1 **Migration to freshwater increases growth rates in a facultatively catadromous tropical**

2 **fish**

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16 *Our study provides the first evidence that catadromy confers a growth advantage. We provide*

17 *new insights into the evolutionary and ecological factors that may shape the expression of*

18 *diadromy in fish.*

19

Declaration of authorship

20   **Abstract**

21   Diadromy is a form of migration where aquatic organisms undergo regular movements

22   between fresh and marine waters for the purposes of feeding and reproduction. Despite

23   having arisen in independent lineages of fish, gastropod molluscs and crustaceans, the

24   evolutionary drivers of diadromous migration remain contentious. We test a key aspect of the

25   'productivity hypothesis', which proposes that diadromy arises in response to primary

26   productivity differentials between marine and freshwater habitats. Otolith chemistry and

27   biochronology data are analyzed in a facultatively catadromous tropical fish (barramundi,

28   *Lates calcarifer*) to determine the effect of freshwater residence on growth rates. Individuals

29   that accessed fresh water grew ~25% faster on average than estuarine residents in the year

30   following migration, suggesting that catadromy provides a potential fitness advantage over

31   non-catadromous (marine/estuarine) life-histories, as predicted by the productivity

32   hypothesis. Although diadromous barramundi exhibited faster growth than non-diadromous

33   fish, we suggest that the relative reproductive success of diadromous and non-diadromous

34   contingents is likely to be strongly influenced by local environmental variability such as

35   temporal differences in river discharge, and that this may facilitate the persistence of diverse

36   life history strategies within populations.

37   **Key words**

38   Diadromy, partial migration, life history, biochronology, otolith chemistry

39   **Introduction**

40   Diadromy, where aquatic fauna migrate between fresh and marine biomes, represent some of

41   nature's most well-known and spectacular migrations. Three forms are recognised:

42   *anadromy*, where adults migrate from the sea to fresh water to spawn; *catadromy*, where

43   adults migrate from fresh water to spawn in marine habitats; and *amphidromy*, where

44   individuals undertake predictable migrations between marine and fresh waters that are

45   unrelated to spawning (Myers 1949; McDowall 1988). Understanding the mechanisms

46   underpinning the evolution and maintenance of diadromous migrations is important given

47   their impact on a variety of ecosystem processes in aquatic environments. Diadromy shapes

48   the biogeography and evolution of species (McDowall 1998) and plays a key role in the

49   transportation of nutrients across marine and freshwater ecotones, thus influencing food web

50   and ecosystem dynamics (Wipfli et al. 2003). Scientific interest in diadromy also has a strong

51   practical basis, with many diadromous species targeted for commercial and recreational

52   fishing and being increasingly challenged by anthropogenic disruptions to migratory

53   pathways due to dams and other disturbances (Crook et al. 2015).

54   Despite the physiological and osmoregulatory challenges associated with transitioning

55   between marine and freshwater habitats, diadromous life-histories have independently arisen

56   across several lineages of fish, gastropod molluscs and crustaceans (McDowall 1999). The

57   pathways leading to the evolution of diadromy across this broad range of taxa remain

58   contentious. Gross (1987) and Gross et al. (1988) proposed a conceptual model ('productivity

59   hypothesis' (Bloom and Lovejoy 2014)), contending that the tendency for diadromous

60   species to exhibit anadromy in temperate regions and catadromy in the tropics was

61   attributable to global patterns in marine and freshwater productivity. They posited that (1) the

62   proximate cause of diadromy is a differential between freshwater and marine primary

63   productivity, with relatively high marine productivity driving anadromy in temperate

64   latitudes, compared with relatively high freshwater productivity driving catadromy in the

65   tropics; and (2) that anadromy and catadromy represent intermediate evolutionary phases

66   between exclusively marine and freshwater lifecycles, respectively. The generality of the

67   second premise of this hypothesis has not been supported by recent phylogenetic studies

68   (Feutry et al. 2013; Bloom and Lovejoy 2014). The role of aquatic productivity in shaping the

69   evolution of diadromy has also been challenged based on a lack of substantiating evidence

70   (e.g., (McDowall 1997). However, to date there has been little empirical study of the

71   influence of productivity differentials on the relative fitness of migratory organisms.

