



Riding the tide: estuarine movements of a sciaenid fish, *Argyrosomus japonicus*

Tor Fredrik Næsje^{1,2,*}, Paul Denfer Cowley², Ola Håvard Diserud¹, Amber-Robyn Childs², Sven Ebo Kerwath^{3,4}, Eva Bonsak Thorstad¹

¹Norwegian Institute for Nature Research, 7485 Trondheim, Norway

²South African Institute for Aquatic Biodiversity, Grahamstown 6140, South Africa

³Department of Agriculture, Forestry and Fisheries, Rogge Bay 8012, South Africa

⁴Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

ABSTRACT: The movement behaviour of juvenile dusky kob *Argyrosomus japonicus* ($n = 25$) was studied in the 12 km long Great Fish Estuary, South Africa, by collecting telemetry data in relation to tidal conditions over 6.5 mo. Two behavioural patterns were observed. Tagged fish either moved in circatidal rhythms over long stretches up and down the estuary, corresponding to the speed and direction of the rise and fall of the tide, or remained stationary, often in deeper or structured habitats. All individuals alternated between moving (mean 61% of the time) and stationary behaviour. Moving periods occurred during both light and dark periods. However, up-estuary movements were initiated most frequently at night, while down-estuary movements were initiated most frequently at dawn and dusk. The mean distance of the unidirectional movements was approximately 3.2 km. Ground speed for up-estuary movements (0.29 m s^{-1}) was faster than for down-estuary movements (0.22 m s^{-1}). These findings suggest that juvenile *A. japonicus* adopt 2 distinct feeding strategies within their turbid estuarine nursery habitats. 'Riding the tide', with minimal energy expenditure, may be a successful strategy when feeding on prey that follow the tidal current. Alternatively, in periods when they adopt a stationary behaviour, they may fulfil their foraging requirements by feeding on stationary and/or passing prey, while at the same time reducing predation risk in sheltered, structured habitats.

KEY WORDS: Circatidal rhythms · Movement behaviour · Environmental factors · Telemetry · *Argyrosomus japonicus*

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INTRODUCTION

Fundamental questions for understanding animal behaviour are: Why do individuals move? How, where and when should individuals move? What are the ecological consequences of moving? Central to addressing these questions is the need to elucidate the proximate causes for observed movement patterns (Nathan et al. 2008). Animal movements are often cyclic processes initiated by external cues, which may be abiotic factors like temperature and light, or biotic factors like food availability, predator

avoidance and access to reproduction (Lucas & Baras 2001). The timing of cyclic movements may be controlled by exogenous clocks such as the solar and lunar rhythms, which are responsible for periodic changes in light and tidal levels (Wilcockson & Zhang 2008). Circadian or circatidal movements of aquatic animals can be ascribed to several functions such as foraging, predator avoidance, reproduction and the selection of optimal environmental conditions (Gibson 2003, Chabot & Watson 2010). These functions are not mutually exclusive, and individual behaviour may be a trade-off among several of these.

*Email: tor.naesje@nina.no

Many mammals, fishes, crustaceans, annelids and molluscs that live in estuarine and coastal habitats are influenced by the cyclic tidal changes (Wilcockson & Zhang 2008). The tide typically causes large and predictable fluctuations in food availability, salinity, temperature, current, predators and turbidity (Burrows et al. 1994, Wilcockson & Zhang 2008), and has been shown to cause significant circatidal movements in animal populations (Forward & Tankersley 2001, Gibson 2003).

The variation in environmental factors in estuaries is closely linked to the freshwater input and tidal phase (Wallace et al. 1984). The influence of environmental factors on the movement patterns of estuarine fish species, however, is poorly understood, although some studies have examined the relationship between estuarine fish behaviour and salinity, temperature and turbidity (Cyrus & Blaber 1987, Whitfield 1994).

The dusky kob *Argyrosomus japonicus* is a large estuarine-dependent sciaenid found in the coastal waters of South Africa and Mozambique, and in Indo-Pacific waters to Japan and Australia in the east and Pakistan in the west (Heemstra & Heemstra 2004, Silberschneider & Gray 2008). It is one of South Africa's most sought-after commercial, recreational and subsistence fishery species (Brouwer et al. 1997, Griffiths 1997a). *A. japonicus* can live in excess of 40 yr and attain a body mass of 75 kg; they sexually mature at approximately 100 cm (Griffiths & Heemstra 1995, Griffiths 1996). Spawning occurs in the marine environment. Early juveniles (<15 cm total length, TL) occur exclusively in estuaries, while older juveniles (up to <100 cm TL) are found in estuaries and the surf zones (Griffiths 1996). In South Africa, *A. japonicus* is currently managed as a single stock.

Over-fishing poses the single biggest threat to estuarine-associated fishes in South Africa (Whitfield & Cowley 2010), and the juvenile estuarine-dependent phase has been viewed as a life history bottleneck (Lamberth & Turpie 2003). The spawner biomass per recruit ratio of *Argyrosomus japonicus* has been reduced to between 1.0 and 4.5% of its unfished condition, probably caused by over-fishing during the juvenile estuarine-dependent phase (Griffiths 1997a). While much is known of the biology of *A. japonicus* (Griffiths 1996, 1997b), little information exists on its movements (Taylor et al. 2006, Cowley et al. 2008). An understanding of the driving forces for the movements of individuals is important to gain insights into the ecology of estuarine-dependent fishes and contribute to the corrective management of overexploited species.

