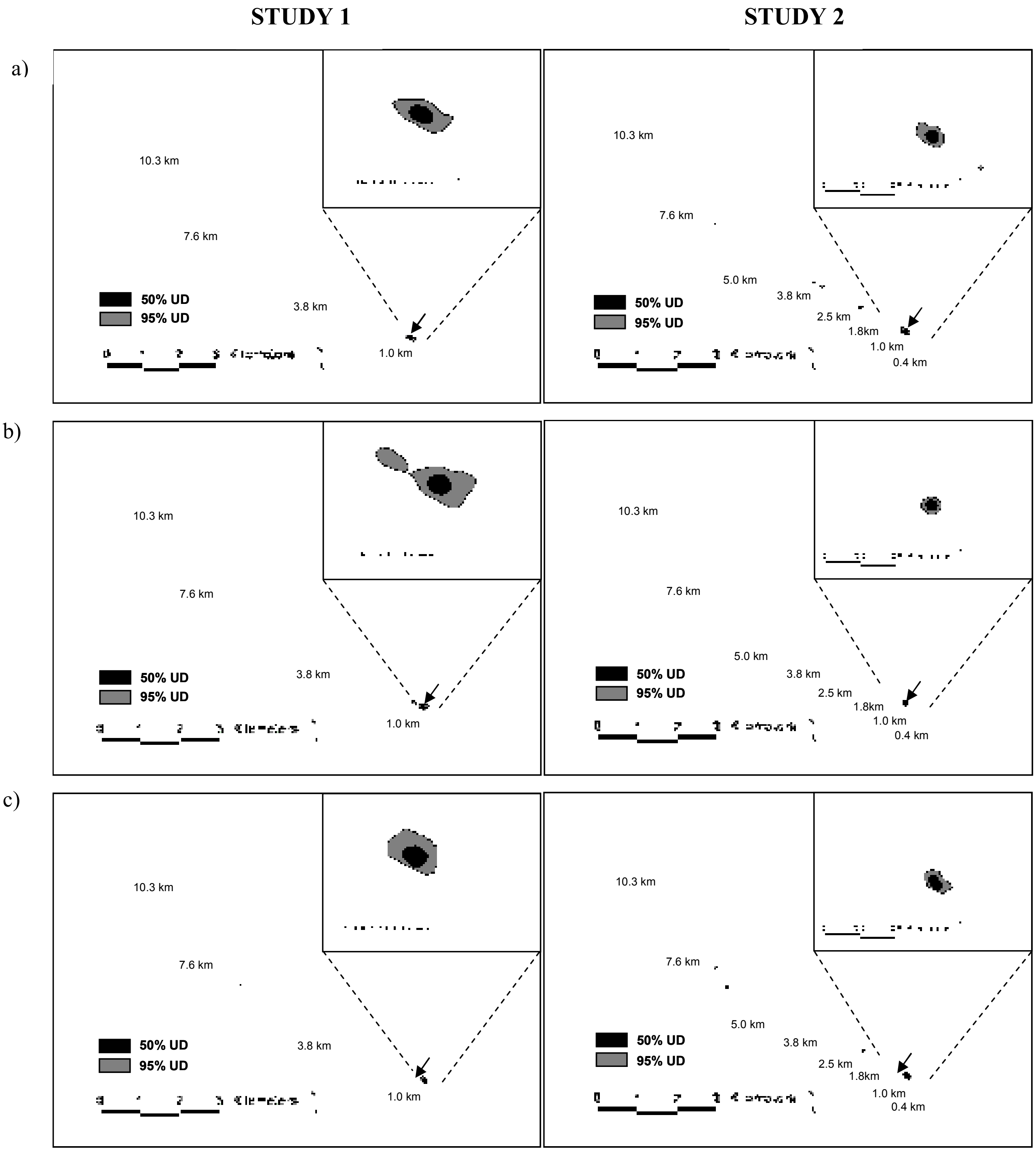


Figure 4.8. Map of the Great Fish River Estuary showing the home range (95% UD, grey shaded area and 50% UD, black shaded area) of a) Fish 29 (377 mm TL), b) Fish 30 (308 mm TL) and c) Fish 32 (318 mm TL) during study 1 (7 February 2003 – 24 March 2003) and study 2 (29 September 2003 – 15 November 2003).

DISCUSSION

To date, there is a lack of information describing the home range of fishes in estuarine environments worldwide and particularly in South Africa.

Spotted grunter in the Great Fish Estuary showed a high degree of temporal and spatial variation in their home range size and core areas of activity. This variation was most pronounced in the length of the home range, which ranged from 0.23 km to 13.02 km. Despite differences in geographical location, high variability in home range size and space use appears to be a common denominator amoungst all fish. Table 4.3 summarises the findings of telemetry studies estimating the home range size of fish in the marine environment. The average and range in home range and core area size of spotted grunter was much larger and wider than that observed in other marine teleosts (Table 4.3). However, those studies were all conducted on reef habitat and are therefore not directly comparable.

Although there was a high variability in the home range estimates of the fish, two common behavioural patterns were identified. Two thirds of the tagged fish exhibited roaming behaviour, with numerous 95% UD areas extending along the length of the entire estuary. The remaining individuals exhibited resident behaviour. The home ranges of the latter were mostly confined to the lower reaches of the estuary, with occasional movements out of this area. Both residency and roaming behaviour have also been observed in other haemulids (e.g. Helfman & Shultz, 1984; Tulevech & Recksiek, 1994; Burke, 1995; Ogden & Ehrlich, 1977), and species in other families (Jadot *et al.*, 2002; Parsons *et al.*, 2003; Egli & Babcock, 2004). Furthermore, Cowley (1999) found that late-juvenile white steenbras *Lithognathus lithognathus* in the marine environment were resident, while some individuals undertake longshore migrations.

Most of the fish (62%) had one high use or core area within their home range, which was generally confined to the lower reaches of the estuary. Many fish species have been observed to spend most of their time in a small core area or preferred site within their home range (Holland *et al.*, 1993a; Bradbury *et al.*, 1995; Zeller, 1997; Baade & Fredrich, 1998; Lowry & Suthers, 1998; Eristhee & Oxenford, 2001; Jadot *et al.*, 2002; Parsons *et al.*, 2003; Hartill *et al.*, 2003; Lowe *et al.*, 2003). A similar trend has also been observed in other animals, such as Cape clawless otters *Aonyx capensis* (Somers & Nel, 2004), white-lipped *Tayassu pecari* and collared *Tayassu tajacu* peccaries (Keuroghlian *et al.*, 2004) and Malayan sun bears, *Helarctos malayanus* (Wong *et al.*, 2004).

Many of the core areas of the tagged fish overlapped. The extent of overlap was highest (60 %) in a short stretch between 1 and 2 km from the estuary mouth. Two other areas where overlapping was most pronounced was in the lower reaches, 2-3 km from the estuary mouth, and in the upper reaches, 7-8 km from the estuary mouth. A high degree of overlap between the home ranges has also been observed in other species (Holland *et al.*, 1993ab; Zeller, 1997; Meyer *et al.*, 2000; Parsons *et al.*, 2002). Eristhee and Oxenford (2001) found that the home ranges and preferred sites of Bermuda chub *Kyphosus sectatrix* tagged in a marine reserve strongly overlapped. Kelp bass *Paralabrax clathratus* tagged in a marine reserve also showed a high degree of overlap in home ranges, even between fish that exhibited large variability in space use (Lowe *et al.*, 2003).

Table 4.3. Documented studies representing the variation in the home range size of marine fish species

Common name	**Species**	**Sample size**	**Length (mm)**	**Region**	**Habitat**	**Home range (m^2) ± SE (range) (95% UD)**	**Core area (m^2) ± SE (range) (50% UD)**	**No. Core areas (50% UD)**
White Goatfish [1]	*Mulloides flavolineatus*	4	284 - 318 FL	Hawaii	Patch Reef	2 533 (1 200 - 3 200)	NA	NA
Cunner [2]	*Tautogolabrus adspersus*	8	195 - 250 TL	Newfoundland	Rocky Reef	5 999 ± 2862 (2 025 - 11 743)	NA	NA
Coral Trout [3]	*Plectropomus leopardus*	39	376 - 675 FL	Australia	Fringing Reef	10 458 ± 962	NA	NA
Coral Trout [3]	*Plectropomus leopardus*				Patch Reef	18 797 ± 3189	NA	NA
Red morwong [4]	*Cheilodactylus fuscus*	68	160 - 440 FL	Australia	Subtidal Reef	1 865 ± 268	706 ± 108	NA
Whitesaddle Goatfish [5]	*Parupeneus porphyreus*	5	205 - 257 FL	Hawaii	Patch Reef	19 201 ± 10 339 (9 070 - 35 163)	NA	NA
Bermuda Chub [6]	*Kyphosus sectatrix*	6	325 - 455 FL	West Indies	Fringing and Patch Reef	30 514 ± 5 104 (14 973 - 52 544)	NA	1 - 2
Bermuda Chub [6]	*Kyphosus sectatrix*	5	260 - 305 FL		Patch Reef	39 114 ± 3 745 (29 402 - 51 416)	NA	1 - 3
Strepie [7]	*Sarpa salpa*	6	249 - 317 FL	Mediterranean Sea	Rocky Reef	21 633 ± 14 584 (8 530 - 42 950)	3 675 ± 2011 (1 470 - 6 230)	NA
Dusky grouper [8]	*Epinephelus marginatus*	7	205 - 400 TL	Mediterranean Sea	Rocky Reef	5 312 (1 848 - 18 626)	NA	NA
Snapper [9]	*Pagrus auratus*	5	400 - 532 FL	New Zealand	Shallow Reef	55 500 ± 6 200 (28 400 - 99 500)	5 600 ± 900 (1 900 - 12 200)	1 - 4
Snapper [9]	*Pagrus auratus*	11	250 - 532 FL	New Zealand	Shallow Reef	(3 877 - 50 329)	NA	1 - 2
Kelp bass [10]	*Paralabrax clathratus*	12	250 - 400 SL	California	Rocky Reef with kelp beds	3 349 ± 3 328 (33 - 11 224)	NA	NA

[1] = Holland *et al*. (1993), [2] = Bradbury *et al*. (1995), [3] = Zeller (1997), [4] = Lowry & Suthers (1998), [5] = Meyer et al. (2000), [6] = Eristhee & Oxenford (2001), [7] = Jadot *et al*. (2002), [8] = Lembo *et al*. (2002), [9] = Parsons *et al*. (2003), [10] = Lowe *et al*. (2003).

Daily activity patterns of an animal are a complex compromise between optimal foraging time, social activities and environmental constraints (Ashoff, 1964). Many factors are known to influence the space use patterns of fish. These include fish size, and thus relative spatial requirements (Helfman *et al.*, 1982; Lowry & Suthers, 1998; Meyer *et al.*, 2000; Hartill *et al.*, 2003; Egli & Babcock, 2004), genetic individual behavioural variability (Parsons *et al.*, 2003; Egli & Babcock, 2004), social interactions (Egli & Babcock, 2004), diel activity (Ogden & Erlich, 1977; Holland *et al.,* 1993a; Tulevech & Recksiek, 1994; Burke, 1995), and environmental variables. More specifically, prey availability (Lowry & Suthers, 1998; Taverny *et al.*, 2002), predator avoidance (Erlich & Erlich, 1973; Savino & Stein, 1982; Baldwin *et al.*, 2002), habitat composition (Morrisey & Gruber, 1993; Zeller, 1997), and abiotic parameters such as tidal state (Helfman *et al.*, 1983; Szedlmayer & Able, 1993; Almeida, 1996; Hartill *et al.*, 2003) and water temperature (Morrisey & Gruber, 1993; Bradbury *et al.*, 1995; Baldwin *et al.*, 2002) have also influenced space use in fishes.

Although variation was observed between individuals, the home range estimates of spotted grunter were related to the size of the fish. The average size and length of the home range increased with fish size. The average number of home range and core areas was also higher for the larger spotted grunter. However, the size of the core areas was similar for large and small spotted grunter. There was a significant positive relationship between fish length and (i) the size of the home range, ii) the number of 95% UD areas, and (iii) the length of the home range. Similarly, Meyer *et al.* (2000) also found a positive trend between the home range size and fish length in whitesaddle goatfish *Parupeneus porphyreu*s. From a data set assembled from published literature, Minns (1995) found that home range size increased with body size in temperate freshwater fishes. Kramer & Chapman (1999) suggested that an increase in home range size with body size may be a combination of the increase in resource requirements and to the decreased relative cost of swimming in larger individuals. In fish species that exhibit territoriality, Grant (1997) showed that territory size also increases with the size of the fish.

Resident behaviour was most commonly observed in smaller spotted grunter, which showed fidelity to one particular site. A similar trend has been observed in other haemulids. Helfman *et al.* (1982) found that schools of juvenile French (*Haemulon flavolineatum*) and white grunts (*H. plumieri*) remained in a particular location for months or even years. It has been hypothesised that the evolutionary advantages of frequent use of a limited number of preferred sites (or core areas) include reduced risk of predation and improved feeding efficiency due to extreme familiarity with localised areas (Bradbury *et al.*, 1995; Zeller, 1997; Kramer & Chapman, 1999; Eristhee & Oxenford, 2002). Larger individuals, on the other hand, were more mobile and displayed roaming behaviour, with more than one core area.

McFarland *et al*. (1979) and Tulevech & Recksiek (1994) suggested that several grunt species (Haemulidae) undergo a significant behavioural change with increasing size or with the onset of maturity. Therefore, the results of this study fully substantiate the suggestions of McFarland *et al*. (1979) and Tulevech & Recksiek (1994). An ontogenetic shift in habitat use has also been observed in other fish species. Lowry & Suthers (1998) and Meyer *et al.* (2000) found that larger individuals of red morwong *Cheilodactylus fuscus* and whitesaddle goatfish *P. porphyreus*, respectively, occupied deeper habitats. Zeller (1997) also found that larger coral trout established wider home ranges on patch reefs than smaller coral trout.

