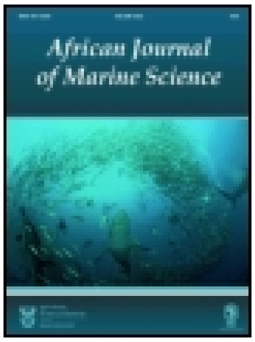

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African Journal of Marine Science

ISSN: 1814-232X (Print) 1814-2338 (Online) Journal homepage: https://www.tandfonline.com/loi/tams20

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To cite this article: A-R Childs , PD Cowley , TF Næsje , AJ Booth , WM Potts , EB Thorstad & F Økland (2008) Estuarine use by spotted grunter *Pomadasys commersonnii* in a South African estuary, as determined by acoustic telemetry, African Journal of Marine Science, 30:1, 123-132, DOI: 10.2989/AJMS.2008.30.1.12.462

To link to this article: https://doi.org/10.2989/AJMS.2008.30.1.12.462

Published online: 08 Jan 2010.

African Journal of Marine Science 2008, 30(1): 123–132

AFRICAN JOURNAL OF
MARINE SCIENCE
EISSN 1814–2338
doi: 10.2989/AJMS.2008.30.1.12.462

Estuarine use by spotted grunter *Pomadasys commersonnii* in a South African estuary, as determined by acoustic telemetry

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Manuscript received September 2007; accepted January 2008

Factors influencing estuarine use and marine excursions by spotted grunter *Pomadasys commersonnii* in the Great Fish Estuary, South Africa, were studied using manual and automated telemetry methods. In all, 20 individuals, ranging from 362 mm to 698 mm total length (TL), were caught and tagged with acoustic-coded transmitters in the estuary. Tagged individuals spent most time in the estuary (67%), interspersed with a number of marine excursions — 15 in all. The number (6–53) and mean duration (0.8–9.5 days) of sea excursions varied among individuals, and were correlated significantly with tide, time of day, fish size and various environmental conditions. On average, fish departed the estuary on the outgoing tide at night and returned to the estuary on the incoming tide during the day. Spotted grunter <400 mm TL spent more time in the estuary than larger fish (403–698 mm TL). The number of fish recorded in the estuary was significantly correlated with barometric pressure, wind direction and sea temperature. The spotted grunter under study exhibited a high degree of estuarine use, highlighting the importance of this habitat to this overexploited, estuarine-dependent fishery species.

Keywords: environmental variables, estuarine-dependence, estuarine conservation, fish movement, Great Fish River

Introduction

Estuaries are important in the life history and the maintenance of the diversity of coastal fish species because of their function as nursery areas for juveniles as well as feeding grounds for adults (Cyrus 1991). The dependence of many fish species on estuaries is well documented (e.g. Wallace *et al.* 1984, Lenanton and Potter 1987, Blaber *et al.* 1989, Whitfield 1990, Hoss and Thayer 1993). Spotted grunter *Pomadasys commersonnii* (Haemulidae) (Lacepède 1801) is an estuarine-dependent species which spawns in the KwaZulu-Natal inshore coastal waters, between August and December (Wallace 1975b, Wallace and van der Elst 1975, Harris and Cyrus 1997, 1999). The eggs and larvae are transported southwards by the Agulhas Current, and juveniles between 20 mm and 50 mm TL recruit into the KwaZulu-Natal and south-eastern Cape estuaries (Wallace and van der Elst 1975, Whitfield 1990). Juvenile spotted grunter make use of the abundant food resources in estuaries, where they grow rapidly and remain for a period of 1–3 years (Wallace and Schleyer 1979, Day *et al.* 1981). Upon attaining sexual maturity (at between 300 mm and 400 mm TL), they return to the marine environment (Wallace 1975b). Some adults, however, return to estuaries to feed and to regain condition after spawning (Wallace 1975b, Whitfield 1994). The return of post-spawning fish coincides with increased catches by fishers in estuaries between July and January. These events are known as 'grunter runs' (Wallace 1975a, Marais and Baird 1980, Marais 1988, Pradervand and Baird 2002). It is suggested that adults spend up to several months in estuaries, before moving back to sea where they undergo gonadal development and ultimately spawn (Wallace 1975b, Wallace and van der Elst 1975). It is believed that adult fish also enter estuaries in a pre-spawning state to gain condition *en route* to their spawning grounds in KwaZulu-Natal (Webb 2002).

Spotted grunter is one of the most important linefishery species along the South African coastline and, although it dominates the catch of recreational and subsistence fishers in most estuaries in the Eastern Cape and KwaZulu-Natal (James *et al*. 2001, Mann *et al*. 2002, Pradervand and Baird 2002), it is far less prevalent in the marine shore-based fishery (Coetzee *et al*. 1989, Bennett *et al*. 1994, Brouwer *et al*. 1997). Increased fishing pressure placed on estuarine systems (Lamberth and Turpie 2003) and the estuarine-dependent nature of spotted grunter render them vulnerable to exploitation during both their juvenile and post-spawning adult phases. Consequently, an understanding of the degree

Published online 08 Jan 2010

of estuarine use and the factors influencing estuarine use is fundamental to the design of management strategies.

