Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry

A.-R. Childs*, P.D. Cowley, T.F. Næsje, A.J. Booth, W.M. Potts, E.B. Thorstad and F. Økland

*Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown, 6140, South Africa

Abstract

Telemetry methods were used to investigate the influence of selected environmental variables on the position and movement of an estuarine-dependent haemulid, the spotted grunter *Pomadasys commersonnii* (Lacepède 1801), in the Great Fish Estuary, South Africa. Forty individuals (263–698 mm TL) were surgically implanted with acoustic coded transmitters and manually tracked during two periods (7 February to 24 March 2003; *n* = 20 and 29 September to 15 November 2003; *n* = 20). Real-time data revealed that spotted grunter are euryhaline (0–37) and are able to tolerate large variations in turbidity (4–356 FTU) and temperature (16–30 °C). However, the fish altered their position in response to large fluctuations in salinity, temperature and turbidity, which are characteristic of tidal estuarine environments. Furthermore, tidal phase had a strong influence on the position of spotted grunter in the estuary.

1. Introduction

Estuarine-dependent fish species are defined as those who would be adversely affected by the loss of estuarine habitats (Whitfield, 1994c). Estuaries, like many other types of wetland worldwide, are under long-term threat of damage and destruction. Human degradation, coupled with an increase in fishing pressure on estuarine systems ([Wallace et al., 1984], [Houde and Rutherford, 1993], [Cattrijse et al., 2002], [Hartill et al., 2003] and [Lamberth and Turpie, 2003]), places estuarine fish species under threat. As a result, the importance of estuarine systems to fish species is widely acknowledged ([Lenanton and Potter, 1987], [Potter et al., 1990] and [Hartill et al., 2003]). Although, studies on the relationships between estuarine fish and environmental factors, such as salinity ([Whitfield, 1994a] and [Shervette et al., 2007]), temperature (Marshall and Elliot, 1998), turbidity (Cyrus and Blaber, 1987) and tidal currents (Szedlmayer and Able, 1993) have been examined world-wide, the relationship between fish movement and environmental factors in estuaries is not well documented. Studies of this nature require knowledge on the real-time movement of estuarine fishes in relation to the fluctuating environmental factors characteristic of estuarine environments. Such high resolution studies can only be conducted using telemetry techniques. Telemetry enables the monitoring of real-time movements of individual fish, and as a result determine the exact abiotic environment in which fish are found. Previous studies have only examined the effect of environmental factors on fish distribution, abundance and/or assemblages, and only a limited number of studies, namely (Almeida, 1996), (Szedlmayer and Able, 1993) and (Taverny et al., 2002) and Kelly et al. (2007), have tested the influence of these factors on fish movements in estuarine environments. Knowledge on the relationship between environmental factors and estuarine fish movements within an estuary is essential to improve our biological understanding of estuarine-dependent species.

The spotted grunter *Pomadasys commersonnii*, is an estuarine-dependent species found in inshore coastal regions and estuaries of the Western Indian Ocean (Smith and Heemstra, 2003). It spawns at sea and juveniles enter estuaries where they remain for a period of up to three years before returning to the marine environment ([Wallace, 1975a] and [Wallace, 1975b]). Consequently, early juveniles are considered to be entirely dependent on estuaries, while adult fish frequent estuaries, presumably to feed ([Wallace, 1975b] and [Whitfield, 1994c]). The survival of spotted grunter and other estuarine-dependent species in South African waters is determined by the existence of numerous estuarine systems along the coast ([Wallace et al., 1984] and [Whitfield, 1994c]). These estuaries are dynamic, unpredictable environments characterized by large environmental variation. Frequent, abrupt changes in salinity, temperature and turbidity place considerable physiological demands on fishes that occupy these systems (Harrison and Whitfield, 2006). Although estuarine fishes have evolved to tolerate large environmental fluctuations, they can also use movements to decrease environmental stress by finding areas that better suit their physiological needs ([Whitfield, 1994b] and [Whitfield, 1994c]). The aim of this study was to determine whether an estuarine-dependent haemulid, the spotted grunter, tolerates large fluctuations in salinity, temperature and turbidity, or if it uses behavioural responses such as tidal transport to move in response to fluctuating environmental conditions.

2. Materials and methods

2.1. Study site

The Great Fish River enters the Indian Ocean approximately halfway between the coastal cities of Port Elizabeth and East London at 33° 29′ 28″S, 27° 13′ 06″E (Fig. 1). It receives large volumes of freshwater from an interbasin transfer scheme, which ensures a continuous input of nutrients and suspended particles, resulting in a highly productive, but turbid estuary. The estuary is riverine in appearance, with an increase in turbidity towards the upper reaches. The perennial river flow together with the tidal exchange ensures a permanently open connection to the sea (Grange et al., 2000). The Great Fish Estuary is approximately 12 km in length and has a tidal prism of 1.6×10^6 m^3 (Whitfield et al., 1994). The spring tidal range is between 1 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 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). 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 bathymetry of the Great Fish Estuary is uniform and is mostly shallow, ranging between 1 and 2 m (mean 1.4 m), except for an area in the lower (±3–4 m), middle (3 m) and two areas in the upper reaches (±5–6 m). The shallow nature of the estuary is a result of the large fluvial sediment load from the catchment (Grange et al., 2000). The mouth region is restricted by the presence of extensive sand banks. The estuary is characterised by strong longitudinal and vertical physico-chemical gradients. The abiotic characteristics of the Great Fish Estuary were monitored at eight fixed stations during both study periods (the same locations as the ALS sites in the second period, see Fig. 1). Salinity (Practical Salinity Scale, Atago handheld refractometer), temperature (°C, digital/electronic thermometer), turbidity (FTU, Hanna 93703 turbidity meter), depth (m, graduated weighted rope) and current speed (m s^{-1}) were recorded. Current speed was calculated from the time that it took a neutrally buoyant object to move 2 m on the water surface. Water samples were taken approximately 30 cm above the bottom using a Van Doorn water sampler. River discharge (m s^{-1}) and conductivity (m s m^{-1}) were supplied by the Department of Water Affairs and Forestry, South Africa.