The location of core areas in the Great Fish Estuary was also dependent on fish length. Most (72 %) of the core areas of the smaller spotted grunter were predominantly in the lower reaches (1 - 2 km from the estuary mouth), while the core areas of the large group were predominantly in the upper reaches (7 - 8 km from the estuary mouth). A greater proportion of the core areas of large grunter were in the mouth region when compared to the smaller group. However, the location of core areas could have been influenced by water temperature. Larger spotted grunter were only tagged in the second study when the sea temperature was lower. For the initial stages of this study, a substantial decrease in the temperature coincided with the fish moving to the warmer upper reaches of the estuary (see Chapter 5). Therefore, temperature may have been a major factor influencing the distribution of the core areas of the larger fish. However, smaller spotted grunter in the second study did not have core areas in the upper reaches. This suggests that fish size may have influenced their distribution. It has been suggested that the larger spotted grunter may return from the marine environment into the upper freshwater regions of estuaries to rid themselves of parasites (A.K. Whitfield, SAIAB, Personal communication, 2004). This may explain the dominance of larger fish in the upper reaches of the estuary.

In this study, the home range of smaller spotted grunter coincided with the highest abundance of their preferred prey items, mud prawn *Upogebia africana* and sand prawn *Callianassa krausii* in the Great Fish Estuary (Hecht & van der Lingen, 1992; Webb, 2002; Marais, 1984). Spotted grunter capture their prey by 'blowing' them from their burrows (van der Elst, 1988). This feeding technique is only found in one other estuarine-dependent species, namely the white steenbras *L. lithognathus*. Since, it has been shown in other animals that the pattern of home range establishment may change as individuals compete for space and resources (King, 2002), the specialised feeding mechanism adopted by spotted grunter and white steenbras could allow them to almost exclusively exploit anomurans buried in the mud or sand, reducing inter-specific competition with other estuarine fishes. Other studies have also shown that variation in the diversity and abundance of prey items can influence home range (Lowry & Suthers, 1998; Wong *et al.*, 2004). Spotted grunter generally displayed fidelity to the area where their primary food items were most abundant. This reduces intra- and inter-specific competition for food in this species, and the hypothesis of increased efficiency of resource use due to familiarity of a small area may hold true for these fish. European sturgeon (*Acipenser sturio*) tagged in the Gironde Estuary, France, were also resident to a particular area where their favourite prey item was most abundant (Taverny *et al.*, 2002).

The overlapping core areas of many spotted grunter suggest that they may shoal or group. Fish in shoals find food faster, spend more time feeding despite the threat of predators, are less timid, are collectively more vigilant, sample the habitat more effectively, and transfer information about feeding sites more quickly (Pitcher & Parish, 1993). Haemulids are thought to form resting shoals to avoid predators (Erlich & Erlich, 1973). Furthermore, haemulids may shoal to learn migration routes or to optimise feeding (Schultz, 1984). However, intra-specific competition in shoals is high and shoaling is only advantageous if prey densities are high (Eggers, 1976, cited in Pitcher & Parish, 1993). Since the prey of spotted grunter is abundant in the Great Fish Estuary, shoaling behaviour would be an effective method to increase feeding efficiency, reduce the risk of predation and provide learning opportunities for individuals (Pitcher & Parish, 1993). Shoaling would be particularly beneficial to smaller spotted grunter since they are at a higher risk of predation and are less experienced at obtaining food and may explain their overlapping home ranges.

Several authors have shown that abiotic variables influences the space use of fishes (Szedlmayer & Able, 1993; Morrisey & Gruber, 1993; Bradbury *et al*. 1995; Baldwin *et al*. 2002). The effect of environmental variables on the movement and distribution of spotted grunter in the Great Fish Estuary are addressed in Chapter 5. Many fish species undergo regular diel migrations between different habitats (Meyer *et al*., 2000; Holland *et al*., 1993a,b & 1996, Lowry & Suthers, 1998; Jadot *et al*., 2002; Eristhee & Oxenford, 2001), including haemulids (e.g. Burke, 1995; Tulevech & Recksiek, 1994; Ogden & Ehrlich, 1977; Helfman & Schultz, 1984). However, studies on the diel activities in estuarine and riverine species are limited (e.g. Bramblett & White, 2001; Helfman *et al*., 1983; Almeida, 1996; Baade & Fredrich, 1998; Szedlmayer & Able, 1993; Hartill *et al*., 2003). Lowry & Suthers (1998) showed that the home range and core area of red morwong *C. fuscus* was significantly greater at night than during the day. Holland *et al.* (1993b) also found the average total area covered by white goatfish *Mulloides flavolineatus* tagged on a patch reef was larger at night (avg. 8267 m²; range. 5200 – 11 600 m²) than during the day (avg. 2533 m²; range. 1200 – 3200 m²). Holland *et al.* (1993a) also showed the activity rates and the size of core activity spaces of hammerhead shark pups increased at night. Since laboratory studies (Du Preez *et al*., 1996) revealed a nocturnal peak in the oxygen consumption of spotted grunter (thought to be due to an endogenous rhythm), it is possible that the home range estimates of spotted grunter might be influenced by the diel cycle. Circumstantial evidence of nocturnal feeding behaviour was presented in Chapter 3. Furthermore, fisher catches of spotted grunter in the lower reaches of the Great Fish Estuary have been found to increase during the night (W.M. Potts, DIFS, Personal communication, 2004).

This study showed that the space use of individual fish remained fairly similar over an extended period. The importance of long term data collection has been emphasised, and additional alternative methods to manual tracking have been suggested (Lowry & Suthers, 1998; Parsons *et al.*, 2003). The results of the ALS data collected during the manual tracking period and the three month period after manual tracking indicated that the ALS data can be used to infer space use patterns of fish over an extended time period. The trends in space use observed by the home range analysis was confirmed by the data recorded on the listening stations. Resident behaviour was highlighted by unimodal peaks in the total detections at a particular listening station, and roaming behaviour by the uniform distribution of total detections at each listening station. From this data, the spatial requirements of different sized individuals could also be inferred, with smaller fish having single large peaks, and larger fish having a more equal distribution in the total number detections between the different listening stations. The above results highlights the importance of employing two telemetric techniques.

The long term trends in space use of spotted grunter were also assessed using the data collected from three individual fish that were tagged in the first study and which were still found in the estuary during the second study. The home range estimates of the three individual fish during the first study (7 February 2003 to 24 March 2003) and the second study (29 September 2003 to 15 November 2003) were similar. The location of the core areas of each fish was identical in both studies, which indicated that these individuals exhibited site fidelity over an eight month period. Parsons *et al.* (2003) found snapper to be highly resident in the CROP marine reserve, where all of the five tagged fish were resident within the reserve over the five month monitoring period, and four of the five tagged individuals were located within their home ranges one year after release. Lowe *et al.* (2003) also found kelp bass *Paralabrax clathratus* to remain in their home ranges for up to four months, and some were even sighted in their home ranges after three years. Of the spotted grunter that exhibited long term residency over the two study periods, two individuals showed an increase in the home range estimates (size, number and length), while the third individual showed a decrease in the home range estimates from the first study to the second study. The larger size of the home range and numerous 95% UD areas could be attributed to both the growth in these individuals and the change in season (see Chapter 5). The largest individual (Fish 29; 377 mm TL) had the largest increase in home range length, from 0.32 km in the first study to 6.33 km in the second study, while the smallest (308 mm TL) of the three fish had a decrease in the size, number and length of home range. These results provide further evidence that spotted grunter undergo ontogenetic changes in behaviour, which affects home range estimates (see Chapter 3).

In conclusion, the findings of this study suggest that estuarine-dependent adolescent spotted grunter have evolved to initially select a small home range in a single area characterised by high food availability and possibly a reduced risk of predation. With growth, and reduced risk of predation, they utilise more areas and move regularly in a larger home range. Shoaling may have evolved to reduce the risk of predation and to increase feeding time and efficiency. Larger spotted grunter have larger home ranges and utilise a large portion of the estuary. Larger fish tend to utilise the upper reaches and mouth reaches more than small fish. Utilisation of the upper reaches may be a consequence of reduced sea temperature or may be an adaptive strategy to remove marine parasites.

CHAPTER 5

FACTORS INFLUENCING SPOTTED GRUNTER DISTRIBUTION IN THE GREAT FISH ESTUARY

INTRODUCTION

Estuarine-dependent fishes utilise a wide variety of habitats in coastal environments as well as in estuaries (Hoss & Thayer, 1993). Most estuarine-dependent species spend part of their life in the more stable and predictable marine environment (Whitfield, 1994b,c). When they enter estuaries, which are more dynamic and unpredictable, they have to find areas within the estuary that best suits their physiological needs.

The distribution of fish in South African estuaries has been related to various abiotic factors such as salinity, temperature and turbidity (e.g. Cyrus, 1992; Whitfield, 1994a; Ter Morshuizen *et al.,* 1996; Whitfield & Paterson, 2003), and to biotic factors, such as predator avoidance and prey availability (Griffiths, 1997). The most commonly used techniques to examine the effect of a range of environmental variables on fish distribution and abundance in the marine environment and in estuaries is multivariate analyses (Morin *et al.,* 1992; Polacheck & Volstad, 1993; Thiel *et al.,* 1995; Marshall & Elliot, 1998; Gregr & Trites, 2001; Sampson, 2002; Strydom *et al.,* 2003; Whitfield & Patterson, 2003; Su *et al.,* 2004). However, none of these have been species specific, and all have used conventional sampling techniques, which are limited to pre-determined sites. Consequently, these studies have only provided broad estimates of the preferred abiotic parameters of fish in their environment.

Considering the paucity of information on the general abiotic and biotic factors governing fish distribution in estuaries, this chapter provides the first attempt at developing a statistical model using telemetry data to describe the effects of abiotic parameters on the spatial utilization of spotted grunter in the Great Fish Estuary.

The aims of this chapter are to describe the abiotic environment in which tagged spotted grunter were located in space and time and to determine the effects of certain abiotic variables on the movement and distribution patterns of spotted grunter in the Great Fish Estuary.

METHODS AND MATERIALS

A detailed description of the study site and research approach is outlined in Chapter 2. While manual tracking in the first (7 February 2003 to 24 March 2003) and second (29 September 2003 to 15 November 2003) study, salinity, temperature, turbidity, depth and current speed were recorded when obtaining a positional fix for each fish.

All data were entered onto a spreadsheet, and then imported into a GIS (ArcView® GIS 3.2). This allowed the distribution of tagged fish along the length of the estuary in relation to the various environmental variables to be mapped. Since spotted grunter are benthic foragers (Whitfield, 1990, 1998), the environmental variables measured at the bottom were used in all analyses. Given the longitudinal nature of the estuary, the spatial position of the fish was expressed as ‘distance from the estuary mouth’.

Distribution of spotted grunter in the estuary

The estuary was divided into 500 m sections from the mouth to the ebb and flow region, and the number of positional fixes within each 500 m stretch was presented as a frequency histogram.

Abiotic environment of spotted grunter

A frequency histogram for each abiotic variable was plotted to determine the number of observations (positional fixes) located within each category. A two-tailed binomial test, with a bonferroni adjustment to reduce Type I error, was conducted to test the hypothesis that the number of observations in each category was not significantly different from the average.

Pearson product-moment correlation was used to assess the relationships between salinity, temperature and turbidity.

Sea Temperature

Sea temperature data was obtained from an underwater temperature recorder (UTR) situated 25 km west of the Great Fish Estuary mouth (Marine and Coastal Management, unpubl. data). The effect of sea temperature on the distribution of spotted grunter was assessed using a linear regression. However, sea temperature data during the second study was not available from the 7 November 2003 (8 days prior to the end of the manual tracking study) until April 2004. Since the daily sea temperature and water temperature collected during the second study at station 1 (0.4 km from the estuary mouth) were significantly correlated ($p < 0.0001$; $R^2 = 0.62$), estuary mouth temperature from station 1 was used to determine the effect of sea temperature on spotted grunter distribution in the estuary during the second study. The residuals of all variables were analysed and assessed for randomness and departure from normality.

Tidal phase

During the second study eight ALSs were deployed along the length of the estuary. The up and downriver movement of spotted grunter could therefore be monitored accurately. It was assumed that the fish moved along the longitudinal axis of the estuary. The pinger search feature in the VEMCO software package was used to follow the movements of each individual fish during the entire 137-day monitoring period. The pinger search feature searches all the data files downloaded from the ALSs for all occurrences of a specific transmitter and combines this data into a search file. A search file, containing the receiver number, the arrival date and time, the departure date and time and the number of hits that occurred while in the detection range of each listening station, was computed for each fish. Each search file was imported into a working spreadsheet. An upriver or downriver movement was only considered if an individual fish passed more than one ALS in the same direction. However, in the cases where the ALSs were situated > 1 km away from each other (ALS-5 to ALS-6, ALS-6 to ALS -7, and ALS-7 to ALS-8), then movement to each of these receivers was considered as an upward or downward movement. All upriver movements were assigned a 1 and downriver movements a 2. To investigate the relationship between the direction of fish movement and tidal phase, the corresponding tidal state was assigned to each of the upriver (1) or downriver (2) movements. For each fish, the number of movements upriver and downriver, as well as with the tide and/or against the tide was calculated. A binomial test, corrected with the bonferroni adjustment, was used to determine the probability of movement with and against the tide. The chi-square test of independence was used to test the hypothesis that the direction of movement was dependent on the tidal phase.

Circular statistics (Batschelet, 1981) was used to test the hypothesis that the distribution of the fish along the length of the estuary was random and was not influenced by the tidal phase. For this calculation the estuary was divided into 1 km stretches, and the mean time (in hours), after low tide, of all fish positions located in each of these 1 km stretches was calculated as theta (Ø). Theta is the mean direction of the resultant vector (measured in radians). The distribution of the fish in relation to the tidal phase was statistically tested using a Rayleigh test of randomness.

Modelling the effect of abiotic factors on the change in fish position

Autocorrelation (as described in Chapter 3) provides a means with which to predict an animal's position based on its previous position. Given the inherent autocorrelation generally found within telemetry data (Dunn & Gibson, 1977; Swihart & Slade, 1985a; De Solla *et al.,* 1999, see Chapter 3), and the autocorrelation found in the present data, the relationship between the relative change in a fish's position from time t to $t+1$, and the relative change in salinity, temperature and turbidity from time t to $t+1$, were modelled using linear regression. Since only smaller adolescent spotted grunter were tagged in the first study, the data from the second study with equal number of small adolescent (< 450 mm TL) and large adult (> 450 mm TL) fish was analysed to check for significant differences with fish size. Since no significant difference was found ($p > 0.05$), the data from the two studies was pooled. One dummy variable was added to the model: season (summer = study 1 and spring = study 2). The dependent variable was the relative change in position (distance from the mouth) from time *t* to *t+1*, and the independent variables were the relative change in salinity, temperature, and turbidity, and the categorical variable season.