In this study, we aimed to investigate the effects of the tidally influenced estuarine environment on juvenile *Argyrosomus japonicus* movements by answering the following questions: (1) Are there any movement patterns, and how can they potentially be described? (2) Are fish movements correlated with tidal movements? (3) Do up- and down-estuary movements vary with respect to distance moved, movement speed and time of the day? (4) Can fish with potentially restricted movements be linked to more structured habitats in the estuary? To achieve this, 25 juvenile *A. japonicus* equipped with acoustic transmitters were monitored for 195 d in their estuarine nursery habitat, where the tidal dynamics were concurrently monitored with data-logging depth sensors. We hypothesized that the direction, duration and timing of fish movements would be correlated with the tidal flow.

MATERIALS AND METHODS

Study area

The 650 km long Great Fish River enters the Indian Ocean on the South African coast (33° 29' S and 27° 13' E, Fig. 1). The tidally influenced estuary is 12 km long, 30 to 100 m wide, highly turbid, and mostly 1 to 2 m deep (maximum depth 6 m; Grange et al. 2000). The deeper parts were found in pools in the lower reaches (ca. 1 km), middle reaches (ca. 4 to 5 km) and upper reaches (ca. 7 km; Childs et al. 2008b). Besides the pylons of the existing and old road bridges, 1 km from the mouth, there are no significant submerged structures. Cowley et al. (2008) showed that tagged juvenile *Argyrosomus japonicus* made extensive use of the estuary, from the mouth to the top (10.3 km).

Physico-chemical environment

The estuary has a large tidal prism volume ($1.6 \times 10^6 \text{ m}^3$) that exceeds the river volume by approximately 6 times during an average tidal cycle (Whitfield 1994). Due to freshwater inputs from an inter-basin transfer system, the estuary exhibits a net outflow of residual water.

Physico-chemical variables were studied in February to March and September to November 2003 (Childs 2005, Childs et al. 2008b). The estuary was characterized by strong longitudinal and vertical physico-chemical gradients, with bottom salinities ranging from 0.0 to 33.0 (Fig. 1), temperatures from

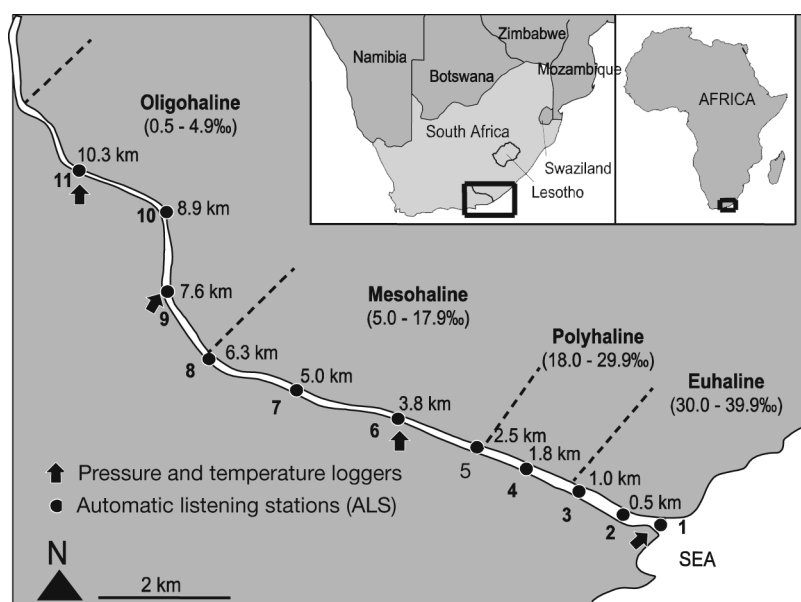


Fig. 1. Location of the Great Fish Estuary in the Eastern Cape Province of South Africa, and a map divided into salinity zones according to the Venice System (1959), with the positions of stationary receivers (automatic listening station, ALS-1 to ALS-11) and pressure and temperature loggers

15 to 30°C and turbidity from 4 to 762 Formazin Turbidity Unit (FTU). Flood and ebb mean tidal current speeds were 0.21 and 0.41 m s⁻¹ in the lower, 0.33 m and 0.34 m s⁻¹ in the middle, and 0.21 and 0.11 m s⁻¹ in the upper reaches. The water temperature increased and the difference between surface and bottom temperatures decreased up-estuary, while the mean salinity and the difference between surface and bottom salinities decreased over the same stretches. Mean turbidity and the difference between surface and bottom turbidities increased up-estuary. The environmental variables temperature, salinity and turbidity were strongly correlated (r^2 : 0.25 to 0.66, $p < 0.001$), with the strongest correlation between temperature and salinity, and the weakest between temperature and turbidity. The variation in temperature should therefore be a good indicator for the variation in salinity and turbidity.

During the present study, the tidal dynamics of the estuary were monitored using 4 stationary data-logging pressure (depth) and temperature sensors (VEMCO Minilog, Fig. 1). Data-loggers were used to record temperatures, quantify the tidal flux (m), daily tidal cycle (high and low tides), duration (h, min) and direction (up- or down-estuary) of each half tidal cycle, and lunar tidal cycle (spring and neap tides). The variation in temperature, both within and between tidal cycles, expressed as standard deviation, were largest in the mouth (within SD = 0.89, between

SD = 0.64) and lower part of the estuary at 3.8 km (within SD = 0.95, between SD = 0.74). The variation in temperature at 7.6 km (within SD = 37, between SD = 0.22) and at the top of the estuary at 10.3 km (within SD = 0.29, between SD = 0.14) were small. Correspondingly, the cross-correlation between tide and temperature were strongest at lag 0, i.e. the temperature decreased when the tide rose in the estuary mouth and at 3.8 km (estuary mouth: cross correlation function (CCF) lag 0 = -0.20, $p < 0.001$; 3.8 km: lag 0 = -0.41, $p < 0.001$). However, at the stations at 7.6 and 10.3 km, the tidal variation within the tidal cycle did not explain the temperature variation.