72   Similar to other major taxa (e.g., birds (Lundberg 1988); mammals (Ball et al. 2001);

73   insects (Hansson and Hylander 2009)), recent research on diadromous fishes has

74   demonstrated the widespread co-existence of distinct migratory phenotypes within

75   populations: a phenomenon often referred to as 'partial migration' (see Chapman et al. 2012).

76   Partial migration is thought to be driven primarily by individual physiological and

77   behavioural asymmetries, and may arise as evolutionary stable strategies (Chapman et al.

78   2011; De Leenheer et al. 2017). According to the productivity hypothesis, diadromous

79   migration from breeding grounds to more productive feeding habitats should confer a growth

80   advantage relative to the non-diadromous state. Thus, populations of partially diadromous

81   fishes present an opportunity to examine the consequences of contrasting life-history

82   strategies among individuals. Although the effect of diadromy on growth has received some

83   attention among anadromous fishes in temperate regions (e.g., Snyder 1991; Kendall et al.

84   2014; Bond et al. 2015), such relationships have received limited attention among

85   catadromous fishes.

86   In this study, we test the hypothesis that growth rates of a facultatively catadromous

87   fish in tropical Australia are enhanced during freshwater residence, as predicted by the

88   productivity hypotheses. Whilst reproductive success, the ultimate measure of fitness, may be

89   influenced by a range of factors (e.g., Durham and Wilde 2009), growth is a key determinant

90   of individual fitness because it can be correlated positively with fecundity and offspring

91   quality (Barneche et al. 2018), mating success (Bisazza and Marconato 1988) and escape

92   from size-specific predation (Perez and Munch 2010). We reconstruct individual salinity

93   histories by analysing strontium isotope ratios ($^{87}Sr/\,^{86}Sr$) of barramundi otoliths. Annual

94   otolith growth increments are then measured to estimate somatic growth rates throughout

95   ontogeny and in relation to ambient salinity to determine whether migration into freshwater

96   confers a growth advantage to catadromous individuals. The results of our study are

97   discussed with regards to the potential fitness consequences of catadromous migration in the

98   context of the productivity hypothesis.

99   **Materials and methods**

100   **Study species**

101   Barramundi is a large, high order predator that is widespread throughout coastal regions and

102   freshwater habitats in the Indo-West Pacific region. The species supports substantial

103   commercial, recreational, subsistence and aquaculture fisheries across its range. Barramundi

104   are sequential hermaphrodites, maturing first as males at 3-4 years of age, before

105   transitioning into females at 6-8 years of age (Grey 1987). Spawning occurs exclusively in

106   marine or estuarine habitats during the monsoonal wet season, where larvae hatch and are

107   thought to spend the first few months of life inhabiting tidal areas. In Australian populations,

108   a proportion of juveniles migrate upstream into the freshwater reaches of rivers and

109   floodplain lakes (known locally as billabongs) towards the end of the wet season. Individuals

110   that forgo catadromous migration in their first year typically remain resident in marine or

111   estuarine habitats throughout life, although a small proportion migrates into freshwater in

112   their second and third years (Crook et al. 2017). After a period of up to 10 years of fresh

113   water residency, catadromous individuals return to the spawning grounds to breed. Most fish

114   continue to reside in saline or brackish water for the remainder of the life-history after

115   spawning (Crook et al 2017). Fish typically breed first as males before undergoing sexual

116   inversion and transitioning into females. Some individuals directly develop or transition into

117 females during the freshwater residency phase without returning to the estuary to spawn as

118 males (Crook et al. 2017).

Growth and salinity proxies

120 The microstructure and chemistry of barramundi otoliths (earstones) were analysed to explore

121 growth and migration behaviour. As with other bony fishes, calcareous material is deposited

122 incrementally on the otolith surface continually throughout life, at a rate that is generally

123 correlated with somatic growth (Campana and Thorrold 2001). Analogous to

124 dendrochronological analyses performed on growth rings in trees, the distances between

125 annual growth rings laid down within otoliths may be measured to determine favourable

126 years for growth (Morrongiello and Thresher 2015). Additionally, trace elements from

127 ambient water are incorporated into the calcium carbonate matrix of otoliths. As this material

128 is not physiologically reworked, otolith microchemistry may be analysed to infer the ambient

129 water chemistry (in this case, salinity) experienced at different stages of fish life-histories and

130 thus the timing of migrations (Elsdon et al. 2008). Sr isotope ratios are an ideal proxy to

131 detect diadromous migrations, because unlike trace element concentrations, they directly

132 reflect ambient salinity and are not influenced by physiology, diet or other environmental

133 factors (Eldson et al. 2008; Hughes et al. 2014).