The change in a fish's position was estimated as follows:

$$\Delta \text{ Fish position} = \beta_1 (\Delta \text{ Salinity}) + \beta_2 (\Delta \text{ Temperature}) + \beta_3 (\Delta \text{ Turbidity}) + \beta_4 (\text{Season}) + \varepsilon$$

where Δ is the relative change from time *t* to *t+1*, and ε is the error structure associated with the model.

RESULTS

Distribution of spotted grunter in the estuary

In the first study, the distribution of spotted grunter in the Great Fish Estuary extended from the mouth to 12.12 km upriver. However, only four individual fish were recorded by the uppermost ALS, and only two fish were tracked manually above this point. Most of the fish (89%) were located within 6 km of the estuary mouth, of which 70% were found within the first 3 km and approximately half (49%) of the total observations were recorded between 1 and 1.5 km from the mouth (Figure 5.1a).

In the second study, the distribution of the fish in the Great Fish Estuary extended from the mouth of the estuary to 13.36 km upriver. Five fish were recorded by the uppermost ALS and above its location during manual tracking. The distribution of the fish along the estuary was bimodal, with 45% of the observations between the mouth and 3 km upriver and one third (32%) of the observations in the upper reaches (6 - 8 km upriver). Only 18% were found in the middle reaches (3 - 6 km) and 5% in the uppermost region (8 - 13.5 km upriver) (Figure 5.1b).

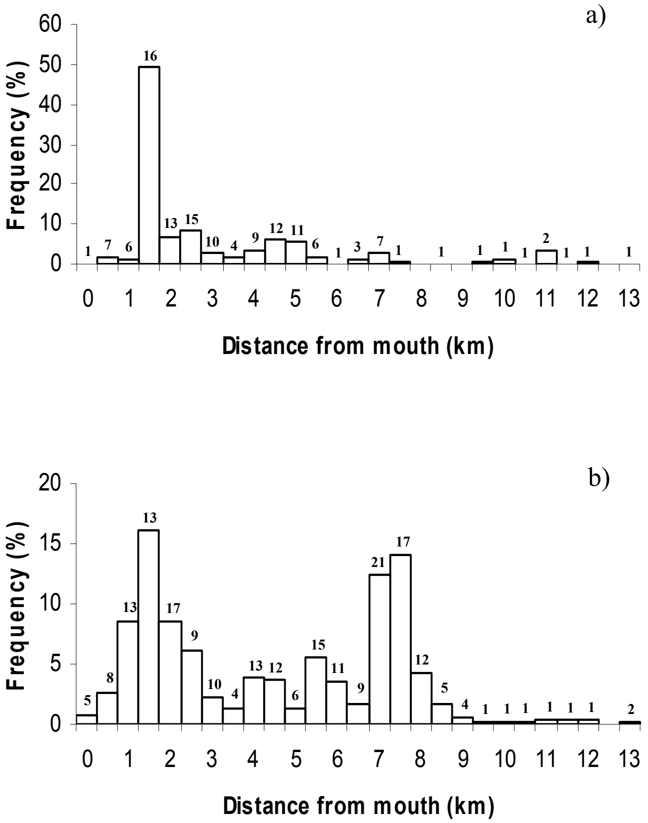


Figure 5.1. Distribution of tagged spotted grunter *Pomadasys commersonnii* along the length of the Great Fish Estuary, based on the percentage of positions per 500m zone, during the a) first study (7 February 2003 - 24 March 2003) (n = 468) and b) second study (29 September 2003 - 15 November 2003) (n = 635). Numerical values above the bars indicate the number of different individuals recorded in each 500 m zone.

Influence of environment variables on spotted grunter distribution

The mean salinity, temperature, turbidity, depth and current speed recorded at each positional fix for all tagged spotted grunter in the first (Fish 20-39) and second (Fish 50A-69) manual tracking studies are summarised in Table 5.1.

Table 5.1. Mean abiotic variables, and range in parenthesis, recorded for each *Pomadasys commersonnii* in the Great Fish Estuary during the first study (Fish 20-39) and the second study (Fish 50A to 69).

Fish code	Salinity (‰)	Temperature (°C)	Turbidity (FTU)	Depth (m)	Current ($m.s^{-1}$)
20	5.2 (0-36)	26.5 (23-31)	159.3 (56-302)	1.6 (0.7-3.2)	0.22 (0.00-0.83)
21	16.2 (4-35)	24.0 (19-28)	187.3 (27-457)	1.4 (0.6-2.1)	0.34 (0.00-0.68)
22	14.8 (2-34)	25.3 (23-31)	184.4 (70-351)	1.4 (0.9-2.8)	0.35 (0.05-0.67)
23	26.4 (12-35)	21.5 (18-28)	78.3 (47-300)	1.7 (0.6-2.3)	0.31 (0.00-0.76)
24	14.6 (2-35)	24.8 (23-27)	201.1 (41-567)	1.4 (1-2)	0.32 (0.04-0.67)
25	23.6 (5-35)	23.7 (20-27)	109.7 (30-327)	1.6 (0.4-3.4)	0.34 (0.07-0.76)
26	25.9 (5-35)	22.2 (18-25)	92.6 (27-264)	1.5 (0.8-2.2)	0.37 (0.00-0.83)
27	26.3 (9-35)	22.9 (21-26)	107.7 (12-264)	1.8 (0.5-3.4)	0.25 (0.00-0.44)
28	23.7 (5-36)	22.3 (17-27)	93.7 (23-323)	1.6 (0.9-3.4)	0.33 (0.09-0.70)
29	27.3 (9-35)	21.4 (17-26)	70.6 (21-260)	1.6 (0.1-2.4)	0.33 (0.00-0.71)
30	27.0 (5-35)	21.3 (18-25)	66.8 (21-230)	1.6 (0.4-2.3)	0.33 (0.00-0.76)
31	26.3 (10-36)	23.0 (19-26)	136.7 (8-264)	1.5 (1-2.5)	0.35 (0.06-0.68)
32	24.2 (5-35)	22.1 (18-26)	86.1 (20-260)	1.2 (0.4-2.4)	0.35 (0.04-0.71)
33	31.2 (20-36)	23.1 (19-25)	82.7 (13-239)	1.9 (1.3-2.5)	0.44 (0.10-0.72)
34	18.9 (6-27)	24.5 (22-30)	147.4 (47-264)	1.3 (0.8-1.5)	0.23 (0.00-0.42)
35	27.1 (16-36)	23.1 (22-24)	101.3 (24-145)	1.8 (1-2.4)	0.31 (0.11-0.46)
36	27.9 (9-36)	22.1 (19-26)	84.7 (12-260)	1.8 (0.5-2.6)	0.25 (0.00-0.83)
37	6.9 (0-35)	24.9 (22-30)	161.7 (6-351)	1.7 (0.8-3.6)	0.24 (0.00-0.62)
38	23.0 (9-35)	24.1 (21-26)	100.2 (27-167)	1.4 (1-2.2)	0.34 (0.05-0.65)
39	25.6 (9-35)	22.3 (18-26)	94.7 (23-479)	1.5 (0.5-2.2)	0.37 (0.04-0.83)
50A	8.1 (0-16)	20.9 (18-23)	93.1 (19-161)	2.4 (1-4.1)	0.27 (0.06-0.52)
50B	11.7 (0-34)	21.4 (18-25)	98.1 (24-217)	1.9 (0.8-4.6)	0.38 (0.2-0.59)
51	13.9 (0-35)	20.5 (17-25)	78.9 (15-168)	1.4 (0.5-3.2)	0.26 (0.05-0.6)
52	18.2 (0-36)	19.9 (17-25)	56.5 (22-164)	1.3 (0.6-2)	0.24 (0.03-0.57)
53	21.6 (0-27)	19.3 (17-24)	74.0 (16-186)	1.8 (0.7-3.2)	0.3 (0.07-0.58)
54	13.7 (0-35)	20.3 (17-23)	95.0 (26-183)	1.3 (0.4-2.9)	0.33 (0.03-0.8)
55	13.7 (0-37)	20.4 (17-25)	104.6 (4-337)	1.8 (1-3.9)	0.27 (0.05-0.58)
56	16.9 (0-36)	20.2 (17-25)	100.1 (24-273)	2.2 (0.9-5.2)	0.29 (0.05-0.69)
57	18.5 (0-35)	20.1 (17-25)	76.9 (21-188)	1.6 (0.8-3)	0.27 (0.03-0.52)
58	15.5 (0-35)	19.9 (16-23)	95.3 (11-205)	1.9 (0.6-5.2)	0.28 (0.02-0.35)
59	20.3 (0-36)	19.1 (16-23)	73.4 (8-195)	2.0 (0.6-4.4)	0.3 (0.03-0.48)
60	16.8 (0-36)	19.8 (17-23)	101.8 (10-259)	1.9 (0.8-5)	0.28 (0.05-0.48)
61	8.6 (0-36)	21.4 (18-25)	118.4 (6-221)	1.9 (1-1.4)	0.27 (0.03-0.48)
62	15.0 (0-36)	20.3 (17-23)	111.5 (5-300)	2.0 (0.9-5)	0.23 (0.03-0.5)
63	6.3 (0-30)	21.3 (19-24)	154.8 (26-358)	2.4 (1.1-5.9)	0.27 (0.03-0.69)
64	14.3 (0-30)	20.4 (18-25)	89.9 (21-194)	1.4 (0.8-3.2)	0.27 (0.05-0.69)
65	17.4 (0-33)	19.6 (17-23)	77.8 (15-183)	1.5 (0.6-2.7)	0.34 (0.05-0.8)
66	19.6 (0-36)	19.5 (17-24)	59.6 (6-162)	1.2 (0.4-2)	0.24 (0.07-0.65)
67	15.7 (0-37)	20.3 (17-25)	87.9 (6-290)	1.5 (0.8-3.3)	0.24 (0.01-0.54)
68	17.0 (0-37)	20.0 (17-23)	83.7 (5-211)	1.4 (0.8-2.9)	0.28 (0.04-0.93)
69	10.1 (0-34)	21.2 (18-25)	102.5 (36-273)	1.6 (0.6-5.3)	0.23 (0.03-0.52)

Salinity

Spotted grunter were found in salinities ranging between 0 and 36 ‰ in both studies. The mean salinity for all fish observations was 22.1 ‰ and 15.5 ‰ in the first and second studies, respectively. Observations were not uniformly distributed (Figure 5.2). During the first study a significantly large percent of observations (36%) were found in the euhaline range (Figure 5.2), while 29% of observations were recorded in the oligohaline range during the second study (Figure 5.2).

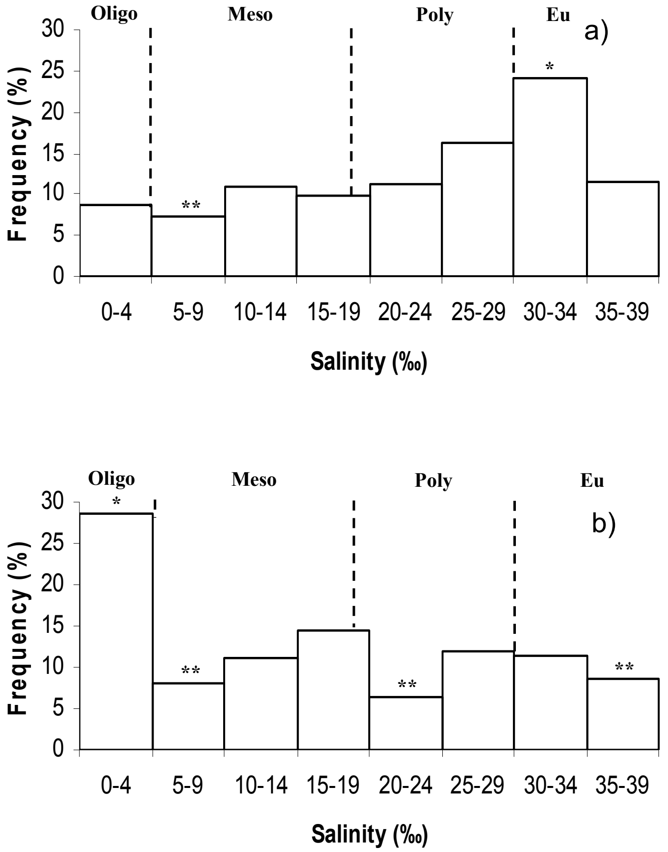


Figure 5.2. Frequency histogram of the salinity at which all spotted grunter *Pomadasys commersonnii* were recorded in the Great Fish Estuary during the a) first study (7 February 2003 - 24 March 2003) and b) second study (29 September 2003 - 15 November 2003). * = significantly higher number of observations; ** = significantly lower number of observations. (Oligo = oligohaline region; Meso = mesohaline region; Poly = polyhaline region; Eu = euhaline region).

Temperature

Mean water temperature at which spotted grunter were located was 23.0ºC (range. 17.3ºC - 30.5ºC) in the first study and 20.2°C (range. 16.3°C - 25.3°C) during the second study. The distribution of observations at each temperature range was not uniform (Figure 5.3). In the first study, a significantly large percent of observations (63 %) were found in temperatures between 22ºC and 25ºC, while in the second study a significantly large percentage of observations (65%) were found in temperatures ranging between 18ºC and 21ºC (Figure 5.3). In addition, although only 10 % of observations in the first study were recorded in water temperatures higher than 25ºC, no fish were recorded in this range during the second study (Figure 5.3).