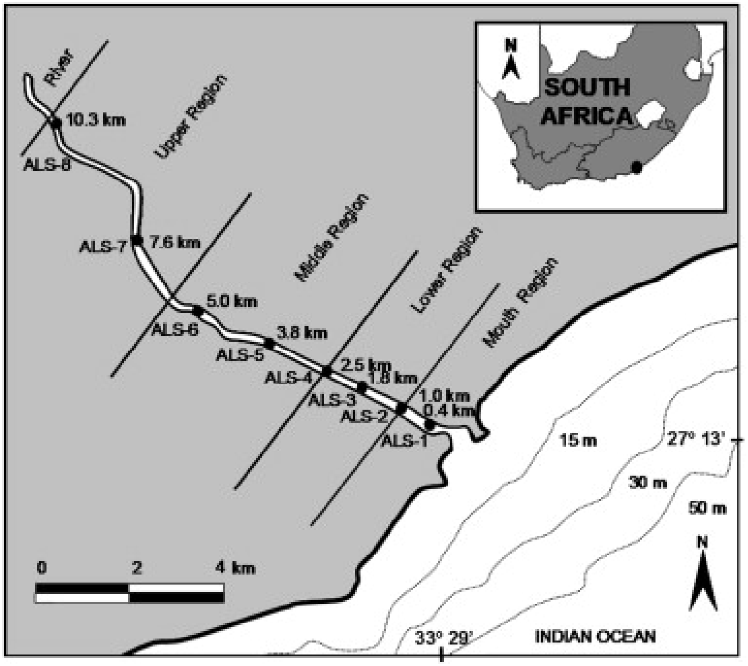

Fig. 1. Map of South Africa showing the location of the Great Fish River and a detailed map showing the position of the automated listening stations (ALSs) (black dots) in the Great Fish Estuary during the second period (29 Sep 2003 to 12 Feb 2004).

2.2. Research approach

Acoustic telemetry methods were used to track the movements of spotted grunter in the Great Fish Estuary during two periods. In the first period (7 February to 24 March 2003), 20 individuals between 263 and 387 mm TL (mean 336 mm TL) (Table 1) were tagged with VEMCO V8SC-2L-R256 (VEMCO Ltd, Halifax, Canada) coded transmitters (69 kHz). These tags had an expected battery life of 112 days, were 8.5 mm in diameter, 28 mm in length and weighed approximately 3.1 g in water being on average 0.75% of the fish body mass (min 0.5%, max 1.6%). In the second period (29 September to 15 November 2003), 20 fish between 362 and 698 mm TL (mean 478 mm TL) (Table 1) were tagged with VEMCO V13SC-1L-R256 coded transmitters (69 kHz). These tags had an expected battery life of 130 days, were 13 mm in diameter, 36 mm in length and weighed approximately 6 g in water being 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. Prior to this study, a pilot laboratory test was conducted on spotted grunter. Fish were tagged with 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. In addition, field trials were conducted by Kerwath et al. (2005), which revealed that the adopted techniques were appropriate for an acoustic telemetry study on this species. According to Wallace's (1975b) estimated size at sexual maturity (300–400 mm TL), the fish tagged in the first study period were mainly juveniles, while both adults and juveniles were tagged in the second period. Manual tracking of spotted grunter commenced 6 and 4 days after the last fish was released in the first and second periods, respectively, 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.

Table 1.

Details of the 40 acoustically tagged spotted grunter manually tracked in the Great Fish Estuary during the first (7 Feb to 24 Mar 2003) and second (29 Sep to 15 Nov 2003) periods, and acoustically monitored during the extended 137-day second period (29 Sep 2003 to 12 Feb 2004). Asterisks (*) indicate the end of the study period

Study period	Fish code	Total length (mm)	No. positional fixes	Date last recorded: manual tracking	Date last recorded: ALS monitoring (Period 2 only)
1	20	317	25	16 March 2003	
1	21	334	34	24 March 2003*	
1	22	297	20	7 March 2003	
1	23	380	36	24 March 2003*	
1	24	330	18	1 March 2003	
1	25	313	19	3 March 2003	
1	26	314	35	24 March 2003*	
1	27	328	12	19 February 2003	
1	28	382	34	24 March 2003*	
1	29	377	36	24 March 2003*	
1	30	308	36	24 March 2003*	
1	31	357	12	10 March 2003	
1	32	318	36	24 March 2003*	
1	33	329	13	9 March 2003	
1	34	263	8	17 February 2003	

Study period	Fish code	Total length (mm)	No. positional fixes	Date last recorded: manual tracking	Date last recorded: ALS monitoring (Period 2 only)
1	35	357	8	18 February 2003	
1	36	387	15	25 February 2003	
1	37	363	23	23 March 2003	
1	38	319	12	23 February 2003	
1	39	355	36	24 March 2003*	
2	50A[a]	449	12	11 October 2003	11 October 2003
2	50B[b]	515	15	15 November 2004*	28 January 2004
2	51	469	32	15 November 2004*	12 February 2004*
2	52	385	42	15 November 2004*	12 February 2004*
2	53	428	37	15 November 2004*	12 February 2004*
2	54	620	22	15 November 2004*	12 February 2004*
2	55	432	29	10 November 2003	10 November 2003
2	56	440	42	15 November 2004*	12 February 2004*
2	57	364	42	15 November 2004*	12 February 2004*
2	58	625	21	15 November 2004*	12 February 2004*
2	59	472	28	15 November 2004*	12 February 2004*
2	60	527	29	15 November 2004*	12 February 2004*
2	61	489	30	15 November 2004*	28 January 2004
2	62	504	29	15 November 2004*	12 February 2004*
2	63	534	20	15 November 2004*	25 December 2003
2	64	387	35	15 November 2004*	12 February 2004*
2	65	698	20	15 November 2004*	26 January 2004
2	66	403	42	15 November 2004*	12 February 2004*
2	67	428	35	15 November 2004*	12 February 2004*
2	68	538	32	15 November 2004*	12 February 2004*
2	69	362	41	15 November 2004*	12 February 2004*

[a] Fish that was caught during study.

[b] Fish that was caught and tagged during the study.

Tagged fish were manually tracked for 36 days in the first, and 42 days in the second period. Each period included two 16-consecutive day sampling sessions and an interim period of 14 days, during which fish were tracked every third day in the first and every second day in the second period. Each 16-consecutive day session was standardised according to the lunar phase and tracking was conducted over two semi-lunar cycles. Each session began 2 days prior to the first quarter (waxing) moon, and the last day of each session was the last quarter (waning) moon.

Manual tracking was conducted using a VEMCO VR60 receiver and VH10 hydrophone from a motorised boat. The position of each fish was recorded once a day. Manual tracking sessions began at the river mouth at approximately 08:00 h. When a fish was located, the boat was anchored, the coordinates were recorded using a GPS (Garmin 12) and water chemistry variables (salinity, temperature, turbidity, depth and current speed) were measured, as described above, when obtaining a positional fix for each fish. If all the fish were not recorded in the estuary, the sampling was extended into the riverine environment between 13 and 14 km upstream. 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 18:00 h. The number of positional fixes per fish varied during both sampling periods, as some fish undertook short-term sea trips or emigrated and did not return during the respective study periods (Table 1). Tests were conducted to determine the precision of tracking, using transmitters that were hidden at random locations within the estuary. On each occasion, the position was recorded within 1 m of the transmitter location.

