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1   Running head: Intra-population structure of an estuarine species

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

3   **species**

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12   ABSTRACT: Habitat connectivity is a fundamental component of estuary-associated fish

13   behaviour. Understanding this is critical to understanding population dynamics and the nursery

14   role of estuarine habitats. This study aimed to elucidate the intra-population structure of juvenile

15   *Argyrosomus japonicus*, and the role of estuarine and coastal habitats for this widely distributed,

16   iconic, estuary-dependent, coastal fishery species. The movements of 85 juvenile *A. japonicus,*

17   tagged with acoustic transmitters in the estuarine (n = 65) and marine (n = 20) environment, were

18   monitored from May 2008 to June 2010, by 44 stationary acoustic receivers deployed in the

19   Eastern Cape, South Africa. While one third of tagged fish visited adjacent marine or estuarine

20   habitats, the majority exhibited high levels of residency to their respective estuarine or coastal

21   tagging site. This high level of residency suggests that juvenile *A. japonicus* exist as a meta-

22   population with several non-dispersing subpopulations, each with distinct estuarine and marine

23   contingents. The estuarine contingent had a higher recapture (mortality) rate (35%) than the

24   marine contingent (15%), and within the estuarine contingent the recapture rate was higher for

25   resident individuals (41%) than migratory individuals (23%). Species with different contingents

26   each exhibiting retentive and migratory/exploratory behaviours (i.e. partial migration) may

27   therefore be more resilient to fishing pressure. Conversely, however, certain behavioural

28   strategies, particularly estuarine residency, may be more vulnerable to exploitation, suggesting

29   that management interventions are necessary in this habitat. This paper demonstrates how

30   ecological concepts should be incorporated to better describe diverse patterns in habitat use and

31   migratory behaviour of estuary-dependent species.

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33   KEY WORDS: acoustic telemetry · contingent theory · estuary-dependent ·estuarine connectivity

34   · partial migration

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40 **INTRODUCTION**

41 Animal movements are fundamental population processes, yet are relatively poorly understood.

42 Interactions among life history, physiology, behaviour and habitat make individual movement an

43 exceptionally complex phenomenon (Patterson et al. 2008). Estuary-associated species, in

44 particular, have spatially and temporally complex life histories and commonly exhibit

45 ontogenetic variation in habitat use and migratory patterns (Able 2005). This is due, in part, to

46 estuaries being dynamic transition zones that link terrestrial, freshwater and marine habitats.

47 Connectivity between coastal and estuarine habitats is thus a critical property of estuary-

48 associated fish ecology (Gillanders et al. 2003). Knowledge of this connectivity is fundamental

49 to understanding the life cycles (Secor & Rooker 2005), estuarine dependence (Able 2005) inter-

50 and intra-population structure and dynamics (Kerr et al. 2009, Vasconcelos et al. 2010) and

51 alternative life history strategies of estuary-associated species, and the roles of estuarine and

52 marine environments as nursery habitats (Beck et al. 2001). Despite the ecological significance

53 of such information and its importance to the design of effective conservation and management

54 strategies, globally there is a dearth of information on movement and connectivity between

55 estuarine and coastal fish habitats (Gillanders et al. 2012).

56

57 Recent literature suggests that fish movement ecology may be more complex than previously

58 assumed (e.g. Kerr et al. 2009, 2010, Kerr & Secor 2012). Kraus and Secor (2004) proposed that

59 the simultaneous occurrence of conspecifics in multiple habitats during a given life stage, which

60 is common in estuary-associated species, could represent population 'contingents'. Secor (1999)

61   defined a 'contingent' as a level of fish aggregation based on i) "divergent migratory behaviour"

62   or ii) "divergent habitat use" within a population. In addition, populations or contingents may

63   display partial migration (Kerr et al. 2009), with fish exhibiting retentive and/or

64   exploratory/migratory behaviour. This is most often influenced by season and ontogeny (Secor &

65   Rooker 2000). Partial migration is the phenomenon of coexisting groups exhibiting migratory

66   and resident behaviour within the same population (Chapman et al. 2012, Jonsson & Jonsson

67   1993). It is a widely applicable and useful concept for understanding life cycle diversity of

68   fishes, as it provides a mechanistic understanding of alternative migratory behaviour. Such intra-

69   population variation in movement has been documented in a wide array of animal taxa, and may

70   be more widespread than generally recognised (Dingle 1996, Chapman et al. 2012). However,

71   there is a paucity of information on the mechanisms driving divergent migratory behaviour and

72   habitat use of estuary-associated fish species.

73

74   Knowledge of habitat use and connectivity are also important for fisheries management and the

75   conservation of essential habitats, such as estuaries. The collapsed stock status of several

76   estuary-dependent species and a need for alternative management interventions, such as spatial

77   management, makes a quantitative understanding of the extent of exchange between estuarine,

78   riverine and coastal marine habitats imperative. Understanding contingent behaviour is also

79   important for the conservation and management of stocks, as identification of a contingent within

80   a population may be useful in assessing divergent behaviour in stock dynamics (Secor 1999).

81

82 *Argyrosomus japonicus* (Temminck & Schlegel 1843) is a marine spawning, estuary-dependent

83 Sciaenid, distributed from South Africa to Pakistan, the northwest coast of India, Australia, Hong

84 Kong, Korea and Japan (Griffiths & Heemstra 1995, Trewavas 1977). Adults are predominantly

85 found in the nearshore zone, while juveniles utilise estuaries and surf-zones throughout their

86 distributional range (Griffiths 1996). It is an important fishery species, mainly due to its large

87 size. In South Africa, high levels of growth and recruitment overfishing, in conjunction with the

88 late attainment of sexual maturity (50% sexual maturity at 1070 mm TL/6 years for females and

89 920 mm TL/5 years for males), have led to stock collapse (Griffiths 1996). Understanding

90 juvenile residency in estuarine, riverine and coastal marine habitats and the temporal

91 characteristics of habitat connectivity is essential for assessing the importance of habitats to this

92 species. The occurrence of juvenile *A. japonicus* in estuaries and the coastal zone (Cowley et al.

93 2008, Griffiths 1996) may be evidence of distinct estuarine and marine contingents within the

94 population, based on divergent habitat use. Additionally, it is possible that within these separate

95 contingents, *A. japonicus* exhibits divergent migratory behaviour i.e. 'partial migration'.

96 Acoustic telemetry offers a useful tool for studying fish movement behaviour and assessing

97 habitat connectivity, as it allows individual residency and movement patterns to be quantified

98 (Able & Grothues 2007b) through 'real-time' and continuous acquisition of data. This approach

99 has enabled researchers to address complex aspects of behavioural ecology, by quantifying

100 movements over varying spatial and temporal scales (Espinoza et al. 2011, Heupel et al. 2006,

101 Næsje et al. 2012). However, despite its broad application for determining population

102 connectivity and identifying essential fish habitats, few telemetry studies (e.g. Abecasis et al.

103 2009, Able & Grothues 2007a, Childs et al. 2008, Cowley et al. 2008) have focused on multiple

104   habitat connectivity or estuarine dependence of estuary-associated fishes (e.g. Able & Grothues

105   2007b, Sackett et al. 2007). While telemetry has recently been used as a tool in partial migration

106   research (Chapman et al. 2012), these studies are limited to the freshwater environment and none

107   have directly addressed divergent migratory behaviour in estuary-associated fishes.

108   This study assessed the intra-population structure of, and the role of estuarine and coastal

109   habitats to an estuary-dependent species, by quantifying the spatial and temporal movements of

110   individuals caught and tagged in an estuary and the associated marine environment. The specific

111   objectives of this study were to elucidate whether juvenile *A. japonicus* 1) exist as separate

112   estuarine and marine contingents, and/or 2) exhibit partial migration.

113

114   **MATERIALS AND METHODS**

115   **Study Site**

116   The study was conducted in the Sundays Estuary and the adjacent coastal embayment, Algoa

117   Bay, within the warm-temperate biogeographic region of South Africa. The Sundays River is

118   310 km long, and enters Algoa Bay at 33°43'S, 25°51'E (Fig. 1). The estuary is a large,

119   permanently open system, approximately 21 km long and roughly 50 m wide over most of its

120   length (lower and middle reaches), with an average depth of 2.5 m (Wooldridge & Bailey 1982).

121   It drains a catchment of 20 730 km^2, with a mean annual runoff of 200 x 10^6 m^3 and a mean

122   annual rainfall of 323 mm (Reddering & Esterhuysen 1981). It has a relatively high freshwater

123   inflow through an inter-basin transfer system (Scharler & Baird 2005). The estuary supports

124 recreational and subsistence fisheries, but is dominated by the recreational sector, with *A.*

125 *japonicus* constituting one of the two most targeted species in the estuary (Cowley et al. 2013).

