

Habitat connectivity and intra-population structure of an estuary-dependent fishery species

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ABSTRACT: Habitat connectivity is a fundamental component of estuary-associated fish behaviour. Understanding this is critical to understanding population dynamics and the nursery role of estuarine habitats. This study aimed to elucidate the intra-population structure of juvenile *Argyrosomus japonicus* and the role of estuarine and coastal habitats for this widely distributed, iconic, estuary-dependent, coastal fishery species. The movements of 85 juvenile *A. japonicus*, tagged with acoustic transmitters in the estuarine (n = 65) and marine (n = 20) environment, were monitored from May 2008 to June 2010 by 44 stationary acoustic receivers deployed in the Eastern Cape, South Africa. While one-third of the tagged fish visited adjacent marine or estuarine habitats, the majority exhibited high levels of residency to their respective estuarine or coastal tagging site. This high level of residency suggests that juvenile *A. japonicus* exist as a meta-population with several non-dispersing subpopulations, each with distinct estuarine and marine contingents. The estuarine contingent had a higher recapture (mortality) rate (35%) than the marine contingent (20%), and within the estuarine contingent, the recapture rate was higher for resident individuals (41%) than migratory individuals (23%). Species with different contingents each exhibiting retentive and migratory/exploratory behaviours (i.e. partial migration) may therefore be more resilient to fishing pressure. Conversely, certain behavioural strategies, particularly estuarine residency, may be more vulnerable to exploitation, suggesting that management interventions are necessary in this habitat. This study demonstrates how ecological concepts should be incorporated to better describe diverse patterns in habitat use and migratory behaviour of estuary-dependent species.

KEY WORDS: Acoustic telemetry · Contingent theory · Estuary-dependent · Estuarine connectivity · Partial migration

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INTRODUCTION

Animal movements are fundamental population processes yet are relatively poorly understood. Interactions among life history, physiology, behaviour and habitat make individual movement an exceptionally complex phenomenon (Patterson et al. 2008). Estuary-associated species, in particular, have spatially and temporally complex life histories and commonly exhibit ontogenetic variation in habitat use and migratory patterns (Able 2005). This is due, in part, to estuaries being dynamic transition zones that link

terrestrial, freshwater and marine habitats. Connectivity between coastal and estuarine habitats is thus a critical property of estuary-associated fish ecology (Gillanders et al. 2003). Knowledge of this connectivity is fundamental to understanding the life cycles (Secor & Rooker 2005), estuarine dependence (Able 2005) inter- and intra-population structure and dynamics (Kerr et al. 2009, Vasconcelos et al. 2010) and alternative life history strategies of estuary-associated species as well as the roles of estuarine and marine environments as nursery habitats (Beck et al. 2001). Despite the ecological significance of such informa-

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tion and its importance to the design of effective conservation and management strategies, globally there is a dearth of information on movement and connectivity between estuarine and coastal fish habitats (Gillanders et al. 2012).

Recent literature suggests that fish movement ecology may be more complex than previously assumed (e.g. Kerr et al. 2009, 2010, Kerr & Secor 2012). Kraus & Secor (2004) proposed that the simultaneous occurrence of conspecifics in multiple habitats during a given life stage, which is common in estuary-associated species, could represent population 'contingents'. Secor (1999) defined a 'contingent' as a level of fish aggregation based on either (1) 'divergent habitat use' or (2) 'divergent migratory behaviour' within a population. In addition, populations or contingents may display partial migration (Kerr et al. 2009), with fish exhibiting retentive and/or exploratory/migratory behaviour. This is most often influenced by season and ontogeny (Secor & Rooker 2000). Partial migration is the phenomenon of co-existing groups exhibiting migratory and resident behaviour within the same population (Jonsson & Jonsson 1993, Chapman et al. 2012). It is a widely applicable and useful concept for understanding life cycle diversity of fishes because it provides a mechanistic understanding of alternative migratory behaviour. Such intra-population variation in movement has been documented in a wide array of animal taxa and may be more widespread than generally recognised (Dingle 1996, Chapman et al. 2012). However, there is a paucity of information on divergent migratory behaviour and habitat use of estuary-associated fish species.

Knowledge of habitat use and connectivity are also important for fisheries management and the conservation of essential habitats, such as estuaries. The collapsed stock status of several estuary-dependent species and a need for alternative management interventions, such as spatial management, makes a quantitative understanding of the extent of exchange between estuarine, riverine and coastal marine habitats imperative. Understanding contingent behaviour is also important for the conservation and management of stocks because identification of a contingent within a population may be useful in assessing divergent behaviour in stock dynamics (Secor 1999).

Argyrosomus japonicus (Temminck & Schlegel 1843) is a marine spawning, estuary-dependent Sciaenid, distributed from South Africa to Pakistan, the northwest coast of India, Australia, Hong Kong, Korea and Japan (Trewavas 1977, Griffiths & Heemstra 1995). Adults are predominantly found in the

nearshore zone, while juveniles utilise estuaries and surf-zones throughout their distributional range (Griffiths 1996, Silberschneider & Gray 2008). It is an important fishery species, mainly due to its large size. In South Africa, high levels of growth (overexploitation of juveniles) and recruitment (overexploitation of mature individuals) overfishing, in conjunction with the late attainment of sexual maturity (50% sexual maturity at 1070 mm total length [TL]/6 yr for females and 920 mm TL/5 yr for males), have led to stock collapse (Griffiths 1996, Mirimin et al. 2015). Understanding juvenile residency in estuarine, riverine and coastal marine habitats and the temporal characteristics of habitat connectivity is essential for assessing the importance of habitats to this species. The occurrence of juvenile *A. japonicus* in estuaries and the coastal zone (Cowley et al. 2008, Griffiths 1996) may be evidence of distinct estuarine and marine contingents within the population, based on Secor's (1999) definition of divergent habitat use. Additionally, according to the definition of 'partial migration' by Kerr et al. (2009), it is possible that within these separate contingents, *A. japonicus* exhibits divergent migratory behaviour.