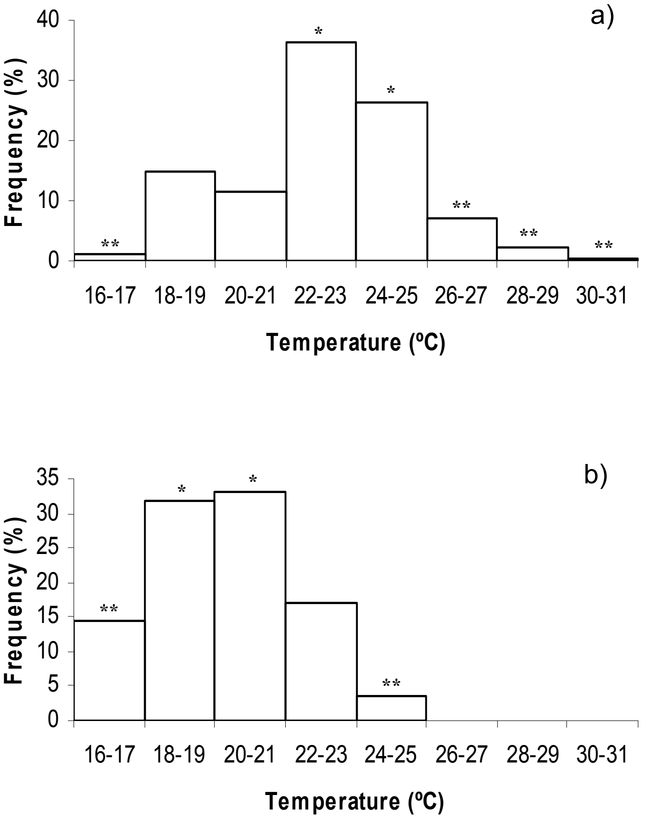


Figure 5.3. Frequency histogram representing the temperatures at which spotted grunter *Pomadasys commersonnii* were recorded in the Great Fish Estuary during the a) first study (7 February 2003 - 24 March 2003 and b) second study (29 September 2003 - 15 November 2003). * = significantly higher number of observations; ** = significantly lower number of observations.

There was a significant negative relationship between the average distance from the mouth and sea temperature during the first ($p = 0.0004$; $R^2 = 0.31$) and second ($p = 0.0001$; $R^2 = 0.33$) study. At low sea temperatures, spotted grunter were located further upriver (Figure 5.4).

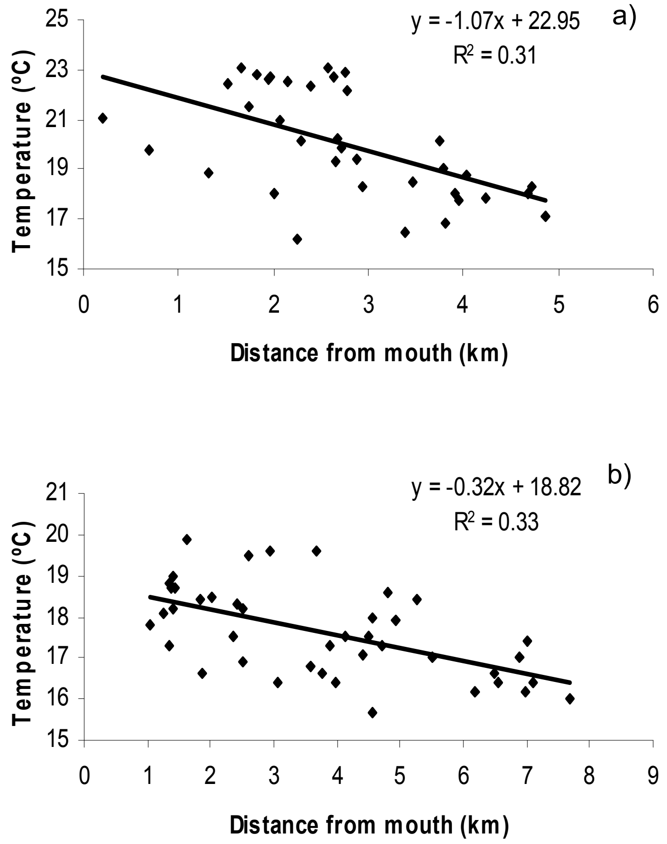


Figure 5.4. Relationship between the distribution of spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary and sea temperature during the a) first study (7 February 2003 - 24 March 2003) and b) second study (29 September 2003 - 15 November 2003).

Turbidity

Spotted grunter were located in water of varying turbidity, ranging from 6.0 FTU to 567.0 FTU (avg. 111.5 FTU ± 83.5 SD) in the first study, and from 4.1 FTU to 358.0 FTU (avg. 92.7 FTU ± 63.4 SD) in the second study. A significantly greater frequency of occurrence in both the first (55%) and second (61%) studies was recorded in water of 20 - 100 FTU, and a significantly small percentage of observations in both the first (1%) and second (4%) studies were found in water less than 20 FTU. A relatively large percentage of observations were found in very turbid water (> 100 FTU) in both the first (44%) and second (35%) studies (Figure 5.5).

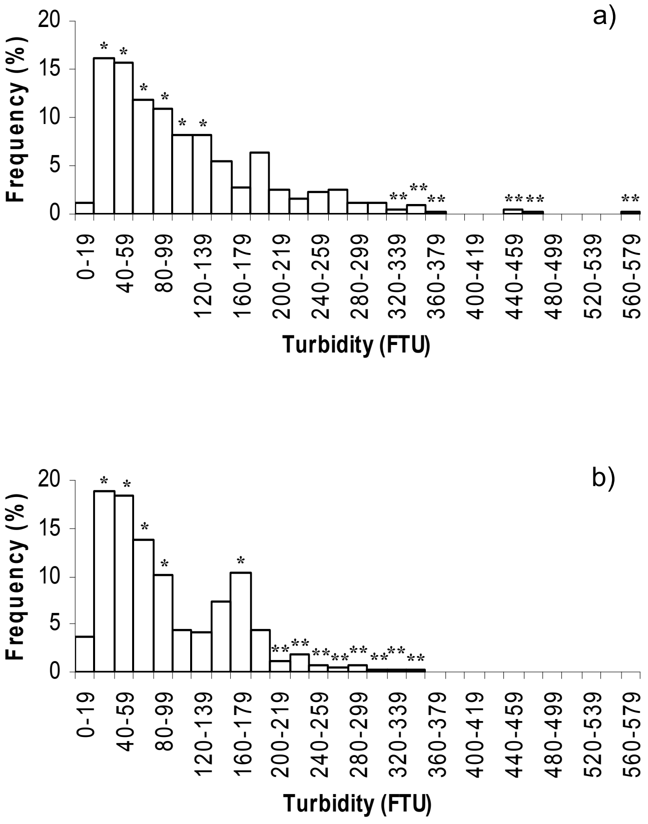


Figure 5.5. Frequency histogram representing the turbidity at which spotted grunter *Pomadasys commersonnii* were recorded in the Great Fish Estuary during the a) first study (7 February 2003 - 24 March 2003) and b) second study (29 September 2003 - 15 November 2003). * = significantly higher number of observations; ** = significantly lower number of observations.

Depth

Spotted grunter were found at an average depth of 1.6 m (range. 0.1 m – 3.6 m) in the first study and at 1.7 m (range. 0.4 m – 5.9 m) in the second study. A significantly greater proportion of fish were located at depths between 1 and 2 m in both the first (78%) and the second (65%) study. A significantly smaller percentage of observations were recorded in depths less than 1 m, in both the first (9%) and second

(11%) studies. Spotted grunter were located 14% and 25% in water deeper than 2 m in the first and second study, respectively (Figure 5.6).

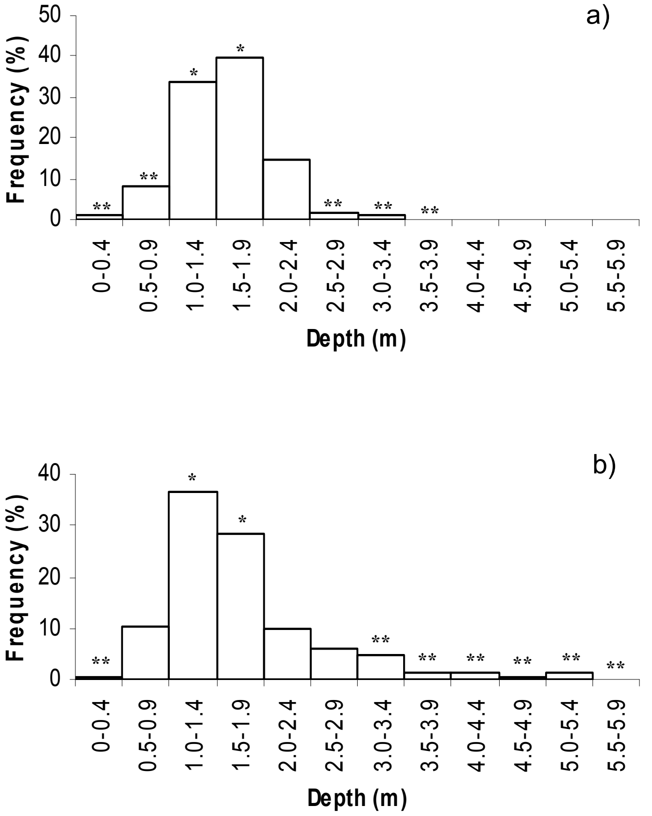


Figure 5.6. Frequency histogram of the depth at which spotted grunter *Pomadasys commersonnii* were recorded in the Great Fish Estuary during the a) first study (7 February 2003 - 24 March 2003) and b) second study (29 September 2003 - 15 November 2003). * = significantly higher number of observations; ** = significantly lower number of observations.

Current Speed

Spotted grunter were located at an average surface current speed of 0.32 $m.s^{-1}$ (range. 0 - 0.83 $m.s^{-1}$) in the first, and 0.27 $m.s^{-1}$ (range. 0 - 0.93 $m.s^{-1}$) in the second study. The distribution of observations was not uniformly distributed. A significantly larger percentage of observations were recorded at current speeds ranging between 0 $m.s^{-1}$ and 0.39 $m.s^{-1}$ in both the first (62%) and the second (80%) studies (Figure 5.7).

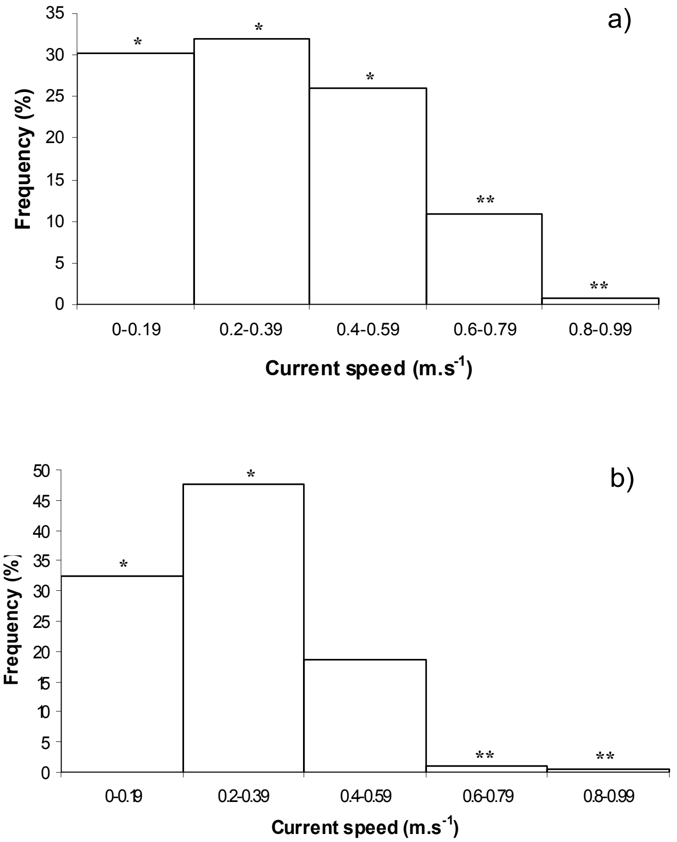


Figure 5.7. Frequency histogram of the surface current speed at which all spotted grunter *Pomadasys commersonnii* were located in the Great Fish Estuary during the a) first study (7 February 2003 - 24 March 2003) and b) second study (29 September 2003 - 15 November 2003). * = significantly higher number of observations; ** = significantly lower number of observations.

Tidal Phase

The distribution of spotted grunter in the estuary was significantly influenced by the tidal phase in both studies (Figure 5.8 and 5.9).

During the first study, with the exception of the mouth region, spotted grunter were found in the lower reaches (1-4 km) of the estuary around low tide, and in the middle and upper reaches during the high tide (Figure 5.8). The number of observations in each stretch of the estuary varied, with a higher number of observations recorded in the lower reaches (Figure 5.8). The significance of these observations could only be tested when more than five observations were recorded. The Rayleigh test showed that the observations were not random ($p < 0.05$), but that the distribution of tagged fish was significantly influenced by the tidal cycle in the stretches of estuary between 0 - 1 km (mean time after low tide, Ø = 08:36), 1 – 2 km (Ø = 11:47), 2 - 3 km (Ø = 01:40), 3 – 4 km (Ø = 11:24), 5 – 6 km (Ø = 05:23), and 6 - 7 km (Ø = 05:52) (Figure 5.8).

During the second study, the number of observations was also greatest in the lower reaches (Figure 5.9). The location of tagged fish over the tidal cycle was significantly influenced by the tide between 1 - 2 km (mean time after low tide, Ø = 00:55) and 2 - 3 km (Ø = 01:49) and between 6 - 7 km (Ø = 05:52) and 8 - 9 km (Ø = 05:04) respectively (Figure 5.9).