126

Research approach

128 The movements of *A. japonicus* between estuarine and coastal habitats were assessed using

129 acoustic telemetry. A total of 85 juveniles (237–832 mm total length (TL)), approximately 0.2 to

130 4.4 years (after Griffiths & Hecht 1995), were tagged with uniquely coded acoustic transmitters

131 from May 2008 to June 2009 (Fig. 1, Appendix 1). Sixty-five fish (mean: 485 mm TL, range:

132 237–832 mm TL) were caught and tagged in the Sundays Estuary in three batches during the

133 study period: Autumn 2008 (mean: 545 mm TL, range: 396–832 mm TL, THELMA LP-7-R04K

134 transmitters), Summer 2009 (mean: 566 mm TL, range: 447–820 mm TL, THELMA MP-9-

135 R04K transmitters), Autumn 2009 (mean: 416 mm TL, range: 237–584 mm TL, VEMCO V13-

136 1L-R64K transmitters). These fish were captured between 3 and 12 km from the estuary mouth

137 (Fig. 1). In addition, twenty juveniles (mean: 589 mm TL, range: 446–812 mm TL, VEMCO

138 V13-1L-R64K and THELMA MP-13-R04K transmitters) were captured in the Woody Cape

139 coastal zone from December 2008 to June 2009 (Fig. 1). The spatial and temporal movements of

140 tagged fish were monitored using a network of 44 stationary automated acoustic receivers

141 (VEMCO, model VR2W) deployed in the Sundays Estuary, its coastal embayment (Algoa Bay)

142 and adjacent estuaries along 300 km of the South African coastline (Fig. 1).

143

144   Fig. 1

145

146   Fish were caught with barbless hooks on rod and line. Acoustic transmitters were surgically

147   implanted into the peritoneal cavity, following the procedure described by Cowley et al. (2008).

148   All fish were tagged and released at their capture site. A nine-month tag retention study

149   conducted on juvenile *A. japonicus* revealed a 100% tag retention rate and no negative effects of

150   surgical implantation of acoustic transmitters on growth or behaviour (Childs et al. 2011).

151   Detections from the first 24 hours after surgery were excluded from analyses. Sixteen receivers

152   were deployed in the Sundays Estuary, from 2 to 21 km upstream of the estuary mouth (Fig. 1).

153   Receivers, except the uppermost receiver, were placed approximately 1 km apart (mean: 1 km,

154   range: 0.7 to 1.1 km), to ensure continuous coverage of the estuary. The uppermost receiver

155   (receiver 16) was placed 3.7 km upriver of receiver 15, at the river-estuary interface, to ascertain

156   if and when tagged *A. japonicus* visited the riverine environment, i.e. displayed 'estuarine-

157   riverine connectivity'. Detections on the lowermost receivers (receivers 1 and 2) were used to

158   quantify when fish moved between the marine and estuarine environments, i.e. displayed

159   'estuarine-coastal connectivity' (Fig. 1). The detection range throughout the estuary ranged from

160   200 to 600 m at different phases of the tide and various weather conditions, with an average

161   recording of 450 m. To determine multiple habitat connectivity, receivers (n = 28) were placed at

162   various sites within Algoa Bay, two commercial harbours and seven adjacent estuaries (Fig. 1).

163   These included three estuaries to the west of the Sundays Estuary (Swartkops, Gamtoos and

164   Kromme) and four to the east (Bushmans, Kariega, Kowie and Great Fish) (Fig. 1).

165

166 **Data analysis**

167 **Monitoring of tagged fish**

168 The movements of juvenile *A. japonicus* were analysed in two groups (Appendix 1), namely: (i)

169 the 65 Estuarine-tagged fish tagged in three batches (transmitters with variable battery life), and

170 (ii) the 20 Marine-tagged fish (1-year transmitters), tagged in the Woody Cape coastal zone. A

171 generalized linear model with a binomial distribution and logit link function was used to model

172 the effect of batch (Batch 1, Batch 2, Batch 3), fish size and catch site (distance from estuary

173 mouth) on the recapture rate (1 = recaptured, 0 = not recaptured) of estuarine-tagged fish.

174

175 **Residency to different habitats**

176 For each estuarine-tagged fish, time spent in the estuary was calculated as the sum of the

177 proportions of time the fish spent in the vicinity of each receiver (Cowley et al. 2008), where

178 total time at each receiver was determined as the sum of (i) the time between consecutive

179 detections at a single receiver, and (ii) half the time between consecutive detections at

180 neighbouring receivers (i.e. time between detections at neighbouring receivers was divided

181 equally between receivers). Given the 3.7-km distance between receivers 15 and 16, and the

182 unknown location of a tagged fish moving between these two receivers; time spent in the riverine

183 environment was calculated as the sum of i) time between consecutive detections at receiver 16

184 and ii) half the time taken to move between receivers 15 and 16. Time spent in the marine

185   environment was calculated from the time an individual was last recorded on the lowermost

186   receiver (receiver 1) until it returned to the estuary and was again recorded on receiver 1 or until

187   it was detected on any receivers in adjacent estuaries. For fish that did not return to the estuary (n

188   = 6), time spent in the marine environment was calculated from the time the fish left the estuary

189   until the end day of its minimum estimated battery life (provided by the tag manufacturer). For

190   marine-tagged fish, time spent in the Sundays Estuary, Sundays riverine environment and

191   adjacent estuaries, was calculated as for the estuarine-tagged fish. Time spent in the marine

192   environment was calculated from the time the fish was tagged until the end of its minimum

193   estimated battery life, excluding time in estuarine or riverine environments, or if the fish was

194   recaptured.

195   Within each group tagged, non-parametric Kruskal-Wallis ANOVA by ranks and a post-hoc

196   multiple comparison test or a non-parametric Kolmogorov two-sample test were run to test for

197   differences in times spent in the Sundays Estuary, Sundays riverine environment, adjacent

198   estuaries and the marine environment. For estuarine-tagged fish, a generalised linear model with

199   a normal distribution and log link function was used to test the effect of catch site (distance from

200   mouth), fish size and batch (Batch 1, Batch 2 and Batch 3) on the combined time spent in the

201   estuarine and riverine environment. Owing to the boundedness, non-constant variance and non-

202   normal error typical of proportional data, the response variable was logit transformed. A non-

203   linear least squares regression, using an inverse logistic with three parameters, was used to

204   describe the relationship between fish length and the proportion of time spent in estuarine and

205   marine environments during the study period, and to estimate the length after which *A. japonicus*

206   spend less time in the estuarine environment.

207

Marine, estuarine and riverine excursions

209 An estuarine-tagged fish was considered to have undertaken a 'marine excursion' if it passed the

210 lowermost estuarine receiver (receiver 1) and was only recorded again in the estuary $\geq$ 12 h later.

211 A marine-tagged fish was considered to visit the estuarine environment (i.e. undertaking an

212 'estuarine excursion') if it was recorded on receiver 1.

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

214 uppermost receiver (receiver 16), situated 21 km upstream of the estuary, at the river-estuary

215 interface (REI). Detections of tagged *A. japonicus* at this receiver were defined as a 'riverine

216 excursion'. A new 'riverine excursion' was considered if a tagged fish was last recorded on this

217 receiver and was only recorded again $\geq$ 12 h later. For estuarine-tagged fish, a generalised linear

218 model with binomial distribution and logit link function was used to test the effect of catch site

219 (distance from mouth), fish size and batch (Batch 1, Batch 2 and Batch 3) on whether the fish

220 undertook marine and riverine excursions.

221 For estuarine-tagged fish that visited the marine environment and returned to the estuary and

222 riverine environment, generalised linear models with a Poisson and normal distribution were

223 used to test the effect of catch site (distance from estuary mouth), fish size and batch (Batch 1,

224 Batch 2, Batch 3) on the number and the duration of excursions across the estuarine-marine and

225 estuarine-riverine interfaces, respectively. For the latter model, fish that visited the marine

226 environment once and did not return to the estuary were excluded from analyses. If the residuals

227   indicated overdispersion, a quasi-Poisson model was used instead of Poisson (Bolker et al.

228   2008).

229   The various analyses used in this study were conducted using R 3.03 (R Development Core

230   Team 2013), STATISTICA 12 (StatSoft Inc. 2011) and Microsoft Excel (2010). Prior to

231   analyses, exploratory data analyses, involving graphical examination of all data, were conducted

232   to assess the suitability of model application. Residuals were also checked for normality and the

233   appropriate analyses were used thereafter. The 'Wald' Chi-square statistic (W) and its *p-level*

234   were used to test the significance of each regression coefficient.

235

236   **RESULTS**

237   **Monitoring of tagged fish**

238   Estuarine-tagged *A. japonicus* were monitored for periods ranging from 13 to 519 days (mean:

239   217 ± 106 days, n = 65) (Fig. 2a). Twenty-three (35%) of these fish were recaptured in the local

240   fishery (length at tagging: mean: 499 ± 179, range: 237 – 832 mm TL; length at recapture: mean:

241   675 ± 212, range: 400 – 1 300 mm TL) (Fig. 2a, Appendix 1), after an average of 429 days post

242   tagging (range: 16 – 1 463 days). Nineteen (83%) recaptures were made in the Sundays Estuary,

243   three (14%) in the adjacent surf-zone and one (4%) outside of Algoa Bay in the Gamtoos

244   Estuary, 110 km west of the Sundays Estuary (Appendix 1). There was no significant effect of

245   batch ($P > 0.05$, $W(2) = 3.64$), catch site (distance from mouth) ($P > 0.05$, $W(1) = 0.52$) or fish

246   size ($P > 0.05$, $W(1) = 1.26$) on recapture rate of estuarine-tagged fish.

