Long-term patterns in estuarine fish growth across two climatically divergent regions

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28   **Abstract**

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30   Long-term ecological datasets are vital for investigating how species respond to changes in their

31   environment, yet, there is a critical lack of such datasets from aquatic systems. We developed otolith

32   growth 'chronologies' to reconstruct the growth history of a temperate estuarine fish species

33   (*Acanthopagrus butcheri*). Chronologies represented two regions in south-east Australia: South

34   Australia, characterised by a relatively warm, dry climate, and Tasmania, characterised by a relatively

35   cool, wet climate. Using a mixed modelling approach, we related inter-annual growth variation to air

36   temperature, rainfall, freshwater inflow (South Australia only), and El Niño-Southern Oscillation

37   events. Otolith chronologies provided a continuous record of growth over a 13 and 21 year period for

38   fish from South Australia and Tasmania respectively. Even though fish from Tasmania were sourced

39   across multiple estuaries they showed higher levels of growth synchronicity across years, and greater

40   year-to-year growth variation, than fish from South Australia, which were sourced from a single, large

41   estuary. Growth in Tasmanian fish declined markedly over the time period studied and was negatively

42   correlated to temperature. In contrast, growth in South Australian fish was positively correlated to both

43   temperature and rainfall. The stark contrast between the two regions suggests that Tasmanian black

44   bream populations are more responsive to regional scale environmental variation and may be more

45   vulnerable to global warming. This study highlights the importance of examining species response to

46   climate change at the intra-specific level and further validates the emerging use of growth chronologies

47   for generating long-term ecological data in aquatic systems.

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49   **Key words:** climate change, growth history, otolith chronology, southeast Australia

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Introduction

Somatic growth is a key driver of population productivity in aquatic systems and understanding what drives variation in growth rate is central to predicting how aquatic communities will change in the future (Audzijonyte et al. 2013; Rountrey et al. 2014). Long-term ecological datasets are vital for determining how species and populations respond to changes in various environmental parameters, however, such datasets in the aquatic environment are rare and can be expensive and logistically difficult to obtain via traditional observational approaches (Poloczanska et al. 2007; Richardson and Poloczanska 2008). Extensive pre-existing archives of calcified tissues, such as fish ear bones (otoliths), mollusc shells, and mammal teeth, represent an alternative, underutilised resource in which long-term ecologically-relevant data can be generated retrospectively. A key attribute of these tissues is that they typically grow incrementally relative to somatic growth. The analysis of annual growth increment patterns or 'growth chronologies' can thus be used to reconstruct continuous, annually-resolved growth histories of individuals and populations (e.g. Black et al. 2011; Hamilton et al. 2013; Kendall et al. 2010).

Fish are undoubtedly essential components of healthy, functioning aquatic environments, as well as being an important component of the human socio-economic system, contributing to global food security and the economy (Garcia and Rosenberg 2010) and providing a suite of ecosystem services vital for human welfare (Holmlund and Hammer 1999). To effectively manage and optimise fishery resources in the future, an understanding of what changes may occur to fish populations is required. Even small changes in fish growth and body size, for instance, can lead to significant changes in mortality, biomass and catch (Audzijonyte et al. 2013). There is a paucity of long-term growth data on fish, particularly in the Southern Hemisphere; nonetheless, a handful of Australian studies have pioneered the use of otolith growth chronologies to generate long-term growth records from archived otolith collections (Gillanders et al. 2012; Morrongiello et al. 2011; Morrongiello et al. 2014; Neuheimer et al. 2011; Rountrey et al. 2014; Thresher et al. 2007).

83   A variety of approaches have been used to develop growth chronologies (Morrongiello et al. 2012),

84   with traditional dendrochronological time-series modelling, and more recently, mixed-effects

85   modelling, the two most commonly adopted for fish-based research. A key advantage of mixed

86   modelling is that it allows extrinsic (e.g. environmental conditions) and intrinsic (e.g. age) drivers of

87   growth variation to be analysed simultaneously and effectively partitioned so that detailed comparisons

88   and interactions among the two can be made; this provides a more comprehensive, biologically-relevant

89   understanding of how fish respond to environmental variability (Morrongiello and Thresher 2015;

90   Weisberg et al. 2010). Such novel analyses are not possible with the more established

91   dendrochronological approach that is designed to maximise environmental-growth relationships though

92   a series of detrending and standardisation steps (Morrongiello et al. 2012). Dendrochronological

93   methods are also less statistically appropriate for analysing relatively short, decadal growth histories

94   derived from shorter-lived, and typically commercially targeted, fish species.