Acoustic telemetry offers a useful tool for studying fish movement behaviour and assessing habitat connectivity because it allows individual residency and movement patterns to be quantified (Able & Grothues 2007b) through 'real-time' and continuous acquisition of data. This approach has enabled researchers to address complex aspects of behavioural ecology by quantifying movements over varying spatial and temporal scales (Heupel et al. 2006, Espinoza et al. 2011, Næsje et al. 2012). However, despite its broad application for determining population connectivity and identifying essential fish habitats, few telemetry studies (e.g. Able & Grothues 2007a, Childs et al. 2008, Cowley et al. 2008, Abecasis et al. 2009, Freedman et al. 2015) have focused on multiple habitat connectivity or estuarine dependence of estuary-associated fishes (e.g. Able & Grothues 2007b, Sackett et al. 2007). While telemetry has recently been used as a tool in partial migration research (Chapman et al. 2012), these studies are limited to the freshwater environment, and none have directly addressed divergent migratory behaviour in estuary-associated fishes.

This study assessed the intra-population structure of and the role of estuarine and coastal habitats for an estuary-dependent species by quantifying the spatial and temporal movements of individuals caught and tagged in an estuary and the associated marine environment. The specific objectives of this study were to

elucidate whether juvenile *A. japonicus* (1) exist as separate estuarine and marine contingents and/or (2) exhibit partial migration.

MATERIALS AND METHODS

Study site

The study was conducted in the Sundays Estuary and the adjacent coastal embayment, Algoa Bay, within the warm-temperate biogeographic region of South Africa. The Sundays River is 310 km long and enters Algoa Bay at 33° 43' S, 25° 51' E (Fig. 1). The estuary is a permanently open system, ~21 km long and roughly 50 m wide over most of its length (lower and middle reaches), with an average depth of 2.5 m (Wooldridge & Bailey 1982). It drains a catchment of 20 730 km², with a mean annual runoff of 200×10^6 m³ and a mean annual rainfall of 323 mm (Reddering

& Esterhuysen 1981). It has a relatively high fresh-water inflow through an inter-basin transfer system (Scharler & Baird 2005). The estuary supports both recreational and subsistence fisheries. According to Cowley et al. (2013), *Argyrosomus japonicus* dominated catches in the Sundays Estuary with a yield of 3.4 t yr⁻¹ (43% of total yield) and a catch per unit effort (CPUE) of 0.06 fish angler⁻¹ h⁻¹. This species is also the primary target in the adjacent coastal (surf zone) fishery, with a CPUE of 0.01 fish angler⁻¹ h⁻¹ (R. Chalmers pers. comm.).

Research approach

The movements of *A. japonicus* between estuarine and coastal habitats were assessed using acoustic telemetry. A total of 85 juveniles (237–832 mm TL), approximately 0.2 to 4.4 yr (after Griffiths & Hecht 1995), were tagged with uniquely coded acoustic

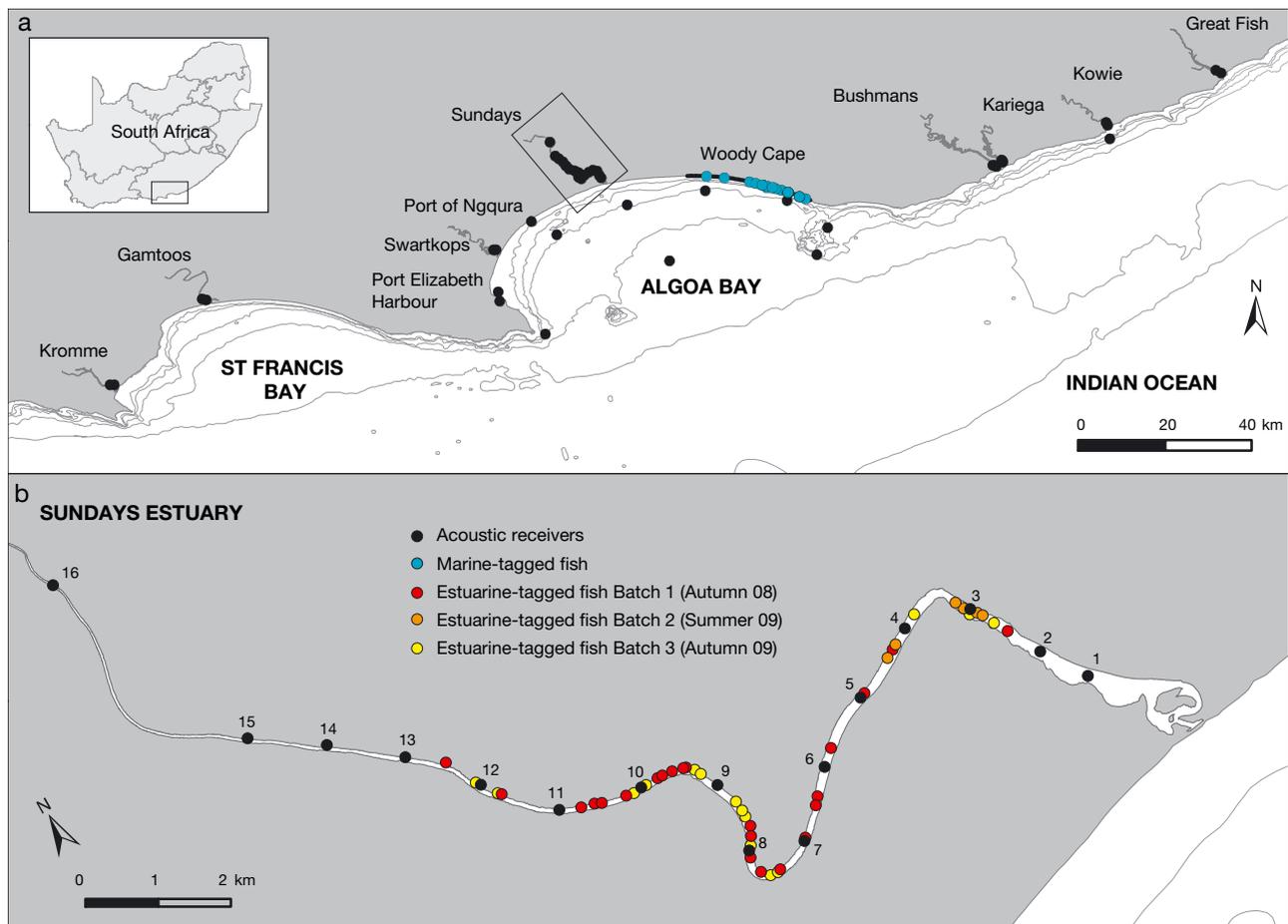


Fig. 1. (a) Study area in South Africa showing estuarine and coastal acoustic receiver positions (●) and catch-sites of marine-tagged fish in the Woody Cape coastal zone (●). (b) Sundays Estuary showing the location of acoustic receivers in the estuary (black dots 1–16) and catch-sites of juveniles caught and tagged in 3 batches throughout the estuary