Conventional tag-and-recapture techniques are considered to be cost-effective to monitor fish movements. However, the animal has to be physically recaptured to obtain the data (Heupel *et al*. 2006) and, more importantly, a description of small-scale localised movements is not possible owing to the lack of information on movements between the fish's release and recapture (Egli and Babcock 2004, Matthews 1990). Although newer, alternative techniques (e.g. otolith microchemistry) are also available to quantify patterns of migration between estuarine and coastal habitats (Gillanders 2005, Secor and Piccoli 2007), particularly at a life-history level, telemetry is the only method that can establish the precise real-time movements of individual fish and provide fine-scale temporal and spatial data that are essential for behavioural ecology (Baldwin *et al*. 2002). The use of acoustic monitoring systems is expanding worldwide and is likely to continue to increase in the field of aquatic sciences (Heupel *et al*. 2006). However, only a few studies have used telemetry to determine the extent of estuarine use by a fish species (Able and Grothues 2007, Hartill *et al*. 2003, Miller and Sadro 2003). In South Africa, Kerwath *et al*. (2005) and Næsje *et al*. (2007) have used acoustic telemetry methods to examine the temporal and spatial use of estuaries by spotted grunter, but only Cowley *et al.* (in press) have used a fixed array of automated data-logging listening stations to accurately determine estuarine residence of a estuarine-dependent species, the dusky kob *Argyrosomus japonicus*. Although Kerwath *et al*. (2005) conducted a pilot study on spotted grunter in a small temporarily open estuary, and Næsje *et al*. (2007) provided the first comprehensive attempt of describing the movement patterns of undersized spotted grunter in a permanently open estuary, neither study provided detailed information on the factors influencing estuarine use.

Environmental factors play an elemental role in fish distribution and recruitment patterns in estuaries (e.g. Abookire *et al*. 2000, Marshall and Elliot 1998). However, there is a lack of information on the influence of environmental conditions on fish movement and researchers have only recently investigated the influence of these factors on estuarine use (Able and Grothues 2007, Hartill *et al*. 2003, Sackett *et al*. 2007). The objectives of this study were to determine the extent of estuarine use by spotted grunter, to quantify their movements between the estuarine and marine environments and to examine the factors influencing these movements.

Material and Methods

Study site

The Great Fish River is 650 km long and enters the Indian Ocean between Port Elizabeth and East London at 33°29′28″ S, 27°13′06″ E (Figure 1). The estuary is approximately 12 km long with a uniform bathymetry (mean 1.4 m), and has a surface area of 192.7 ha (Whitfield *et al.* 1994). Although variable, the estuary receives large volumes of freshwater from an interbasin transfer scheme, which accounts for continuous nutrient inputs and elevated phytoplankton production. Consequently, the Great Fish Estuary is a highly productive and turbid system. Perennial river flow (mean annual river discharge of 250–650 × 10^6 m^3) and tidal exchange ensures a permanently open connection to the sea (Grange and Allanson 1995, Grange *et al.* 2000). 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 spring tidal prism is 1.6 × 10^6 m^3 and the spring tidal range is between 1.0 m and 1.5 m in the lower reaches and decreases towards the head (Whitfield *et al.* 1994).

Research approach

Acoustic telemetry methods were used to track the movements of spotted grunter in the Great Fish Estuary between 29 September 2003 and 12 February 2004. This 137-day study period coincided with the known time spotted grunter enter estuaries along the South African coastline (Webb 2002). A total of 20 fish of between 362 mm and 698 mm TL (mean 478 mm TL) was tagged with VEMCO V13SC-1L-R256 coded transmitters. The transmitters (69 kHz) had an expected battery life of 130 days, were 13 mm in diameter, 36 mm in length and weighted approximately 6 g in water — on average 0.5% of the fish's body mass (min: 0.2%, max: 1.2%). Each transmitter emitted a unique acoustic pulse train randomly every 5–15 s. According to Wallace (1975b), the length-at-50% maturity of spotted grunter is 300 mm TL for males and 360 mm TL for females, so those under study were likely a mix of both juveniles and adults.

Tagging of fish

Fish were caught from a boat using rod-and-line with baited barbless hooks. After capture, each fish was immediately placed in a plastic container with about 100 l of estuary water containing 2-phenoxyethanol (c. 1.0 ml l^{-1}). Once anaesthetised, each fish was measured to the nearest millimetre and placed ventral side up in a wet towel on a V-shaped foam cradle. During surgery, the 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 average duration of the surgical process was 2.8 min. Following surgery, fish were placed in a recovery bath filled with estuarine water, which was flushed regularly with new water. Once the fish was in a stable, upright position and swimming, it was released into the estuary at the catch site. Manual tracking of spotted grunter commenced four days after the last fish was released to allow for acclimation. 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.