Study sites

135 Barramundi otoliths were obtained from samples collected between 2008 and 2015 from the

136 Daly and Mary rivers, and to a lesser extent, the South Alligator, Roper and McArthur rivers

137 in the Northern Territory, Australia (Table S1). All rivers are located within Australia's

138 wet/dry tropics and are free of major dams and other artificial barriers to migration. Samples

139 from coastal marine, estuarine and freshwater habitats were collected using commercial,

140   recreational and scientific fishing practices to ensure that both migratory and resident fish

141   were represented in the analyses.

142   **Otolith preparation and analyses**

143   Otoliths from 131 barramundi were embedded in epoxy resin, sectioned through the

144   primordium, then polished and mounted on glass slides. Chemical analysis was conducted on

145   each otolith section using a multi-collector Laser Ablation Inductively Coupled Plasma Mass

146   Spectrometer (LA-ICPMS) operated at the University of Melbourne, Australia, following the

147   methods of Woodhead et al. (2005). $^{87}Sr/^{86}Sr$ ratios were measured along a transect,

148   following the axis of growth from the otolith core to the proximal edge. Otolith $^{87}Sr/^{86}Sr$ data

149   were then examined alongside water $^{87}Sr/^{86}Sr$ salinity mixing models previously constructed

150   for the Daly, Mary, Roper and South Alligator rivers to recreate the lifetime salinity history

151   for each fish (Table S2; see Crook et al. 2017). An additional $^{87}Sr/^{86}Sr$ salinity mixing model

152   was constructed for the McArthur river using the methods described by Crook et al. (2017).

153    $^{87}Sr/^{86}Sr$ values corresponding to salinities <1ppt were considered to represent freshwater

154   residency, whereas $^{87}Sr/^{86}Sr$ values above this value were considered to represent residency

155   in more saline estuarine or marine habitats.

156   Sectioned otoliths were viewed under a dissecting microscope, photographed and

157   distances (µm) measured from the inside of each opaque zone (i.e., annual increment; Stuart

158   and McKillup (2002)) to the inside of the next opaque zone using image analyses software

159   (Leica Application Suite, v. 4.2, Figure 1). Measurements were taken along the laser-ablated

160   transect, allowing us to estimate ambient salinity in relation to annual increment formation.

161   Reconstruction of growth histories via otolith increment analysis assumes that otolith growth

162   is proportional to somatic growth across the life history (Campana 1990). In our barramundi

163   samples, regression analysis demonstrated a strong linear relationship between otolith size

164   and fish length (Figure S1). We assumed a November 1 birthdate for all fish (Stuart and

165   McKillup 2002), and assigned each annulus a growth year (November 1- October 31) based

166   on back-calculation from known date of capture. Each annual growth measurement was

167   assigned a categorical salinity value: 'freshwater' or 'estuarine' if an entire growing year was

168   spent in either habitat (freshwater: $^{87}Sr/\,^{86}Sr$ <1 ppt, estuarine: $^{87}Sr/\,^{86}Sr$ >1 ppt). Annual

169   growth measurements were classified as 'mixed' if a portion of a year was spent in each

170   habitat.

171   **Data analysis**

172   A mixed effects modelling framework was used to investigate the effect of salinity on growth

173   (increment width, µm) (Morrongiello and Thresher 2015). A series of models were developed

174   using the *lme4* package (Bates et al. 2013) in R Studio 1.0.143 (RStudio Team 2016)

175   containing different combinations of intrinsic and extrinsic predictors, and their interactions.

176   The first increment was excluded from the analyses because the protracted spawning period

177   of barramundi (September-March) may result in different length growth periods prior to

178   deposition of the first increment among individuals. Similarly, we excluded growth

179   increments beyond age eight from our analyses because nearly all fish had returned to the

180   estuary and resided there or associated coastal habitats by this age. Our analyses therefore

181   included data for ages 2-8 from 131 individuals (67 collected in fresh water, 64 collected

182   from estuarine or coastal habitats).