transmitters from May 2008 to June 2009 (Fig. 1, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m537p233_supp.pdf). In total, 65 fish (mean: 485 mm TL, range: 237–832 mm TL) were caught and tagged in the Sundays Estuary in 3 batches during the study period: Autumn 2008 (mean: 545 mm TL, range: 396–832 mm TL, THELMA LP-7-R04K transmitters), Summer 2009 (mean: 566 mm TL, range: 447–820 mm TL, THELMA MP-9-R04K transmitters), Autumn 2009 (mean: 416 mm TL, range: 237–584 mm TL, VEMCO V13-1L-R64K transmitters). These fish were captured between 3 and 12 km from the estuary mouth (Fig. 1). In addition, 20 juveniles (mean: 589 mm TL, range: 446–812 mm TL, VEMCO V13-1L-R64K and THELMA MP-13-R04K transmitters) were captured in the Woody Cape coastal zone from December 2008 to June 2009 (Fig. 1). The spatial and temporal movements of tagged fish were monitored using a network of 44 stationary automated acoustic receivers (VEMCO, model VR2W) deployed in the Sundays Estuary, its coastal embayment (Algoa Bay) and adjacent estuaries along 300 km of the South African coastline (Fig. 1). To determine multiple habitat connectivity, receivers ($n = 28$) were placed at various sites within Algoa Bay, 2 commercial harbours and 7 adjacent estuaries (Fig. 1). These included 3 estuaries to the west of the Sundays Estuary (Swartkops, Gamtoos and Kromme) and 4 to the east (Bushmans, Kariega, Kowie and Great Fish) (Fig. 1).

Fish were caught with barbless hooks on rod and line. Acoustic transmitters were surgically implanted into the peritoneal cavity, following the procedure described by Cowley et al. (2008). All fish were tagged and released at their capture site. A 9 mo tag retention study conducted on juvenile *A. japonicus* revealed a 100% tag retention rate and no negative effects of surgical implantation of acoustic transmitters on growth or behaviour (Childs et al. 2011). Detections from the first 24 h after surgery were excluded from analyses to avoid any abnormal behaviour associated with the tagging procedure (Kreiberg 2000). Sixteen receivers were deployed in the Sundays Estuary, from 2 to 21 km upstream of the estuary mouth (Fig. 1). Receivers, except the uppermost receiver, were placed ~1 km apart (mean: 1 km, range: 0.7 to 1.1 km) to ensure continuous coverage of the estuary. The uppermost receiver (Receiver 16) was placed 3.7 km upriver of Receiver 15, at the river-estuary interface to ascertain if and when tagged *A. japonicus* visited the riverine environment, i.e. displayed 'estuarine-riverine connectivity'. Salinity (Atago hand-held refractometer) recordings mea-

sured bimonthly at receiver locations throughout the study period confirmed that Receiver 16 (mean bottom salinity: 2.0, range: 0.0–3.0) and Receiver 15 (mean bottom salinity: 7.6, range: 1.0–25.0) were indeed placed at the river estuary interface (REI) region and within the estuary, respectively.

Detections on the lowermost receivers (Receivers 1 and 2) were used to quantify when fish moved between the marine and estuarine environments, i.e. displayed 'estuarine-coastal connectivity' (Fig. 1). *In situ* range tests, following the procedure described by Childs et al. (2008), indicated that the detection range throughout the estuary ranged from 200 to 600 m at different phases of the tide and various weather conditions, with an average recording of 450 m.

Data analysis

Monitoring of tagged fish

The movements of juvenile *A. japonicus* were analysed in 2 groups (Table S1): (1) the 65 estuarine-tagged fish tagged in 3 batches (transmitters with variable battery life) and (2) the 20 marine-tagged fish (1 yr transmitters), tagged in the Woody Cape coastal zone. A generalized linear model with a binomial distribution and logit link function was used to model the effect of batch (Batch 1, Batch 2 and Batch 3), fish size and catch site (distance from estuary mouth) on the recapture rate (1 = recaptured, 0 = not recaptured) of estuarine-tagged fish.

Residency to different habitats

For each estuarine-tagged fish, time spent in the estuary was calculated as the sum of the proportions of time the fish spent in the vicinity of each receiver (Cowley et al. 2008), where total time at each receiver was determined as the sum of (1) the time between consecutive detections at a single receiver and (2) half the time between consecutive detections at neighbouring receivers (i.e. time between detections at neighbouring receivers was divided equally between receivers). Given the 3.7 km distance between Receivers 15 and 16, and the unknown location of a tagged fish moving between these 2 receivers, time spent in the riverine environment was calculated as the sum of (1) time between consecutive detections at Receiver 16 and (2) half the time taken to move between Receivers 15 and 16. Time

spent in the marine environment was calculated from the time an individual was last recorded on the low-estmost receiver (Receiver 1) until it returned to the estuary and was again recorded on Receiver 1 or until it was detected on any receivers in adjacent estuaries. For fish that did not return to the estuary ($n = 6$), time spent in the marine environment was calculated from the time the fish left the estuary until the end day of its minimum estimated battery life (provided by the tag manufacturer). For marine-tagged fish, time spent in the Sundays Estuary, Sundays riverine environment and adjacent estuaries was calculated as for the estuarine-tagged fish. Time spent in the marine environment was calculated from the time the fish was tagged until the end of its minimum estimated battery life, excluding time in estuarine or riverine environments, or the time when the fish was recaptured.

Within each group tagged, non-parametric Kruskal-Wallis ANOVA by ranks and a post-hoc multiple comparison test or a non-parametric Kolmogorov 2-sample test were run to test for differences in times spent in the Sundays Estuary, Sundays riverine environment, adjacent estuaries and the marine environment. For estuarine-tagged fish, a generalised linear model with a normal distribution and log link function was used to test the effect of catch site (distance from mouth), fish size and batch (Batch 1, Batch 2 and Batch 3) on the combined time spent in the estuarine and riverine environment. Owing to the boundedness, non-constant variance and non-normal error typical of proportional data, the response variable was logit transformed. A non-linear least squares regression, using an inverse logistic with 3 parameters, was used to describe the relationship between fish length and the proportion of time spent in estuarine and marine environments during the study period and to estimate the length after which *A. japonicus* spend less time in the estuarine environment.