247   Marine-tagged fish were monitored for periods ranging from 182 to 684 days (Fig. 2b, Appendix

248   1). While it was possible to estimate the total number of days monitored for marine-tagged fish,

249   the lack of spatially continuous coverage (provided by the array in the marine environment)

250   reduced the accuracy of the estimation. Marine-tagged fish were detected in the estuarine and

251   marine receiver array for 7 to 408 days (Fig. 2b, Appendix 1). Four (20%) of these fish were

252   recaptured (length at tagging: mean: 543 ± 59, range: 498 – 630 mm TL; length at recapture:

253   mean: 767 ± 83, range: 658 – 860 mm TL) (Appendix 1). Three (75%) were recaptured in the

254   surf-zone, approximately 500 m from the Sundays Estuary mouth, and one in the near-shore zone

255   38 km west of the Sundays Estuary (Appendix 1), near the end of their transmitter's expected

256   battery life.

257

258   Fig. 2

259

260   **Residency to different habitats**

261   The estuarine-tagged *A. japonicus* spent significantly more time in the Sundays Estuary (mean:

262   94 ± 12%, range: 46 – 100%), than the riverine (mean: 3 ± 8%, range: 0 – 38%), marine (mean: 3

263   ± 8% range: 0 – 54%) or adjacent estuarine (mean: 0.04 ± 0.30, range: 0 – 2.4%) environments

264   ($H_{(3, 260)} = 186.15$; $P < 0.001$) (Fig. 3a). There were no significant differences among the times

265   spent in the riverine, marine and adjacent estuarine environments ($P < 0.05$). Only two

266   individuals visited other estuaries during the study period; namely the Kariega and Gamtoos

267   estuaries (Appendix 1, Fig. 1).

268   Thirty-nine (60%) of the 65 *A. japonicus* remained resident in the estuary and never ventured

269   into the marine environment throughout their respective monitoring periods (Appendix 1). Time

270   spent within the estuary was influenced by fish size (P < 0.05, W(1) = 5.51), but not by batch (P

271   > 0.05, $W(2) = 0.89$) or catch site (distance from mouth) (P > 0.05, W(1) = 0.70). Time spent in

272   the riverine region was not affected by batch (P > 0.05, W(2) = 0.03), catch site (P > 0.05, W(1)

273   = 2.97) or fish size (P > 0.05, W(1) = 1.00).

274   Marine-tagged fish spent significantly more time in the marine environment (mean: $97.9 \pm 6.4\%$,

275   range: 75 – 100%) than the Sundays estuarine (mean: $2.1 \pm 6.4\%$, range: 0 – 25%, n = 6 fish) or

276   riverine (0.01%, n = 1 fish) ($H_{(2, 45)} = 36.01$; $P < 0.001$) environments (Fig. 3b).

277

278   **Movements across the estuarine-marine interface**

279

280   Twenty-six (40%) of the 65 estuarine-tagged *A. japonicus* undertook marine excursions. Batch

281   (P > 0.05, W(2) = 0.86), catch site (P > 0.05, W(1) = 2.06) and fish size (P > 0.05, W(1) = 0.38)

282   had no effect on whether estuarine-tagged fish undertook marine excursions. Seven (27%) of

283   these 26 fish were recaptured (two from Batch 1, one from Batch 2 and four from Batch 3)

284   (Appendix 1). Proportionally more fish (41%, n = 16 fish) that remained resident in the estuary

285   (n = 39) were recaptured during the study period.

286   Most individuals undertook a single marine excursion, although some fish undertook up to six

287   such excursions (mean: 1.8 ± 1.5) (Appendix 1). Batch (P > 0.05, W(2) = 0.90), catch site (P >

288   0.05, W(1) = 0.36) and fish size (P > 0.05, W(1) = 0.38) had no effect on the number of marine

289   excursions. Their durations ranged from 1.2 to 68.8 days (mean: 9.2 ± 13.1 days) (Appendix 1),

290   although most (74%) excursions (calculated as the sum of the mean proportion) were less than

291   one week (7 days). The longest marine excursions were undertaken by different individuals, and

292   were 19.3, 23.3, 39.2 and 68.8 days. There was no effect of batch (P > 0.05, W(2) = 2.25), catch

293   site (P > 0.05, W(1) = 0.17) or fish size (P > 0.05, W(1) = 0.41) on the mean duration of marine

294   excursions. Eight (31%, mean: 400 mm TL, range: 326–486 mm TL) of the 26 estuarine-tagged

295   fish that undertook marine excursions were recorded on receivers within Algoa Bay. One of

296   these fish was detected in the nearby Kariega Estuary, and the other seven in the Port of Ngqura;

297   of which one was also detected in the PE Harbour and another in the Gamtoos Estuary. The

298   maximum number of days each fish was detected in the Port of Ngqura was two.

299   Six (30%) marine-tagged fish entered the Sundays Estuary during the study period, of which one

300   did not return to the marine environment, but was recaptured in the estuary (Appendix 1). The

301   number (mean: 2.2 ± 2.4, range: 1 – 7) and duration (mean: 6.9 ± 12.3 days, range: 0.75 to 45

302   days) of estuarine excursions varied among individuals (Appendix 1). However, excluding Fish

303   M17 (which never left the estuary) reduced the mean (3.5 ± 3.1 days) and maximum (10 days)

304   duration of estuarine excursions considerably. None of the marine-tagged fish visited other

305   estuaries in the acoustic array and only two individuals visited the Port of Ngqura (for one day)

306   during the study period (Appendix 1).

307

Movements across the estuarine-riverine interface

309 Twenty-five (38%) of the 65 estuarine-tagged *A. japonicus* visited the uppermost receiver

310 (Receiver 16) situated at the REI region, 21 km from the estuary mouth, of which ten (40%) also

311 undertook marine excursions. There was no effect of batch (P > 0.05, W(2) = 0.82), fish size (P >

312 0.05, W(1) = 0.21) or catch site (P > 0.05, W(1) = 3.91) on whether estuarine-tagged fish

313 undertook riverine excursions.

314 Riverine excursions totalled 422 (individual mean: 16.9 ± 26.6, range: 1 – 111), and were

315 relatively short (mean: 0.4 ± 0.5 days, range: 27 minutes to 3.4 days), with most (74%) lasting

316 less than six hours. There was no effect of batch (P > 0.05, W(2) = 2.81), catch site (P > 0.05,

317 W(1) = 0.22) or fish size (P > 0.05, W(1) = 3.66) on the number of riverine excursions.

318 Similarly, there was no effect of batch (P > 0.05, W(2) = 1.46), catch site (P > 0.05, W(1) = 0.96)

319 or fish size (P > 0.05, W(1) = 0.09) on the mean duration of riverine excursions. Only one of the

320 marine-tagged fish (M17) visited the riverine receiver, and only on a single occasion.

321

Effect of fish size on habitat connectivity

323 Smaller estuarine-tagged *A. japonicus* (< 746 mm TL) spent more time in the estuary than larger

324 juveniles ($F_{(1, 63)} = 92.04$, $R^2 = 0.32$; $P < 0.01$) (Fig. 4a), and the number of marine excursions

325 undertaken was positively related to fish length ($R^2 = 0.10$, $P < 0.05$) (Fig. 4b). Fish length had

326   no significant effect on time spent in the riverine environment ($R^2 = 0.03$, $P > 0.05$), or the

327   number of riverine excursions ($R^2 = 0.01$, $P > 0.05$), for estuarine-tagged fish.

328

329   Fig. 4

330

331   Owing to the low number of individuals that undertook estuarine excursions and the low

332   proportions of time spent in the estuary, non-linear least squares regression was not suitable to

333   model the time spent in the estuary by marine-tagged *A. japonicus*. However, there were no

334   correlations between fish length and either time spent in the estuary (Spearman rank order

335   correlation: $r = -0.13$, $P > 0.05$), or the number of estuarine excursions undertaken ($r = -0.09$, $P >$

336   0.05), for marine-tagged fish.

337

338   **DISCUSSION**

339   *Identification of 'contingent' and 'partial migration' strategies*

340   Based on the observed residency of estuarine- and marine-tagged *A. japonicus* to their habitats of

341   capture and Secor's (1999) definition of a contingent (a level of fish aggregation based on

342   'divergent habitat use'), it appears that the population consists of two separate juvenile

343   contingents (i.e. estuarine and marine). Contingents, mostly based on migratory behaviour, have

344   been documented in moronids (e.g. Kerr et al. 2009, Secor et al. 2001), anguillids (e.g. Tzeng et

345   al. 2003), clupeids (e.g. Mcquinn 1997), pleuronectids (Sagarese & Frisk 2011) and other marine

346   fish taxa (Petitgas et al. 2010). While the majority of tagged *A. japonicus* exhibited residency to

347   their habitat of capture, approximately one third within each contingent (and within each

348   estuarine batch) exhibited exploratory/migratory behaviour and visited the adjacent marine or

349   estuarine habitats. A proportion (40%) within the estuarine contingent also visited the REI

350   region. Such connectivity among the estuarine, marine and freshwater habitats exhibited by

351   individuals within each contingent, suggests that each is regulated by individuals that display

352   exploratory/migratory behaviour (Secor 1999), and may be best described as 'partial migration'

353   i.e. the occurrence of coexisting exploratory/migratory and resident groups within the same

354   population (Kerr et al. 2009)

355

356   Partial migration is a widespread phenomenon in nature, yet although it is well-documented in

357   the avian literature (e.g. Berthold 1999), the reporting of partial migration in fishes has been

358   infrequent (Kerr et al. 2009, Chapman et al. 2012), and generally limited to populations where it

359   is morphologically expressed and easily observed, e.g. salmonid populations exhibiting

360   morphologically different resident and migratory individuals (*inter alia* Jonsson & Jonsson 1993,

361   Olsson et al. 2006). However, Kerr et al. (2009) and Chapman et al. (2012) argue that partial

362   migration is more widespread among fishes than previously recognised. For example, adult red

363   drum *Sciaenops ocellatus*, a Sciaenid with a life-history remarkably similar to *A. japonicus*

364   (Griffiths 1996), exhibited what could have been classified as partial migration, with only a

365   proportion (26%) of tagged fish emigrating to the adjacent continental shelf, while the rest

366   remained resident in the estuary (Reyier et al. 2011).