Fish tagging

Twenty-five juvenile *Argyrosomus japonicus* (mean total length: 334 ± 31 mm, range: 256 to 400) were internally tagged with acoustic transmitters (Table 1). Fish were caught with rod and line between 2.4 and 7.0 km (mean: 4.7 ± 1.6 km) from the estuary mouth during 14 February to 10 March 2004. Surgery and release of the fish took place at the catch site. After being anaesthetised, the fish were measured to the nearest millimetre. During surgery, the gills were continuously flushed with estuarine water, and the transmitter was surgically inserted into the body cavity. The fish was released back into the estuary when fully recovered. For closer description of the method used, see Cowley et al. (2008). The individually-coded transmitters (V8SC-2L-R256, VEMCO) were 28 mm long, 8.5 mm in diameter, weighed 3.1 g in water (average 0.8% of the fish body mass, range: 0.5 to 1.9%), emitted a signal at a random pulse interval of 10 to 30 s and had an expected battery life of 190 d.

Fish tracking

An array of 11 stationary receivers (automatic listening station, ALS; VEMCO VR2), were deployed 300 to 1400 m apart along the estuary. The receivers were moored to a concrete block positioned on the substrate, and used to monitor fish movements between 3 March and 14 September 2004 (Fig. 1). The first 7 to 16 d after tagging were omitted from the

Table 1. *Agyrosomus japonicus*. Details of the juveniles acoustically tagged and monitored in the Great Fish Estuary between 3 March and 14 September 2004. *: fish caught during the study, CCF: cross-correlation coefficient between movement direction of *A. japonicus* and tidal direction for lag 0. Dates are given as dd/mm. Data collection commenced on 03/03 for all fish except 81 (17/03) and 99 (16/03)

Fish ID	Total length (cm)	Catch site (km from mouth)	Date tagged in 2004	No. of days monitored	CCF
70	36.6	5.1	22/02	195	0.39
71	34.1	5.0	16/02	46	0.54
73	34.7	5.8	14/02	193	0.22
74	36.2	7.0	15/02	123	0.25
75*	31.7	5.1	15/02	15	0.53
77	37.7	5.1	15/02	16	0.62
78	34.9	5.7	14/02	50	0.41
79	35.0	5.0	16/02	194	0.37
80	40.0	5.1	15/02	7	0.82
81	33.5	5.1	10/03	40	0.65
82	31.4	5.0	16/02	27	0.43
83*	33.1	5.9	16/02	27	0.63
84*	30.9	5.0	16/02	68	0.53
85	30.7	5.0	16/02	47	0.65
86	34.2	7.0	15/02	45	0.64
88	32.9	7.0	15/02	10	0.47
89	35.5	5.8	14/02	195	0.41
91	34.9	2.4	18/02	67	0.38
92	30.8	2.4	18/02	47	0.14
94	28.4	2.4	18/02	8	0.74
95	31.4	2.4	18/02	50	0.61
96	35.1	2.4	18/02	47	0.60
97	30.9	3.2	18/02	46	0.44
98*	25.6	2.4	18/02	15	0.60
99	32.2	3.2	09/03	189	0.40

data analysis depending on the date tagged. The ALSs identified and stored the unique identification codes of tagged fish when they were within the reception range, which varied from 110 to 610 m, depending on receiver position and environmental conditions. All receivers, except ALS-1 and ALS-2, had a minimum detection range exceeding the width of the estuary. Hence, all passing fish were recorded. Due to occasionally poor reception ranges in the mouth caused by strong water currents and wave action, some fish passed ALS-1 and ALS-2 on rare occasions without being detected. Therefore, a fish was assumed to be in the sea if detections were recorded by 1 of the 2 lowermost receivers before and after an absence period exceeding 24 h.

Data analysis

The data analysis is organized into (1) estuarine movement patterns, (2) fish and tide movements,

(3) up- and down-estuary movement dynamics and (4) stationary behaviour. In addition, background data of tidal dynamics and the overall time *Argyrosomus japonicus* spent in the estuary are described.

When comparing the behaviour of individual fish, we alternated between 2 different measures of central tendency: the arithmetic mean and the median. The median was used to reduce the influence of extreme values, e.g. fish with a short observation period and few recordings, or unrealistic movement estimates due to inaccuracies in the definition of a few fish locations. In the first example, we present the median of individual means, whereas in the latter example, we first calculated the individual median before taking the mean of all fish.

The variance for each variable (e.g. duration of moving period) is presented as ± 1 SD. When testing whether there was any significant correlation between movement variables and other fish characteristics, such as body length, we applied a test statistic that follows a *t*-distribution with d.f. = $n - 2$ (e.g. Zar 1999).

Data were analysed using the statistical software R 2.11 (R Development Core Team 2009) and the VEMCO VUE software. In order to compare and correlate different time series with varying time steps between transmitter detections, the series were assigned values for each minute. The periods in the series with time gaps larger than 1 min between detections were interpolated. Between consecutive detections of a single transmitter, the interpolated values for receiver locations were set to the average of the 2 actual detections. Therefore, a tagged fish was assumed to remain at the same station if the 2 detections were made on the same receiver, or halfway between stations if the 2 consecutive detections were made on neighbouring receivers (Simpfendorfer et al. 2002).