Marine, estuarine and riverine excursions

An estuarine-tagged fish was considered to have undertaken a 'marine excursion' if it passed the low-estmost estuarine receiver (Receiver 1) and was only recorded again on this receiver after a period exceeding 12 h. A marine-tagged fish was considered to visit the estuarine environment (i.e. undertaking an 'estuarine excursion') if it was recorded on Receiver 1.

A tagged fish was considered to have visited the riverine environment if it was detected on the upper-

most receiver (Receiver 16), situated 21 km upstream of the estuary, at the REI) Detections of tagged *A. japonicus* at this receiver were defined as a 'riverine excursion'. A new 'riverine excursion' was considered if a tagged fish was last recorded on Receiver 16 and was only recorded again after a period exceeding 12 h. For estuarine-tagged fish, a generalised linear model with binomial distribution and logit link function was used to test the effect of catch site (distance from mouth), fish size and batch (Batch 1, Batch 2 and Batch 3) on whether the fish undertook marine and riverine excursions.

For estuarine-tagged fish that visited the marine environment and returned to the estuary and riverine environment, generalised linear models with Poisson and normal distributions were used to test the effect of catch site (distance from estuary mouth), fish size and batch (Batch 1, Batch 2 and Batch 3) on the number and the duration of excursions across the estuarine-marine and estuarine-riverine interfaces, respectively. For the latter model, fish that visited the marine environment once and did not return to the estuary were excluded from analyses. If the residuals indicated over-dispersion, a quasi-Poisson model was used instead of a Poisson model (Bolker et al. 2009).

The various analyses used in this study were conducted using R 3.03 (R Development Core Team 2013), STATISTICA 12 (StatSoft 2011) and Microsoft Excel (2010). Prior to analyses, exploratory data analyses, involving graphical examination of all data, were conducted to assess the suitability of model application. Residuals were also checked for normality, and the appropriate analyses were used thereafter. The 'Wald' chi-squared statistic (W) and its p -level were used to test the significance of each regression coefficient.

RESULTS

Monitoring of tagged fish

Estuarine-tagged *Argyrosomus japonicus* were monitored for periods ranging from 13 to 519 d (mean: 217 ± 106 d, $n = 65$) (Fig. 2). Twenty-three (35%) of these fish were recaptured in the local fishery (length at tagging: mean: 499 ± 179 mm TL, range: 237 to 832 mm TL; length at recapture: mean: 675 ± 212 mm TL, range: 400 to 1300 mm TL) (Fig. 2, see Table S1 in the Supplement), after an average of 429 d post tagging (range: 16 to 1463 d). Nineteen (83%) recaptures were made in the Sundays Estuary, 3 (14%) in the adjacent surf-zone and 1 (4%) outside