183   Fixed intrinsic predictors were the age of the fish at the time of increment formation

184   (*Age*), and the age-at-capture (*AAC*). The former term was included in models to allow for

185   decreasing growth with age while the latter was included to test and account for any potential

186   age selectivity biases associated with sample collection (Morrongiello et al. 2012). We

187   included a random intercept for *FishID* to allow each fish to have higher or lower growth

188   than average (model's overall intercept), and to account for the non-independence of repeated

189   increment measurements from the same fish. We also explored whether allowing for

190   individual-specific deviations from the overall age: growth relationship (random *Age* slopes

191   for *FishID*) improved model performance. We allowed for the possibility that increments

192   formed by different fish in the same year were non-independent by including a *Year* random

193   intercept, because concurrent environmental conditions (i.e. good or poor growing years) may

194   be expected to exert similar effects on groups of individuals. Similarly, we included a *Cohort*

195   random intercept to account for any persistent growth effects among individuals of a common

196   year class. We tested for consistent among-river variation in annual and cohort-specific

197   growth by composing models that included *River: Year* and *River: Cohort* interactions. Fixed

198   extrinsic variables were *River* and *Salinity*. To test for differences in age dependent growth

199   between fresh and estuarine habitats an *Age × Salinity* interaction was fitted to the full model.

200   To satisfy model assumptions, *Growth* (increment width), *Age* and *AAC* were log-

201   transformed. The predictor variables were centred to facilitate model convergence.

202   Different random effects structures were first compared using restricted maximum

203   likelihood estimation (REML). Next, increasingly complex fixed effects structures were fitted

204   using maximum likelihood, ML. The relative support for each model was assessed using

205   Akaike's Information Criterion, adjusted for small sample sizes (AICc). Marginal (proportion

206   of variance explained by fixed effects) and conditional (proportion of variance explained by

207   combined fixed and random effects) R^2 values were calculated for each model using the

208   sem.model.fits function in piecewiseSEM package (see (Nakagawa and Schielzeth 2013)).

209   95% confidence intervals for parameter estimates (fixed effects) and standard deviations

210   (random effects) were derived from 1000 non-parametric bootstrap replicates.

211   **Results**

212   Of the fish sampled from estuarine habitats, the majority (61.5%) had migrated into

213   freshwater during the life history. Catadromous individuals and estuarine/marine residents

214   were present in the Mary, Roper and Daly systems but as samples from the McArthur and

215   South Alligator rivers were obtained solely from fresh water, they only contained

216   catadromous barramundi. Repeated movements between salt and fresh water were relatively

217   infrequent among migrants. Of the fish sampled in fresh water, 90.6% had undergone a single

218   juvenile transition from saline water, and of the catadromous fish sampled in salt water, 60%

219   had undertaken a single return migration after 1-8 years of freshwater residency. A total of

220   267 years of freshwater growth, 212 years of estuarine/marine growth and 131 years of

221   'mixed' growth were recorded across the 131 individuals.

222   The best-supported random effects structure included random intercepts and *Age*

223   slopes for *FishID*, as well as a random intercept for *River*: *Year* (Table S3). This indicates

224   that the *Growth ~ Age* relationship varied between individuals and that the effect of *Year*

225   varied across rivers. The optimum fixed effects structure included an *Age × Salinity*

226   interaction (Table S4; marginal R^2: 0.53; conditional R^2: 0.68). Overall, there was a decline in

227   growth with age, and differences in growth amongst habitats were greatest in the earlier years

228   of life (Table 1, Figure 3). Growth was initially highest in freshwater, lowest in saltwater, and

229   intermediate in years spent partially within freshwater (i.e., mixed), but these habitat-

230   dependent differences became less pronounced as fish age increased (Table 2).

231   **Discussion**

232   Our results demonstrate that catadromous migration into fresh water from the coastal marine

233   spawning grounds confers enhanced growth for juvenile barramundi. This pattern contrasts

234   with temperate anadromous fishes, which are widely reported to achieve higher growth rates

235   while residing in marine habitats (e.g., threespine sticklebacks (Snyder 1991), Atlantic

236 salmon (Fleming 1996), white perch (Kraus and Secor 2004), rainbow trout (Kendall et al.