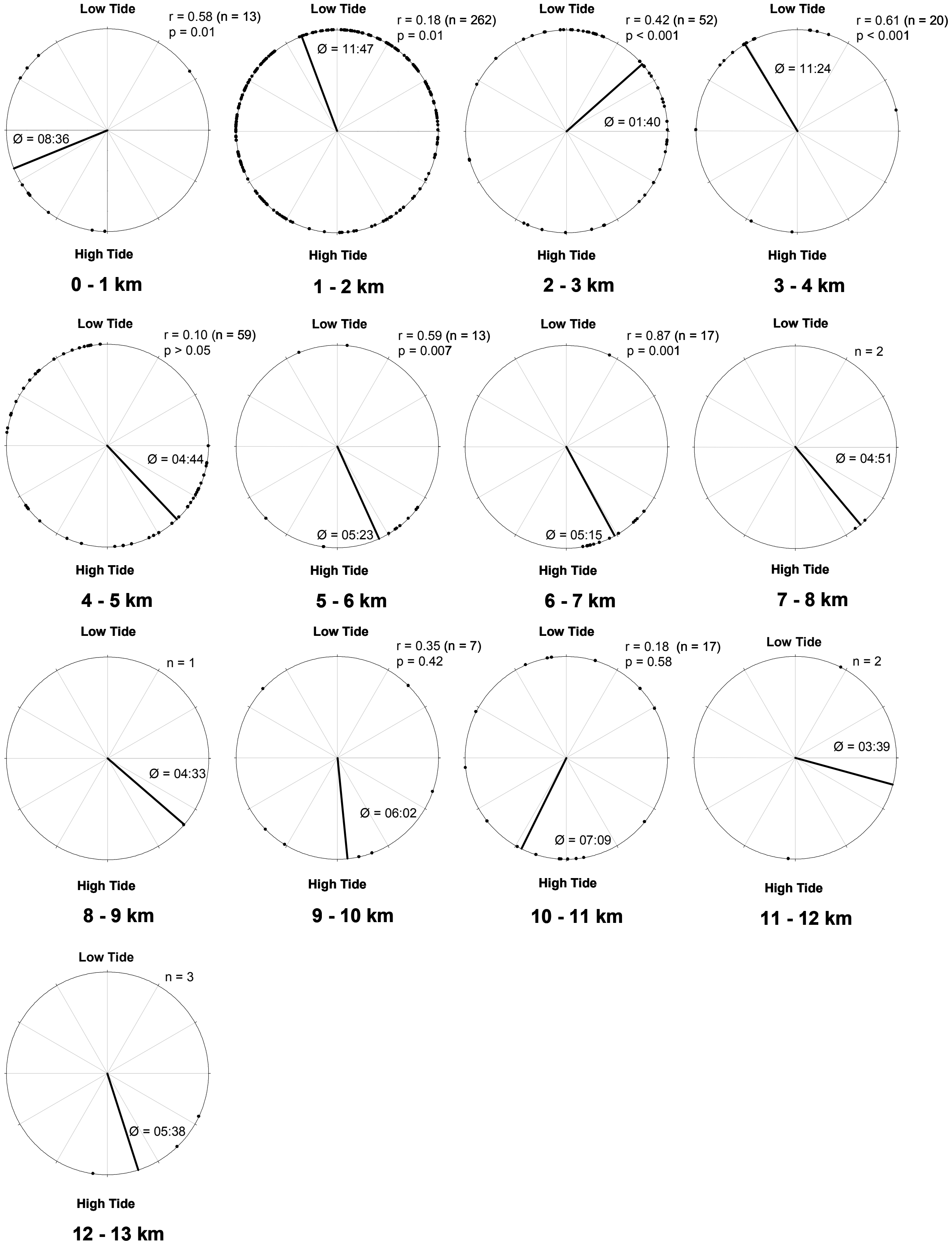


Figure 5.8. Tidal phase and average time after low tide (Ø) of spotted grunter *Pomadasys commersonnii* observations from the mouth to 13 km upriver in the Great Fish Estuary during the first study (7 February 2003 - 24 March 2003). Ø = the mean time after low tide and presented graphically as the mean direction of the resultant vector.

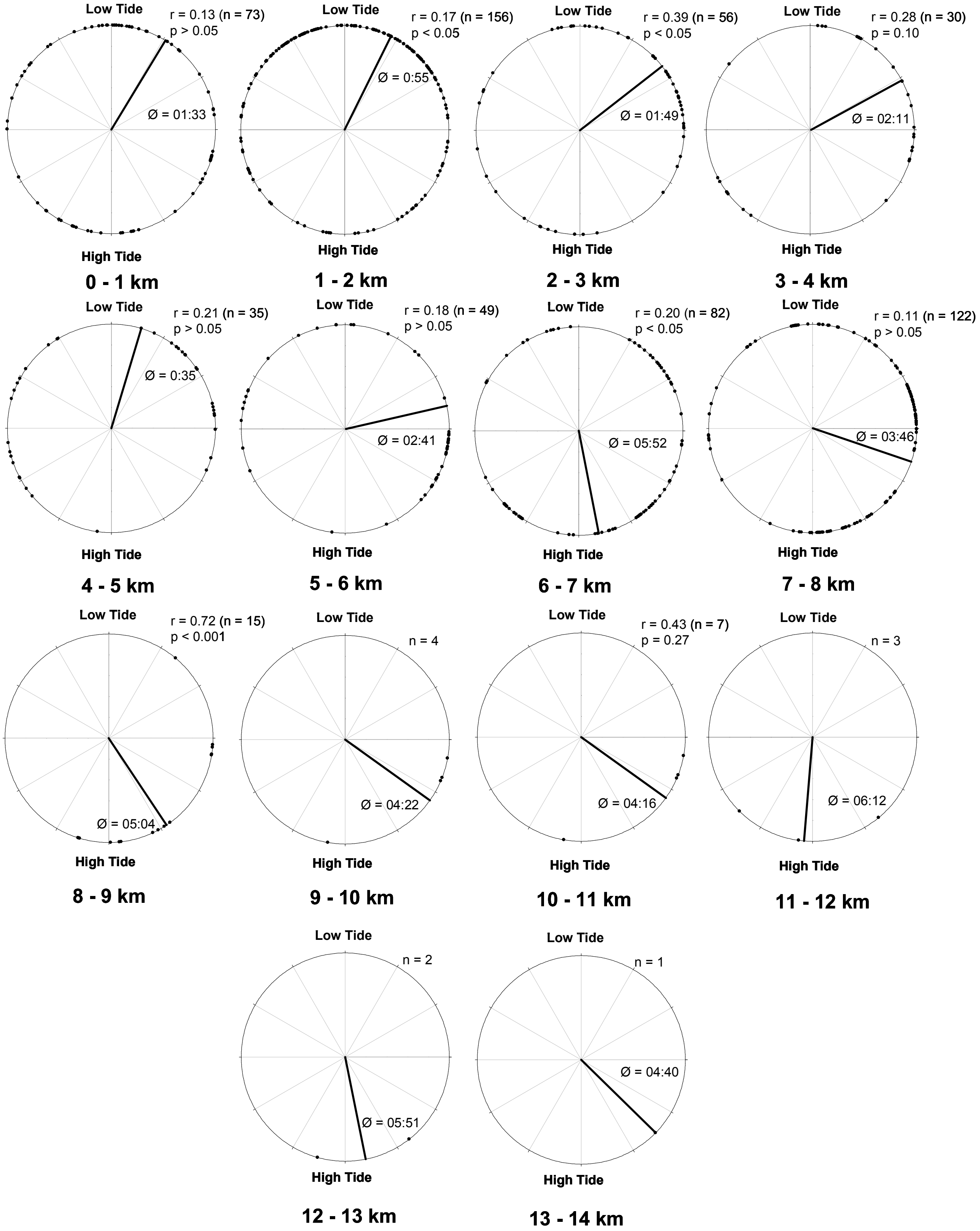


Figure 5.9. Tidal phase and average time after low tide (Ø) of spotted grunter *Pomadasys commersonnii* observations from the mouth to 13 km upriver in the Great Fish Estuary during the second study (29 September 2003 - 15 November 2003). Ø = the mean time after low tide and presented graphically as the mean direction of the resultant vector.

The direction of fish movement was dependent on the tidal cycle ($\chi^2 = 5462.3$; $p < 0.0001$). A binomial test showed that the probability of movements with the tide for each tagged fish was statistically significant ($p < 0.01$) (Table 5.2). In general, upriver movements were made with the incoming tide, while downriver movements were made with the outgoing tide. A large majority of movements (94%) of the tagged spotted grunter were made with the tide, while only 4% of movements were made against the tide. Very few (2%) movements were made during slack tide, of which 1.3% were during high, and 0.7 % during low tide.

Table 5.2. Movements of spotted grunter *Pomadasys commersonnii* recorded by the ALSs during the second study (29 September 2003 - 12 February 2004). The first three columns represent the percentage and probability of movements made with and against the tide. The last four columns represent the percentage of movements made with the incoming and the outgoing tides, and the probability of the direction of movement being dependent on the tidal phase.

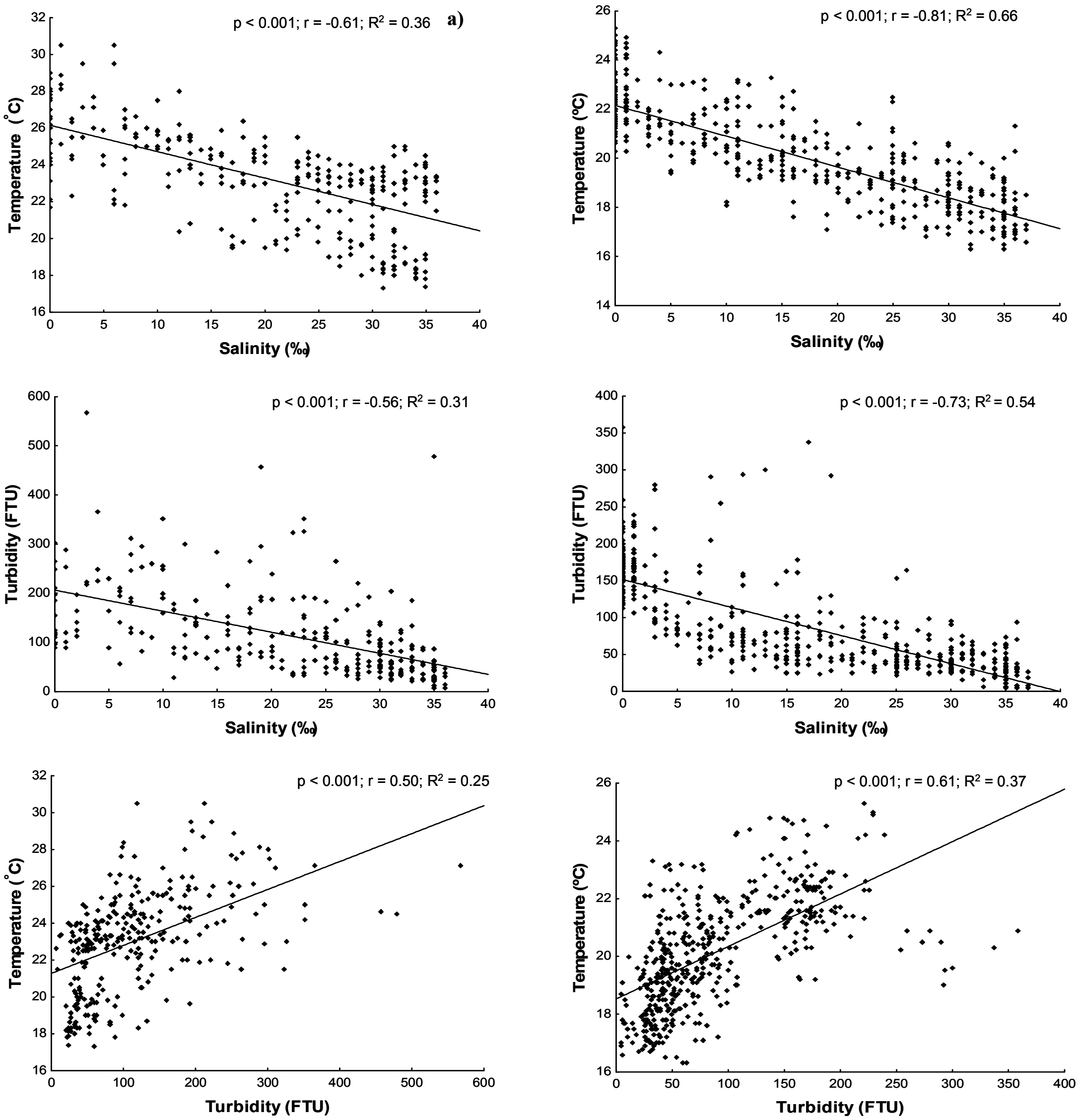
Fish code	With tide (%)	Against tide (%)	Binomial probability	With incoming (%)	With outgoing (%)	χ^2	p-value
51	95	2.9	< 0.0001	95.1	94.9	413.7	<0.0001
52	96.5	2	< 0.0001	98	94.7	178.4	<0.0001
53	95.7	2.5	<0.0001	94.7	96.9	397.2	<0.0001
54	94.7	3	<0.0001	92.4	97	229.5	<0.0001
55	80.4	16.7	<0.0001	70.2	89.1	43.1	<0.0001
56	95.5	4.5	<0.0001	98.3	92.7	255	<0.0001
57	94	3.4	<0.0001	97.4	90.5	320.3	<0.0001
58	97.6	2.2	<0.0001	99.6	95.6	414.7	<0.0001
59	94.6	4.6	<0.0001	95.7	93.4	405.4	<0.0001
60	95.9	3.1	<0.0001	95.3	96.5	447	<0.0001
61	90.2	7.1	<0.0001	89.2	91.2	239.2	<0.0001
62	90.3	6.6	<0.0001	91.7	88.9	229.7	<0.0001
63	98.1	1.3	<0.0001	100	96.5	151.2	<0.0001
64	92.3	5.6	<0.0001	94.2	90.4	397.9	<0.0001
65	88.8	9	<0.0001	90.3	87.5	151.9	<0.0001
66	96.7	1.5	<0.0001	94.4	99	363.5	<0.0001
67	88.8	6	<0.0001	90.1	87.4	289.1	<0.0001
68	91.7	4.8	<0.0001	90.4	93	312.5	<0.0001
69	91	6.5	<0.0001	92.8	89.4	205.2	<0.0001

Modelling the effect of abiotic factors on the change in fish position

All the environmental variables (salinity, temperature, and turbidity) measured at each spotted grunter location were significantly correlated to each other (Figure 5.10). In the first study, the strongest correlation was between salinity and temperature ($r = -0.61$; $R^2 = 0.38$; $p < 0.001$), followed by salinity and turbidity ($r = -0.56$; $R^2 = 0.31$; $p < 0.001$), and temperature and turbidity ($r = 0.50$; $R^2 = 0.25$; $p < 0.001$) (Figure 5.10a). In the second study, the strongest correlation was between salinity and temperature ($r = -0.81$; $R^2 = 0.66$; $p < 0.001$), followed by salinity and turbidity ($r = -0.73$; $R^2 = 0.54$; $p < 0.001$), and temperature and turbidity ($r = 0.61$; $R^2 = 0.37$; $p < 0.001$) (Figure 5.10b).