Estuarine movement patterns

Fish movements were classified as: (1) 'stationary' if a fish was only detected on 1 receiver, or alternating between the same 2 neighbouring receivers for a period exceeding the duration of the tidal cycle (12 h 18 min), or (2) 'moving' if a fish was detected on 3 or more neighbouring receivers (in 1 direction) during a period of less than 12 h 18 min (Fig. 2). As a result, a fish classified as moving travelled a minimum of 800 to 2700 m (i.e. the distance between any 3 receivers), depending on its location within the estuary. Additionally, a fish was defined as having left the estuary

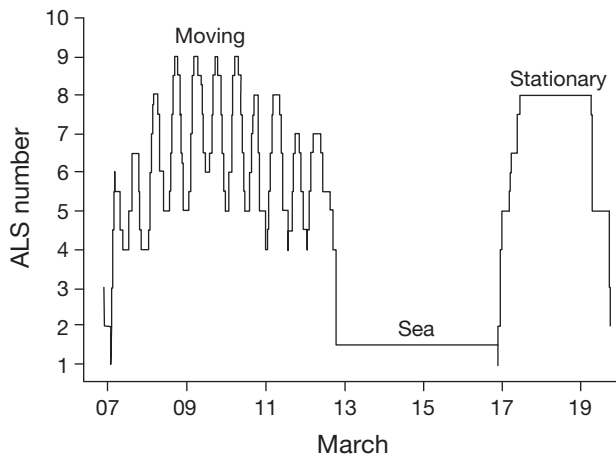


Fig. 2. *Agyrosomus japonicus*. Movement pattern of an individual in the Great Fish Estuary during 7 to 19 March 2004, illustrating moving and stationary periods, and a sea journey. ALS: automatic listening station

permanently if it was last detected on ALS-1 and/or ALS-2, and did not return to the estuary during the study period.

The duration of a single unidirectional movement was defined as the time between the last detection on the first receiver and the first detection on the last receiver in a single direction. The accuracy of each unidirectional movement, in terms of distance, might vary by a few hundred meters due to variable receiver ranges. Also, the receivers did not have overlapping detection ranges, and a movement bout might have started between receivers, resulting in a slightly longer total movement than described. These inaccuracies did not significantly influence the results, as the lengths of the movements were usually more than an order of magnitude larger than the maximum possible deviation from the starting point.

Fish and tide movements

Fish movements were tested for correlations with the tidal cycle and tide direction. The duration of a full tidal cycle, 12 h 18 min based on the tidal dynamics registered by the depth sensors, was chosen as the time period to describe movement patterns.

The relationship between each unidirectional movement and the direction of the tidal current (i.e. changes in depth at the closest pressure logger), was evaluated using the cross-correlation function (Wei 2005). The cross-correlation function correlates 1 univariate time series with an increasingly delayed version of another series. A unidirectional movement

was assigned a value of -1 when the fish moved down the estuary, $+1$ when it moved up and 0 when it was turning or stationary. The direction of tide was classified as -1 for decreasing depth (ebbing), $+1$ for increasing depth (flooding) and 0 if there was no depth change (slack tide). Only the cross-correlations for a time lag of 0 are presented, as there was no indication of a delay between the time when a movement was initiated and a change in depth recorded by the pressure loggers. The cross-correlation was calculated for periods when the fish were classified as 'moving'.

Up- and down-estuary movement dynamics and stationary behaviour

The investigations of the up- and down-estuary movement dynamics of *Argyrosomus japonicus* with respect to duration, distance moved, speed and starting time were based on the registration of individual fish by the automatic listening stations. For these fish movement variables, there were a few extreme values. The median was therefore chosen as a measure of the central tendency when comparing individual movements.

The duration of the unidirectional movements, either up- or down-estuary, was estimated as time between the last detection on the first receiver and the first detection on the last receiver of the unidirectional movement, while length of the same movement was estimated as the distance between the first and last receiver. The minimum movement speed relative to land during a unidirectional movement was estimated as the length of a movement divided by its duration. Some of the movement speeds may be over- or under-estimated due to varying detection ranges, but using the individual median speed in the subsequent analyses reduces the effect of extreme observations. Paired-sample *t*-tests (Zar 1999) were used to test whether there were significant differences in the duration, length or speed between the unidirectional movements up- and down-estuary.

To test whether fish movements were initiated at spring or neap tide, the tidal amplitude when each movement started was compared to the mean tidal amplitude for the whole corresponding spring/neap tide period. For example, if spring tide triggered the movements, the amplitude when a movement started would be expected to be larger than the mean tidal amplitude for that period. A paired-sample *t*-test was used (Zar 1999) to test the difference in the tidal amplitudes.

The areas of the estuary where fish were classified as being stationary were compared with known deeper areas and structures such as bridge pillars in the estuary and the behaviour of the most important prey items of *Argyrosomus japonicus*.

RESULTS

Tidal dynamics

The tide in the Great Fish Estuary has a semi-diurnal cycle with 2 high and 2 low periods daily. The tidal flux in the estuary mouth varied between 0.3 and 2.5 m during the study period (mean: 1.34 m). Based on the recording of the tidal cycle, the average lunar cycle was 28 d, 23 h 40 min, while a full tidal cycle, from 1 high tide to the next, was 12 h 18 min. The study period (195 d) comprised 380.5 tidal cycles.