237 2014), dolly varden (Bond et al. 2015). This suggests that growth differentials between

238 adjacent marine and freshwater habitats may be important in shaping the form of diadromy

239 exhibited by fishes. We note, however, that contrary to the productivity hypothesis

240 catadromous eels in temperate systems tend to grow more rapidly in saline than freshwater

241 habitats (Arai et a. 2004; Cairns et al. 2009), whilst tropical amphidromous gobies (*Awaous*

242 *stamineaus*) have faster growth rates and shorter larval durations associated with marine

243 dispersal, (Hogan et. al. 2014). It is therefore apparent that the expression of diadromy may

244 be shaped by a range of processes and is not strictly regulated by habitat-specific growth rates

245 or latitude across taxa.

246 Habitat-dependent variance in growth rate potentially reflects greater foraging success by

247 barramundi in fresh water compared to saline water, which may in turn be driven by

248 increased access to floodplain-derived food resources. Extensive, highly productive

249 floodplain habitats are a defining characteristic of the large river catchments in the wet/dry

250 tropics of northern Australia (Douglas et al. 2005; Jardine et al. 2012). These systems

251 typically undergo predictable periods of inundation during the monsoon season, although the

252 magnitude and duration of flooding may vary considerably between years (Douglas et al.

253 2005). Floodplain inundation events deliver large-scale energy influxes into aquatic food-

254 webs, providing seasonally abundant food supplies available to consumers (Junk et al. 1989;

255 Jardine et al. 2012). Stable isotope analyses indicate that floodplain-derived prey make a

256 substantial contribution to the diet of barramundi and other large-bodied fishes in freshwaters

257 (Jardine et al. 2012), suggesting that catadromous barramundi may gain access to highly

258 productive food resources that are unavailable to those that remain as estuarine residents. It is

259 also feasible that differences in growth may be partially attributable to habitat-specific

260 differences in energetic costs or mortality rates. For example, residence in macrotidal habitats

261   with very strong tidal currents may entail high energetic costs, potentially constraining

262   energetic investment in growth. Similarly, fish living in different salinities incur different

263   energetic costs associated with osmoregulation (Bœuf and Payan 2001). Differential

264   mortality rates for slow- and fast-growing fish in saline versus freshwater habitats could also

265   potentially contribute to the patterns observed (see Sponaugle et al. 2006). At present,

266   however, little information is available on the energetic costs and mortality rates incurred by

267   fish living in marine/estuarine versus freshwater habitats and this is an important area for

268   future research.

269   Given that body size is positively correlated to a range of fitness traits in fish, our findings of

270   increased growth rates in catadromous barramundi (insofar as it results in larger size-at-age)

271   suggest that migration may have important implications in terms of reproductive fitness. In

272   this respect, our findings provide potential support for the primary production differential

273   aspect of the productivity hypothesis (Gross et al. 1988). However, whilst different migratory

274   strategies may result in divergent growth trajectories, alternate phenotypes may nonetheless

275   persist over generations if lifetime reproductive output is equal among strategies, or if the

276   optimum strategy varies throughout time (Hendry et al. 2004; Gillanders et al. 2015). Thus,

277   our findings of increased growth rates during freshwater residence do not necessarily support

278   the suggestion of Gross (1988) that catadromous fish in tropical regions have generally

279   higher reproductive fitness than non-catadromous fish. Indeed, populations comprising

280   diverse life-histories are increasingly recognised as commonplace (Chapman et al. 2011) and

281   may be shaped by dynamism in the success rates of different reproductive tactics as

282   influenced by changes in local conditions (e.g., temporal variation in river hydrology or

283   changes in the abundance of predators). Thus, co-existing life-history modes frequently arise

284   as evolutionary stable states and represent an example of population-level bet-hedging by

285   enabling species to optimize recruitment in unpredictable environments (Schindler et al.

286   2010). In the case of barramundi, it is possible catadromous individuals migrating onto

287   productive, inundated floodplains obtain fitness advantages over marine/estuarine

288   conspecifics in years of high rainfall, but may be disadvantaged in years with poor wet

289   seasons due to limited hydrological connectivity to breeding and nursery habitats.