367

368   *Evolutionary consequences of alternative life history strategies/behavioural traits*

369   Alternative life history strategies or behavioural traits such as contingent behaviour and partial

370   migration have significant ecological consequences (Kerr et al. 2009, Chapman et al. 2011,

371   Rohde et al. 2014). The expression of diverse life history strategies is particularly advantageous

372   for estuary-dependent fishes, as a means of offsetting environmental variability and ensuring

373   population persistence and regulation (Kerr & Secor 2012, Secor & Kerr 2009). Possibly

374   developed through phenotypic plasticity (Secor 1999), such contingents could offer "rescue

375   effects" for subpopulation declines by buffering population-level responses against

376   anthropogenic impacts and/or unfavourable conditions (e.g. Ray 2005, Kerr et al. 2010, Petitgas

377   et al. 2010). Therefore, alternative life history strategies or behavioral traits could be a beneficial

378   strategy to enhance population regulation and persistence, and could provide a powerful survival

379   mechanism for estuarine fish, especially in combination with dynamic meta-population

380   characteristics, including genetic diversity (Cowen et al. 2007).

381   Petitgas et al. (2010) examined the influence of diverse life cycles on the recovery of previously

382   collapsed marine fish stocks that exhibit resident and migratory contingents and demonstrated

383   the contribution of adopting contingents to the maintenance and recovery of collapsed

384   populations. They showed that the offshore (resident) contingents were the first to collapse and

385   their recovery was dependent on the reappearance phenotypically divergent migratory

386   individuals to re-establish the use of the offshore habitats. They suggested that resident

387   contingents confer stability while migratory contingents confer productivity and resilience, and

388   that the connectivity between the two contingents increases stock size. In the case of *A.*

389   *japonicus*, the existence of separate contingents, coupled with partial migration within each,

390   could allow for population regulation and contribute to the maintenance of the Algoa Bay *A.*

391   *japonicus* population. For example, the recapture rate of estuarine-tagged fish (35%) was almost

392   double that of the marine-tagged fish (20%). Additionally, among the estuarine-tagged fish, the

393   recapture rate of fish that remained resident to the estuary (41%) was almost double that of the

394   fish that exhibited movements across the estuarine-marine interface (23%). This highlights the

395   vulnerability of the estuarine contingent, particularly the resident individuals, to exploitation and

396   the potential benefits of alternative behavioural traits. Simultaneously, this highlights the need

397   for urgent management attention to allow for the recruitment of juveniles to the marine adult

398   population.

399   This study also acknowledges the contribution and importance of the marine contingent in

400   supplementing the coastal adult population, particularly as the connectivity between *A. japonicus*

401   tagged in the Sundays Estuary and adjacent Woody Cape coastal zone and the low levels of

402   dispersal out of Algoa Bay (n = 2 individuals) suggest that juvenile *A. japonicus* exist as a meta-

403   population with several subpopulations, each with distinct estuarine and marine contingents. This

404   supports the hypothesis of Griffiths (1996) and suggestions by Griffiths and Attwood (2005) that

405   juvenile dusky kob consist of several allopatric subpopulations that remain around their nursery

406   estuaries until they reach maturity. Kerr and Secor (2012) hypothesised that natural selection

407   should favour partial migration in estuarine and coastal fishes, but that the consequences of a

408   partial migration strategy should still be considered at a meta-population level, particularly in the

409   context of anthropogenic impacts, where for example, the removal of migratory individuals

410   could decrease connectivity between local populations and hence result in meta-population

411   declines. For example, this study showed that estuarine resident *A. japonicus* were more

412   vulnerable to exploitation. Over time, the removal of these individuals, particularly if residency

413   is a heritable trait, will have consequences at a meta-population level. The extent of such

414   associated consequences for *A. japonicus*, as for other fishes, remains unknown. Nonetheless, the

415   existence of such contingents and partial migration strategies in this case can be seen as

416   beneficial as they may improve the resilience of the species to the impacts of overfishing. The

417   occurrence of such intra-population structure within the *A. japonicus* Algoa Bay population

418   therefore likely improves the species' resilience to major perturbations, caused by anthropogenic

419   (e.g. estuarine degradation) or environmental (e.g. climatic) impacts. This is necessary, given the

420   high overall recapture rate (28%) and degree of residency and the low levels of dispersal and

421   connectivity among estuaries, which render this species vulnerable to exploitation.

422

Habitat connectivity and partial migration

424   Habitat connectivity was not affected by batch or catch site, although there was individual

425   variability in the extent, timing and duration of movements between estuarine, riverine and

426   marine environments. The need to understand individual variability in fish movement has

427   recently gained increased recognition from researchers, as population structure can be dependent

428   on individual movement behaviour (Patterson et al. 2008). According to Chapman et al. (2012),

429 intraspecific variation in migratory behaviour is widespread and appears to be the rule rather than

430 the exception, resulting in such within-population migratory dimorphism being termed partial

431 migration.

432

433 In vertebrates, migratory behaviour can be genetically-controlled, and the movement behavior

434 (i.e. resident or migratory) of fishes can be genetically inherited (Gemperline et al. 2002, Jonsson

435 & Jonsson 1993). However, the adoption of migratory behaviour may also be based on a trade-

436 off, where the benefits and costs of residency and migration are weighed up through their effect

437 on fitness (Gross 1987, Dingle 1996, Mehner & Kasprzak 2011). For an individual to maximise

438 fitness, behaviour should depend on the present conditions and future trade-offs in terms of

439 expected growth and probability of survival as a resident or migratory fish (Forseth et al. 1999).

440 For example, the adoption of migratory behaviour by common bream *Abramis brama* and brown

441 trout *Salmo trutta* was found to be related to an individual's risk of predation (Skov et al. 2011),

442 and by food availability and changes in feeding conditions in that habitat (Olsson et al. 2006),

443 respectively.

444

445 The expression of partial migration may also be affected by anthropogenic impacts that increase

446 productivity, by promoting residency in or migration to a specific habitat (Kerr et al. 2009).

447 *Gilchristella aestuaria,* one of the dominant prey items of juvenile *A. japonicus* (Marais 1984),

448 was found to be most abundant in the upper reaches of the Sundays Estuary (Harrison &

449 Whitfield 1990). Potential increases in abundance of *G. aestuaria*, as a result of increased

450 riverine productivity, could induce migratory behaviour to the REI, thereby promoting partial

451 migration in the *A. japonicus* population. Given that excursions were of relatively short duration

452 (~10 days) and seasonal, estuarine-coastal and riverine connectivity of *A. japonicus* is likely

453 prey- or predatory-related.

454

455 Habitat connectivity of estuarine-tagged *A. japonicus* was largely affected by fish size, with fish

456 < 746 mm TL spending significantly more time in the estuary, and larger fish undertaking more

457 marine excursions. Secor (1999) suggested that ontogeny is one of the most important factors

458 influencing the movements and migrations of fish (Secor 1999). Ontogenetic changes in habitat

459 use are typically associated with refuge, predation, diet and physiological requirements (Bacheler

460 et al. 2009a), allowing life stages to respond individually to the different selection pressures

461 experienced in the environment (Ebenman 1992), and maximise resource use efficiency (Pittman

462 & McAlpine 2001). Ontogenetic shifts in habitat use are common, particularly in estuary-

463 associated species (e.g. Childs et al. 2008, Sagarese & Frisk 2011). Therefore, the influence of

464 ontogeny on estuarine-coastal connectivity of *A. japonicus* in the present study is not surprising.

465 Bacheler et al. (2009a) suggested that the ontogenetic shift of *S. ocellatus* from the estuarine

466 tributaries towards the coast may be explained by the physiological requirements and preference

467 of larger individuals for higher salinity. It is therefore possible that the ontogenetic shift observed

468 in *A. japonicus* in this study may be in preparation for their adult marine phase and may be

469 related to an ontogenetic physiological shift, with larger fish having a reduced tolerance for low

470 salinity environments. It is uncertain whether fish size influences multiple estuary use as only

471 two fish, which were both of similar sizes, displayed such behaviour. The low levels of dispersal

472 may be attributed to the costs associated with moving to new estuaries. Dingle (1996) stated that

473   differential migration, which is the variation in distance travelled, may be facultative owing to

474   certain biological benefits or obligatory as a consequence of gene control. In some cases, the

475   environment and genes interact, such that physical properties can determine the expression of

476   genes and can cause certain individuals to migrate from estuaries when the physical environment

477   is unsuitable (Gillanders et al. 2012). Therefore the benefits of displaying multiple habitat

478   connectivity may also be related to the highly dynamic nature of estuaries or other sheltered

479   environments, such as ports, having varied effects on each individual. Given the low number of

480   estuarine and marine-tagged *A. japonicus* exhibiting multiple habitat connectivity, their

481   connectivity patterns were most likely attributed to individual variability.