In laboratory experiments using dummy transmitters, spotted grunter showed no abnormal behaviour after surgery (Kerwath *et al.* 2005). Also, a pilot laboratory test was conducted on spotted grunter. Fish were tagged with

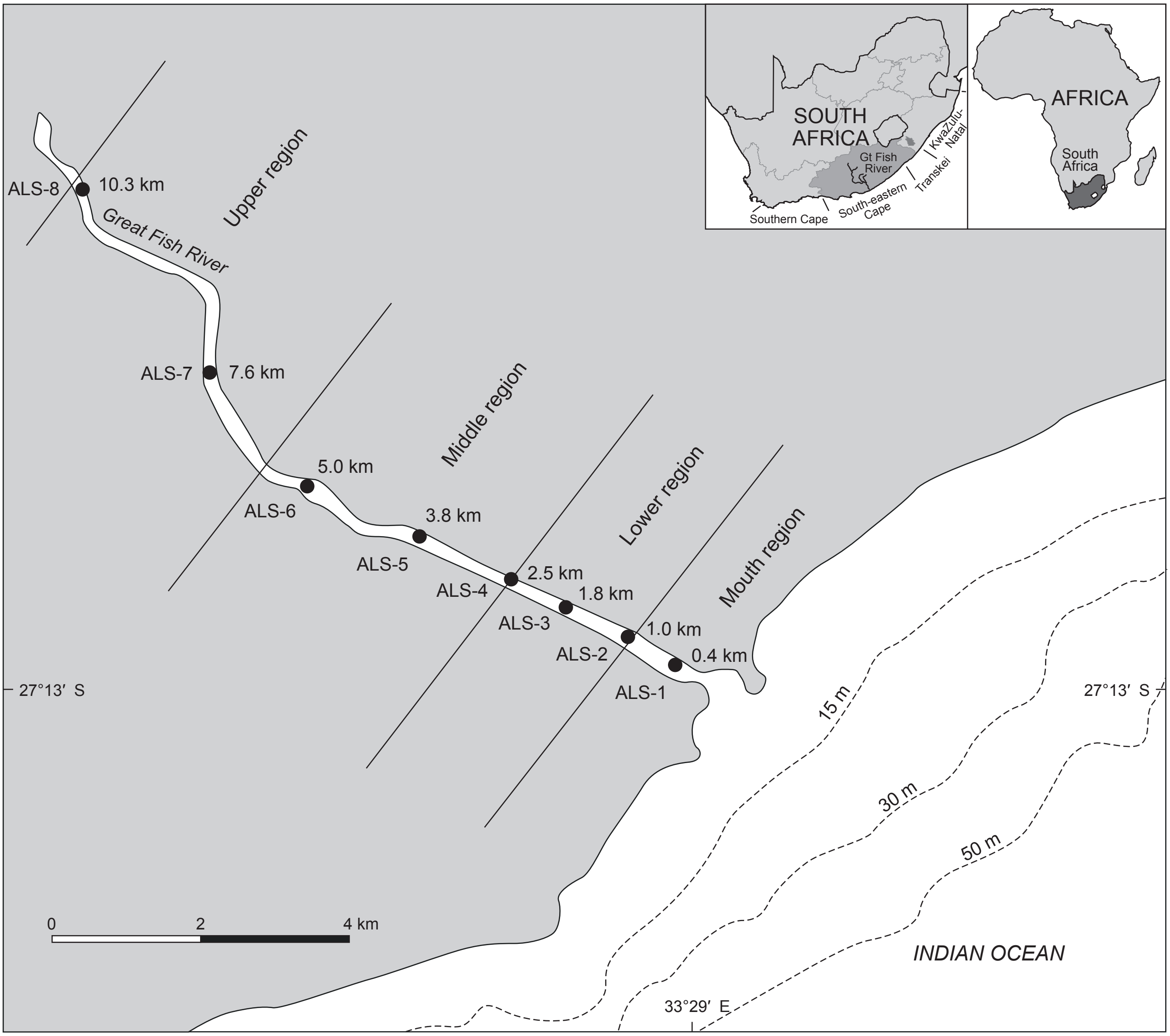

Figure 1: Map of South Africa showing the location of the Great Fish River and a detailed map showing the position of the automated listening stations (ALSs) (black dots) in the Great Fish Estuary during the study (29 September 2003–12 February 2004)

exact replicates (size and weight) of the VEMCO transmitters using the tagging techniques (capture and retention of fish and the appropriate surgical procedure) described by Næsje *et al*. (2007). No post-tagging infection, haemorrhaging or abnormal post-tagging behaviour was observed during the 90-day trial period.

Tracking of fish

Two methods were used to monitor the movements of spotted grunter: (1) manual tracking from a 4.2 m motorised boat using a VEMCO VR60 and VH10 directional hydrophone; and (2) the presence and absence of individual fish using automated listening stations.

Manual tracking

Fish were tracked for 42 days within the 137-day sampling period, which included two 16-consecutive-day sampling sessions that were standardised according to the lunar phase (tracking was conducted over two semi-lunar cycles) and an interim period of 16 days, during which fish were tracked for 10 days. 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. Manual tracking sessions were conducted during daylight hours and the position of each fish was recorded once per day. Once a transmitter signal was received, the location of the fish was established by rotating the hydrophone and monitoring the directional strength of the signal. When the receiver's gain was reduced to zero and the signal strength was equal in all directions, a GPS waypoint was taken to record the position of the fish. Manual tracking was confined to the lower 14 km of the river, i.e. to approx. 2 km above the river/estuarine interface. Tests were conducted to determine the precision of tracking, using transmitters that were hidden at random locations within the estuary. On each test, the position was recorded within 1 m of the transmitter location.