During the second period, eight VEMCO VR2 acoustic listening stations (ALSs) were deployed along the length of the estuary from 29 September 2003 to 12 February 2004 (Fig. 1). The up and downstream movements of spotted grunter were therefore only monitored during the second period. These movements were monitored over the manual tracking period (29 September 2003 to 15 November 2003) and for an additional 95 days.

A reward system and an awareness campaign were implemented to ensure that fishers returned the transmitter of a tagged fish they had caught. One fish (Fish 50A) was caught and returned on 10 October 2003 and was replaced by another (Fish 50B) later in the study (Table 1). Subsequently these fish were excluded from all data analyses.

2.3. Data analyses

Data were analysed using GIS (ArcView® GIS 3.2) and the VEMCO software package. The position of the fish was expressed as ‘distance from the estuary mouth’. Given the longitudinal nature of the estuary, the estuary was divided into 500 m sections and the number of positional fixes recorded for each fish within each 500 m section was calculated as a proportion of the total number of fixes. The proportion of positional fixes calculated for each fish within each stretch was then averaged and presented as a frequency histogram. This ensured that the assumption of independence was not contravened (Grafen and Hails, 2002) and that the contribution of each individual fish was equally weighted.

2.3.1. Environmental variables

The frequency histograms for each of the environmental variables salinity, temperature, turbidity, depth and current speed were calculated as described above. Each environmental variable was binned into specific categories (e.g., 16–17 °C). The proportion of positional fixes for each fish within each category was averaged and the mean proportion of positional fixes within each category was presented as a frequency histogram. A Pearson product–moment correlation was used to assess the relationships between salinity, temperature and turbidity during the first and second periods.

The chi-square test of independence was used to test the hypothesis that the direction of fish movement was dependent on the tidal phase. A binomial test, corrected with the Bonferroni adjustment, was used to determine the probability of movement with and against the tide. An upstream or downstream movement was only considered if an individual fish passed more than one ALS in the same direction within 6 h. However, in the cases where the ALSs were situated more than 1 km away from each other, the assumption of an individual passing more than one ALS to constitute a movement did not apply, but instead the movement to each of these receivers within a 6 h period was considered as an upward or downward movement. All upstream movements were assigned a 1 and downstream movements a 2. The corresponding tidal state was then assigned to each of the upstream or downstream movements. For each fish, the number of movements upstream and downstream, as well as with and/or against the tide was calculated.

The relationship between fish position and tidal phase was analysed using a Rayleigh test of randomness (Batschelet, 1981). For this calculation, the estuary was divided into the lower (0–2 km from the estuary mouth), middle (2–6 km from the estuary mouth), upper (6–11 km from the estuary mouth) and riverine (>11 km from the estuary mouth) regions, based on the mean bottom salinities recorded at the eight fixed positions during the study. The mean time after low tide (h) that the positional fixes were recorded within each region of the estuary was expressed as theta (θ), the mean direction of the resultant vector (measured in radians). Theta for each fish was then used to calculate the mean time after low tide that all fish were recorded in each region. The number of observations in each stretch of the estuary varied and the significance of these observations could only be tested when more than five observations were recorded. The tidal phase was recorded when each fish was located. The time delay of the tide from sea to 10.3 km upstream was calculated using the daily depth values measured at each fixed station and was considered when assigning the tidal phase at each fish position.

2.3.2. Effect of environmental variables on fish movement

A generalized linear model was used to model the relationship between the relative change in a fish's position from time t to $t + 1$ and the relative change in salinity, temperature, turbidity and tide from time t to $t + 1$, fish size and season. Given the inherent autocorrelation generally found within telemetry data ([Dunn and Gipson, 1977], [Swihart and Slade, 1985] and [De Solla et al., 1999]), and hence the autocorrelation found in the present data, the relative change between all variables, dependent and independent, removed the inherent autocorrelation in the data and did not violate the assumptions of the linear regression approach. The 'Wald' statistic (W) and its p-level were used to test the significance of each regression coefficient. The response variable was the relative change in position (distance from the mouth) from time t to $t + 1$, and the continuous independent variables were the relative change in salinity, temperature, turbidity, and tide and the categorical variables were season (summer = period 1 and spring = period 2) and size of fish (small ≤400 mm TL and large >400 mm TL). Since the data of the response variable was continuous, the identity link function was used for variables with a normal distribution (McCullagh and Nelder, 1995). The following parameters were included in the generalized linear model (GLM):

$$\Delta\text{Fish position}=\beta_0+\beta_1(\Delta\text{Salinity})+\beta_2(\Delta\text{Temperature})+\beta_3(\Delta\text{Turbidity})+\beta_4(\Delta\text{Tide})+\beta_5(\text{Season})+\beta_6(\text{Size})+\varepsilon$$

where Δ is the relative change from time t to $t + 1$, β_* are the regression coefficients, and ε is the model residual where $\varepsilon \sim N(0,\sigma^2)$.

Movement was assumed to be upstream if the change was positive and downstream (towards the mouth) if the change was negative. Only data where consecutive days were sampled were included in the model.

Partial correlations (Yule, 1907) were used to test if any of the environmental variables (salinity, temperature, turbidity and tide) had an underlying influence on the relationship between these variables.

3. Results

Bottom temperatures recorded at the eight fixed water chemistry stations ranged from 15.2 to 29.5 °C in the first and from 15.7 to 25.8 °C in the second period. Bottom turbidities recorded at the fixed stations ranged from 12.4 to 762 FTU in the first and from 3.67 to 358 FTU in the second period, and bottom salinities ranged from 0 to 38 in both periods. Using the Venice System (Whitfield, 1998), the bottom salinity profile revealed euhaline conditions (30.0–39.9) from the mouth to 1 km upstream, polyhaline conditions (18.0–29.9) from 1 to 3.5 km upstream, mesohaline conditions (5.0–17.9) from 3.5 to 6 km upstream and oliogohaline conditions (0.5–4.9) from 6 km to the head of the estuary (12 km). Surface current speeds recorded at the fixed stations ranged from 0 to 0.76 m s^{-1} in the first and from 0 to 0.69 m s^{-1} in the second period. 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.