Time spent in the estuary

Over the 195 d study period, 4 individuals were caught in the local fishery and 18 moved to sea and did not return. The mean study period of individual fish within the estuary was 61 ± 67 d (range: 7 to 195 d, Fig. 3). Sixteen fish (64%) made 1 or more sea journeys and returned to the estuary during their respective study periods (Fig. 3). There was no correlation between body length and the proportion of time spent at sea, or time spent in the estuary before leaving the estuary for those not returning (time at sea: $R = 0.33$, $p = 0.11$; time in estuary: $R = 0.20$, $p = 0.33$).

Estuarine movement patterns

While in the estuary, the fish were moving on average $61 \pm 25\%$ (range: 17 to 99%) of the time (Fig. 3). The proportion of time moving decreased with the total time individuals remained in the estuary before permanently leaving ($R = -0.77$, $p < 0.001$). The 4 fish caught by anglers were among the fish with the highest proportion of time moving (mean: 84%, range: 80 to 89%). There was no relationship between body length and the proportion of time spent moving ($R = -0.32$, $p = 0.12$).

The duration of the moving periods varied within and among individuals (Fig. 3). Of the individuals' median moving periods, 68% were longer than 12 h, while 50% were longer than 24 h and 40% longer than 48 h. Hence, 50% of the moving periods per-

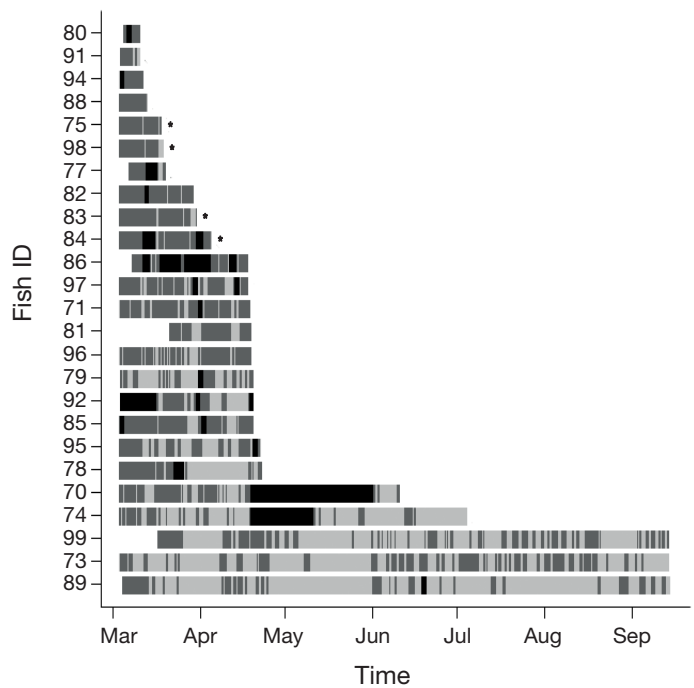


Fig. 3. *Argyrosomus japonicus*. Stationary (light grey) and moving (dark grey) periods in the estuary, and time spent at sea (black) for individually tagged fish in the Great Fish Estuary between 3 March and 14 September 2004. *: fish caught in the estuary

sisted both during light and dark. The mean of the individual median duration of moving periods was 54.0 ± 52.5 h (range: 9.5 to 219.9 h), while the mean of the individual median duration of stationary periods was 30.1 ± 17.2 h (range: 13.6 to 81.4 h).

Fish and tide movements

The direction of fish movements was correlated with the direction of the tide, as most of the moving fish moved up-estuary during flood and down-estuary during ebb tide. For all individuals, there was a highly significant positive cross-correlation ($p < 0.001$) between the time series of the directional movements up or down the estuary, with the direction of the tide (Table 1). All individual cross-correlations had a maximum at lag 0, indicating that there was no time lag between fish movements and tidal changes. The CCF, however, varied among individuals (from 0.14 to 0.82, mean 0.50 ± 0.16). Fish that spent a large proportion of time moving in the estuary had movements that were better correlated with the tidal movements ($R = 0.69$, $p < 0.001$). Exclusion of the 4 fish caught during the study did not change this regression.

The number of unidirectional movements (either up- or down-estuary) within a moving period varied within and among individuals (mean of individual medians: 7.0 ± 7.5 , range: 1 to 34). The duration of most unidirectional movements (73%) was shorter than half a tidal cycle (i.e. 6 h 9 min). The unidirectional movements of only 1 fish (id: 73) moving up-estuary and 3 fish (ids: 70, 73, 74) moving down-estuary had a median movement duration exceeding half a tidal cycle.

Up- and down-estuary movement dynamics

The mean individual duration of down-estuary movements (4.6 ± 1.5 h, range: 1.3 to 7.6 h) was greater (2 sample *t*-test, $p = 0.033$) than the mean individual duration of up-estuary movements (3.7 ± 1.5 h; range: 1.1 to 8.4 h). Maximum duration of movements was obtained for fish with few movements.

The length of the movements up- or down-estuary did not differ, as the mean individual median distance was 3.2 ± 0.8 km (range: 1.2 to 4.4 km) and 3.1 ± 0.7 km (range: 1.4 to 4.4 km), respectively (2 sample *t*-test, $p > 0.05$). Approximately half (54%) of the up-estuary movements started around ALS-2 and ALS-4, and stopped near ALS-7 or ALS-8 (51%). The down-estuary movements started around ALS-7 and ALS-8 (49%) and stopped near ALS-2 and ALS-4 (54%).