Automated listening stations

Eight VEMCO VR2 automated listening stations (ALSs) were deployed along the entire length of the estuary, which provided an additional 95 days of monitoring, and a total of 137 days of fish monitoring. The ALSs were moored to concrete blocks (approximately 40 kg). Range tests were conducted at ALS locations in the mouth (ALS-1), lower (ALS-2), middle (ALS-4) and upper (ALS-7) regions (Figure 1). Transmitters were submerged for a fixed period at allocated positions (three transects) and set distances (every 50 m) from the ALS. The results of the range tests showed variation in the detection capability of the ALSs. The detection range of the ALSs ranged between 110 m and 610 m, but the high variability was ascribed to tidal influences such as altered physico-chemical conditions (e.g. salinity and current speed) and wind speed. Bathymetry, substrate type and physical obstructions (e.g. road bridge pylons) may have also influenced the reception range.

Data analysis

Fish 50A was caught on 10 October 2003 and replaced by Fish 50B later in the study (Table 1). Data obtained from both individuals were excluded from the analysis due to a reduced monitoring period. It was unlikely that any other fish was captured and not reported because of a public awareness campaign and a reward system offered to local fishers.

If a fish was not located in the estuary during manual tracking on a given day, data downloaded from the uppermost ALS (ALS-8) and the lowermost ALS (ALS-1) were checked to establish whether the fish was in the riverine environment or had migrated to the sea.

The percentage time (h) that each tagged fish spent in the estuary was calculated from the ALS data. A tagged fish was considered to be at sea if it passed ALS-1 and was only recorded again ≥6 h later, without being recorded on any other ALS in the estuary. Furthermore, if the same incident occurred, but the fish was not last recorded on ALS-1, but on ALS-2, it was also considered to be a sea trip. This was because of poor reception and/or code collisions on ALS-1 in the mouth region. The number of hours spent at sea was calculated from the time an individual was last recorded on the lowermost ALS-1 until the time it re-entered the estuary and was again recorded on ALS-1. The term 'sea trip' was used when a fish made a marine excursion. The effect of tide and time of day on the sea trips was assessed using circular statistics, which are commonly

Table 1: Details of acoustically tagged spotted grunter, percentage of time each fish was recorded in the Great Fish Estuary and the characteristics of the sea trips made by each tagged spotted grunter during the 137-day sampling period (29 September 2003–12 February 2004)

Fish code	Total length (mm)	Number of positional fixes	Date tagged	Date last recorded	ALS hours in estuary (%)	Date of first sea trip	Number of sea trips	Mean duration of sea trips in days (range)
50A[1]	449	12	24 Sep. 2003	11 Oct. 2003	–	–	0	–
50B[2]	515	15	14 Oct. 2003	28 Jan. 2004	–	27 Oct. 2003	19	3.0 (0.3–19.8)
51	469	32	24 Sep. 2003	12 Feb. 2004*	61	26 Oct. 2003	25	2.1 (0.4–15.3)
52	385	42	24 Sep. 2003	12 Feb. 2004*	100	–	0	–
53	428	37	23 Sep. 2003	12 Feb. 2004*	73	7 Nov. 2003	16	2.3 (0.3–9.8)
54	620	22	23 Sep. 2003	12 Feb. 2004*	54	18 Oct. 2003	14	6.7 (0.3–26.6)
55	432	29	22 Sep. 2003	10 Nov. 2003	26	26 Oct. 2003	10 (9 returned)	0.8 (0.3–2.5)
56	440	42	24 Sep. 2003	12 Feb. 2004*	82	29 Nov. 2003	12	2.0 (0.3–9.9)
57	364	42	24 Sep. 2003	12 Feb. 2004	100	–	0	–
58	625	21	22 Sep. 2003	12 Feb. 2004*	44	7 Oct. 2003	12	6.3 (0.6–17.6)
59	472	28	25 Sep. 2003	12 Feb. 2004*	60	26 Oct. 2003	28	2.0 (0.4–10.7)
60	527	29	23 Sep. 2003	12 Feb. 2004*	53	18 Oct. 2003	18	3.8 (0.5–17.8)
61	489	30	24 Sep. 2003	28 Jan. 2004	57	18 Oct. 2003	23	2.6 (0.3–22.8)
62	504	29	22 Sep. 2003	12 Feb. 2004*	38	17 Oct. 2003	18	4.7 (0.4–19.1)
63	534	20	23 Sep. 2003	25 Dec. 2003	58	17 Oct. 2003	6	9.5 (1.6–28.1)
64	387	35	24 Sep. 2003	12 Feb. 2004*	70	27 Oct. 2003	19	2.2 (0.4–6.3)
65	698	20	22 Sep. 2003	26 Jan. 2004	61	7 Oct. 2003	14	6.0 (0.3–26.3)
66	403	42	22 Sep. 2003	12 Feb. 2004*	100	–	0	–
67	428	35	23 Sep. 2003	12 Feb. 2004*	65	27 Oct. 2003	29	1.7 (0.3–6.8)
68	538	32	22 Sep. 2003	12 Feb. 2004*	47	12 Oct. 2003	53	1.4 (0.3–1.4)
69	362	41	24 Sep. 2003	12 Feb. 2004*	100	–	0	–