River discharge was relatively constant during both the first and second periods, with a mean discharge of 6.28 ± 1.86 m s^{-1} (range 1.48–9.76 m s^{-1}) and 5.13 ± 1.19 m s^{-1} (range 3.21–7.90 m s^{-1}), respectively. Mean conductivity was slightly higher in the second period (mean 176.17 m s m^{-1}; range 159–190 m s m^{-1}) when compared to the first period (mean 137.88 m s m^{-1}; range 121.3–149 m s m^{-1}).

The number of positional fixes per fish varied (range 8–42, mean 28 ± 10 SD) during both sampling periods, as some fish went to sea (Table 1).

In the first period, the position of spotted grunter in the estuary extended from the mouth to 12.1 km upstream. The mean proportion of observations was highest (90%) within 6.0 km of the estuary mouth, of which 68% were within the first 3.0 km and half (50%) between 1.0 and 1.5 km from the mouth (Fig. 2a).

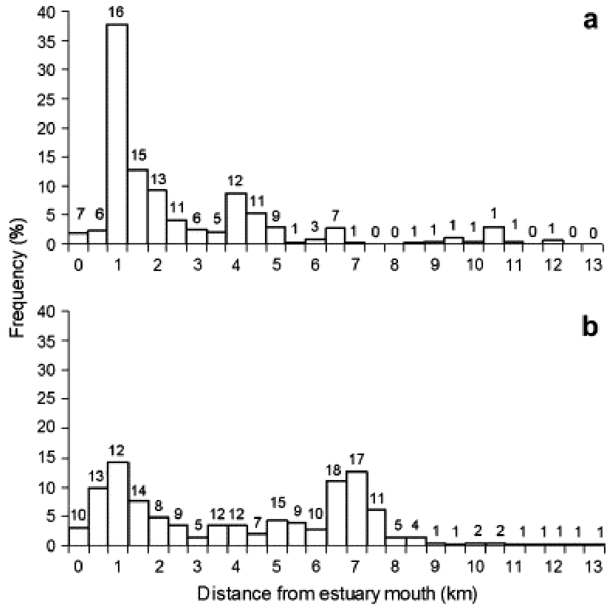

Fig. 2. Position of tagged spotted grunter in the Great Fish Estuary, based on the mean proportion of observations per 500 m zone recorded while manual tracking, during (a) the first (7 Feb 2003 to 24 Mar 2003) and (b) second (29 Sep 2003 to 15 Nov 2003) period. Numerical values above the bars indicate the number of individuals recorded in each 500 m zone.

In the second period, tagged individuals were positioned from the mouth to 13.4 km upstream. The distribution of fish along the estuary was bimodal, with 43% of the mean proportion of positional fixes recorded between the mouth and 3.0 km upstream and one-third (33%) in the upper reaches (6–8 km upstream). Only 19% were found in the middle reaches (3–6 km) and 5% in the uppermost region (8–13.5 km upstream) (Fig. 2b).

3.1. Environmental variables

3.1.1. Salinity

Spotted grunter were found in salinities ranging between 0 and 36 during both periods. The mean salinity in which tagged individuals were recorded was 22.1 and 15.5 in the first and second periods, respectively. Observations were not uniformly distributed (Fig. 3a). During the first period, the mean proportion of observations was highest (35%) in the euhaline range, while during the second period the mean proportion of observations was highest (29%) in the oligohaline range (Fig. 3a).

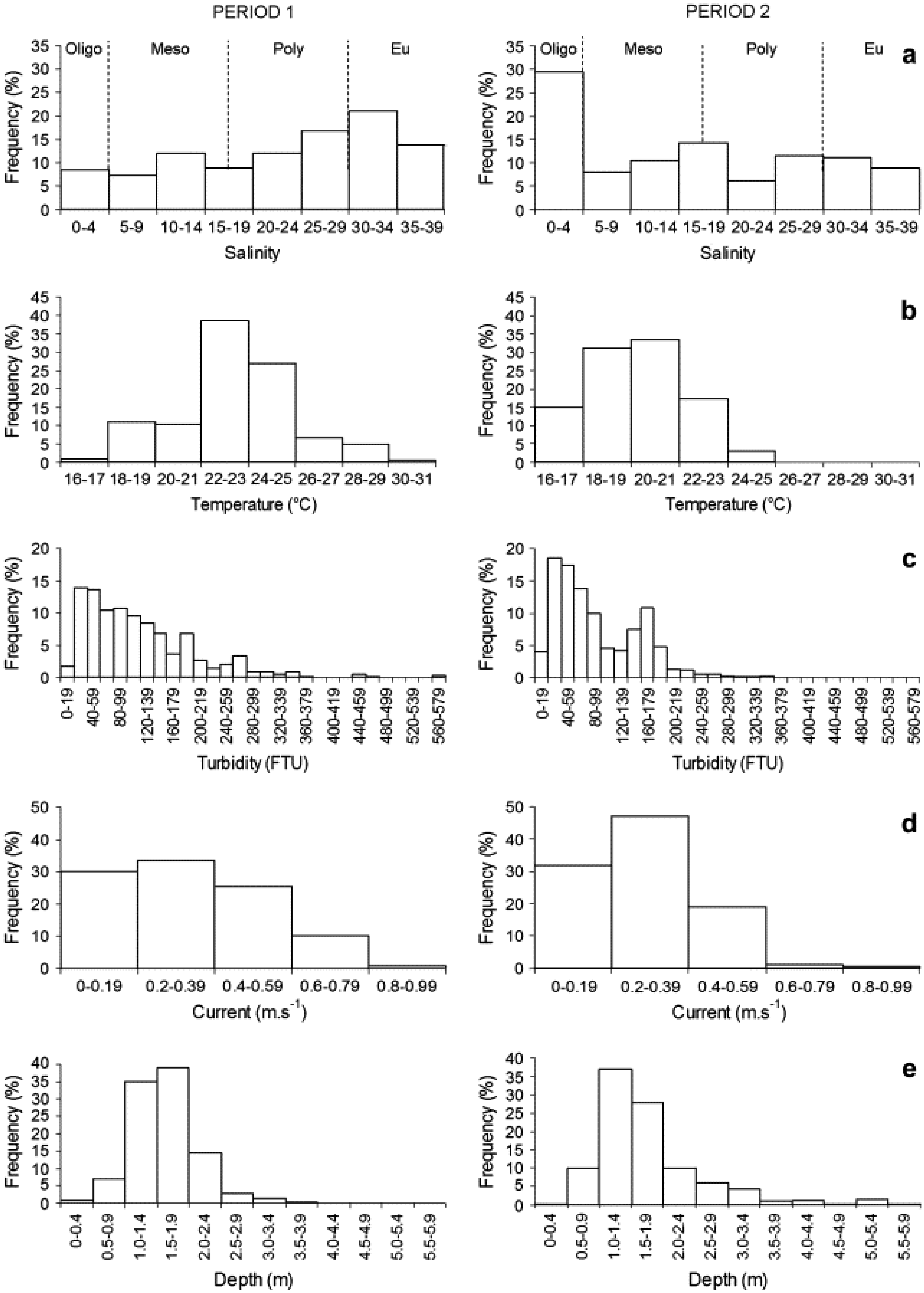
PERIOD 1
PERIOD 2
a
b
c
d
e
Oligo
Meso
Poly
Eu
Frequency (%)
0-4
5-9
10-14
15-19
20-24
25-29
30-34
35-39
Salinity
16-17
18-19
20-21
22-23
24-25
26-27
28-29
30-31
Temperature (°C)
0-19
40-59
80-99
120-139
160-179
200-219
240-259
280-299
320-339
360-379
400-419
440-459
480-499
520-539
560-579
Turbidity (FTU)
0-0.19
0.2-0.39
0.4-0.59
0.6-0.79
0.8-0.99
Current (m.s-1)
0-0.4
0.5-0.9
1.0-1.4
1.5-1.9
2.0-2.4
2.5-2.9
3.0-3.4
3.5-3.9
4.0-4.4
4.5-4.9
5.0-5.4
5.5-5.9
Depth (m)