The ground speeds differed between up- and down-estuary movements (paired *t*-test, $p < 0.001$), with most (88%) of the fish having a higher median movement speed when swimming up the estuary. The mean median speeds were 0.29 ± 0.08 ms⁻¹ for up-estuary and 0.22 ± 0.08 ms⁻¹ for down-estuary movements. There was no correlation between individual median speeds and body length (up-estuary movements: $R = 0.18$, $p = 0.39$; down-estuary movements: $R = 0.19$, $p = 0.36$).

The starting time of movements differed between up- and down-estuary movements (Fig. 4). Up-estuary movements began most frequently at night from 23:00 to 03:00 h, with a smaller peak during the day from 11:00 to 14:00 h. The down-estuary movements started most frequently during dawn and dusk, from 04:00 to 08:00 h and 17:00 to 19:00 h (i.e. 5 to 6 h later than the up-estuary movements). There was no significant difference between the mean tidal amplitude when movements started and the mean tidal amplitude for the entire spring/neap tidal cycle. Hence, movements were neither significantly correlated to spring nor neap tide.

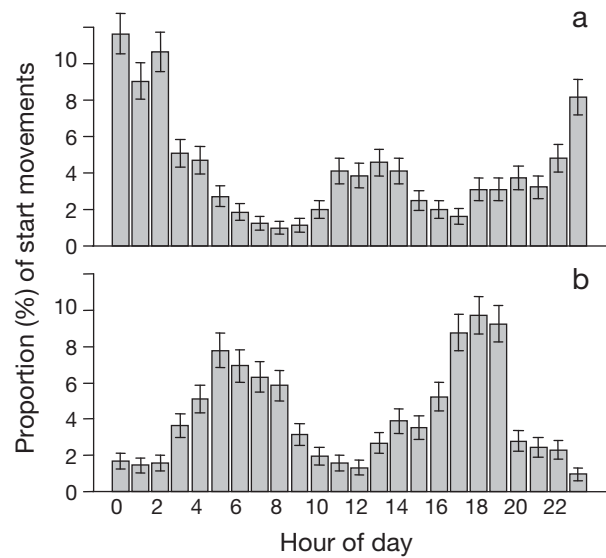


Fig. 4. *Agrosomus japonicus*. Proportion (%) of all (a) up-estuary ($n = 806$) and (b) down-estuary ($n = 822$) movements that started each hour of the day during 3 March to 14 September 2004

Stationary behaviour

During their stationary periods, most fish ($n = 18$) used only 1 area, while some fish ($n = 7$) used 2 areas. These areas occurred throughout the estuary, but most were near ALS-2 and ALS-3 in the lower, ALS-5 in the middle and ALS-8 in the upper part of the estuary (Figs. 1 & 5). After a stationary period, movements were randomly directed (141 up-estuary and 173 down-estuary).

DISCUSSION

Estuarine movement patterns

Individual and temporal variations in movement patterns and habitat utilisation are commonly found among fishes (e.g. Hartill et al. 2003, Childs et al. 2008a). It is also known that space-use patterns can be mediated by the tidal cycle (Potthoff & Allen 2003, Dorenbosch et al. 2004), which was also the case for juvenile *Agrosomus japonicus* in this study. Although the majority of individuals alternated between the estuary and sea for variable time periods, when they were in the estuary, 2 distinct movement patterns were identified, with the fish either 'moving' over long stretches, up and down the estuary, or being 'stationary' with only small local movements. All individuals displayed both patterns, but alter-

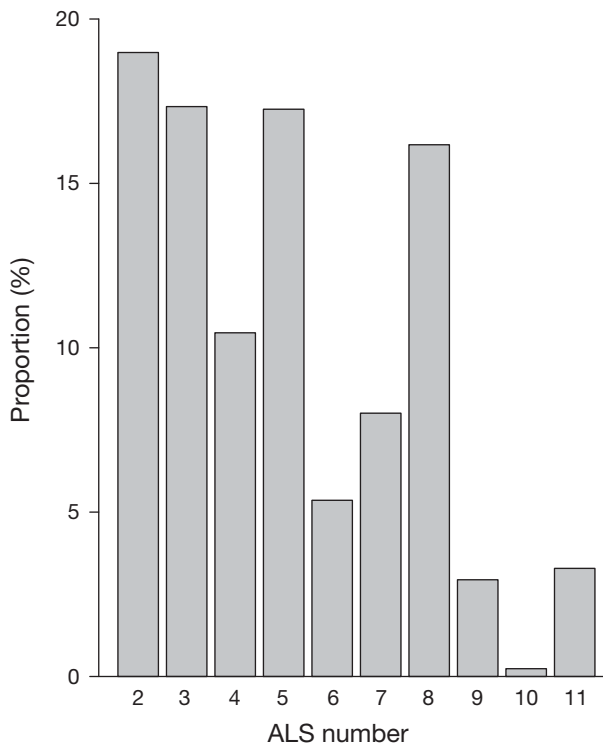


Fig. 5. *Agyrosomus japonicus*. Localisation of stationary periods of individuals ($n = 17$) in the Great Fish Estuary during 3 March to 14 September 2004. Fish with less than 5 stationary periods were excluded from the sample. ALS: automatic listening station

nated between the 2 to a variable degree, although the most frequently observed behaviour was 'moving' (61% of the time). However, there was no synchrony among individuals in the behaviour with respect to moving or stationary periods. In addition, the length of periods with different behaviour varied largely among individuals. Such a dual-behavioural pattern, with 'movers' and 'stayers', has also previously been documented for killifish *Rivulus hartii* (Fraser et al. 2001). The diel cycle seemed to have little influence on the movement patterns of *A. japonicus*, as movement periods often lasted longer than 24 h.