The results from the linear model showed that the change in the environmental variables from time t to $t+1$ had a significant effect on the change in fish position from time t to $t+1$ ($p < 0.0001$; $F(4, 1057) = 160.8$; $R^2 = 0.38$). Partial residuals plots are presented in Figure 5.11. Salinity, temperature and turbidity were all highly significant ($p < 0.0002$). There was no significant difference between season (summer and spring) ($p = 0.50$). Therefore, the relative change (Δ) in spotted grunter distribution within the estuary from time t to $t+1$ was determined by the relative change in salinity, temperature and turbidity from time t to $t+1$. This is described by the equation:

$$\Delta \text{ Fish position} = -0.07 \, \Delta \text{ Salinity} + 0.16 \, \Delta \text{ Temperature} + 0.005 \, \Delta \text{ Turbidity}$$


a)

b)

Figure 5.10. Relationships between the environmental variables measured at each spotted grunter *Pomadasys commersonnii* location within the Great Fish Estuary during a) the first study (7 February 2003 - 24 March 2003) and b) the second study (29 September 2003 - 15 November 2003).

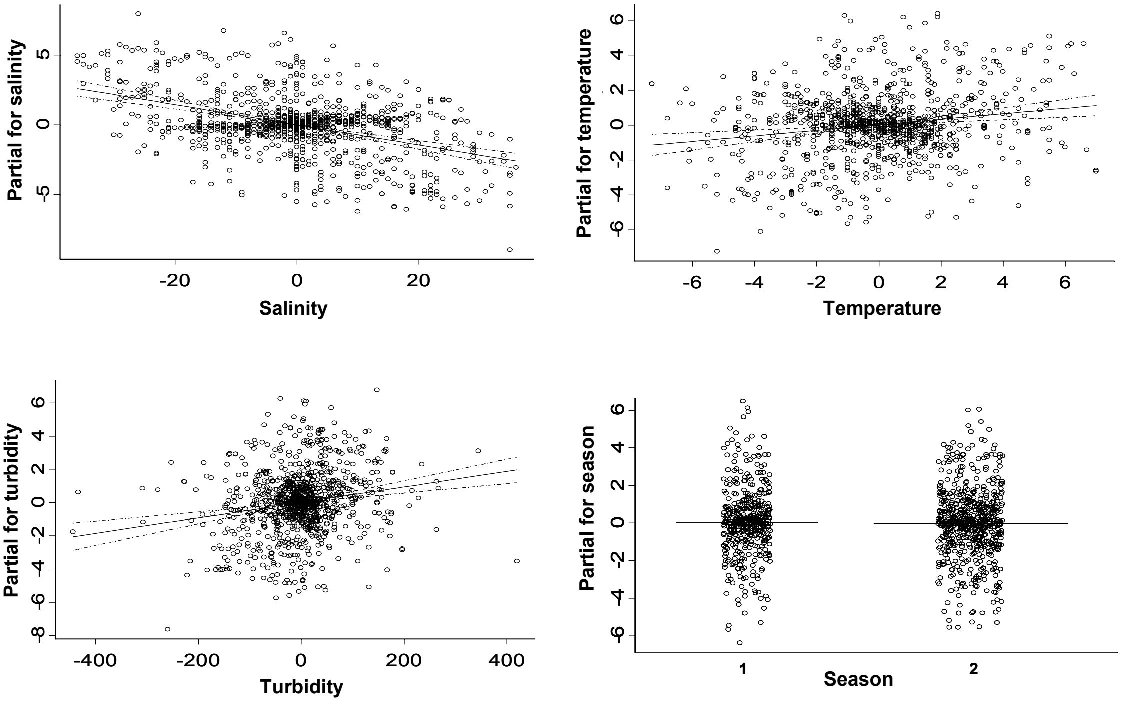


Figure 5.11. Partial residual plots describing the effect of the abiotic variables (salinity, temperature, turbidity and season) on the relative change in spotted grunter *Pomadasys commersonnii* positions in the Great Fish Estuary. Dashed lines indicate the upper and lower twice-standard error bands.

DISCUSSION

The distribution of fish within estuaries has been related to a number of factors. These include salinity (Whitfield, 1994a), temperature (Marshall & Elliot, 1998), turbidity (Cyrus & Blaber, 1987), tidal currents (Szedlmayer & Able, 1993), dissolved oxygen (Russell, 1994), catchment size (Marais, 1988), habitat type (Whitfield, 1986), available food resources (Marais, 1984; Whitfield, 1988), predation (Blaber, 1973; Whitfield & Blaber, 1978), parasite loads (Whitfield & Heeg, 1977; Schramm, 1991), and habitat degradation (Blaber *et al.,* 1984). The distribution and habitat use of fishes in South African estuaries has, however, never been observed directly. Real-time studies of this nature require knowledge on the movement of fishes in relation to the highly fluctuating abiotic factors (salinity, temperature, turbidity) characteristic of estuarine environments. Such high resolution studies can only be addressed through the use of telemetry.

In this chapter, telemetry data was used to determine the influence of the abiotic variables, salinity, temperature, sea temperature, turbidity, depth, current speed and tidal phase, on the movement patterns of spotted grunter. In addition, the combined effect of salinity, temperature and turbidity, on the position of spotted grunter in the estuary was determined.

Influence of abiotic variables on spotted grunter distribution

Traditionally, salinity has been viewed as one of the most important variables influencing the distribution of organisms in estuaries (Whitfield *et al.,* 2003). In South Africa and elsewhere, salinity (Whitfield, 1994a; Ter Morshuizen *et al.,* 1996; Marshall & Elliot, 1998; Strydom *et al.,* 2003) and the combined effects of temperature, turbidity and salinity (Cyrus & MacLean, 1966; Whitfield *et al.,* 1981; Cyrus & Blaber, 1992) have been found to influence fish distribution in estuaries. Spotted grunter is a euryhaline species (Whitfield, 1980) and was located in salinities ranging from 0 ‰ to 36 ‰, with an average of 22.1 ‰ in the first and 15.5 ‰ in the second study. The variation between the first and second studies can be ascribed to the large proportion of fish located in the freshwater upper reaches of the estuary during the initial stages of the second study. Laboratory studies conducted by Deacon & Hecht (1999) on small, juvenile spotted grunter (avg. 51 mm TL) showed that in salinities ranging from 12 ‰ to 35 ‰, growth was equal. They suggested that since estuaries, which are the nursery areas for spotted grunter, are subject to unpredictable and regular salinity changes, the lack of a clear optimum salinity for juvenile spotted grunter could indicate an adaptation to an unstable natural environment. Furthermore, spotted grunter have been recorded in salinities varying from 0 – 90 ‰ (Wallace, 1975a; Day *et al.,* 1981), and can survive in salinities < 1 ‰ for prolonged periods (Blaber & Cyrus, 1981). This is consistent with the opinion of Whitfield *et al.* (1981), that estuarine-associated fish taxa are usually more tolerant of low rather than high salinities. Pradervand & Baird (2002) showed that spotted grunter were the most abundant fishery species in the freshwater dominated Great Fish Estuary and Sundays Estuary and the freshwater deprived Kromme, Kariega, Bushmans, and Kowie estuaries. This provides further evidence of the salinity tolerance of spotted grunter. Ter Morshuizen *et al.* (1996) and Bate *et al.* (2002) suggest that the high conductivity levels of the Great Fish Estuary, promotes the utilisation of the upper and head regions of the estuary by euryhaline fish species, such as the spotted grunter. This is facilitated by the dissolved salts of terrestrial origin which reduce osmotic stress experienced by fish inhabiting the riverine environment (Whitfield, 1998; Whitfield *et al.,* 2003). Conductivity levels in the first study ranged from 121.3 – 149 mS.m^{-1} (avg. 137.88 mS.m^{-1}), and in the second study from 159 – 190 mS.m^{-1} (avg. 176.17 mS.m^{-1}). This is high in comparison to other Eastern Cape rivers, such as the Krom River (41 mS.m^{-1}) and Blaaukrantz River (10 mS.m^{-1}) (Ter Morshuizen *et al.,* 1996). The results confirm the euryhaline nature of spotted grunter and suggest that they have physiologically adapted to survive in both fresh and saltwater.

Temperature (Marshall & Elliot, 1998) and the combined effect of temperature and salinity (Morin *et al.,* 1992; Thiel *et al.,* 1995) were found to influence fish distribution in the Humber (United Kingdom), Maquatua (Canada) and Elbe (Germany) Estuaries, respectively. Temperature has also been found to influence space use by fish (Morrisey & Gruber, 1993; Bradbury *et al*., 1995; Baldwin *et al.,* 2002). Whitfield & Paterson (2003) found that temperature and aquatic vegetation were the primary factors governing the distribution of fish in the freshwater deprived Kariega Estuary. Beitinger & Fitzpatrick (1979) identified temperature as the primary abiotic factor controlling key physiological, biochemical and life-history processes of fish. Generally, fish have a thermal preference that optimizes physiological processes. With the exception of one day where a pocket of cold water was recorded at the mouth, water temperature during the first study did not drop below 17 ºC. Spotted grunter were located in a wide range of temperatures during the first (17.3 ºC - 30.5 ºC) and second (16.3 ºC - 25.3 ºC) study. In summer (study 1), most spotted grunter were located in water temperatures between 22 and 25 °C, while in spring (study 2), most were located in temperatures between 18 and 21 °C.

Ter Morshuizen *et al.* (1996) also recorded most spotted grunter in the Great Fish River at temperatures between 21 ºC and 23 ºC. The thermal preference of 0+ juveniles under culture conditions was found to be between 24 ºC and 25 ºC (Deacon & Hecht, 1995). Lower temperatures are likely to reduce metabolism and growth.

Evidence for the avoidance of low water temperature was found in both studies. There was a significant negative relationship between the average distance of spotted grunter from the estuary mouth and sea temperature. In addition, the very low temperatures (< 16 °C) recorded at the beginning of the second study may have caused the spotted grunter to move to the upper reaches of the estuary, where they maintained position for an extended period of time (10 to 14 days). Furthermore, a greater number of fish were located in the estuary during low sea temperatures (Chapter 3). Egli & Babcock (2004) found that snapper *Pagrus auratus* tagged in a New Zealand marine reserve displayed varying periods of absence from the study site and that the highest number of individuals were absent during low temperatures. Mass fish mortalities attributed to salinity extremes in South African estuaries have been recorded during conditions of low water temperature (< 13 ºC). Whitfield *et al.* (1981) and Cyrus & McLean (1996) suggest that temperature is the key factor initiating such fish kills, and that temperature and other factors will determine how long a fish can survive certain salinity regimes. The findings of this study suggest that spotted grunter have adapted physiologically and behaviourally to temperature variations within estuaries. They are tolerant of a wide range of higher temperatures, and appear to avoid temperatures < 16 ºC.

Turbidity has also been found to influence fish distribution in estuaries (Cyrus, 1992; Blaber & Blaber, 1980; Blaber, 1981; Cyrus & Blaber, 1987; Whitfield *et al.*, 1994). Turbidity is also a major factor influencing both juvenile and adult fish abundance (Blaber, 1981; Marais, 1988). Spotted grunter were found in both exceptionally clear and turbid waters, ranging from 6 FTU to 567 FTU in the first study and from 4 FTU to 358 FTU in the second study. The Great Fish Estuary was more turbid during summer (first study) than during spring (second study). The findings suggest that spotted grunter favour turbid water between 20 – 80 FTU, and avoid areas of very high (> 200 FTU) and very low (< 20 FTU) turbidity. Turbidity has been found to influence feeding success in visual foraging piscivorous fishes in estuaries (Hecht & van der Lingen, 1992; Whitfield *et al.,* 1994). Field sampling and laboratory experiments have shown that spotted grunter are indifferent to turbidity (Cyrus & Blaber, 1987; Hecht & van der Lingen, 1992; Whitfield *et al.,* 1994), probably because they are macrobenthic carnivores and rely primarily on tactile stimuli when foraging (Whitfield, 1998). The results from this study suggest that spotted grunter are physically adapted to tolerate large variations in turbidity, supporting the conclusions reached by Cyrus & Blaber (1987), Hecht & van der Lingen (1992) and Whitfield *et al*. (1994) .

During both studies, the majority of spotted grunter were found at depths between 1 and 2 m. However, on average, during the second study, spotted grunter were located in deeper water and in a wider range of depths. During the second study, spotted grunter were frequently located in deep scoured holes in the upper reaches of the estuary which were not present in the first study.

The Great Fish Estuary has a large tidal prism ($1.6x10^6$ m^3) and strong currents (maximum surface current speeds recorded in the studies reached 0.69 $m.s^{-1}$ in the upper reaches, around 0.8 $m.s^{-1}$ in the lower reaches and 0.93 $m.s^{-1}$ in the mouth of the estuary). Therefore, spotted grunter have to adapt accordingly. It would be advantageous to choose a site where the influence of current, and therefore the energy requirement for maintaining their position is minimal. In this study, the high use area of smaller spotted grunter near the banks of the lower reaches (Chapter 3) coincided with low current flow. Szedlmayer & Able (1993) suggested that habitat use of summer flounder *Paralichthys dentatus*, within the creek of the estuary, maximised energy efficiency as it served as a low-energy holding area during flood and ebb tides.

Due to the controlled but high freshwater input, the Great Fish Estuary is characterized by wide fluctuations in abiotic variables. During the outgoing and low tides, conditions in the lower reaches of the estuary are characteristic of the freshwater environment, while during the incoming and high tides, conditions in the lower reaches are characteristic of the marine environment, with high salinity, cool water, and low turbidity. Despite the noticeable peaks in spotted grunter distribution observed in both studies, and the site fidelity displayed by the fish (see Chapter 3), the tidal phase had a distinct influence on the distribution of tagged fish in the estuary. During the outgoing and low tides most of the fish were found in the lower reaches, while during the incoming and high tides, they were located in the middle and upper reaches of the estuary. The influence of the tidal phase was most pronounced in the second study, probably due to the more sedentary (resident) nature of the smaller spotted grunter tagged in the first study (Chapter 4). This suggests that larger fish (tagged in the second study) utilized the tidal currents more frequently than smaller adolescent individuals. Since the effect of the tidal phase appears to be more pronounced in larger spotted grunter, these fish may use behavioural cues and to a lesser extent physiological adaptations to determine their location within the estuary. The results from the second study showed that spotted grunter use the current, moving upriver during the incoming tide and downriver during the outgoing tide. From the results it is known that spotted grunter have a broad physico-chemical tolerance. However, due to the rhythmic changes of abiotic conditions caused by the tides, it appears that these fish utilize the current to avoid less desirable conditions. Such behaviour would alleviate both osmoregulatory and thermoregulatory stress, and consequently minimize energy expenditure. Szedmayer & Able (1993) showed that age-0 summer flounder *Paralichthys dentatus* used selective tidal transport to optimize feeding and select preferred environmental conditions in Schooner Creek, in southern New Jersey USA. The use of tidal currents for movement thereby minimizing energy expenditure, has also been observed in adult thin-lipped grey mullet *Liza ramada* (Almeida, 1996), American eel *Anguilla rostrata* (Helfman *et al.,* 1983), and salmon smolts *Oncorhynchus kisutch* (Miller & Sadro, 2003). Rangeley & Kramer (1995) also showed that juvenile pollock *Pollachius virens* in an intertidal marine environment made extensive use of tidal currents to move from one habitat to another.