482

483   CONCLUSION

484   This study highlights the value of incorporating movement theory and concepts, such as the

485   contingent hypothesis and partial migration, into fish ecological studies. Such concepts have

486   been previously overlooked in this and many other fish species. It also demonstrates that a

487   comprehensive understanding of behavioural dynamics could be valuable in the effective

488   management and conservation of overexploited estuary-associated species. By quantifying

489   habitat connectivity and intra-population spatial structure, this study not only highlighted the

490   importance of estuaries as nursery habitats but also provided insights into the potential role of

491   acoustic telemetry in contemporary ecological theory and its application.

492

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LITERATURE CITED

501   Abecasis D, Bentes L, Erzini K (2009) Home range, residency and movements of *Diplodus*

502   *sargus* and *Diplodus vulgaris* in a coastal lagoon: Connectivity between nursery and adult

503   habitats. Estuar Coast Shelf Sci 85: 525–529.

504   Able KW (2005) A re-examination of fish estuarine dependence: evidence for connectivity

505   between estuarine and ocean habitats. Estuar Coast Shelf Sci 64: 5–17.

506   Able KW, Grothues TM (2007a) Diversity of estuarine movements of striped bass (*Morone*

507   *saxatilis*): a synoptic examination of an estuarine system in southern New Jersey. Fish Bull

508   105: 426–435.

509   Able KW, Grothues TM (2007b) An approach to understanding habitat dynamics of flatfishes:

510   advantages of biotelemetry. J Sea Res 58: 1–7.

511   Bacheler NM, Paramore LM, Burdick SM, Buckel JA, Hightower JE (2009a) Variation in

512   movement patterns of red drum (*Sciaenops ocellatus*) infered from conventional tagging

513   and ultrasonic telemetry. Fish Bull 107: 405–419.

514   Bacheler NM, Paramore LM, Buckel JA, Hightower JE (2009b) Abiotic and biotic factors

515   influence the habitat use of an estuarine fish. Mar Ecol Prog Ser 377: 263–277.

516   Beck MW, Heck Jr. KL, Able KW, Childers D, Eggleston D, Gillanders BM, Halpern B, Hays

517   C, Hoshino K, Minello T, Orth R, Sheridan P, Weinstein M (2001) The identification,

518   conservation, and management of estuarine and marine nurseries for fish and invertebrates.

519   Bioscience 51: 33−641.

520   Berthold P (1999) A comprehensive theory for the evolution, control and adaptability of avian

521   migration. Ostrich: J Afr Ornith 70(1): 1-11

522   Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHM, White J-SS (2008)

523   Generalized linear mixed models: a practical guide for ecology and evolution. TREE 24

524   (3): 127-135.

525   Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A (2011) The ecology and evolution of

526   partial migration. Oikos 120: 1764–1775.

527   Chapman BB, Skov C, Hulthén K, Brodersen J, Nilsson PA, Hansson L-A, Brönmark C (2012)

528   Partial migration in fishes: definitions, methodologies and taxonomic distribution. J Fish

529   Biol 81: 479–499.

530   Childs A-R, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, Økland F (2008)

531   Estuarine use by spotted grunter (*Pomadasys commersonnii*) in a South African estuary,

532   as determined by acoustic telemetry. Afr J Mar Sci 30: 123–132.

533   Childs A-R, Næsje TF, Cowley PD (2011) Long-term effects of different-sized surgically

534   implanted acoustic transmitters on the sciaenid *Arygyrosomus japonicus*: breaking the 2%

535   tag-to-body mass rule. Mar Freshw Res 62: 432–438.

536   Cowley PD, Kerwath SE, Childs A-R, Thorstad EB, Økland F, Næsje TF (2008) Estuarine

537   habitat use by juvenile dusky kob *Argyrosomus japonicus* (Sciaenidae), with implications

538   for management. Afr J Mar Sci 30: 247–253.

539   Cowley PD, Childs A-R, Bennett RH (2013) The trouble with estuarine fisheries in temperate

540   South Africa, illustrated by a case study on the Sundays Estuary. Afr J Mar Sci 35(1): 117–

541   128.

542   Cowen RK, Gawarkiewic G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity

543   in marine systems: an overview. Oceanography 20: 14–21.

544   Dingle H (1996) Migration: the biology of life on the move. New York: Oxford University Press.

545   Ebenman B (1992) Evolution in organisms that change their niches during the life cycle. Am Nat

546   139: 990–1021

547 Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011) Testing a new acoustic

548   telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish

549   Res 108: 364–371.

550 Forseth T, Næsje TF, Jonsson B, Harsaker K (1999) Juvenile migration in brown trout: a

551   consequence of energetic state. J Anim Ecol 68: 783–793.

552 Gemperline PJ, Rulifson RA, Paramore L (2002) Multi-way analysis of trace elements in fish

553   otoliths to track migratory patterns. Chemom.Intell Lab Syst 60: 135–146.

554 Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of

555   connectivity between juvenile and adult habitats for mobile marine fauna: an important

556   component of nurseries. Mar Ecol Prog Ser 247: 281–295.

557 Gillanders BM, Elsdon TS, Roughan M (2012) Connectivity of Estuaries. In: Wolanski E,

558   McLusky DS (eds), Treat Estuar Coast. Amsterdam: Elsevier.

559 Griffiths MH (1996) Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the

560   east coast of South Africa. S Afr J Mar Sci 17: 135–154.

561 Griffiths MH (1997) Influence of prey availability on the distribution of dusky kob *Argyrosomus*

562   *japonicus* (Sciaenidae) in the Great Fish River Estuary, with notes on the diet of early

563   juveniles from three other estuarine systems. S Afr J Mar Sci 18: 137–145.

564 Griffiths MH, Attwood CG (2005) Do dart tags suppress growth of dusky kob *Argyrosomus*

565   *japonicus*? Afr J Mar Sci 27: 505–508.

566   Griffiths MH, Hecht T (1995) Age and growth of South African dusky kob *Argyrosomus*

567   *japonicus* (Sciaenidae) based on otoliths. S Afr J Mar Sci 16: 119–128.

568   Griffiths MH, Heemstra PC (1995) A contribution to the taxonomy of the marine fish genus

569   *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from

570   southern Africa. Ichthyol Bull JLB Smith Inst Ichthyol. No. 65: 1–40.

571   Gross MR (1987) Evolution of diadromy in fishes. Am Fish Soc Symp 1: 14–25.

572   Harrison TD, Whitfield AK (1990) Composition, distribution and abundance of ichthyoplankton

573   in the Sundays River estuary. S Afr J Zool 25: 161–168.

574   Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals:

575   scales, design, and deployment of listening station arrays. Mar Freshw Res 57: 1–13.

576   Illenberger WI (1988) The Holocene evolution of the Sundays Estuary and adjacent coastal

577   dunefields, Algoa Bay, South Africa. In: Davis GF, Moon BP (eds.), Geomorphological

578   studies in southern Africa. Cape Town: AA Balkema. pp 389–405.

579   Jonsson B, Jonsson N (1993) Partial migration: niche shift versus sexual maturation in fishes.

580   Rev Fish Biol Fish 3: 348–365.

581   Kerr LA, Secor DH (2012) Partial migration across populations of white perch (*Morone*

582   *americana*): A flexible life history strategy in a variable estuarine environment. Estuar

583   Coast 35: 227–236.

584   Kerr LA, Secor DH, Piccoli P (2009) Partial migration of fishes as exemplified by the estuarine-

585   dependent white perch. Fisheries 34:114–123.

586   Kerr LA, Cadrin SX, Secor DH (2010) The role of spatial dynamics in the stability, resilience,

587   and productivity of an estuarine fish population. Ecol Appl 20: 497–507.

588   Kraus RT, Secor DH (2004) Dynamics of white perch *Morone americana* population contingents

589   in the Patuxent River estuary, Maryland, USA. Mar Ecol Prog Ser 279: 247–259.

590   Marais JFK (1984) Feeding ecology of major carnivorous fish from four Eastern Cape estuaries.

591   S Afr J Zool 19: 210–223.

592   McQuinn IH (1997) Metapopulations and the Atlantic herring. Rev Fish Biol Fish 7: 297–329.

593   Mehner T, Kasprzak P (2011) Partial diel vertical migrations in pelagic fish. J Anim Ecol 80:

594   761–770.

595   Næsje TF, Cowley PD, Diserud OH, Childs A-R, Kerwath S, Thorstad EB (2012) Riding the

596   tide: estuarine movements of a sciaenid fish, *Argyrosomus japonicus*. Mar Ecol Prog Ser

597   460: 221–232.

598   Olsson IC, Greenberg EB, Wysujack K (2006) Environmentally induced migration: the

599   importance of food. Ecol Lett 9: 645–651.