Fig. 3. The mean proportion of observations describing (a) salinity (Oligo, oligohaline region; Meso, mesohaline region; Poly, polyhaline region; Eu, euhaline region, according to the Venice System), (b) temperature, (c) turbidity, (d) surface current speed and (e) depth at which tagged spotted grunter were recorded in the Great Fish Estuary during the first (7 Feb 2003 to 24 Mar 2003) (Period 1) and second (29 Sep 2003 to 15 Nov 2003) periods (Period 2).

3.1.2. Temperature

Mean water temperature at which spotted grunter were located was 23.0 °C (range 17.3–30.5 °C) in the first and 20.2 °C (range 16.3–25.3 °C) in the second period. The distribution of observations within each temperature range was not uniform (Fig. 3b). In the first period, the mean proportion of observations was highest (63%) between temperatures of 22 and 25 °C, while in the second period, 65% were in temperatures ranging between 18 and 21 °C (Fig. 3b). Although in the first period, the mean proportion of observations was only 10% in water temperatures higher than 25 °C, no observations were recorded in this range during the second period (Fig. 3b).

3.1.3. Turbidity

Spotted grunter were located in water ranging from 6.0 to 567.0 FTU (mean 111.5 ± 83.5 (SD) FTU) in the first and from 4.1 to 358.0 FTU (mean 92.7 FTU, SD 63.4) in the second period. In both the first (49%) and second (60%) periods, the mean proportion of positional fixes was greatest in water of 20–100 FTU, while in water less than 20 FTU it was low in both the first (1.8%) and second (4%) periods. The mean proportion of observations was also high in turbid water (exceeding 100 FTU) in both the first (49%) and second (36%) periods (Fig. 3c).

3.1.4. Depth

The mean water depth at which spotted grunter were located was 1.6 m (range 0.1–3.6 m) in the first and 1.7 m (range 0.4–5.9 m) in the second period. The mean proportion of positional fixes was highest at depths between 1 and 2 m in both the first (74%) and the second (65%) periods, but much lower in depths less than 1 m, in both the first (7.7%) and second (11%) periods. The mean proportion of observations was only 19% in water deeper than 2 m in the first, and 25% in the second period (Fig. 3d).

3.1.5. 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 period. The maximum surface current speed (0.93 m s^{-1}) in which spotted grunter were recorded was in the mouth region of the estuary. The observations were not uniformly distributed. The mean proportion of observations was highest at current speeds ranging between 0 and 0.39 m s^{-1} in both the first (64%) and second (79%) periods (Fig. 3e).

3.1.6. Tidal phase

The position of spotted grunter in the estuary was influenced by the tidal phase. Spotted grunter were found in the lower reaches of the estuary during low tide and in the upper reaches during the incoming and high tides. In the first period, spotted grunter were located in the lower reaches of the estuary around low tide (mean time after low tide, θ = 11:20 ± 01:59; $p < 0.005$; $r = 0.50$; $n = 20$), in the middle reaches on the incoming tide (mean time after low tide, θ = 01:31 ± 02:15; $p > 0.01$; $r = 0.36$; $n = 18$), and in the upper region of the estuary on the high tide (mean time after low tide, θ = 05:26 ± 00:30; $p < 0.001$; $r = 0.97$; $n = 8$). While only one fish was recorded in the riverine environment, this fish was recorded on average during the incoming and high tide (mean time after low tide, θ = 04:53 ± 01:49). Similarly, in the second period, spotted grunter were found in the lower reaches of the estuary during low tide (mean time after low tide, θ = 00:52 ± 01:48; $p < 0.001$; $r = 0.59$; $n = 17$), in the middle reaches of the estuary on the incoming tide (mean time after low tide, θ = 02:22 ± 01:43; $p < 0.001$; $r = 0.63$; $n = 18$) and in the upper reaches on the incoming tide (mean time after low tide, θ = 03:38±01:16; $p < 0.001$; $r = 0.79$; $n = 19$). Although the number of fish located in the riverine environment was too low to test the significance of the tidal phase on fish position, the three fish recorded in this region were located on average during the high tide (mean time after low tide, θ = 06:06 ± 00:28).

The probability of movements with the tide for each tagged fish was significant (Binomial test: $p < 0.01$). The mean percentage of movements made by the tagged spotted grunter with the tide was 93%, compared with movements made against the tide (5%), during high (1%) and low tide (1%). The direction of fish movement up and downstream was dependent on the tidal cycle ($\chi^2 = 5462.3$; $p < 0.001$). The mean percentage of upstream movements made with the incoming tide was 95%, while the mean percentage of downstream movements made with the outgoing tide was also 95%.

3.2. Effect of environmental variables on fish movement

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

The results from the linear model showed that the change in salinity ($p < 0.001$; $W(1) = 48.76$), temperature ($p < 0.01$; $W = 10.58$), turbidity ($p < 0.01$; $W = 9.58$), and tide ($p < 0.05$; $W = 4.74$) from time t to $t + 1$ had a significant effect on the change in fish position from time t to $t + 1$. There was no significant difference between season (summer and spring) ($p = 0.78$; $W = 0.08$) and fish size ($p = 0.92$, $W = 0.01$). Therefore, the relative change (Δ) in spotted grunter position in the estuary from time t to $t + 1$ was determined by the positive relative change in temperature and turbidity, and negative change in salinity and tide, from time t to $t + 1$. This is described by the equation:

$$\Delta\text{Fish position} = 0.01 - 0.06\Delta\text{Salinity} + 0.16\Delta\text{Temperature} + 0.003\Delta\text{Turbidity} - 0.16\Delta\text{Tide}$$

Partial correlation values revealed that after controlling for salinity, turbidity, temperature and tide, the relationship between these variables remained constant.