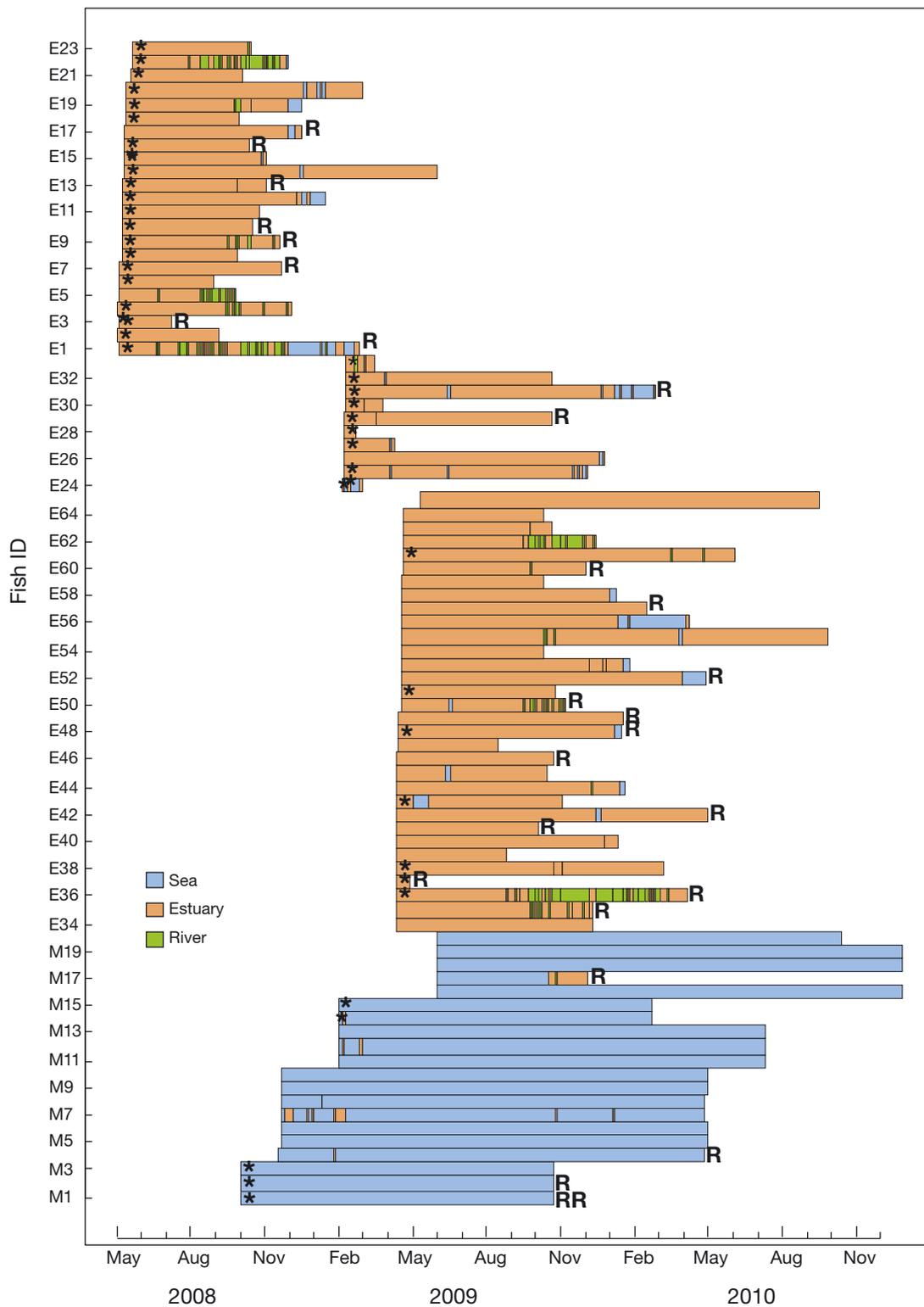


Fig. 2. Abacus plot showing the monitoring periods and daily presence of the 3 batches of estuarine-tagged (E) juvenile *Argyrosomus japonicus* (Batch 1 [E1 to E23], Batch 2 [E24 to E33], and Batch 3 [E34 to E65]) and marine-tagged (M) juvenile *A. japonicus* (M1 to M20). R: fish that were recaptured and kept; RR: a fish that was recaptured and released; *: transmitters that switched off randomly during the study period (shut off period is represented by the end of the monitoring period). Estimated monitoring period for the marine-tagged fish was based on the transmitter battery life provided by the transmitter manufacturer

of Algoa Bay in the Gamtoos Estuary, 110 km west of the Sundays Estuary (Table S1). There was no significant effect of batch ($p > 0.05$, $W2 = 3.64$), catch site (distance from mouth) ($p > 0.05$, $W1 = 0.52$) or fish size ($p > 0.05$, $W1 = 1.26$) on the recapture rate of estuarine-tagged fish.

Marine-tagged fish were monitored for periods ranging from 182 to 684 d (Fig. 2, Table S1). While it was possible to estimate the total number of days monitored for marine-tagged fish, the lack of spatially continuous coverage (provided by the array in the marine environment) reduced the accuracy of the estimation. Marine-tagged fish were detected in the estuarine and marine receiver array for 7 to 408 d (Fig. 2, Table S1). Four (20%) of these fish were recaptured (length at tagging: mean: 543 ± 59 mm TL, range: 498 to 630 mm TL; length at recapture: mean: 767 ± 83 mm TL, range: 658 to 860 mm TL) (Table S1). Three (75%) were recaptured in the surf-zone, ~500 m from the Sundays Estuary mouth, and 1 in the near-shore zone 38 km west of the Sundays Estuary (Table S1), near the end of their transmitter's expected battery life.

Residency to different habitats

The estuarine-tagged *A. japonicus* spent significantly more time in the Sundays Estuary (mean: $94 \pm 12\%$, range: 46–100%) than in the riverine (mean: $3 \pm 8\%$, range: 0–38%), marine (mean: $3 \pm 8\%$, range: 0–54%) or adjacent estuarine (mean: 0.04 ± 0.30 , range: 0–2.4%) environments (Kruskal-Wallis test statistic [H], where $H_{(3,26)} = 186.15$; $p < 0.001$) (Fig.

3a). There were no significant differences among the times spent in the riverine, marine and adjacent estuarine environments ($p < 0.05$). Only 2 individuals visited other estuaries during the study period, namely the Kariega and Gamtoos estuaries (Table S1, Fig. 1).

In total, 39 (60%) of the 65 *A. japonicus* remained resident in the estuary and never ventured into the marine environment throughout their respective monitoring periods (Table S1). Time spent within the estuary was influenced by fish size ($p < 0.05$, $W1 = 5.51$) but not by batch ($p > 0.05$, $W2 = 0.89$) or catch site (distance from mouth) ($p > 0.05$, $W1 = 0.70$). Time spent in the riverine region was not affected by batch ($p > 0.05$, $W2 = 0.03$), catch site ($p > 0.05$, $W1 = 2.97$) or fish size ($p > 0.05$, $W1 = 1.00$).

Marine-tagged fish spent significantly more time in the marine environment (mean: $97.9 \pm 6.4\%$, range: 75 to 100%) than in the Sundays estuarine (mean: $2.1 \pm 6.4\%$, range: 0 to 25%, $n = 6$ fish) or riverine (0.01%, $n = 1$ fish) ($H_{(2,45)} = 36.01$; $p < 0.001$) environments (Fig. 3b).

Movements across the estuarine-marine interface

Twenty-six (40%) of the 65 estuarine-tagged *A. japonicus* undertook marine excursions. Batch ($p > 0.05$, $W2 = 0.86$), catch site ($p > 0.05$, $W1 = 2.06$) and fish size ($p > 0.05$, $W1 = 0.38$) had no effect on whether estuarine-tagged fish undertook marine excursions. Seven (27%) of these 26 fish were recaptured (2 from Batch 1, 1 from Batch 2 and 4 from Batch 3) (Table S1). Proportionally more fish (41%,

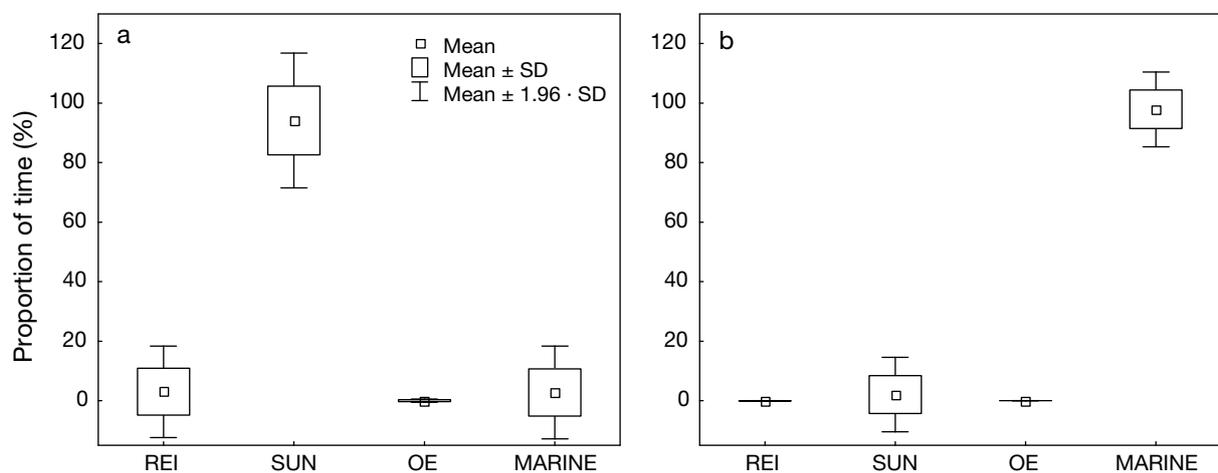


Fig. 3. Mean proportions (%) of time spent by (a) estuarine-tagged *Argynosomus japonicus* ($n = 65$) and (b) marine-tagged *A. japonicus* ($n = 15$) in the Sundays River (river-estuary interface, REI), Sundays Estuary (SUN), other estuaries (OE) and the marine environment (MARINE)

n = 16 fish) that remained resident in the estuary (n = 39) were recaptured during the study period.