Influence of environmental variables on the movement of spotted grunter

During the daily tidal phases, spotted grunter are subjected to large fluctuations in salinity (0 to 36 ‰), turbidity (turbid to clear), and to a fairly wide range in temperature. Although it has been shown that spotted grunter are tolerant of these environmental changes, the results showed a strong influence of salinity, temperature and turbidity on the position of the fish in the estuary. It was evident from the model that season had no effect on the relative change in position of the fish, despite the decrease in temperature and turbidity observed during the second study. However, this study has shown that low temperatures (≤ 16 ºC), typical of the spring season, may have induced a behavioural response in spotted grunter to avoid low temperatures. Although fish length had an influence on home range size (Chapter 4) and estuarine use (Chapter 3), small and large fish responded similarly to changes in the abiotic factors. Even the more sedentary (Chapter 4) smaller adolescent spotted grunter alter their position in response to changes in environmental conditions. This suggested that fish of all sizes have a preference for certain conditions. These are most likely the conditions which best suit their physiological needs. Unlike the findings of Szedlmayer and Able (1993), who suggested that the tidal movements of age-0 summer flounder *Paralichthys dentatus* may be in response to a preferred narrow range of environmental parameters and that small changes in these parameters may cause the fish to move, spotted grunter appear to have a broader range. However, large fluctuations in the environmental variables, characteristic of the Great Fish Estuary, do cause spotted grunter to move.

From the above it appears that the most important abiotic factor governing spotted grunter distribution and movement in the Great Fish Estuary is the tidal phase and the associated changes in salinity, temperature and turbidity. However, low sea temperatures may supersede these factors and determine the distribution of spotted grunter in the estuary.

No biotic parameters were measured in this study. Although the interaction between abiotic and biotic factors is still poorly understood, it is recognised that the distribution and relative change in movement of spotted grunter is not simply a response of environmental variables, but is also effected by biotic variables (e.g. predator-prey interactions and prey availability). The importance of both abiotic and biotic factors have been observed in a number of studies (e.g. Blaber, 1981; Polacheck & Volstad, 1993; Morrissey & Gruber, 1993; Werner *et al.,* 1983). Blaber & Blaber (1980) also showed the importance of turbidity on fish distribution and that it may be linked to reduced predation pressure and food supply. In addition, Marshall & Elliot (1998) observed that environmental variables only partly explained the variance in the distribution patterns of fish and concluded that biotic factors may also affect fish assemblages. Griffiths (1997) observed that the spatial distribution of large juvenile dusky kob *Argyrosomus japonicus* in the Great Fish Estuary was mainly determined by prey availability. Furthermore, theoretical studies on cost-benefit analysis predict that predator avoidance will influence the spatial distribution of fish in their environments (Huntingford, 1993). The above suggest that predation risk and food availability influences habitat selection.

Although fish are likely to occupy positions in an estuary that optimises their physiological needs, Matthews (1990) suggests that strong selection also exists for animals to occupy areas of optimal resource availability. For example, the major food sources of spotted grunter (the thalassinid prawns, *Upogebia africana* and *Callianassa kraussii*) are most abundant and concentrated in the muddy intertidal lower reaches and the inter-and subtidal regions near the estuary mouth, respectively. This mirrors with the noticeable peaks observed in the distribution of spotted grunter in the lower reaches during both studies. Furthermore, although the influence of the tidal cycle on the feeding intensity of spotted grunter is not known, optimal foraging theory (McArthur & Pianka, 1966) suggests that these fish would feed when prey is most readily available to them. Hill (1981) showed that at low tide, mud prawns move to the air-water interface of their burrows. It is therefore possible that these prey items are more vulnerable at low tide and that spotted grunter would concentrate their feeding effort on the submerged mud banks at low tide. Since spotted grunter were mostly found in the lower reaches of the estuary during low tide, this study provides some circumstantial evidence for this hypothesis.

To fully understand the driving mechanisms behind the space utilization of spotted grunter in estuaries, one needs to determine their physiological constraints as well as the importance of biological factors that govern their distribution. Future telemetry studies should therefore attempt to quantify the influence of prey availability and predator avoidance in the space utilisation of this and other species.

CHAPTER 6
GENERAL DISCUSSION

A diverse array of movement patterns have been identified in fish species. These range from highly mobile species that usually exhibit complex and predictable movement patterns (e.g. home range and movements associated with ontogenetic shifts, spawning migrations and larvae recruitment) (Pittman & Mc Alpine, 2001) to largely resident species that exhibit a confined home range usually determined by unpredictable factors such as food availability and predation pressure. Furthermore, studies on fish movement have shown not only differences between species, but between individuals of the same species (Zlokovitz *et al*., 2003; Secor, 1999). Movement patterns of fish are, therefore, thought to reflect ecological and evolutionary responses to the environment (Pittman & McAlpine, 2001) and are determined by genetic inheritance and by learning or experience.

Within a species, different movement patterns are genetically determined and are often associated with ontogenetic change. Ontogenetic shifts are responses to longer term predictable changes in morphology, size or maturity state (Gibson, 1997). For example, in South Africa, juvenile red steenbras *Petrus rupestri*s and carpenter *Argyrozona argyrozona* are resident on inshore reefs where their behaviour is best described as "station keeping", but later join spatially distant populations. Carpenter exhibit an offshore 'natal homing' behaviour, while red steenbras undertake longshore eastward migrations (Griffiths & Wilke, 2002). Besides the influence of genetic inheritance and ontogeny, short term endogenous stimuli, such as hunger can stimulate movements. Foraging movements may be restricted to a temporary extension of an individuals range within its habitat or may result in long range feeding migrations between habitats (Gibson, 1997). Overwhelming evidence suggests that fish movement patterns are genetically determined and environmentally driven, and are ultimately an attempt to maximise growth, survival and reproductive output.

The pattern of fish migration can be explained by a "migration triangle" (Harden Jones, 1968) or by multi-phase ontogenetic shifts in habitat use (Pittman & McAlpine, 2001). Each phase of the triangle can be associated with a spatially and temporally discrete set of movements. The tri-phasic life cycle generally consists of movements involving (1) the youngest stages from the spawning grounds to the nursery area, and then, (2) as the juveniles mature, from the nursery area to the adult habitat, where they undergo a range of routine foraging and shelter movements, and lastly (3) from the adult habitat to the spawning grounds, completing the life cycle or migration triangle (Harden Jones, 1968; Pittman & McAlpine, 2001) (Figure 6.1). Additional complexity is found in migrations that are not for the purpose of spawning and movements that result in a relocation of the home range of an individual that cannot be defined as an ontogenetic shift (Pittman & McAlpine, 2001).

The results of this study have spatial (restricted to one estuary) and temporal (limited to two seasons within one year) boundaries. Furthermore, as with all telemetry studies, the sample size represents only a small portion of the entire stock, and only pertain, albeit important, to a single phase (the estuarine-dependent phase) of their life history. Nonetheless, this study has shown that throughout the life history of spotted grunter, these fish have adapted one or more of the behavioural patterns mentioned above. Since this study deals with the movement patterns of spotted grunter in their nursery habitat and in-part their adult habitat (i.e. the second phase of the migration triangle), the findings are discussed in the context of this simple triangular pattern (Figure 6.1).

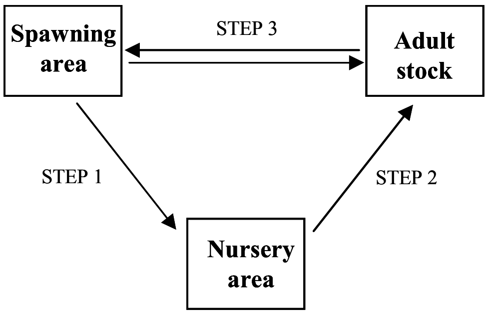


Figure 6.1. The migration triangle, adapted from Harden Jones (1968).

It is well-known that spotted grunter is an estuarine-dependent species (see Chapter 1 for overview). Juveniles are dependent on the estuarine environment, while adults are predominantly marine (Wallace & van der Elst, 1975). The first step in the migration triangle of the spotted grunter is the movement of eggs and larvae from the spawning area (thought to exist in the marine inshore waters of KZN) to the nursery grounds in the estuarine environment along the South African coast (Figure 6.2). Juveniles inhabit the estuarine environment, for a period that lasts between one and three years, after which they reach sexual maturity (between 300 – 400 mm TL) (Wallace, 1975b; Webb, 2002).

When in the Great Fish Estuary, adolescent spotted grunter appear to be highly resident, with a small home range (mean size = 129 167 m^2) that is generally confined to a single core area (Figure 6.2). The lower reaches of the Great Fish Estuary serves as a common high use area for adolescent spotted grunter (see Figure 4.1; Chapter 4) (Figure 6.2). This area is characterised by high food availability and possibly a reduced risk of predation, but is subject to wide abiotic fluctuations. The high use of this region and the dependence (see Chapter 3) of spotted grunter, particularly the juveniles, on the estuary suggests that they are capable of tolerating highly fluctuating abiotic conditions. It appears that they have physiologically adapted to survive in water of varying salinity as they are able to tolerate prolonged periods in both fresh and saltwater, are adapted to survive in highly turbid waters, and are capable of changing their foraging strategies in order to optimize food intake under different turbidity conditions. Spotted grunter are also physiologically and behaviourally adapted to survive in a range of water temperatures where they are able to survive in a range of warm waters, but this study showed that they tend to avoid very cold temperatures (< 16 º C). Although resident and tolerant to the widely fluctuating abiotic conditions, the findings indicated that adolescent spotted grunter move and change their position to avoid wide fluctuations in salinity, temperature and turbidity (see Chapter 5).

The second step in the migration triangle is when the juveniles mature and move from the nursery area in the estuary to the adult stock in the marine environment, where they undergo a range of routine movements (Figure 6.2). Although adolescent spotted grunter in the Great Fish Estuary showed a high degree of estuarine use or "dependence", it appears that at the onset of sexual maturity, the fish begin to undertake short term sea trips (see Chapter 3). These trips may either simply reflect their movement into an expanding estuarine environment during the outgoing and low tide or may (and most probably) indicate the initial stages of an ontogenetic habitat shift from the estuarine to the marine environment. Long term sea trips characterised by the permanent departure of adolescent spotted grunter to the marine environment are most probably the final stage of the ontogenetic habitat shift, which marks the end of their juvenile estuarine-dependent phase (Figure 6.2).

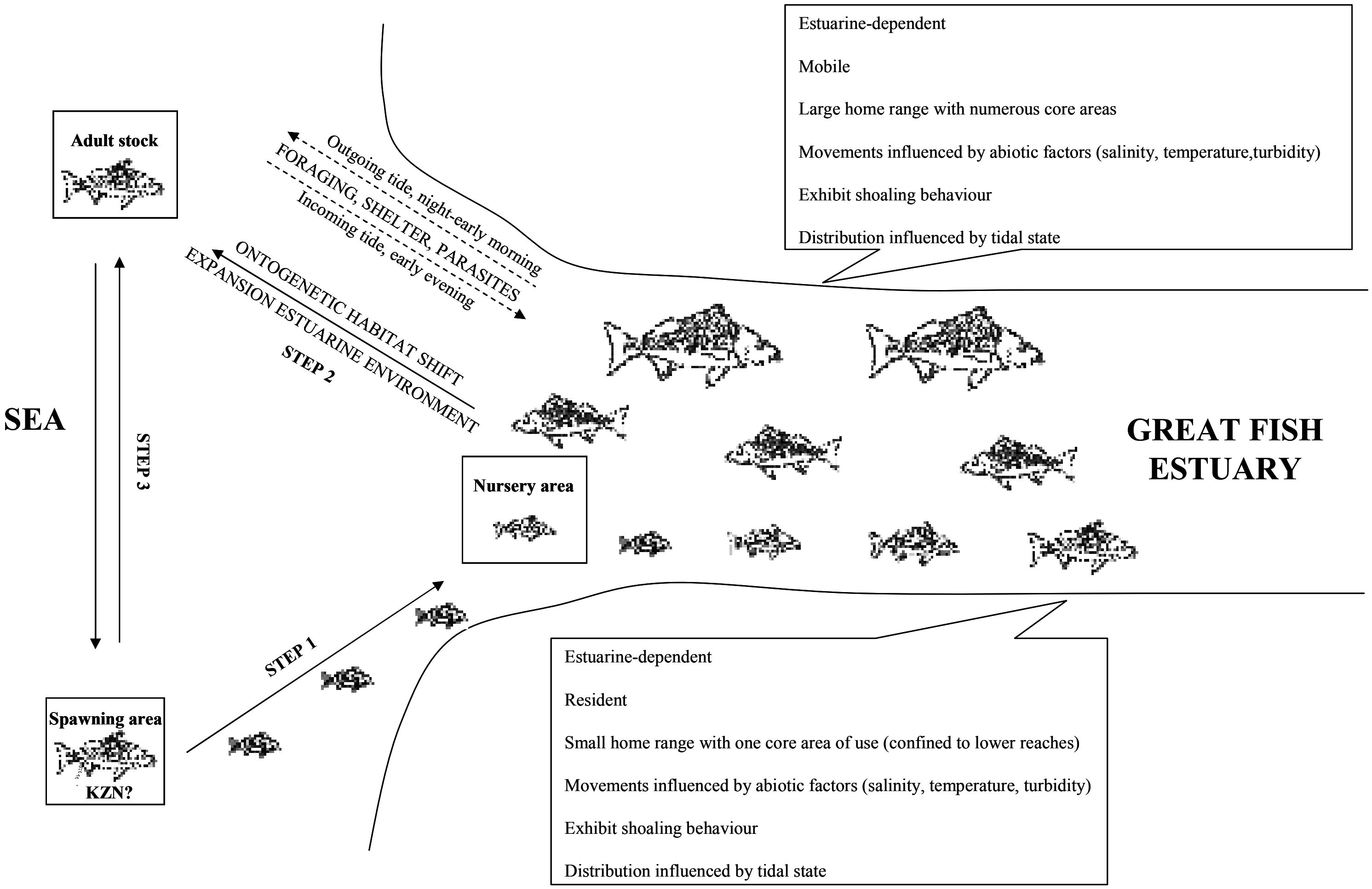
After undergoing an ontogenetic habitat shift, the adult fish are now predominantly marine (Wallace & van der Elst, 1975). However, despite this, adult spotted grunter in the Great Fish Estuary still undertake numerous movements from the marine environment into the estuary (Figure 6.2). These movements were influenced by a number of abiotic and biotic factors and were, expectedly, different to those of their adolescent counterparts (see Chapter 3). Adult fish are thought to frequent estuaries to forage (Wallace, 1975b; Webb, 2002), to find shelter (Stone, 1988) and to possibly rid themselves of parasites (A.K. Whitfield, SAIAB, Personal communication, 2004) (see Chapter 3). Foraging is most probably the primary reason that adult fish enter the Great Fish Estuary as their preferred prey is abundant and available in this system. This is particularly true during the spawning season (spring and summer) when it is thought that pre- and post-spawning spotted grunter move into estuaries to gain and/or regain condition lost (Wallace, 1975b). The Great Fish Estuary also appears to provide shelter for spotted grunter from low sea temperatures (caused by an increase in barometric pressure and easterly winds) (see Figure 3.8, 3.9, 3.10; Chapter 3) and may also act as a refuge from predators (see Chapter 3). The movement of adult fish into and out of the Great Fish Estuary was strongly affected by the time of day (see Figure 3.4; Chapter 3) and was facilitated by the tide (see Figure 3.5; Chapter 3).