4. Discussion

The conservation of biodiversity and management of aquatic environments in particular has become a major concern in recent years. The linear nature of most estuaries, and their high degree of linkage with freshwater and marine ecosystems, makes estuarine habitats highly vulnerable to external perturbations ([Whitfield, 1998] and [Cattrijse et al., 2002]). It was noted more than a decade ago that anthropogenic activities could lead to the periodic or permanent elimination of estuarine-dependent fish species from individual estuarine systems ([Cyrus, 1991], [Peterson et al., 2000] and [Kennish, 2002]). Such activities include poor farming practices which result in siltation (extremely high turbidity levels) and construction of impoundments in the catchment which result in freshwater abstraction (salinity extremes and hypersaline conditions). Since the adults of many estuarine-dependent species are exploited commercially, the preservation of estuarine habitats is critical for the maintenance of many marine fisheries (Lenanton and Potter, 1987). Therefore, knowledge of the response of estuarine fishes to changes in environmental conditions will not only enhance our biological understanding of estuarine fish, but will contribute to our understanding of the potential affects of anthropogenic impacts on estuarine fish species.

Salinity has been viewed as one of the most important variables influencing the utilisation of organisms in estuaries (Marshall and Elliot, 1998). Spotted grunter are euryhaline (Whitfield, 1980) and have been found to tolerate salinities from 0 to 90 (Whitfield et al., 1981). In this study, spotted grunter were located in a wide range of salinities (ranging from 0 to 36). The variation in the mean salinity between the first and second periods 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 period. Ter Morshuizen et al. (1996) and Bate et al. (2002) suggested that the high conductivity levels of the Great Fish Estuary, in comparison to the upper reaches of other Eastern Cape estuaries, promotes the utilisation of the upper and head regions of the estuary by euryhaline fish species, such as the spotted grunter. The higher mean conductivity in the second period, when compared to the first, could have facilitated the utilization of the upper reaches of the Great Fish Estuary by spotted grunter in the second period.

Temperature has been identified as the primary abiotic factor controlling key physiological, biochemical and life-history processes of fish (Beitinger and Fitzpatrick, 1979), and has been found to influence the utilisation of estuaries by fishes worldwide ([Morin et al., 1992], [Thiel et al., 1995], [Baldwin et al., 2002] and [Harrison and Whitfield, 2006]). Generally, fish have a thermal preference that optimizes physiological processes. Spotted grunter were however located in a wide range of temperatures during both periods. The large variation in water temperature, between and within both periods, was due to the large tidal fluctuation in the estuary, with cold incoming seawater and warm outgoing freshwater. Although the mean water temperature at which spotted grunter were located was 23 °C in the first and 20 °C in the second period, the thermal preference of 0+ juveniles under culture conditions was found to be between 24 and 25 °C (Deacon and Hecht, 1995). Lower temperatures are likely to reduce metabolism and growth. The very low sea temperatures (<16 °C) recorded at the beginning of the second period (unpublished data) may account for the noticeable peak in spotted grunter position observed in the upper reaches of the estuary during this period. The upper reaches may have provided a thermal refuge and caused the fish to move to this region where they maintained position for an extended period (10–14 days). This suggests that spotted grunter may use movement in response to temperature variations within the Great Fish Estuary.

Turbidity has also been found to influence the utilization of estuaries by fishes ([Blaber and Blaber, 1980], [Blaber, 1981], [Cyrus, 1992], [Akin et al., 2005] and [Bennett et al., 2005]). Spotted grunter were found in both exceptionally clear and turbid waters. Field sampling and laboratory experiments have also shown that spotted grunter are indifferent to turbidity ([Cyrus and Blaber, 1987], [Hecht and van der Lingen, 1992] and [Whitfield et al., 1994]), probably because they are macrobenthic carnivores and rely primarily on tactile stimuli when foraging (Whitfield, 1998). The real-time data collected in this study suggest that spotted grunter are physically adapted to tolerate large variations in turbidity.

The large tidal prism in the Great Fish Estuary creates wide fluctuations in environmental conditions during a single tidal phase. During low tide, conditions in the lower reaches of the estuary were characterized by reduced salinity, increased turbidity and warmer freshwater (particularly in summer). During high tide, conditions in the lower reaches are characterized by high salinity, low turbidity and cooler sea water. Spotted grunter were found in the lower reaches during the outgoing and low tides, and in the middle and upper reaches during the incoming and high tides. Continuous 24-h data collected in the second period by the eight acoustic listening stations corroborate these findings of the manual tracking data by showing that spotted grunter moved upstream during the incoming tide and downstream during the outgoing tide. Although it was found that spotted grunter have a broad physico-chemical tolerance, this information suggests that spotted grunter may follow a particular suite of environmental variables while making use of the strong currents of the Great Fish Estuary. Such behaviour may alleviate the physiological demands (e.g. thermoregulatory stress) that are placed on fishes that occupy estuarine systems (Harrison and Whitfield, 2006) and consequently minimize energy expenditure. The use of tidal currents for movement thereby minimizing energy expenditure, has been suggested by other authors studying the movements of adult thin-lipped grey mullet *Liza ramado* (Risso 1810) (Almeida, 1996), American eel *Anguilla rostrata* (Lesueur 1817) (Helfman et al., 1983), and salmon smolts *Oncorhynchus kisutch* (Walbaum 1792) (Miller and Sadro, 2003). Although fish are likely to occupy positions in an estuary that optimises their physiological needs, Matthew (1990) suggests that strong selection also exists for animals to occupy areas of optimal resource availability. For example, the major food source of spotted grunter, the mud prawn *Upogebia africana* (Ortmann 1894) are most abundant and concentrated in the muddy intertidal lower reaches of the Great Fish Estuary (Hecht and van der Lingen, 1992). This mirrors with the noticeable peaks observed in the position of spotted grunter in the lower reaches during both periods. Furthermore, while the influence of the tidal cycle on the feeding intensity of spotted grunter is not known, optimal foraging theory (McArthur and 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.