Most individuals undertook a single marine excursion, although some fish undertook up to 6 such excursions (mean: 1.8 ± 1.5) (Table S1). Batch ($p > 0.05$, $W2 = 0.90$), catch site ($p > 0.05$, $W1 = 0.36$) and fish size ($p > 0.05$, $W1 = 0.38$) had no effect on the number of marine excursions. Their durations ranged from 1.2 to 68.8 d (mean: 9.2 ± 13.1 d) (Table S1), although most (74%) excursions (calculated as the sum of the mean proportion) were <1 wk (7 d). The longest marine excursions were undertaken by different individuals and were 19.3, 23.3, 39.2 and 68.8 d. There was no effect of batch ($p > 0.05$, $W2 = 2.25$), catch site ($p > 0.05$, $W1 = 0.17$) or fish size ($p > 0.05$, $W1 = 0.41$) on the mean duration of marine excursions. Eight (31%, mean: 400 mm TL, range: 326–486 mm TL) of the 26 estuarine-tagged fish that undertook marine excursions were recorded on receivers within Algoa Bay. One of these fish was detected in the nearby Kariiega Estuary, and the other 7 were detected in the Port of Ngqura, of which one was also detected in the Port Elizabeth (PE) Harbour and another in the Gamtoos Estuary. The maximum number of days each fish was detected in the Port of Ngqura was 2.

Six (30%) marine-tagged fish entered the Sundays Estuary during the study period, of which one (M17) did not return to the marine environment but was recaptured in the estuary (Table S1). The number (mean: 2.2 ± 2.4 , range: 1 to 7) and duration (mean: 6.9 ± 12.3 d, range: 0.75 to 45 d) of estuarine excursions varied among individuals (see Table S1). However, excluding Fish M17 (which never left the estuary) reduced the mean (3.5 ± 3.1 d) and maximum (10 d) duration of estuarine excursions considerably. None of the marine-tagged fish visited other estuaries in the acoustic array, and only 2 individuals visited the Port of Ngqura (for 1 d) during the study period (Table S1).

Movements across the estuarine-riverine interface

Twenty-five (38%) of the 65 estuarine-tagged *A. japonicus* visited the uppermost receiver (Receiver 16) situated at the REI region, 21 km from the estuary mouth, of which 10 (40%) also undertook marine excursions. There was no effect of batch ($p > 0.05$, $W2 = 0.82$), fish size ($p > 0.05$, $W1 = 0.21$) or catch site ($p > 0.05$, $W1 = 3.91$) on whether estuarine-tagged fish undertook riverine excursions.

Riverine excursions totalled 422 (individual mean: 16.9 ± 26.6 , range: 1 to 111) and were relatively short

(mean: 0.4 ± 0.5 d, range: 27 min to 3.4 d), with most (74%) lasting <6 h. There was no effect of batch ($p > 0.05$, $W2 = 2.81$), catch site ($p > 0.05$, $W1 = 0.22$) or fish size ($p > 0.05$, $W1 = 3.66$) on the number of riverine excursions. Similarly, there was no effect of batch ($p > 0.05$, $W2 = 1.46$), catch site ($p > 0.05$, $W1 = 0.96$) or fish size ($p > 0.05$, $W1 = 0.09$) on the mean duration of riverine excursions. Only 1 of the marine-tagged fish (M17) visited the riverine receiver and only on a single occasion.

Effect of fish size on habitat connectivity

Smaller estuarine-tagged *A. japonicus* (<746 mm TL) spent more time in the estuary than larger juveniles ($F_{(1,63)} = 92.04$, $R^2 = 0.32$; $p < 0.01$) (Fig. 4a), and the number of marine excursions undertaken was positively related to fish length ($R^2 = 0.10$, $p < 0.05$) (Fig. 4b). Fish length had no significant effect on time spent in the riverine environment ($R^2 = 0.03$, $p > 0.05$) or the number of riverine excursions ($R^2 = 0.01$, $p > 0.05$) for estuarine-tagged fish.

Owing to the low number of individuals that undertook estuarine excursions and the low proportions of time spent in the estuary, non-linear least squares regression was not suitable to model the time spent in the estuary by marine-tagged *A. japonicus*. However, there were no correlations between fish length and either time spent in the estuary (Spearman rank order correlation: $r = -0.13$, $p > 0.05$) or the number of estuarine excursions undertaken ($r = -0.09$, $p > 0.05$) for marine-tagged fish.

DISCUSSION

Identification of 'contingent' and 'partial migration' strategies

Based on the observed residency of estuarine- and marine-tagged *Argyrosomus japonicus* to their habitats of capture and Secor's (1999) definition of a contingent (a level of fish aggregation based on 'divergent habitat use'), it appears that the population consists of 2 separate juvenile contingents (i.e. estuarine and marine). Contingents, mostly based on migratory behaviour, have been documented in moronids (e.g. Secor et al. 2001, Kerr et al. 2009), anguillids (e.g. Tzeng et al. 2003), clupeids (e.g. McQuinn 1997), pleuronectids (Sagarese & Frisk 2011) and other marine fish taxa (Petitgas et al. 2010). While the majority of tagged *A. japonicus* exhibited residency to their