Fish movements and environmental factors

Some estuarine and tidal zone species have endogenous circatidal rhythms, as indicated by continued movement patterns when the individuals are taken into the laboratory in a constant environment (Naylor 2005, Wilcockson & Zhang 2008). However, the variable and non-synchronous behavioural pattern of

either being stationary or rhythmically moving may indicate that *Agyrosomus japonicus* independently time their movements to external cues and not to endogenous circatidal rhythms. Estuarine-associated fishes may adapt to the large environmental fluctuations in these habitats by making use of the tidal cycle. Such behavioural responses may minimise energy expenditures (Almeida 1996), minimise predation risks (Gibson 1986) and/or maximise foraging success and prey availability (Szedlmayer & Able 1993). The observed movements of juvenile *A. japonicus* were mostly rhythmic and corresponded to the speed and direction of the rise and fall of the tide. On a spatial scale, the up- and down-estuary movements occurred during the flood and ebb tide, respectively. Subsequently, up-estuary movements were usually initiated lower in the estuary than down-estuary movements. On a temporal scale, the duration of most uni-directional movements was in accordance with the tidal phase and did not exceed half a tidal cycle.

Agyrosomus japonicus may adapt to the large environmental fluctuations in the Great Fish Estuary by making use of the tidal cycle. During the flood tide, more saline and dense water with reduced turbidity and temperature is pushed up-estuary along the bottom in the form of a salt-water wedge. During the ebb tide, fresh water with lower density, high turbidity and higher temperature is pushed down-estuary on top of the water column. Moving with tidal currents may minimise the energy expenditure, alleviating physiological stress as individuals remain in the similar environmental conditions while moving (e.g. Almeida 1996, Miller & Sadro 2003, Childs et al. 2008b). *A. japonicus*, however, are able to tolerate wide fluctuations in salinity, from 0 to 66 (Wallace 1975, Ter Morshuizen et al. 1996). They are also well equipped to forage in turbid estuaries, being carnivorous predators that hunt mainly by smell and lateral line senses and to a lesser extent by sight (van der Elst 1988). The species is particularly abundant in turbid estuaries (Whitfield 1998). Juveniles may be found at temperatures between 12 and 28°C (Bernatzeder & Britz 2007). Despite the broad tolerance to environmental fluctuations, the physiological cost of staying in different environmental conditions may vary. Hence, when utilising the tide to move, juvenile *A. japonicus* may reduce physiological stress caused by a variable physico-chemical environment.

The use of tidal rhythms may optimise the foraging success of individuals (Wirjoatmodjo & Pitcher 1984, Szedlmayer & Able 1993), as it enables fish to explore an extensive area with minimal energy expenditure

(Rangeley & Kramer 1995, Hartill et al. 2003). Due to a higher metabolic rate (Damuth 2001), adopting a strategy that optimises foraging success is particularly important for smaller fish. For example, Griffiths (1997b) showed that small *Argyrosomus japonicus* fed more frequently than larger individuals. Griffiths (1997b) also suggested that the spatial distribution pattern of *A. japonicus* juveniles in the Great Fish Estuary was mainly determined by predator avoidance and optimised feeding.

Dominant prey items of juvenile *Argyrosomus japonicus* include mysids, prawns and teleosts (Marais 1984, Griffiths 1997b, Taylor et al. 2006). In the Great Fish Estuary, teleosts (Mugilidae and small pelagic estuarine round herring *Gilchristella aestuaria*) and mysids (*Mesopodopsis slabberi* and *Rhopalophthalmus terranatalis*) were the most dominant prey items (Griffiths 1997b). If the density of dominant prey items differs spatially and temporally, as in tidal estuaries, it may be advantageous for a predator to sample multiple sub-habitats (Fraser et al. 2001). *A. japonicus* may therefore have adopted the 'moving' behaviour to optimise its foraging success. The use of strong tidal currents may further optimise the energy balance by minimising the energy spent on active swimming. *M. slabberi* adults utilised lateral migration moving with the tide as a means of maintaining position in the estuary (Wooldridge & Erasmus 1980). Therefore, both *A. japonicus* and one of its most important prey items, *M. slabberi*, may be 'riding the tide'.

Up- and down-estuary movement dynamics

The longer duration of down- than up-estuary movements may be linked to different foraging behaviours. *Rhopalophthalmus terranatalis* keeps its position primarily by lateral movements (Wooldridge & Erasmus 1980). The population remains in greater numbers near the bottom during ebb tide, thereby avoiding the outgoing currents, but uses the flood tide to move up-estuary. It is therefore possible that the longer duration of downward movements of *Argyrosomus japonicus* during the ebb tide could be caused by exploratory feeding on *R. terranatalis* concentrated on the bottom substrate. The shorter duration of up-estuary movements of *A. japonicus* could be caused by feeding on *R. terranatalis* and/or *Mesopodopsis slabberi* during their up-estuary movement when utilising the tidal currents higher in the water column.

The faster up-estuary movements, which were mainly initiated during the night, may also be related

to fish feeding, in particular nocturnal feeding on *Gilchristella aestuaria*. In 4 other estuaries in South Africa, *G. aestuaria* was the single most important prey item of juvenile *Argyrosomus japonicus* (Marais 1984). In the Great Fish Estuary, mugilids and *G. aestuaria* were of similar importance as prey (Griffiths 1997b). Since *G. aestuaria* is most abundant in the upper reaches of estuaries (Harrison & Whitfield 1995, Whitfield & Paterson 2003), it is possible that the faster up-estuary movements may also be linked to feeding on *G. aestuaria*.