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96   Estuaries are productive and dynamic environments between marine and freshwater systems. They are

97   highly heterogenous, both temporally and spatially, and can be influenced by a complex interplay of

98   environmental drivers (Gillanders et al. 2011). Due to this complexity, many interacting environmental

99   factors can influence the growth of estuarine species over a range of hierarchical levels (e.g. individual,

100   population and species). Freshwater inflows, influenced by water abstraction and regulation,

101   evapotranspiration, groundwater attributes and precipitation, are, however, considered a primary

102   determinant of estuarine dynamics, and can influence salinity, water-column stratification, water

103   quality, nutrients and primary productivity (Gillanders et al. 2011; Gillanders and Kingsford 2002;

104   Statham 2012). These factors, in turn, can impact the phenology and physiology (i.e. growth) of

105   estuarine species, as well as distribution and abundance (e.g. Jenkins et al. 2010; Morrongiello et al.

106   2014; Sakabe et al. 2011). The influence of temperature on estuarine environments has received less

107   attention; however, it can directly affect the physiology of individuals (Morrongiello et al. 2014), as

108   well as estuarine attributes such as water quality, nutrient cycling and salinity (Gillanders et al. 2011;

109   Scavia et al. 2002).

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111   Climate change is predicted to have a major impact on estuarine environments around the world, with

112   current and forecasted changes to temperature and precipitation (Gillanders et al. 2011; Scavia et al.

113   2002; Statham 2012). Estuaries in temperate southern Australia are particularly vulnerable, with the

114   region undergoing significant climatic change. Air temperature is warming faster than the global

115   average and sea surface temperature is also increasing, particularly along the eastern coastline, which

116   is a notable climate change 'hotspot' (Hobday and Pecl 2014; Lough and Hobday 2011). Although

117   rainfall trends (used as proxies of freshwater inflow) are subject to high levels of inter-annual

118   variability, declines are evident with effects exacerbated by increasing evaporation (Lough and Hobday

119   2011). Within this context we reconstructed the growth history of a commercially and recreationally

120   important estuarine fish species, black bream (*Acanthopagrus butcheri*, Munro 1949), using otolith

121   growth chronologies. The chronologies represented two climatically divergent regions in temperate

122   southern Australia with the first characterised by a warmer, drier climate (South Australia), and the

123   second characterised by a cooler, wetter climate (Tasmania). We used mixed-effect modelling to

124   examine extrinsically-driven, inter-annual growth variation among the two regions and then determined

125   if environmental predictors, representative of temperature and hydrological change in estuarine

126   systems, drive growth variation in black bream.

127

128   **Material and Methods**

129

130   *Study species*

131   Black bream is an estuarine-dependent sparid found throughout temperate southern Australia and

132   constitutes valuable fisheries throughout its distributional range. Black bream live for at least 29 years

133   (Morison et al. 1998) with age at maturity varying from 2 to 4 years (Sarre and Potter 1999). The species

134   spawns multiple times over a prolonged period during the austral spring and summer; however, timing

135   of spawning can vary among regions and years (Ferguson and Ye 2008; Haddy and Pankhurst 1998;

136   Sakabe et al. 2011; Sarre and Potter 1999). Black bream is an euryhaline species and can tolerate fresh

137   to hypersaline waters up to 60 ppt (Partridge and Jenkins 2002). It completes its entire life cycle within

138   an estuarine system (Potter and Hyndes 1999), spawning in the upper reaches of estuaries. Larval

139 recruitment and settlement occurs within the parent estuary, therefore, mixing between populations is

140 typically restricted to the movement of adults during flood events. Climate change impacts are largely

141 unknown for the species, but a recent risk assessment on commercial fishery species in south-east

142 Australia classified black bream as relatively high risk to climate change due to life history

143 characteristics, habitat preference and potential sensitivity to changes in key climate change drivers

144 (Pecl et al. 2014).