[1] Fish caught during study period
[2] Fish tagged to replace Fish 50A during the study period; data excluded from the analysis
* End of study period
ALS = Automated listening stations

used for cyclical or periodical data (Batschelet 1981). The mean tide and time of day of the sea trips for each fish was calculated as theta (θ), the mean direction of the resultant vector (measured in radians). In order to not contravene the assumption of independence (Grafen and Hails 2002), θ for each fish was then used to calculate mean θ or mean tide and time of day that tagged spotted grunter undertook sea trips. The Rayleigh test of randomness (Batschelet 1981) was used to test whether the sea trips were random or whether they exhibited 'directedness/non-randomness' towards a specific tidal phase and to a specific time of day.

Non-linear 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 entire study period.

The effect of sea temperature, wind direction and atmospheric pressure on the number of tagged fish located in the estuary was determined using the manual tracking data. Wind and barometric pressure data were supplied by the South African Weather Service, and sea temperature was collected daily at the estuary mouth using a digital/electronic thermometer. Using circular statistics, the mean daily wind direction (θ), and mean direction (in radians) of the resultant vector (Batschelet 1981) were calculated. To find the optimal combination of parameters, the fit of the different models was assessed using the Akaike information criterion (AIC; Akaike 1973), and the 'Wald' statistic (W) and its p-level were used to test the significance of each regression coefficient. The number of fish located in the estuary on a given day during manual tracking was used as the response variable. Temperature and barometric pressure were used as continuous independent variables and wind as an independent categorical variable. Because the data of the response variable were discrete and Poisson-distributed, the log-link function was used in the analyses (McCullagh and Nelder 1995). The effect of a one-day and two-day lag on the independent variable and barometric pressure was also considered. The parameter wind was discarded in *a priori* AIC analysis and a two-sample t-test was then used to test for differences between the number of tagged fish located in the estuary during an east and west wind. To model the number of fish recorded in the estuary on a given day, the following parameters were included in a generalised linear model (GLM):

$$\text{Number fish in estuary} = \beta_0 + \beta_1 \text{ (sea temperature)} + \beta_2 \text{ (barometric pressure)} + \varepsilon$$

where β is the parameter vector and $\varepsilon \sim N(0, \sigma^2)$.

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

Results

Time spent in the estuary

Between 19 and 20 spotted grunter remained in the estuary for the first 18 days of the manual tracking period, after which between five and 17 fish were recorded daily. Fifteen fish were located in the estuary on the last day of the manual tracking period. In all, five fish did not go to sea during the manual tracking period and three permanently left the estuary after 15, 49 and 94 days (Table 1). Tagged fish were in the estuary for 67% of the entire sampling period (range 26–100%; Table 1).

Sea trips

A total of 15 fish undertook sea trips during the sampling period. Taking into account the time lag of 6 h, the number of sea trips made by each of the 15 individuals ranged between 6 and 53 (mean 19.7 ± 11.4 [SD], Table 1) and the mean duration of sea trips made by those 15 fish ranged between 0.8 ± 0.67 days and 9.5 ± 0.42 days, with an overall mean of 3.6 ± 2.5 days (Table 1). The minimum and maximum duration of sea trips made by each fish was 0.25 days and 28.1 days respectively (Table 1). Approximately half (52%) of the mean proportion of sea trips for each individual were short (6–24 h); 21% were between one and three days (Figure 2). Four individuals went to sea for a period of 3–4 weeks.

There were significant trends regarding the departure and arrival times of sea trips. The mean time (θ) that spotted grunter undertook sea trips was at 00:22 ± 01:52 (Rayleigh test: $p < 0.001$, $r = 0.88$, $n = 15$), whereas the mean time that they returned to the estuary was at 18:07 ± 02:51 (Rayleigh test: $p < 0.001$, $r = 0.72$, $n = 15$) (Figure 3). The sum of the mean proportion of departures recorded for each fish was 75% between 19:00 and 05:00, and the sum of mean proportion of return trips (arrivals) was 81% between 12:00 and 00:00.

The mean time after high tide that tagged spotted grunter left the estuary was 02:25 ± 02:35, i.e. on the outgoing tide, whereas the mean time that they returned to the estuary was 04:36 ± 00:48 after low tide, i.e. on the incoming tide (Figure 4). There was no significant relationship between the tidal phase and when spotted grunter undertook sea trips (Rayleigh test: $p > 0.05$, $r = 0.16$, $n = 15$), and no significant