290   The strength of selection on different migratory contingents can fluctuate throughout

291   ontogeny as individuals maximise spawning investment at contrasting life-history stages

292   (Monro and Marshall 2014). For example, because barramundi are protandrous

293   hermaphrodites, relative fitness may involve complex trade-offs between male and female

294   spawning investment. Individuals that utilise productive freshwater habitats, delay sexual

295   maturation and maximise energetic investment into somatic growth may increase the chances

296   of ultimately attaining female status; however, delayed maturation also incurs an increased

297   risk of mortality prior to the commencement of reproductive activity. At the other end of the

298   spectrum, foregoing migration and adopting slower-growing lives in estuaries may facilitate

299   successful reproduction during the initial male adult phase, but may reduce the chances of

300   successful transition into large, highly fecund females in later life. It appears likely that such

301   trade-offs promote the co-existence of divergent life-histories in barramundi, although further

302   detailed analyses are required to shed light on relationships between migration strategies and

303   relative fitness.

304   In conclusion, our study provides new insights into the potential drivers of diadromy and

305   highlights the complex interaction between life history characteristics and individual fitness.

306   The results also serve to demonstrate the importance of preserving highly productive tropical

307   freshwater habitats, especially in the face of increasing demand for water resources and a

308   changing climate. If access to high quality freshwater habitat is reduced by human activities,

309   or connectivity between floodplains, rivers and estuaries is compromised, then the

310   productivity of diadromous fishes and their associated fisheries will likely decline.

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459   **Table 1.** Model parameter estimates with 95% CI describing fixed and random sources of

460   growth variation in barramundi.

Fixed effects				Random effects				
Covariate	**Estimate**	**Lower**	**Upper**	**Covariate**	**SD**	**Lower**	**Upper**	**Corr**
Intercept (Salinity Estuarine)	5.349	5.310	5.388	FishID	0.103	0.077	0.128	
Age	-0.407	-0.474	-0.331	Age|FishID	0.131	0.065	0.182	0.49
Salinity Freshwater	0.100	0.050	0.149	River:Year	0.031	0.000	0.056	
Salinity Mixed	0.054	0.008	0.108	Residual	0.176	0.163	0.188	
Age × Salinity Freshwater	-0.137	-0.236	-0.047					
Age × Salinity Mixed	-0.045	-0.163	0.043					

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473   **Table 2.** Growth advantages of freshwater and mixed salinity residence at ages 2-8, relative

474   to residency in saline environments.

Age	2	3	4	5	6	7	8
Freshwater	+24.17%	+17.26%	+12.59%	+9.10%	+6.33%	+4.04%	+2.09%
Mixed	+11.18%	+8.63%	+6.86%	+5.50%	+4.41%	+3.49%	+2.71%

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Figure Legends

Fig. 1 Transverse otolith section from a 5+ year-old *Lates calcarifer* illustrating location of ablated laser transect and annual growth increments

Fig. 2 Examples of core-to-edge transects of otolith $^{87}Sr/^{86}Sr$ for an estuarine resident (black unbroken line) and a catadromous fish (grey unbroken line) that entered freshwater in its first year and returned to the estuary/marine environment at age 5. Grey broken line represents salinity of 1ppt and the black broken line represents salinity of 35 ppt (i.e., sea water) based on water $^{87}Sr/^{86}Sr$ mixing models. Values of otolith $^{87}Sr/^{86}Sr$ above the grey broken line infer freshwater residency and those below infer estuarine or marine residency. Corresponding diamonds indicate the location of annual growth increments along the ablated transect for each fish

Fig. 3 Estimated age and salinity (i.e., habitat type) effects on growth. Shaded areas represent 95% CI
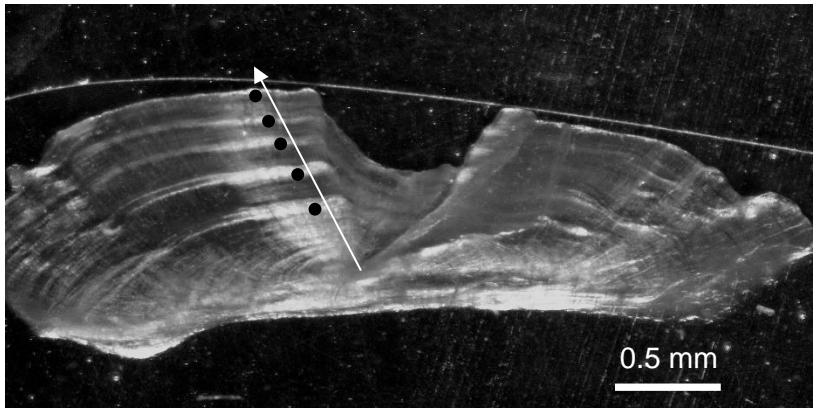
512   **Fig. 1**