Theoretical studies on cost-benefit relationships predict that predator avoidance will influence the spatial distribution of fish (Huntingford 1993). Both predator avoidance and food availability play important roles for the estuarine distribution of juvenile *Argyrosomus japonicus* (Griffiths 1997b). Most probably the main predators of juvenile *A. japonicus* in the Great Fish Estuary were their larger conspecifics, as both field (Griffiths 1997b, Marais 1984) and laboratory (Timmer & Magellan 2011) studies have shown *A. japonicus* to be cannibalistic. Young-of-the-year mainly inhabit the upper reaches of large turbid estuaries to seek refuge from large predators, such as their larger conspecifics, which are more abundant in the less turbid water of the middle and lower reaches (Griffiths 1996). As they grow, the increased spatial requirements need to be weighed against the predation risk. Therefore, if juvenile *A. japonicus* were to venture to the lower reaches of an estuary, it would be advantageous to avoid predators as well as minimise energy expenditures by staying in turbid freshwater-dominated currents. The bull shark *Carcharhinus leucas* may also feed on *A. japonicus* and is known to favour turbid estuaries (Cliff & Dudley 1991, Simpfendorfer et al. 2005), and had a daily habitat use of less than 5 km in a North American estuary, moving up-estuary during the day and down-estuary during the night (Heupel et al. 2010). Since the up-estuary movements of *A. japonicus* occurred most frequently at night, this could reduce predation by *C. leucas*.

Stationary behaviour

Despite 'moving' being the dominant behaviour, stationary periods were also frequently observed. The duration of stationary periods varied largely within and among individuals, and for some individuals lasted for several weeks. *Argyrosomus japonicus* are fast-growing predators (Griffiths 1996), and the long stationary periods suggest that they must feed

while being stationary. The uneven distribution of stationary sites within the estuary indicates that these areas were not randomly chosen.

Fraser et al. (2001) suggested that the behavioural polymorphism, such as 'moving' or 'stationary' behaviour, may be a consequence of ecological factors. For example, if foraging success varies temporally, then it would be advantageous for fish to sample multiple habitats, but if certain areas are safer or more productive, it would be more advantageous to exhibit 'stationary' behaviour. Taylor et al. (2006) classified deeper areas with bottom structures and submerged cliffs as key habitats and holding sites for juvenile *Argyrosomus japonicus*, which are structured habitats that may reduce the predation risk. The Great Fish Estuary has a uniform bathymetry with few underwater structures or deep pools. However, the area near ALS-2 and ALS-3, the most important area of 'stationary' behaviour, is close to the only major structure in the estuary, a road bridge with several large concrete pillars and a deep area just below the bridge. The area around ALS-8 may also be linked to deeper pools in the estuary (Childs et al. 2008b). At ALS-5, however, the bottom was uniform, but the estuary was wider with less strong current. Habitat choice involves a trade-off between predation risk and optimal foraging behaviour (Mittelbach 2002). Structured habitats with increased habitat complexity may hold more prey items, but the typically cryptic and resident nature of organisms that occupy structured habitats may make them more difficult to capture. Therefore, it is proposed that *A. japonicus* use the structured areas to 'hide' and ambush passing prey that utilise the tide, such as *Gilchristella aestuaria*, *Mugil* spp. and *Mesopodopsis slabberi*, or feed on stationary *Rhopalophthalmus terranatalis*. Although the main area of 'stationary' behaviour was in the lower part of the estuary, which has relatively lower turbidity during flood tide, the structure and depth of the habitat may compensate for the increased predation risk from visual predators in the clearer water.

Management implications

The predictable circatidal movements of *Argyrosomus japonicus* renders them vulnerable to capture in the fishery. This was supported by the fact that the 4 fish caught by anglers during the study were among the individuals with the highest proportion of time spent moving. The predictable diel and tidal movements of the sub-adult red drum *Sciaenops ocellatus*

enhanced their vulnerability to angling, but also provided an opportunity to manage the timing and location of fishing effort of the species (Dresser & Kneib 2007). Area-based management measures might not have merit for juvenile *A. japonicus* in the Great Fish Estuary, due to the extensive movements covering most parts of the estuary. For a no-take zone to be effective, the protected area would have to extend from the mouth to approximately 6.5 km up-estuary, covering 65% of the entire estuary. As this is a rural estuary, with many subsistence livelihoods dependent on fishing, the socio-economic ramifications of implementing such a management measure would be complex and require further investigation. Nonetheless, the results of this study demonstrate how knowledge of the movements and the mechanisms responsible for the observed movement patterns may facilitate management of this over-exploited fishery species.

CONCLUSION

Results from this study suggest that it is biologically and ecologically advantageous for juvenile *Argyrosomus japonicus* to adopt 2 different behavioural strategies in a river-like permanently open tidal estuary: (1) moving with the tidal currents, and (2) remaining stationary in deep or structured habitats. There are several advantages to utilising the tide, with the most evident being the minimisation of energy expenditures while moving. *A. japonicus* may also use the tidal currents to reduce predation risk by remaining in a turbid environment, and optimise foraging success by covering an extensive area and sampling multiple sub-habitats while minimising energy expenditure. When adopting the alternative 'stationary' behaviour, *A. japonicus* may reduce their predation risk, particularly in clear water, by remaining in deep or structured habitats, while still upholding their foraging requirements by feeding on prey that follow the tidal currents.

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