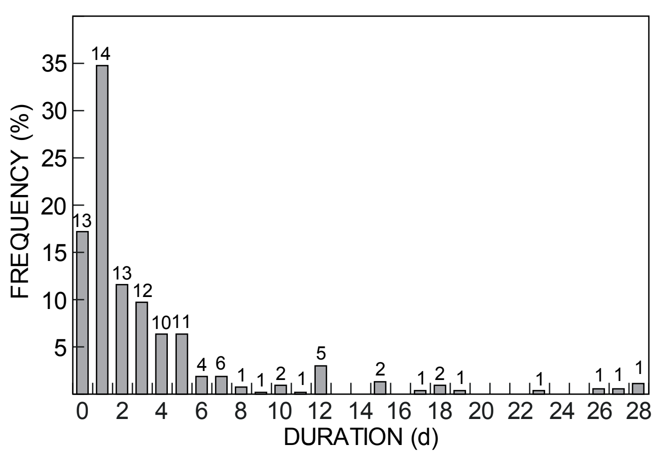

Figure 2: The mean proportion of sea trips of given duration made by each spotted grunter in the Great Fish Estuary during the study period (29 September 2003–12 February 2004). Number of individuals that undertook a sea trip of the given duration is shown above each bar

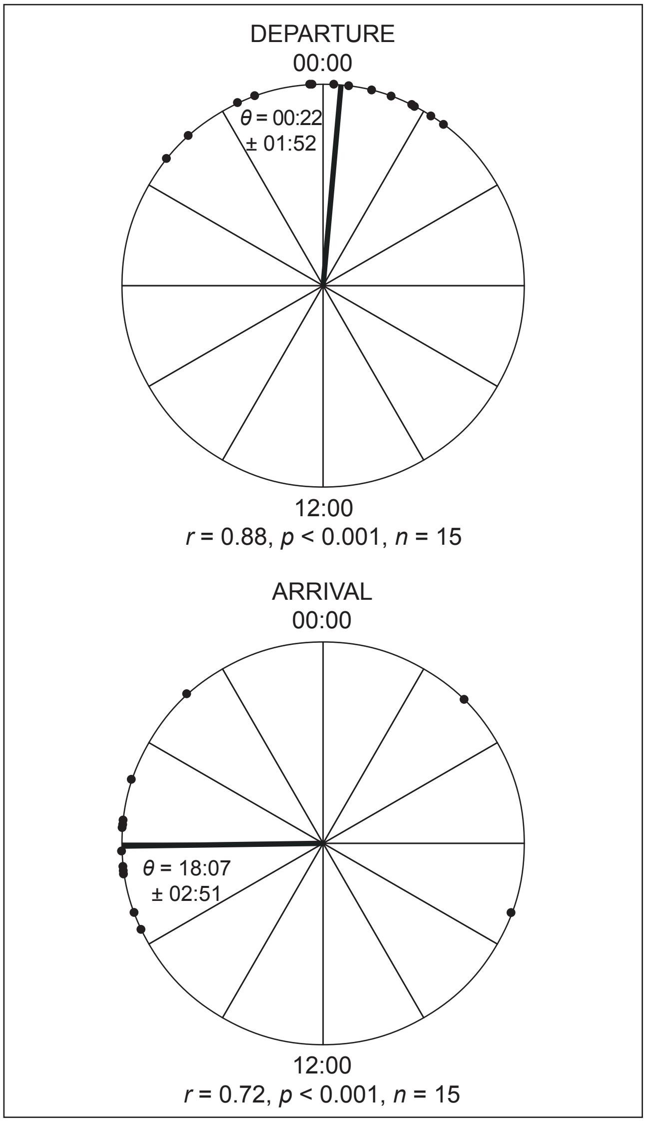

Figure 3: Mean (θ) departure and arrival times of tagged spotted grunter that undertook sea trips during the study (29 September 2003–12 February 2004)

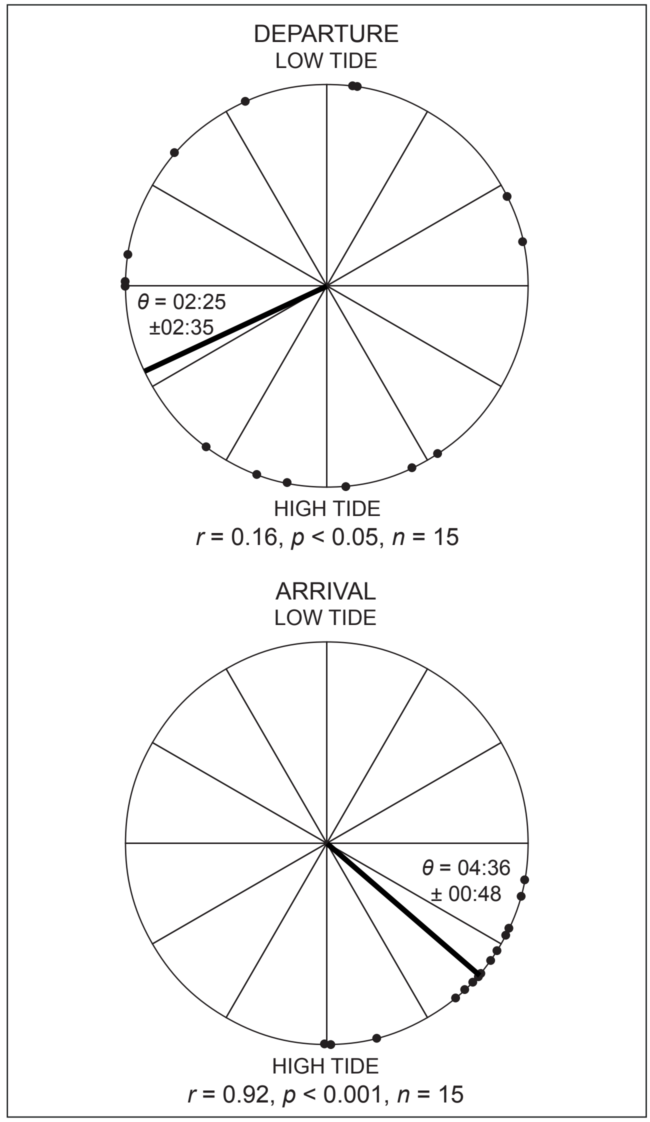

Figure 4: Tidal phase and mean (θ) time after low tide of tagged spotted grunter that undertook sea trips during the study (29 September 2003–12 February 2004)