Most fish entered the estuary on the incoming tide during the afternoon and early evening, and exited on the outgoing tide during the night and early morning.

Spotted grunter undergo a behavioural change with increased size. With increasing size, fish generally have larger spatial requirements and the risk of predation is reduced (Kramer & Chapman, 1999; Minns, 1995). Larger spotted grunter began to occupy a larger home range with numerous core areas within the Great Fish Estuary (Figure 6.2). Even with the increased home range size there was still a high degree of overlap in their space use. It appeared that adult spotted grunter also showed an increased behavioural response to fluctuations in salinity, temperature, and turbidity (see Chapter 5). By making frequent use of the tidal currents (see Table 5.2; Chapter 5), larger fish avoided less desirable abiotic conditions. Consequently, their distribution in the Great Fish Estuary was influenced by the tide and, generally, fish were located further upriver during incoming and high tide and closer to the mouth during the outgoing and low tide (see Figure 5.9; Chapter 5).

The final step in the migration triangle is the movement of adults to their spawning grounds (Figure 6.2). It is thought that spotted grunter from the southeastern Cape migrate to KZN to spawn (Webb, 2002). No direct evidence for these movements was apparent from the study. However, the long term sea trips undertaken by some of the adolescent spotted grunter could have been spawning migrations to KZN (see Chapter 3) (Figure 6.2). Since no reproductively active specimens have been found in the Great Fish Estuary (Webb, 2002), and other KZN estuaries (Wallace, 1975b), it appears that adult fish undergo gonadal maturation at sea. Two fish undertook extended sea trips and were recaptured in the Great Fish Estuary approximately one year later (see Chapter 3). It is possible that these individuals could have migrated to KZN where they spawn (Webb, 2002), and returned to the Great Fish Estuary. If so, this would suggest that natal homing may be a strategy adopted by this species. Since the second study was conducted during the spawning season of these fish, it is likely that the tagged adult fish were in a post-spawning condition. Therefore, it was not surprising that only one long term sea trip was observed during this study (see Chapter 3).

The results of this study have described the degree of estuarine use, home range, and movement patterns. However, according to Willis *et al.* (2001), assumptions about homogenous behaviour cannot always be made for a species. From the results it is evident that spotted grunter exhibit several different behavioural traits, which is common among many species (Attwood & Bennett, 1994; Jadot *et al.* 2002; Secor, 1999; Hartill *et al*. 2003; Parsons *et al.* 2003; Zlokovitz *et al*., 2003; Egli & Babcock, 2004; Attwood & Cowley, in press.). Secor (1999) suggested that over a single generation, ontogeny is one of the most important factors that influences migrations, but over many generations, variable migratory behaviour should be a key tactic in population persistence. A high degree of variation was observed in the behavioural modes (resident and roaming), home range estimates (size, number, location), the frequency and duration of sea trips, the abiotic environment in which each spotted grunter was found and the use of the tidal currents. Although some of this variation in behaviour can be attributed to ontogenetic behavioural shifts, this unpredictable and versatile behaviour displayed by individual spotted grunter appears to be a successful adaptive strategy evolved by the population.



Estuarine-dependent

Mobile

Large home range with numerous core areas

Movements influenced by abiotic factors (salinity, temperature,turbidity)

Exhibit shoaling behaviour

Distribution influenced by tidal state

Estuarine-dependent

Resident

Small home range with one core area of use (confined to lower reaches)

Movements influenced by abiotic factors (salinity, temperature, turbidity)

Exhibit shoaling behaviour

Distribution influenced by tidal state

Figure 6.2. Diagrammatic representation of the proposed life cycle and movement patterns of spotted grunter *Pomadasys commersonnii* from the Great Fish Estuary.

Another estuarine-dependent species has developed a similar adaptive strategy to that of the spotted grunter. The New Zealand snapper *Pagrus auratus* has a similar life history to spotted grunter. Juvenile snapper are found in estuarine waters and coastal embayments, with adults moving to a range of coastal habitats in waters less than 50 m deep. Parsons *et al.* (2003) found that snapper in the Cape Rodney to Okakari Point (CROP) marine reserve, New Zealand, had more than one core area. Like that of spotted grunter (see Chapter 4), they also found that the home ranges and core areas of this fish overlapped considerably. In the Mahurangi Estuary, New Zealand, Hartill *et al.* (2003) also showed a high degree of overlap in the space use patterns of snapper. Similarly to spotted grunter (see Chapter 4) individual snapper in the CROP reserve displayed resident and mobile behavioural patterns (Parsons *et al.,* 2003; Egli & Babcock, 2004). As was found with spotted grunter in the Great Fish Estuary (see Chapter 5), Hartill *et al*. (2003) showed that half of the tagged snapper, in the Maruhangi Estuary, exhibited tidal biorhythms and suggested that utilising tidal currents enables the fish to explore an extensive estuarine area with minimal energy expenditure. They also found that small, mainly immature snapper showed a high degree of residency, with some individuals migrating to the marine environment. They suggested that, amongst other factors (e.g. feeding and spawning), marine migrations are possibly related to fish size and that they reflected the larger fish's necessary spatial requirements. This was also observed in spotted grunter (see Chapter 3). Egli & Babcock (2004) suggested that the extended excursions made out of the CROP reserve could be related to fish size (larger snapper were found to be more mobile), individual behavioural variability and possibly social interaction. Parsons *et al.* (2003) suggested that the variation in home range estimates in the CROP reserve could be due to individualised behavioural traits. This seemingly similar behaviour exhibited by snapper and spotted grunter is surprising as the species occupy different trophic niches. However, the co-evolution of this behavioural strategy by two species in different biogeographical regions may suggest that this strategy is successful in estuarine and inshore marine environments.

Management Implications

The stock status of spotted grunter is considered to be slightly over-exploited (Fennessy, 2000). However, when compared with other estuarine-dependent angling species such as dusky kob *Argyrosomous japonicus* and white steenbras *Lithognathus lithognathus,* this species is in a relatively healthy state (Mann, 2000). The most probable reason for this is that the rate of exploitation of the species in the marine environment is negligible.

It is also possible that the high degree of variability in the space use, home range and movements of individual spotted grunter makes this species less predictable to anglers, thus reducing their catchability. The current stock status of spotted grunter suggests that bag and size limit regulations have curbed the over-exploitation to some degree. However, estuarine degradation due to freshwater abstraction (Cyrus, 2000), increased fishing pressure placed on estuarine systems (Lamberth & Turpie, 2003), and lack of compliance to fishing regulations (Potts *et al*., 2004), may cause spotted grunter numbers to decline in the future.

The maintenance and conservation of estuarine environments which serve as both migratory pathways and resident habitats during the early life history stages of estuarine-dependent linefish species must be considered as an integral part in the management of these fish species (Cowley, 1999). This and other studies have identified estuaries as important nursery areas and as essential habitats in the life history of spotted grunter and other estuarine-dependent species. The degradation of these environments is of serious concern for spotted grunter and other estuarine-dependent species. It is imperative that estuaries be protected from further degradation, and if possible, be rehabilitated. Of major concern to estuaries is the damming of water and alien invasive plant species in the catchment. These reduce freshwater flow into estuaries and severely influence their ecological functions. Every effort should be made to increase and ensure adequate supply of freshwater flow into estuaries in affected catchments by regulating the flow of water from the dams and by removing alien vegetation. It is suggested that freshwater be released during spring/summer, the period of early juvenile recruitment.

A growing body of research suggests that the spatial structure of fish stocks and their movement patterns cannot be ignored to ensure effective management. Future fishery regulations for this species could witness the inclusion of estuarine protected areas (EPAs). These areas could include the closure of entire estuaries or only specific parts of certain estuaries. However, such regulations are subject to research on the movement patterns, activity and home range size of the target species for the design of a closed area (Attwood & Bennett, 1994; Holland *et al*. 1996; Zeller, 1997; Kramer & Chapman, 1999). This study has provided information on the movement patterns and home range size of adolescent and adult spotted grunter. In addition to being wholly dependent on estuaries as juveniles, this study has confirmed that adolescent and adult spotted grunter are also dependent on estuarine environments. This dependence creates a bottleneck in their life history and suggests that EPAs would have merit for this species. This is in agreement with Lamberth & Turpie (2003) who stated that the most sensible policy would be to conserve estuarine stocks as nursery and source areas for marine fishes. In addition, Wallace & van der Elst (1975) stated that conservation measures of estuarine-dependent species should be directed at the most vulnerable part of their life cycle, which, given the considerable fishing pressure placed on estuaries, would be the time spent in the estuarine environment. However, while there are many marine protected areas, no estuarine protected areas currently exist in South Africa. Since this study focussed on one estuary, the results can only be used to suggest the optimal position of a closed area in the Great Fish Estuary. The results from this study show that after additional long term assessments, the region from the estuary mouth to 2 km upriver would be worthy of consideration. However, the implementation of this strategy, particularly in the rural Great Fish Estuary, may be unrealistic as the livelihood of permanent subsistence dwellers is dependent on the fishery resource.

Future research

Although this study has contributed to the understanding of the autecology of spotted grunter in the Great Fish Estuary, much information on the species is still required to fully and comprehensively understand its life history.

Long term telemetry studies are required to gain an understanding of seasonal and inter-annual trends in spotted grunter behaviour. Such studies are necessary to understand the long term patterns of space use in the estuary and to establish whether natal homing exists in this species. Long term studies that monitor the space use, home range and movements of spotted grunter and other estuarine-dependent species are critical for the development of alternative management strategies, such as EPAs. In addition, this study suggests that spotted grunter may exhibit alternative nocturnal behaviour. Preliminary analysis of ALS data showed that spotted grunter moved to the lower reaches of the estuary during the night. This coincides with increased catches by fishers at this time (W.M. Potts, DIFS, Personal communication, 2004). The perceived vulnerability of spotted grunter to capture by fishers at night suggests that gaining an understanding of the nocturnal movements of spotted grunter has management implications and is worthy of future research attention.

Since this study only investigated the movement patterns of a fraction of the spotted grunter population in only one estuary, spatial aspects involving the long term monitoring of home range and space use of spotted grunter in different estuaries is necessary both at an ecological and management level. Such studies would not only further our knowledge on the movement patterns of the spotted grunter population, but also provide effective information for the implementation of EPAs. An effective EPA would also require knowledge on the spatial and temporal use of the home range relative to fishing effort (i.e. the overlap between fishing effort and high use areas). It would, therefore, be advantageous to simultaneously monitor the space use of the fish as well as the fisher. Consequently, management options could include zoning resource use practices within estuarine environments.

The information obtained in this study has provided the fundamentals for future ecological and behavioural investigations, and may serve as a foundation for the development of EPAs that could assist in sustaining susceptible estuarine-dependent fish stocks. Since the success of EPAs depends on the amount of time that individuals spend in the estuary or protected area, a precise knowledge on the long term space use, home range and movement patterns of each fish species is imperative if one is to make suitable recommendations for this management strategy. This study has provided evidence that ultrasonic telemetry is a valuable method to establish such information necessary for the effective management of estuarine-dependent species within the estuarine environment.

To achieve effective management of a fish stock, critical information on the life history of the species is essential. In the case of spotted grunter, much information on their life history is still needed (in particular, the final step in the migration triangle). The hypothesis, proposed by Webb (2002), that adult spotted grunter from the southern and eastern Cape undertake an annual spring/summer migration to spawn in KZN has not been addressed. This has major implications as a single stock species, which would be the case if spotted grunter all spawned in KZN, should be managed very differently to a species with meta populations (multiple stocks). A genetic study on the species is currently being conducted to establish if the spotted grunter population is a single stock throughout its distributional range (P.D. Cowley, SAIAB, Personal communication, 2004). Secondly, Webb's hypothesis should be addressed by identifying the spawning location of spotted grunter. An understanding of the spatial and temporal patterns of longshore migration of spotted grunter can be achieved through the use of otolith microchemistry. Otolith microchemistry could also establish if spotted grunter exhibit natal homing, and will identify the most important nursery estuaries. Since otolith microchemistry is expensive, alternative methods such as conventional tagging programs could assist in the understanding of longshore migrations and will provide evidence of natal homing. A suite of conventional techniques could be used to identify the spawning grounds of this species. This would involve a comprehensive study on the reproduction, seasonal abundance (inter-annual variability in catch rate), and larval distribution (inter-annual recruitment variability and factors influencing recruitment) of spotted grunter within estuaries and the inshore marine environment along their entire distributional range. Furthermore, continued long term fishery studies in selected estuaries are suggested to monitor the status of the spotted grunter stock. Using information from past studies, target reference points, based on the catch rate, may be used as an indicator of the health of the stock. If the catch rate declines below a pre-determined level, then alternative management strategies, such as EPAs or closed seasons, should be implemented, or in extreme cases, the fishery should be closed.

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