600   Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models

601   of individual animal movement. TREE 23: 87–94.

602 Petitgas P, Secor DH, McQuinn I, Huse G, Lo N (2010) Stock collapses and their recovery:

603   mechanisms that establish and maintain lifecycle closure in space and time. ICES J Mar Sc

604   67: 1841–1848.

605 Pittman SJ, McAlpine CA (2001) Movements of marine fish and decapod crustaceans: Process,

606   Theory and Application. Adv Mar Biol 44: 206–272.

607 Ray GC (2005) Connectivities of estuarine fishes to the coastal realm. Estuar Coast Shelf Sci

608   64:18–32.

609 Reddering JSV, Esterhuysen K (1981) Sedimentation in the Sundays Estuary. University of Port

610   Elizabeth, ROSIE Report No. 3: 1-48.

611 Reyier EA, Lowers RH, Scheidt DM, Adams DH (2011) Movement patterns of adult red drum,

612   *Sciaenops ocellatus*, in shallow Florida lagoons as inferred through autonomous acoustic

613   telemetry. Environ Biol Fishes 90: 343–360.

614 Rohde J, Fresh KL, Quinn TP (2014) Factors affecting partial migration in Puget Sound Coho

615   Salmon. Nor Am J Fish Manag 34: 559–570.

616 Sackett DK, Able KW, Grothues TM (2007) Dynamics of summer flounder, *Paralichthys*

617   *dentatus,* seasonal migrations based on ultrasonic telemetry. Estuar Coast Shelf Sci 74:

618   119–130.

619 Sagarese SR, Frisk MG (2011) Movement patterns and residence of adult winter flounder within

620   a Long Island Estuary. Mar Coast Fish 3: 295–306.

621 Scharler UM, Baird D (2005) The filtering capacity of selected Eastern Cape estuaries, South

622   Africa. Water SA 31: 483–490.

623 Secor DH (1999) Specifying divergent migrations in the concept of stock: the contingent

624   hypothesis. Fish Res 43: 13–34.

625 Secor DH, Kerr LA (2009) A lexicon of life cycle diversity in diadromous and other fishes. In:

626   Haro A, Smith KL, Rulifson RA, Moffitt CM, Klauda RJ, Dadswell MJ, Cunjak RA,

627   Cooper JE, Beal KL, Avery TS (eds), Challenges for diadromous fishes in a dynamic

628   global environment, Am Fish Soc Symp Vol. 69. USA: American Fisheries Society. pp

629   537–556.

630 Secor DH, Rooker JR (2000) Is otolith strontium a useful scalar of life cycles in estuarine fishes?

631   Fish Res 46: 359–371.

632 Secor DH, Rooker JR (2005) Connectivity in the life histories of fishes that use estuaries. Estuar

633   Coast Shelf Sci 64: 1–3.

634 Secor DH, Rooker JR, Zlokovitz E, Zdanowicz VS (2001) Identification of riverine, estuarine,

635   and coastal contingents of Hudson River striped bass based upon otolith elemental

636   fingerprints. Mar Ecol Prog Ser 211: 245–253.

637 Silberschneider V, Gray CA (2008) Synopsis of biological, fisheries and aquaculture-related

638   information on mulloway *Argyrosomus japonicus* (Pisces: Sciaenidae), with particular

639   reference to Australia. J Appl Ichthyol 24: 7–17.

640   Skov C, Baktoft H, Brodersen J, Brönmark C, Chapman BB, Hansson L-A, Anders Nilsson P

641   (2011) Sizing up your enemy: individual predation vulnerability predicts migratory

642   probability. Proc Roy Soc Biol Sci 278: 1414–1418.

643   Trewavas E (1977) The sciaenid fishes of the Indo-West Pacific. Transactions of the Royal

644   Society, London 33: 253–541.

645   Tzeng WN, Iizuka Y, Shiao JC, Yamada Y, Oka HP (2003) Identification and growth rates

646   comparison of divergent migratory contingents of Japanese eel (*Anguilla japonica*).

647   Aquaculture 216:77–86.

648   Vasconcelos RP, Reis-Santos P, Maia A, Fonseca V, França S, Wouters N, Costa MJ, Cabral

649   HN. 2010. Nursery use patterns of commercially important marine fish species in estuarine

650   systems along the Portuguese coast. Estuar Coast Shelf Sci 86: 613–624.

651   Wallace JH (1975) The estuarine fishes of the east coast of South Africa. I. Species composition

652   and length distribution in the estuarine and marine environments. II. Seasonal abundance

653   and migrations. Invest Rep Ocean Res Inst. 40: 1–72.

654   Wooldridge TH, Bailey C (1982) Euryhaline zooplankton of the Sundays Estuary and notes on

655   trophic relationships. S Afr J Zool 17: 151–163.

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659   Fig. 1. Map of A) South Africa showing the location of acoustic receivers in the telemetry array

660   situated in Algoa Bay and eight estuaries along the South African coastline (green dots) and in

661   the coastal zone (blue dots), B) Sunday Estuary and catch-sites of juveniles caught and tagged in

662   three batches throughout the estuary and C) fish caught and tagged in the Woody Cape coastal

663   zone.

664   Fig. 2. Abacus plots showing the monitoring periods and daily presence of a) the three batches of

665   estuarine-tagged juvenile *A. japonicus* (E1 – E65); b) marine-tagged juvenile *A. japonicus* (M1 –

666   M20) ('R' = fish that were recaptured and kept, 'RR' = fish that were recaptured and released,

667   asterisk (*) denotes transmitters that switched off randomly during the study period. Note:

668   estimated monitoring period for the marine-tagged fish was based on the transmitter battery life

669   provided by the transmitter manufacturer).

670   Fig. 3. Mean proportions (%) of time spent by a) estuarine-tagged *A. japonicus* (n = 65) and b)

671   marine-tagged *A. japonicus* (n = 15); in the Sundays River (REI), Sundays Estuary (SUN), other

672   estuaries (OE) and the marine environment (MARINE).

673   Fig. 4. Relationships between estuarine-tagged *A. japonicus* size (mm TL) and a) the proportion

674   of time spent in the estuary (time in estuary = TIE) (solid markers represent observed time in

675   estuary and solid line represents estimated time in estuary) and b) number of marine excursions

676   undertaken.

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679   Fig. 1
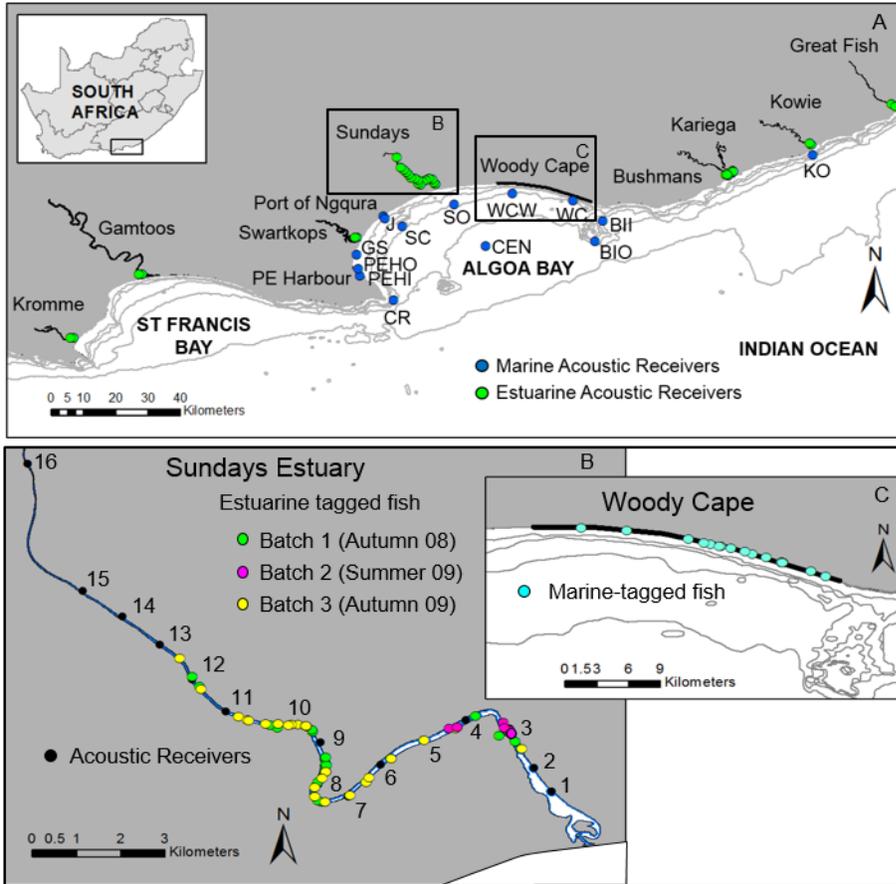
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687   Fig. 2

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714   Appendix 1. Details of the 85 juvenile *A. japonicus* acoustically tagged in the Sundays Estuary

715   and Woody Cape coastal zone from May 2008 to June 2009.