Although this study has found that spotted grunter are tolerant to large fluctuations in salinity and turbidity, and to a fairly wide range in temperature during the daily tidal phases, the results also indicate that a change in tide and the subsequent changes in salinity, temperature and turbidity do cause a change in position of spotted grunter in the estuary. Season had no effect on the relative change in position of the fish, despite the decrease in temperature and turbidity observed during the second period. However, low temperatures (≤16 °C), typical of the spring season, may have induced a behavioural response in spotted grunter to evade low temperatures by moving upstream. The size of fish had no effect on the relative change in position of the fish and even the smaller individuals (whose distribution was confined to the lower reaches of the estuary in the first period) altered their position with changes in environmental conditions. Spotted grunter may well be physiologically adapted to survive in this wide range of environmental conditions, but it appears that they use movement and selective use of tidal currents to minimise energy expenditure and remain in optimal environmental conditions.

5. Conclusion

The results of this study suggest that the most important environmental factor governing the movement of the estuarine-dependent spotted grunter in the Great Fish Estuary is tidal phase and the associated changes in salinity, temperature and turbidity. However, low sea temperatures may supersede these factors and determine the position of spotted grunter in the estuary. These results suggest that anthropogenic impacts (construction of dams, water abstraction, and inter-basin transfer schemes) that are able to cause large environmental fluctuations, particularly in salinity and turbidity, could influence the movement of spotted grunter in estuarine environments.

Acknowledgements

We would like to thank Rupert Harvey most sincerely for his dedicated support during the fieldwork. Tia and Hendrik Swart are thanked for providing access to the caravan park and its facilities during the study. This research was funded by the SA/Norway program on research co-operation (2003–2005). The collaborating institutions, SAIAB and NINA, are thanked for additional financial and infrastructure support.

References

Akin, S., Buhan, E., Winemiller, K.O., Yilmaz, H. Fish assemblage structure of Koycegiz Lagoon-Estuary, Turkey: Spatial and temporal distribution patterns in relation to environmental variation (2005) Estuarine, Coastal and Shelf Science, 64 (4), pp. 671-684.

Almeida, P.R. Estuarine movement patterns of adult thin-lipped grey mullet, Liza ramada (Risso) (Pisces, Mugilidae), observed by ultrasonic tracking (1996) Journal of Experimental Marine Biology and Ecology, 202 (2), pp. 137-150.

Batschelet, E. (1981) Circular Statistics in Biology. Academic Press, London 371 pp.

Baldwin, C.M., Beauchamp, D.A. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry (2002) Transactions of the American Fisheries Society, 131 (1), pp. 143-158.

Bate, G.C., Whitfield, A.K., Adams, J.B., Huizinga, P., Wooldridge, T.H. The importance of the river-estuary interface (REI) zone in estuaries (2002) Water SA, 28 (3), pp. 271-279.

Beitinger, T.L., Fitzpatrick, L.C. Physiological and ecological correlates of preferred temperature in fish (1979) American Zoology, 19 (1), pp. 319-329.

Bennett, W.R., Edmondson, G., Lane, E.D., Morgan, J. Juvenile white sturgeon (Acipenser transmontanus) habitat and distribution in the Lower Fraser River, downstream of Hope, BC, Canada (2005) Journal of Applied Ichthyology, 21 (5), pp. 375-380.

Blaber, S.J.M. The zoogeographical affinities of estuarine fishes in south-east Africa. (1981) South African Journal of Science, 77 (7), pp. 305-307.

Blaber, S.J.M., Blaber, T.G. Factors affecting the distribution of juvenile estuarine and inshore fish (1980) Journal of Fish Biology, 17, pp. 143-162.

Cattrijse, A., Codling, I., Conides, A., Duhamel, S., Gibson, R.N., Hostens, K., Mathieson, S., (...), McLusky, D.S. Estuarine development/habitat restoration and re-creation and their role in estuarine management for the benefit of aquatic resources (2002) Fishes in Estuaries, pp. 266-321. Cited 6 times. Elliot M., and Hemingway K.L. (Eds), Blackwell Science Ltd, UK

Cyrus, D.P. Fish conservation in South African estuaries: pressures, problems and prospects (1991) South African Journal of Aquatic Science, 17, pp. 19-27.

Cyrus, D.P. Turbidity gradients in two indo-pacific estuaries and their influence on fish distribution (1992) South African Journal of Aquatic Science, 18 (1-2), pp. 51-63.

Cyrus, D.P., Blaber, S.J.M. The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. (1987) Continental Shelf Research, 7 (11-12), pp. 1411-1416.

Deacon, N., Hecht, T. Observations on the thermoregulatory behaviour of juvenile spotted grunter, Pomadasys commersonnii (Haemulidae: Pisces) (1995) Journal of Applied Ichthyology, 11 (1-2), pp. 100-110.

De Solla, S.R., Bonduriansky, R., Brooks, R.J. Eliminating autocorrelation reduces biological relevance of home range estimates (1999) Journal of Animal Ecology, 68 (2), pp. 221-234.

Dunn, J.E., Gipson, P.S. Analysis of radio telemetry data in studies of home range (1977) Biometrics, 33 (1), pp. 85-101.

Grafen, A., Hails, R. (2002) Modern Statistics for the Life Sciences. Oxford University Press Inc., New York

Grange, N., Whitfield, A.K., De Villiers, C.J., Allanson, B.R. The response of two South African east coast estuaries to altered river flow regimes (2000) Aquatic Conservation: Marine and Freshwater Ecosystems, 10 (3), pp. 155-177.

Harrison, T.D., Whitfield, A.K. Temperature and salinity as primary determinants influencing the biogeography of fishes in South African estuaries (2006) Estuarine, Coastal and Shelf Science, 66 (1-2), pp. 335-345.

Hartill, B.W., Morrison, M.A., Smith, M.D., Boube?e, J., Parsons, D.M. Diurnal and tidal movements of snapper (Pagrus auratus, Sparidae) in an estuarine environment (2003) Marine and Freshwater Research, 54 (8), pp. 931-940.

Helfman, G.S., Stoneburner, D.L., Bozeman, E.L., Christian, P.A., Whalen, R. Ultrasonic telemetry of American eel movements in a tidal creek (1983) Transactions of the American Fisheries Society, 112, pp. 105-110.

Hecht, T., van der Lingen, C.D. Turbidity-induced changes in feeding strategies of fish in estuaries (1992) South African Journal of Zoology, 27 (3), pp. 9-107.

Hill, B. Respiratory adaptations of three species of Upogebia (Thalassinidea, Crustacea) with special reference to low tide periods (1981) Biological Bulletin, 160 (2), pp. 272-279.