relationship was found between the tidal phase and when they returned to the estuary ($p < 0.001$, $r = 0.92$, $n = 15$).

Effect of fish length

Spotted grunter <400 mm TL spent significantly more time in the estuary than larger individuals ($p < 0.01$, $r^2 = 0.62$, $F(1, 17) = 44.82$; Figure 5). Non-linear least squares regression estimated that the minimum time tagged individuals spent in the estuary during the entire study period was 53%. The effect of fish length on the number of sea trips was most evident in four of the five smallest fish, which remained resident in the estuary throughout the entire study period. The largest of those fish (Fish 51) went to sea for the first time after the manual tracking period (Table 1).

Effect of sea temperature, barometric pressure and wind direction

A significantly higher number of tagged fish were recorded in the estuary during cool sea temperatures (GLM: $p < 0.05$; $W(1) = 18.68$), high barometric pressure with a two-day lag (GLM: $p < 0.05$; $W(1) = 6.375$), and after an east wind ($p = 0.01$; $t(1, 36) = 2.66$).

Discussion

Spotted grunter use estuaries as nursery areas and are thought to move from the estuary to the marine environment with the onset of sexual maturity (Wallace 1975a). The present study supports this belief, by showing that spotted grunter <400 mm TL spent more time in the estuary than

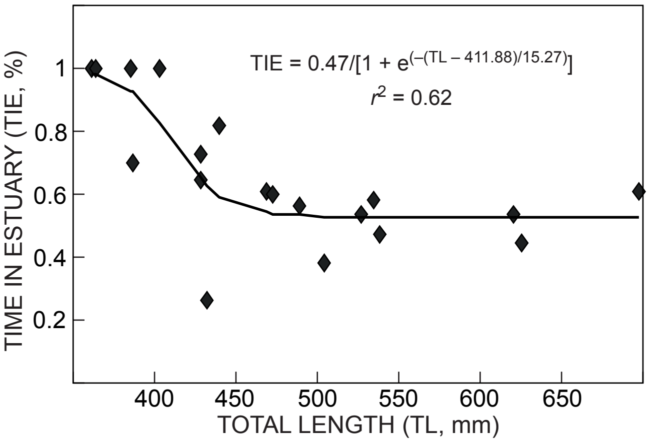

Figure 5: Relationship between the proportion of time (%) spent in the estuary and fish length for tagged spotted grunter in the Great Fish Estuary during the study (29 September 2003–12 February 2004)

larger fish. Short sea trips were more frequent in fish between 400 mm and 450 mm TL, and were less frequent, but longer, in fish >450 mm TL. More frequent use of the marine environment with increasing size may reflect the beginning of the marine phase of mature or maturing spotted grunter. Ontogenetic habitat shifts are common in fish (Gibson 1997). Such ontogenetic changes allow life stages to respond individually to the different selection pressures experienced in the environment (Ebenman 1992). In addition, effective use of resources often requires different movement patterns during the fish's lifetime (Pittman and McAlpine 2001). Tulevech and Recksiek (1994) identified a behavioural change in the movement patterns of white grunt *Haemulon plumieri,* which they attributed to an ontogenetic shift or a consequence of maturity. Hartill *et al.* (2003) found that the sea trips by the estuarine-dependent snapper *Pagrus auratus* in the Maruhangi Estuary, New Zealand, were in part related to fish length, with larger individuals undergoing more sea trips. The ontogenetic habitat shift found in the fish under study could therefore be explained by their onset of maturity, in the support of Wallace (1975b).

There was a high degree of estuarine use by the larger fish. Adult spotted grunter are believed to frequent estuaries seasonally to feed, particularly during their post-spawning phase (Wallace 1975a, 1975b, Bok 1988, Whitfield 1990, 1994) and possibly in a pre-spawning state (Webb 2002). The current study period coincided with the post-spawning phase. Feeding aggregations are often associated with adult post-spawning fish (Harden-Jones 1968, Pittman and McAlpine 2001) and estuaries along the South African coast function as feeding grounds for adults of many fish species (Cyrus 1991). The high abundance of mud prawn *Upogebia africana*, the preferred prey of spotted grunter in the Great Fish Estuary (Hecht and van der Lingen 1992), suggests that this estuary is an important feeding ground for adult spotted grunter.