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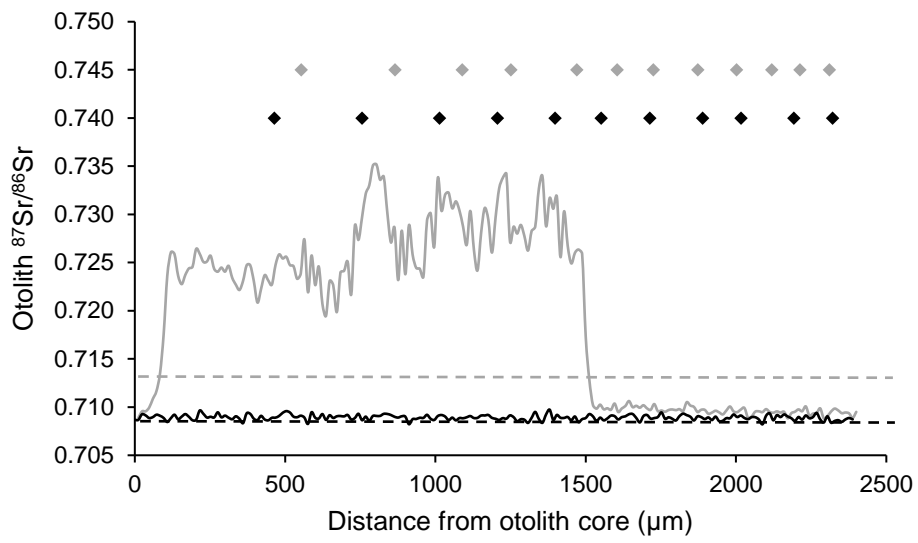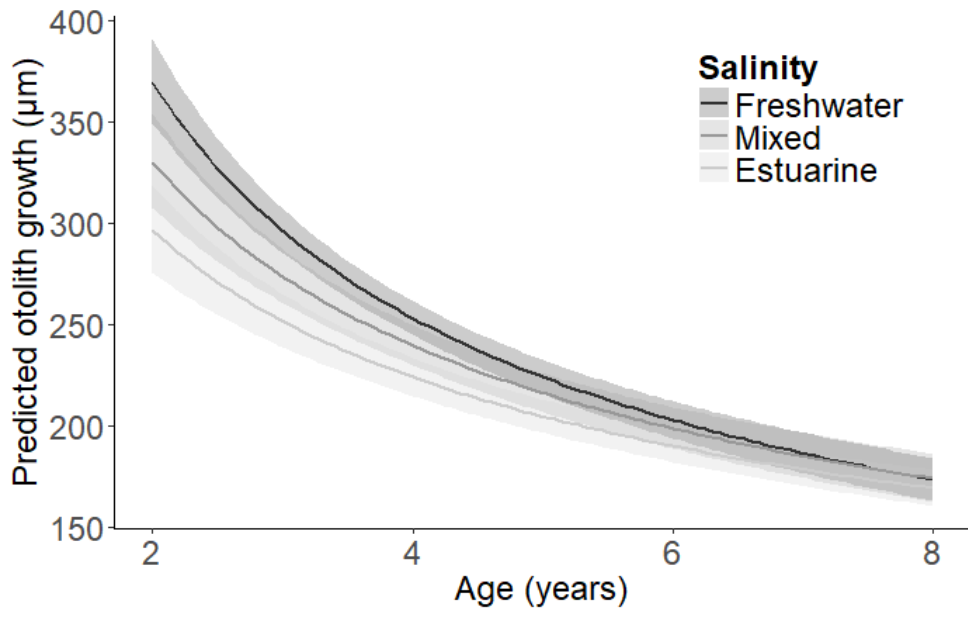
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527   **Fig. 2**

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540 **Fig. 3**

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