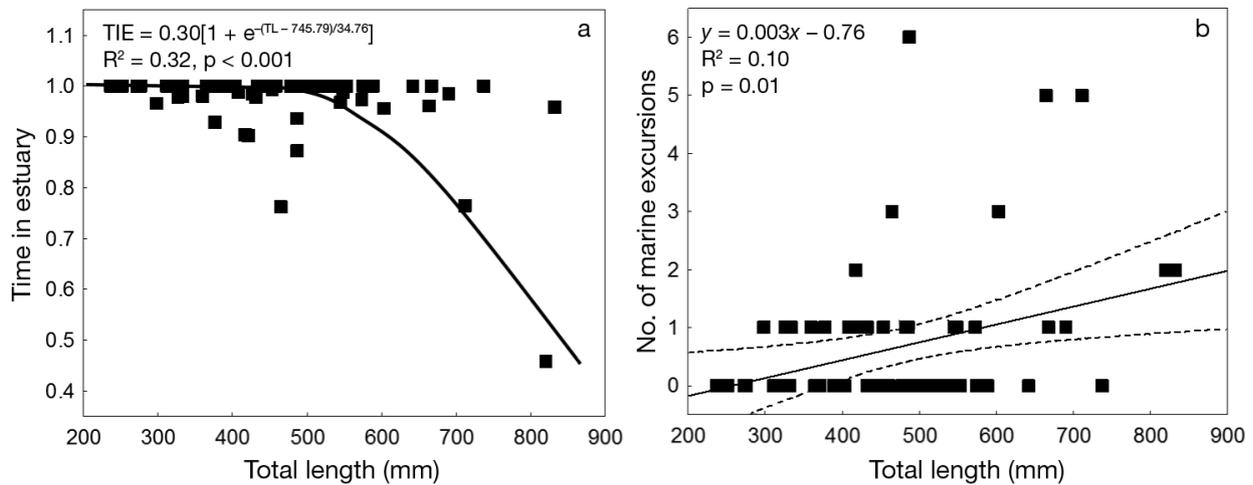


Fig. 4. Relationships between estuarine-tagged *Argyrosomus japonicus* size (mm total length, TL) and (a) the proportion of time spent in the estuary (TIE) (■: observed TIE; solid line: estimated TIE) and (b) number of marine excursions undertaken (solid line: trend; dashed lines: confidence intervals)

habitat of capture, approximately one-third of each contingent (and within each estuarine batch) exhibited exploratory/migratory behaviour and visited the adjacent marine or estuarine habitats. A proportion (40%) within the estuarine contingent also visited the REI region. Such connectivity among the estuarine, marine and freshwater habitats exhibited by individuals within each contingent suggests that each is regulated by individuals that display exploratory/migratory behaviour (Secor 1999) and may be best described as 'partial migration', i.e. the occurrence of co-existing exploratory/migratory and resident groups within the same population (Kerr et al. 2009).

Partial migration is a widespread phenomenon in nature, and although it is well-documented in the avian literature (e.g. Berthold 1999), the reporting of partial migration in fishes has been infrequent (Kerr et al. 2009, Chapman et al. 2012) and generally limited to populations where it is morphologically expressed and easily observed, e.g. salmonid populations exhibiting morphologically different resident and migratory individuals (inter alia Jonsson & Jonsson 1993, Olsson et al. 2006). However, Kerr et al. (2009) and Chapman et al. (2012) argue that partial migration is more widespread among fishes than previously recognised. For example, adult red drum *Sciaenops ocellatus*, a sciaenid with a life-history remarkably similar to *A. japonicus* (Griffiths 1996), exhibited what could have been classified as partial migration, with only a proportion (26%) of tagged fish emigrating to the adjacent continental shelf, while the rest remained resident in the estuary (Reyier et al. 2011).

Evolutionary consequences of alternative life history strategies/behavioural traits

Alternative life history strategies or behavioural traits such as contingent behaviour and partial migration have significant ecological consequences (Kerr et al. 2009, Chapman et al. 2011, Rohde et al. 2014). The expression of diverse life history strategies is particularly advantageous for estuary-dependent fishes, as a means of offsetting environmental variability and ensuring population persistence and regulation (Secor & Kerr 2009, Kerr & Secor 2012). Possibly developed through phenotypic plasticity (Secor 1999), such contingents could offer 'rescue effects' for subpopulation declines by buffering population-level responses against anthropogenic impacts and/or unfavourable conditions (e.g. Ray 2005, Kerr et al. 2010, Petitgas et al. 2010). Therefore, alternative life history strategies or behavioural traits could be a beneficial strategy to enhance population regulation and persistence and could provide a powerful survival mechanism for estuarine fish, especially in combination with dynamic meta-population characteristics, including genetic diversity (Cowen et al. 2007).

Petitgas et al. (2010) examined the influence of diverse life cycles on the recovery of previously collapsed marine fish stocks that exhibit resident and migratory contingents and demonstrated the contribution of adopting contingents to the maintenance and recovery of collapsed populations. They showed that the offshore (resident) contingents were the first to collapse, and the recovery of these contingents

was dependent on the reappearance of phenotypically divergent migratory individuals to re-establish the use of the offshore habitats. They suggested that resident contingents confer stability, while migratory contingents confer productivity and resilience, and that the connectivity between the 2 contingents increases stock size. In the case of *A. japonicus*, the existence of separate contingents, coupled with partial migration within each, could allow for population regulation and contribute to the maintenance of the Algoa Bay *A. japonicus* population. For example, the recapture rate of estuarine-tagged fish (35%) was almost double that of the marine-tagged fish (20%). Additionally, among the estuarine-tagged fish, the recapture rate of fish that remained resident to the estuary (41%) was almost double that of the fish that exhibited movements across the estuarine-marine interface (23%). This highlights the vulnerability of the estuarine contingent, particularly the resident individuals, to exploitation and the potential benefits of alternative behavioural traits. Simultaneously, this highlights the need for urgent management attention to allow for the recruitment of juveniles to the marine adult population. The potential of the marine contingent to 'rescue' or buffer the effects of a collapsed estuarine contingent is further supported by the lower catch rates of *A. japonicus* in the coastal zone (R. Chalmers pers. comm.) compared to the adjacent estuarine nursery habitat (Cowley et al. 2013).