The frequency and duration of sea trips varied among individuals. According to Willis *et al.* (2001), assumptions of homogeneous behaviour cannot always be made for a species. Individual behavioural traits are common among many fish species (e.g. Attwood and Bennett 1994, Jadot *et al.* 2002, Secor 1999, Hartill *et al*. 2003). During our study, all but one spotted grunter undertook sea trips of less than 28 days, suggesting that they did not leave the estuary for reproductive activity. The large percentage (50%) of short (6–24 h) sea trips undertaken may have simply been an expansion of the estuarine environment out of the estuary mouth at low tide. This would concur with the findings of Childs *et al*. (in press) that spotted grunter move upstream during the incoming tide and downstream during the outgoing tide. Fish 55 left the estuary permanently on the 10 November 2003 and had not returned by the end of the study period (approximately three months). This fish may have been predated or caught (by a fisher) while in the sea, or may have begun the marine phase of its life history and/or undertaken a spawning migration north-eastwards to KwaZulu-Natal (Wallace 1975b, Wallace and van der Elst 1975) (Figure 1). Bullen and Mann (2000, 2004) found that adult spotted grunter are capable of considerable long-shore coastal migrations in both north-east and south-westward directions.

The movements of spotted grunter between the estuarine and marine environments appear to be affected by tidal currents, and the number of fish in the estuary was significantly correlated with time of day, sea temperature, wind and barometric pressure. Spotted grunter left the estuary on the outgoing tide and returned to the estuary on the incoming tide. According to Gibson (2003), tidal migrations serve several functions that increase the fitness of individuals. Hartill *et al*. (2003) showed that half of tagged snapper *Pagus auratus* in the Maruhangi Estuary, New Zealand, exhibited tidal movements and suggested that utilising tidal currents enables the fish to explore an extensive estuarine area with minimal energy expenditure. Also, Tytler *et al.* (1978) suggested that Atlantic salmon *Salmo salar* smolts leave the estuary during ebb tides.

Most spotted grunter left the estuary between the evening and early morning, and most fish returned between mid-day and midnight. Hartill *et al.* (2003) found that the largest snapper during their study left the estuary 27 times over a two-month period, each time leaving in the early morning and returning in the afternoon. Spotted grunter left the estuary during the night and returned from mid-day onwards. Given that adult fish use estuaries predominantly for feeding (Whitfield 1994), it is possible that they enter the estuary on the incoming tide in the evening and night to feed and possibly depart on the outgoing tide. Fishers have reported higher catch rate of spotted grunter in the Great Fish Estuary at night than during the day (Potts *et al*. 2005).

Temperature appeared to influence the number of fish returning to and/or leaving the estuary, with a higher number of fish being recorded in the estuary during cold sea temperatures. Stone (1988) suggested that many fish species seek the warmer water of estuaries when the sea is cold. Even non-estuarine marine fish have been reported to take temporary refuge in warmer estuarine systems during cold upwelling events in the southern Cape coast (Hanekom *et al*. 1989, Whitfield 1996). After periods of high barometric pressure, the dominant easterly winds cause cold bottom water to upwell along some areas of the South Coast, resulting in rapid decline in the inshore temperature

(Schumann 1998). On the other hand, warmer sea temperatures predominate under low barometric pressure and are characterised by westerly winds and the absence of upwelling events. Spotted grunter were found mostly in waters of between 21 °C and 23 °C and appear to avoid water <16 °C (Childs *et al*. in press). This may explain why more tagged spotted grunter were recorded in the estuary during low sea temperatures and high barometric pressure.

Wind appeared to be a good predictor of the proportion of fish that were at sea. The average number of tagged fish in the estuary was higher after easterly winds than after westerly winds. This is perhaps because wind speed and direction influences and determines sea temperature (Schumann *et al*. 1982).

The results of this study have implications for fisheries management. In recent years, there has been a marked increase in fishing effort in estuaries along the South African coast (Lamberth and Turpie 2003). Furthermore, compliance with regulations regarding bag and size limits is low (Mann *et al.* 2002). Estuarine use by spotted grunter may render this species vulnerable to exploitation during both juvenile and post-spawning adult phases and alternative estuarine conservation measures could be beneficial for this species. Lamberth and Turpie (2003) suggested that an appropriate policy would be to conserve estuarine stocks as nursery and source areas for marine fish. Also, Wallace and van der Elst (1975) suggested 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 (Peterson *et al*. 2000, Lamberth and Turpie 2003), may be the time spent in the estuarine environment. This study has identified estuaries as essential habitats in the life history of spotted grunter. The degradation of such environments is of serious concern for estuarine-dependent fish (Wallace *et al*. 1984, Houde and Rutherford 1993). Given that estuaries serve as both migratory pathways and resident habitats during the early life-history stages of spotted grunter and other estuarine-dependent fish, the maintenance and conservation of estuarine environments should be an integral part in the management of these fish.

Acknowledgements — We sincerely thank Rupert Harvey for his dedicated support during the fieldwork, as well as Don Reynolds, Simon Daniel and Aidan Wood for help in the field. This research was funded by the South Africa / Norway Programme on Research Co-operation (National Research Foundation of South Africa, and the Research Council of Norway) (2003–2005). The collaborating institutions were the South African Institute for Aquatic Biodiversity and the Norwegian Institute for Nature Research, which are thanked for additional financial and infrastructure support.

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