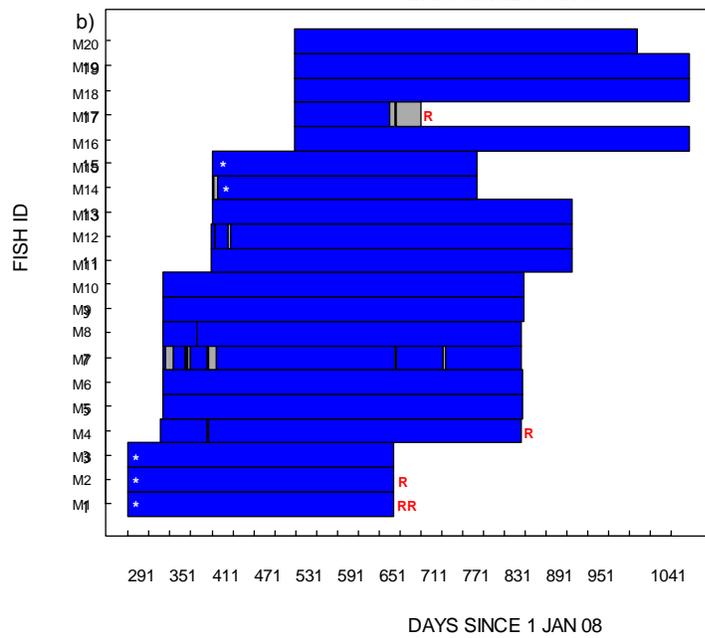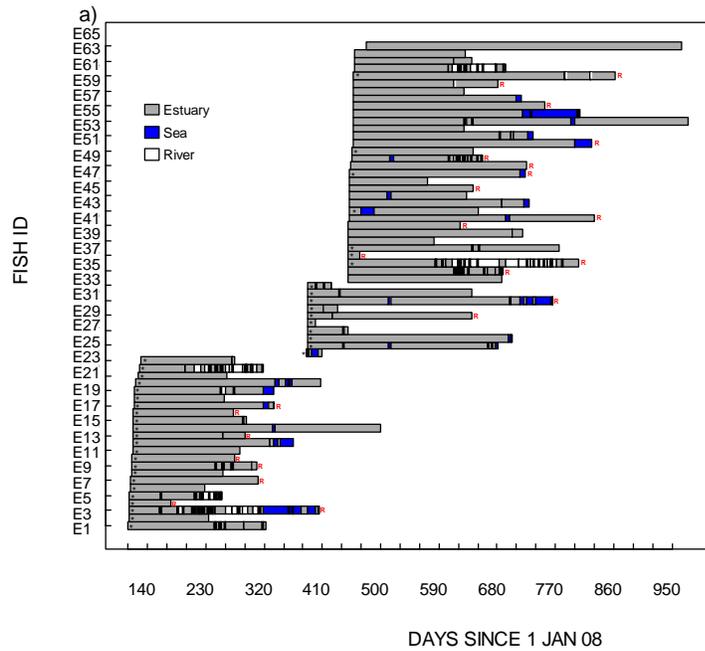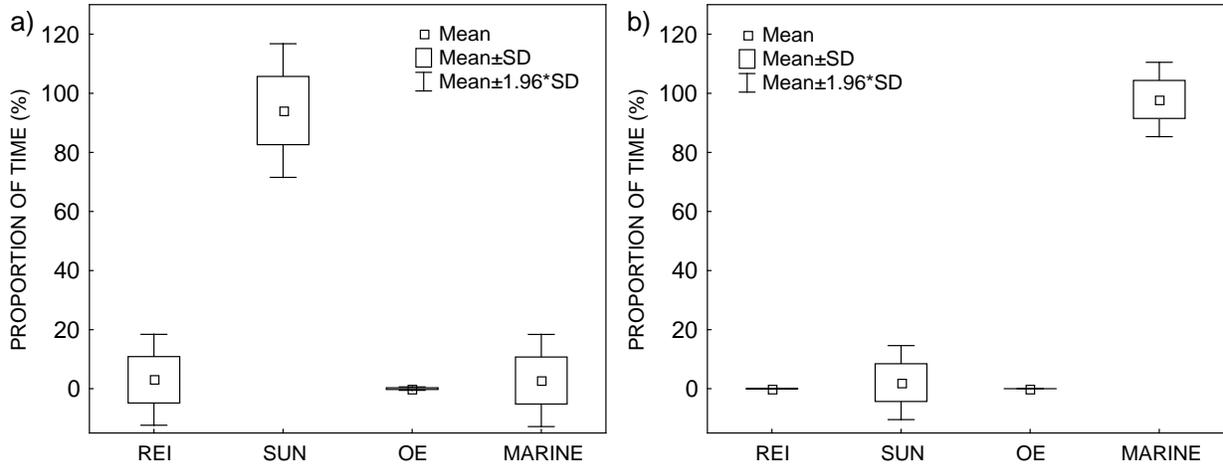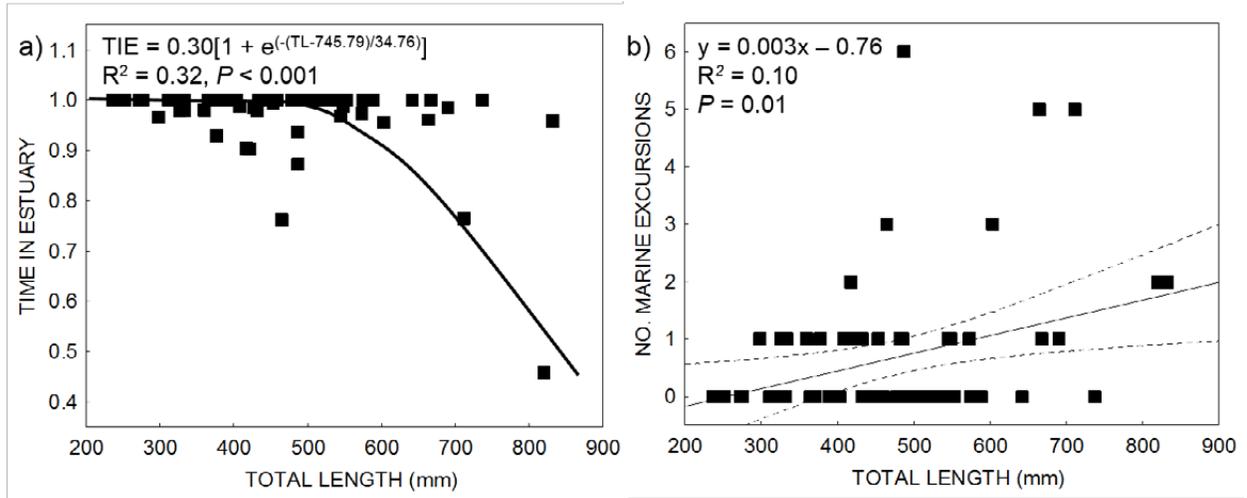| Fish No.	Tag type	Date tagged (yy/mm/dd)	Tag Location (SE=Sundays Estuary, SS=Sundays surfzone, WC=Woody Cape)	Total Length in mm (Age in years**)	No. days monitored	Time spent in habitat of capture (%)	Time spent in other estuaries (%)	Fate of Fish	No. and duration (mean days) of marine/estuarine excursions. NR=never returned. Other habitats visited in acoustic array given in parenthesis.	No. and duration (mean days) of riverine excursions	Recapture date (Distance from tag location)
						Estuarine-tagged juveniles					
						Batch 1					
E1*	V13	08/05/20	SE	433 (1.5)	212	94	-	TB	-	12 (0.17)	-
E2*	V13	08/05/21	SE	642 (2.9)	124	100	-	TB	-	-	-
E3*	V13	08/05/22	SE	712 (3.4)	292	52	-	TB-C	5 NR (16.9)	63 (0.33)	2011/02/23 (2 km)
E4*	V13	08/05/22	SE	737 (3.6)	64	100	-	TB-C	-	-	2009/07/11 (0 km)
E5*	V13	08/05/22	SE	532 (2.2)	143	85	-	TB	-	28 (0.19)	-
E6*	V13	08/05/23	SE	575 (2.5)	115	100	-	TB	-	-	-
E7*	V13	08/05/23	SE	450 (1.6)	198	100	-	TB-C	-	-	2009/06/16 (0 km)
E8*	V13	08/05/26	SE	516 (2.1)	140	100	-	TB	-	-	-
E9*	V13	08/05/26	SE	531 (2.2)	193	98	-	TB-C	-	9 (0.09)	2009/01/19 (0 km)
E10*	V13	08/05/26	SE	535 (2.2)	159	100	-	TB-C	-	-	2009/07/05 (2 km)
E11*	V13	08/05/27	SE	510 (2.0)	166	100	-	TB	-	-	-
E12*	V13	08/05/27	SE	417 (1.4)	246	90	2 (Kariega)	S (TB)	2 NR (6.2) (Kariega Estuary)	1 (0.14)	-
E13*	V13	08/05/27	SE	551 (2.3)	174	100	-	TB-C	-	1 (0.001)	2009/05/30 (0 km)
E14*	V13	08/05/28	SE	548 (2.3)	380	99	-	TL	1 (3.4)	-	-
E15*	V13	08/05/28	SE	427 (1.5)	174	99	-	TB	1 (2.3)	-	-
E16*	V13	08/05/28	SE	534 (2.2)	154	100	-	TB-C	-	-	1-May-09 (0 km)
E17*	V13	08/05/29	SE	832 (4.4)	215	96	-	S (TB)	2 NR (8.9)	-	3-Sep-12 (0 km)
E18*	V13	08/05/30	SE	403 (1.3)	138	100	-	TB	-	-	-