Houde, E.D., Rutherford, E.S. Recent trends in estuarine fisheries: predictions of fish production and yield (1993) Estuaries, 16 (2), pp. 161-176.

Kelly, J.T., Klimley, A.P., Crocker, C.E. Movements of green sturgeon, Acipenser medirostris, in the San Francisco Bay estuary, California (2007) Environmental Biology of Fishes, 79 (3-4), pp. 281-295.

Kennish, M.J. Environmental threats and environmental future of estuaries (2002) Environmental Conservation, 29 (1), pp. 78-107.

Kerwath, S.E., Go?tz, A., Cowley, P.D., Sauer, W.H.H., Attwood, C. A telemetry experiment on spotted grunter Pomadasys commersonnii in an African estuary (2005) African Journal of Marine Science, 27 (2), pp. 389-394.

Lamberth, S.J., Turpie, J.K. The role of estuaries in South African fisheries: Economic importance and management implications (2003) African Journal of Marine Science, 25, pp. 131-157.

Lenanton, R.C.J., Potter, I.C. Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. (1987) Estuaries, 10 (1), pp. 28-35.

Marshall, S., Elliott, M. Environmental influences on the fish assemblage of the Humber estuary, U.K. (1998) Estuarine, Coastal and Shelf Science, 46 (2), pp. 175-184.

Matthews, K.R. An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (Sebastes spp.) (1990) Environmental Biology of Fishes, 29 (3), pp. 161-178.

McArthur, R.H., Pianka, E.R. On optimal use of a patchy environment (1966) The American Naturalist, 100 (916), pp. 603-609.

McCullagh, P., Nelder, J.A. Log-linear models (1995) Generalized Linear Models McCullagh P., and Nelder J.A. (Eds), Chapman and Hall, London

Miller, B.A., Sadro, S. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon (2003) Transactions of the American Fisheries Society, 132 (3), pp. 546-559.

Morin, B., Hudon, C., Whoriskey, F.G. Environmental influences on seasonal distribution of coastal and estuarine fish assemblages at Wemindji, eastern James Bay (1992) Environmental Biology of Fishes, 35 (3), pp. 219-229.

Næsje, T.F., Childs, A.-R., Cowley, P.D., Potts, W.M., Thorstad, E.B., Økland, F. Movements of undersized spotted grunter (Pomadasys commersonnii) in the Great Fish Estuary, South Africa: Implications for fisheries management (2007) Hydrobiologia, 582 (1), pp. 25-34.

Peterson, C.H., Summerson, H.C., Thomson, E., Lenihan, H.S., Grabowski, J., Manning, L., Micheli, F., Johnson, G. Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat (2000) Bulletin of Marine Science, 66 (3), pp. 759-774.

Potter, I.C., Beckley, L.E., Whitfield, A.K., Lenanton, R.C.J. Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa (1990) Environmental Biology of Fishes, 28 (1-4), pp. 143-178.

Shervette, V.R., Ibarra, N., Gelwick, F. Influences of salinity on growth and survival of juvenile pinfish Lagodon rhomboides (Linnaeus) (2007) Environmental Biology of Fishes, 78 (2), pp. 125-134.

Smith, M.M., Heemstra, P.C. (2003) Smiths' Sea Fishes Struik Publishers, Cape Town, South Africa 1047 pp.

Swihart, R.K., Slade, N.A. Testing for independence of observations in animal movements. (1985) Ecology, 66 (4), pp. 1176-1184.

Szedlmayer, S.T., Able, K.W. Ultrasonic telemetry of age-0 summer flounder, Paralichthys dentatus, movements in a southern New Jersey estuary (1993) Copeia, 1993 (3), pp. 728-736.

Taverny, C., Lepage, M., Piefort, S., Dumont, P., Rochard, E. Habitat selection by juvenile European sturgeon Acipenser sturio in the Gironde estuary (France) (2002) Journal of Applied Ichthyology, 18 (4-6), pp. 536-541.

Ter Morshuizen, L.D., Whitfield, A.K., Paterson, A.W. Distribution patterns of fishes in an Eastern Cape estuary and river with particular emphasis on the ebb and flow region (1996) Transactions of the Royal Society of South Africa, 51, pp. 257-280.

Thiel, R., Sepulveda, A., Kafemann, R., Nellen, W. Environmental factors as forces structuring the fish community of the Elbe Estuary (1995) Journal of Fish Biology, 46 (1), pp. 47-69.

Wallace, J.H. The estuarine fishes of the east coast of South Africa. I. Species composition and length distribution in the estuarine and marine environments. II. Seasonal abundance and migrations (1975) Investigational Report of the Oceanographic Research Institute, 40, pp. 1-72.

Wallace, J.H. The estuarine fishes of the east coast of South Africa. III. Reproduction (1975) Investigational Report of the Oceanographic Research Institute, 41, pp. 1-51.

Wallace, J.H., Kok, H.M., Beckley, L.E., Bennett, B., Blaber, S.J.M., Whitfield, A.K. South African estuaries and their importance to fishes. (1984) South African Journal of Science, 80 (5), pp. 203-207.

Whitfield, A.K. A quantitative study of the trophic relationships within the fish community of the Mhlanga Estuary, South Africa (1980) Estuarine and Coastal Marine Science, 10, pp. 417-435.

Whitfield, A.K. Abundance of larval and O+ juvenile marine fishes in the lower reaches of 3 southern African estuaries with differing freshwater inputs (1994) Marine Ecology Progress Series, 105 (3), pp. 257-268.

Whitfield, A.K. Fish species diversity in southern African estuarine systems: An evolutionary perspective (1994) Environmental Biology of Fishes, 40 (1), pp. 37-48.

Whitfield, A.K. An estuary-association classification for the fishes of southern Africa (1994) South African Journal of Science, 90 (7), pp. 411-417.

Whitfield, A.K. Biology and ecology of fishes in southern African Estuaries. Ichthyological Monographs of the J.L.B (1998) Smith Institute of Ichthyology, 2, pp. 1-223.

Whitfield, A.K., Blaber, S.J.M., Cyrus, D.P. Salinity ranges of some southern African fish species occurring in estuaries (1981) South African Journal of Zoology, 16, pp. 151-155.

Whitfield, A.K., Paterson, A.W., Bok, A.H., Kok, H.M. A comparison of the ichthyofaunas in two permanent open eastern Cape estuaries (1994) South African Journal of Zoology, 29 (2), pp. 175-185.

Yule, G.U. On the theory of correlation for any number of variables treated by a new system of notation (1907) Proceedings of the Royal Society. Series A, 79, pp. 182-193.