This study also acknowledges the contribution and importance of the marine contingent in supplementing the coastal adult population, particularly because the connectivity between *A. japonicus* tagged in the Sundays Estuary and adjacent Woody Cape coastal zone and the low levels of dispersal out of Algoa Bay ($n = 2$ individuals) suggest that juvenile *A. japonicus* exist as a meta-population with several subpopulations, each with distinct estuarine and marine contingents. This supports the hypothesis of Griffiths (1996) and suggestions by Griffiths & Attwood (2005) that juvenile dusky kob consist of several allopatric subpopulations that remain around their nursery estuaries until they reach maturity. Results from a recent genetic study also suggested that *A. japonicus* in South Africa display 'some degree of subtle, but patchy population segregation' (Mirimin et al. 2015). Kerr & Secor (2012) hypothesised that natural selection should favour partial migration in estuarine and coastal fishes, but that the consequences of a partial migration strategy should still be considered at a meta-population level, particularly in the context of anthropogenic impacts, where for example, the removal of migratory individuals could decrease con-

nectivity between local populations and hence result in meta-population declines. For example, this study showed that estuarine-resident *A. japonicus* were more vulnerable to exploitation. Over time, the removal of these individuals, particularly if residency is a heritable trait, will have consequences at a meta-population level. The extent of such associated consequences for *A. japonicus*, as for other fishes, remains unknown. Nonetheless, the existence of such contingents and partial migration strategies in this case can be seen as beneficial because they may improve the resilience of the species to the impacts of overfishing. The occurrence of such intra-population structure within the *A. japonicus* Algoa Bay population therefore likely improves the species' resilience to major perturbations, whether anthropogenic (e.g. estuarine degradation) or environmental (e.g. climatic impacts). This is necessary, given the high overall recapture rate (28%) and degree of residency and the low levels of dispersal and connectivity among estuaries, which render this species vulnerable to exploitation.

Habitat connectivity and partial migration

Habitat connectivity was not affected by batch or catch site, although there was individual variability in the extent, timing and duration of movements between estuarine, riverine and marine environments. The need to understand individual variability in fish movement has recently gained increased recognition from researchers, as population structure can be dependent on individual movement behaviour (Patterson et al. 2008). According to Chapman et al. (2012), intraspecific variation in migratory behaviour is widespread and appears to be the rule rather than the exception, resulting in such within-population migratory dimorphism being termed partial migration.

In vertebrates, migratory behaviour can be genetically controlled, and the movement behavior (i.e. resident or migratory) of fishes can be genetically inherited (Jonsson & Jonsson 1993, Gemperline et al. 2002). However, the adoption of migratory behaviour may also be based on a trade-off, where the benefits and costs of residency and migration are weighed through their effect on fitness (Gross 1987, Dingle 1996, Mehner & Kasprzak 2011). For an individual to maximise fitness, behaviour should depend on the present conditions and future trade-offs in terms of expected growth and probability of survival as a resident or migratory fish (Forseth et al. 1999). For

example, the adoption of migratory behaviour by common bream *Abramis brama* and brown trout *Salmo trutta* was related to an individual's risk of predation (Skov et al. 2011) and to food availability and changes in feeding conditions in that habitat (Olsson et al. 2006), respectively.

The expression of partial migration may also be affected by anthropogenic impacts that increase productivity, by promoting residency in or migration to a specific habitat (Kerr et al. 2009). *Gilchristella aestuaria*, one of the dominant prey items of juvenile *A. japonicus* (Marais 1984), was most abundant in the upper reaches of the Sundays Estuary (Harrison & Whitfield 1990). Potential increases in abundance of *G. aestuaria*, as a result of increased riverine productivity, could induce migratory behaviour to the REI, thereby promoting partial migration in the *A. japonicus* population. Given that excursions were of relatively short duration (~10 d), estuarine-coastal and riverine connectivity of *A. japonicus* is likely prey- or predatory-related.

Habitat connectivity of estuarine-tagged *A. japonicus* was largely affected by fish size, with fish <746 mm TL spending significantly more time in the estuary and larger fish undertaking more marine excursions. Secor (1999) suggested that ontogeny is one of the most important factors influencing the movements and migrations of fish (Secor 1999). Ontogenetic changes in habitat use are typically associated with refuge, predation, diet and physiological requirements (Bacheler et al. 2009), allowing life stages to respond individually to the different selection pressures experienced in the environment (Ebenman 1992) and to maximise resource use efficiency (Pittman & McAlpine 2003). Ontogenetic shifts in habitat use are common, particularly in estuary-associated species (e.g. Childs et al. 2008, Sagarese & Frisk 2011). Therefore, the influence of ontogeny on estuarine-coastal connectivity by *A. japonicus* in the present study is not surprising. Bacheler et al. (2009) suggested that the ontogenetic shift of *S. ocellatus* from the estuarine tributaries towards the coast may be explained by the physiological requirements and preference of larger individuals for higher salinity. It is therefore possible that the ontogenetic shift observed in *A. japonicus* in this study may be in preparation for their adult marine phase and may be related to an ontogenetic physiological shift, with larger fish having a reduced tolerance for low-salinity environments. It is uncertain whether fish size influences multiple estuary use because only 2 fish, which were both of similar sizes, displayed such behaviour. The low levels of dispersal

may be attributed to the costs associated with moving to new estuaries. Dingle (1996) stated that differential migration, which is the variation in distance travelled, may be facultative owing to certain biological benefits or obligatory as a consequence of gene control. In some cases, the environment and genes interact, such that physical properties can determine the expression of genes and can cause certain individuals to migrate from estuaries when the physical environment is unsuitable (Gillanders et al. 2012). Therefore, the benefits of displaying multiple habitat connectivity may also be related to the highly dynamic nature of estuaries or other sheltered environments, such as ports, having varied effects on each individual. Given the low number of estuarine- and marine-tagged *A. japonicus* exhibiting multiple habitat connectivity, their connectivity patterns were most likely attributed to individual variability.

CONCLUSION

This study highlights the value of incorporating movement theory and concepts, such as the contingent hypothesis and partial migration, into fish ecological studies. Such concepts have been previously overlooked in this and many other fish species. It also demonstrates that a comprehensive understanding of behavioural dynamics could be valuable in the effective management and conservation of overexploited estuary-associated species. By quantifying habitat connectivity and intra-population spatial structure, this study not only highlighted the importance of estuaries as nursery habitats but also provided insights into the potential role of acoustic telemetry in contemporary ecological theory and its application. However, given the current limitation of battery life for acoustic transmitters suitable for juvenile (small) fishes, to fully explore partial migration and contingent behaviours throughout the life history of this and other estuary-associated fish species, complimentary methods, such as otolith microchemistry (Kerr et al. 2009), could be employed. Furthermore, investigations into the genetic basis responsible for fish migration (e.g. Lorgen et al. 2015) would greatly enhance our understanding of the evolution of alternative migratory behaviours.

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