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E19*	V13	08/05/30	SE	486 (1.9)	213	92	-	S (TB)	1 NR (Port of Ngqura, PE Harbour)	7 (0.23)	-
E20*	V13	08/05/31	SE	604 (2.7)	287	96	-	TB	3 (4.2)	-	-
E21*	V13	08/06/05	SE	396 (1.3)	136	100	-	TB	-	-	-
E22*	V13	08/06/07	SE	667 (3.1)	189	62	-	S (TB)	1 NR	57 (0.22)	-
E23*	V13	08/06/08	SE	486 (1.9)	144	100	-	TB	-	1 (0.1)	-
Batch 2											
E24*	V13	09/02/19	SE	820 (4.3)	25	46	-	TB	2 (6.2)	-	-
E25*	V13	09/02/21	SE	664 (3.1)	295	96	-	TB	5 (2.3)	-	-
E26*	V13	09/02/21	SE	690 (3.3)	317	99	-	TB	1 (4.1)	-	-
E27*	V13	09/02/21	SE	545 (2.2)	62	97	-	TB	1 (1.9)	-	-
E28*	V13	09/02/21	SE	588 (2.5)	13	100	-	TB	-	-	-
E29*	V13	09/02/21	SE	447 (1.6)	253	100	-	TB-C	-	1 (0.42)	19-Nov-09 (0 km)
E30*	V13	09/02/22	SE	485 (1.8)	45	100	-	TB	-	1 (0.03)	-
E31*	V13	09/02/22	SE	487 (1.9)	377	87	-	TB-C	6 NR (9.5)	-	5-Mar-10 (0 km)
E32*	V13	09/02/22	SE	453 (1.6)	252	99	-	TB	1 (1.4)	-	-
E33*	V13	09/02/22	SE	483 (1.8)	35	94	-	S (TB)	1 NR	3 (0.74)	-
Batch 3											
E34	V13 TP	09/04/25	SE	552 (2.3)	238	100	-	TL	-	-	-
E35	V13 TP	09/04/25	SE	459 (1.7)	240	90	-	TL-C	-	17 (0.38)	4-Oct-10 (0 km)
E36*	V13	09/04/25	SE	486 (1.9)	354	65	-	TL-C	-	111 (0.56)	14-Apr-10 (0 km)
E37*	V13	09/04/25	SE	527 (2.1)	17	100	-	C	-	-	11-May-09 (0 km)
E38*	V13	09/04/25	SE	524 (2.1)	325	100	-	TB	-	2 (0.05)	-
E39	MP-9	09/04/25	SE	324 (0.8)	133	100	-	TL/C?	-	-	-
E40	MP-9	09/04/25	SE	371 (1.1)	270	99	-	TL	-	1 (0.01)	-
E41	MP-9	09/04/25	SE	365 (1.1)	173	100	-	C	-	-	14-Oct-09 (0 km)
E42*	V13	09/04/26	SE	548 (2.3)	379	99	-	TB-C	1 (4.1)	-	26-Apr-11 (0 km)
E43	MP-9	09/04/26	SE	421 (1.4)	200	73	-	TL/C?	1 (19.3)	34 (0.40)	-
E44	MP-9	09/04/26	SE	326 (0.8)	271	98	-	TL/C?	1 NR (Port of Ngqura)	1 (0.1)	-
E45	MP-7	09/04/26	SE	298 (0.6)	182	97	-	TL/C?	1 (6.1)	-	-

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ID	Tag	Date	Area								
E46	MP-7	09/04/26	SE	237 (0.2)	191	100	-	TLC	-	-	24-Feb-10 (0 km)
E47*	V13	09/04/27	SE	554 (2.3)	121	100	-	TB	-	-	-
E48	MP-9	09/04/27	SE	334 (0.9)	265	98	-	TLC	1 NR (Port of Ngqura)	-	23-Jan-10 (20 km)
E49	MP-9	09/04/28	SE	539 (2.2)	273	100	-	TLC	-	-	25-Jan-10 (0 km)
E50*	V13	09/05/01	SE	573 (2.4)	201	82	-	TB-C	1 (5.3)	20 (0.12)	24-Jan-10 (0 km)
E51	MP-7	01-May-09	SE	251 (0.3)	187	100	-	TL/C?	-	-	-
E52	MP-9	02-May-09	SE	377 (1.1)	368	93	0.4 (Gamtoos)	SC	1 NR (Gamtoos Estuary, Port of Ngqura)	-	6-Jan-11 (110 km)
E53	MP-9	02-May-09	SE	360 (1.0)	271	94	-	TL/C?	1 NR (Port of Ngqura)	4 (0.10)	-
E54	MP-9	02-May-09	SE	502 (2.0)	171	100	-	TL/C?	-	-	-
E55	MP-9	02-May-09	SE	408 (1.3)	518	99	-	TL	1 (5.9)	3 (0.27)	-
E56	MP-9	02-May-09	SE	465 (1.7)	349	76	-	S	3 NR (40.9) (Port of Ngqura)	-	-
E57	MP-9	02-May-09	SE	333 (0.8)	297	100	-	C	-	-	22-Feb-10 (0 km)
E58	MP-9	02-May-09	SE	432 (1.5)	254	98	-	S	1 NR (Port of Ngqura)	-	-
E59	MP-7	02-May-09	SE	272 (0.4)	172	100	-	TL/C	-	-	-
E60*	V13	03-May-09	SE	584 (2.5)	223	100	-	TB-C	-	1 (0.02)	4-Jan-10 (0 km)
E61	MP-9	03-May-09	SE	312 (0.7)	404	100	-	TL/C?	-	3 (0.15)	22-Oct-10 (0 km)
E62	MP-9	04-May-09	SE	389 (1.2)	235	82	-	TL/C?	-	40 (0.13)	-
E63	MP-9	04-May-09	SE	478 (1.8)	181	100	-	TL/C?	-	1 (0.07)	-
E64	MP-7	04-May-09	SE	276 (0.5)	171	100	-	TL/C	-	-	-
E65	MP-9	23-May-09	SE	437 (1.5)	394	100	-	TL	-	-	-
Marine-tagged juveniles											
M1*	V13	18-Oct-08	WC	498 (1.9)	TB	-	-	TB	-	-	18-Dec-09 (56 km) (Released)
M2*	V13	18-Oct-08	WC	630 (2.8)	TB	-	-	TB	-	-	5-Jan-11 (36 km)
M3*	V13	18-Oct-08	WC	560 (2.3)	TB	-	-	TB	-	-	-
M4	V13	03-Dec-08	WC	518 (2.1)	517 (68)	99.8	-	S	1 (1.1)	-	13-Oct-12 (36 km)
M5	V13	06-Dec-08	WC	684 (3.2)	517 (0)	100	-	S	-	-	-
M6	V13	06-Dec-08	WC	716 (3.5)	517 (0)	100	-	S	-	-	-

M7	V13	06-Dec-08	WC	536 (2.2)	517 (408)	94.3	-	S	7 (4.2)	-	-
M8	V13	06-Dec-08	WC	696 (3.3)	517 (399)	99.9	-	S	1 (0.7) (Port of Ngqura)	-	-
M9	V13	07-Dec-08	WC	738 (3.6)	517 (0)	100	-	S	-	-	-
M10	V13	07-Dec-08	WC	465 (1.7)	517 (0)	100	-	S	-	-	-
M11	V13	14-Feb-09	WC	597 (2.6)	517 (326)	100	-	S	0 (Port of Nqura)	-	-
M12	V13	14-Feb-09	WC	571 (2.4)	517 (27)	99.5	-	S	2 (2.6)	-	-
M13	V13	15-Feb-09	WC	812 (4.2)	517 (0)	100	-	S	-	-	-
M14*	V13	15-Feb-09	WC	595 (2.6)	TB (7)	-	-	TB	1 (4.1)	-	-
M15*	V13	2009/02/15	WC	588 (2.5)	TB	-	-	TB	-	-	-
M16	MP-13	2009/06/13	WC	491 (1.9)	684 (0)	100	-	S	-	-	-
M17	MP-13	2009/06/13	WC	524 (2.1)	182	75.4	-	TL-C	1 NR (45)	1 (0.05)	19-Aug-11 (36 km)
M18	MP-13	2009/06/13	WC	553 (2.3)	684 (0)	100	-	S	-	-	-
M19	MP-13	2009/06/13	WC	446 (1.6)	684 (0)	100	-	S	-	-	-
M20	MP-13	2009/06/13	WC	570 (2.4)	492 (0)	100	-	S	-	-	-

716   * = Transmitters that switched off randomly during the study period between May 2008 and June 2009.

717   ** = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995). Note:

718   TB = Transmitter battery switched off at random intervals, TB-C = Transmitter battery switched off randomly then caught, C =

719   Caught, TL = Transmitter lifespan completed, TL-C = Transmitter lifespan completed then caught, TL/C? = Transmitter lifespan

720   completed or caught, S (TB) = Sea but unknown because transmitter battery could have switched off randomly, S = Sea, S-C = Sea

721   then caught.

722

723

724

725