145

146 *Sample sites*

147 Sectioned otoliths were obtained from archived collections representing two regions in temperate south-

148 east Australia: the Murray River estuarine system in South Australia and the east coast of Tasmania

149 (represented by nine estuaries across a 230 km stretch of coastline) (Table 1, Fig 1). The Murray River

150 estuary region has a relatively dry, warm climate with a mean annual rainfall of 463 mm and a mean

151 daily temperature of 16°C. The Murray River estuary is the terminus of Australia's largest river, the

152 Murray–Darling, and is a large, complex, and highly modified system. It is separated by barrages from

153 the freshwater Lower Lakes (Bucater et al. 2013; Gillanders et al. 2011) and water abstraction from

154 upstream systems has reduced natural flow into the estuary by 80% (Ferguson et al. 2013). As a

155 consequence, to maintain connectivity with the sea the estuary opening has been dredged during severe

156 drought (from 2002 to 2010) and under low flow conditions since January 2015. In contrast, eastern

157 Tasmania has a relatively wet, cool climate with a mean annual rainfall ranging from 601 to 659 mm

158 across the region and a mean daily air temperature of 13 to 14°C. Estuaries along the east coast are

159 relatively unmodified and characteristically small and shallow with low tidal ranges and flushing rates

160 and include closed, seasonally closed and open systems (Table 1).

161

162 *Annual growth estimation*

163 Otoliths were sectioned through the core (primordium), and examined under a compound microscope

164 (Leica DMLB) using transmitted light at 50x magnification. Each section was photographed with a

165 digital camera (Leica DF320) and analysed using ImagePro Plus software (version 6.0). Annual growth

166 increment counts were used to estimate fish age (*Age-at-capture*) (see Morison et al. 1998 for more

167   details), taking into account the width of the marginal increment, date-of-capture and time of increment

168   formation. Widths between each increment were subsequently measured along a transect running from

169   the core to edge of the otolith along the dorsal side of the *sulcus acusticus*, which provides a robust,

170   temporally-resolved proxy of somatic growth (*Growth*) (see Fig S1). Each growth increment was

171   assigned a calendar growth year (*Year*) and an age (*Age*) based on back calculation from year-of-capture

172   and age-at-capture respectively. This latter step was automated in R (version 3.0.2) (R Development

173   Core Team 2008) using the method developed by Weisberg et al. (2010). The growth year was defined

174   as the 1st October to 30th September (e.g. 2006 = October 2006 to September 2007), based on a previous

175   study on black bream that suggests that growth increments form in October (Elsdon and Gillanders

176   2006). The marginal increment and the first two years of growth were not measured, with the latter due

177   to poor visualisation in the inner region of the otolith. Consequently, growth data represented the 3rd

178   year of the fish's life onwards to the last full year of growth. Regionally, each growth year was

179   represented by a minimum of five increment measurements (i.e. five individuals) with most years

180   having more than 50 measurements (see Fig 2).

181

182   *Growth predictors*

183   A range of predictor variables were selected to investigate sources and drivers of inter-annual growth

184   variation (Table 2). Fixed intrinsic (biological) variables included *Age* and *Age-at-capture*, with the

185   latter included to test for potential bias in the dataset associated with 'age selectivity' and to ensure that

186   estimates of temporal growth variation were not influenced by certain phenotypes (i.e. longer-lived

187   individuals) (Morrongiello et al. 2012; Morrongiello et al. 2014).

188

189   A range of fixed extrinsic (environmental) variables were included with regional and global scale

190   influence (see Table 2 and Supporting Information for additional methods). Based on data availability,

191   air temperature (*Temperature*) was used as a proxy for water temperature across both regions and

192   rainfall (*Rainfall*) was used as a proxy of freshwater inflows in Tasmania (see Supporting Information

193   and Fig S2). Freshwater flow (*Flow*) data were also included in the South Australian analysis as flow

194   and rainfall were poorly correlated. The Southern Oscillation Index (*SOI*) was included as a measure of

195   El Niño-Southern Oscillation (ENSO) events, with negative values (El Niño episodes) generally

196   corresponding to warmer sea surface temperatures and drier conditions in the region, and vice versa for

197   positive values (La Niña episodes) (Holbrook et al. 2009). Growth response to environmental predictor

198   variables was examined across three biologically-relevant time periods: annual growth year (October

199   to September), spawning season (August to December) (Ferguson and Ye 2008; Sakabe et al. 2011),

200   and season when maximum otolith growth occurs, hereafter termed 'summer' (December to February)

201   (Elsdon and Gillanders 2006). However, if variables were highly correlated among time periods (within

202   a predictor) (Pearson's correlation = 0.9 to 1), they were removed from analysis. Rainfall, flow (South

203   Australia), air temperature and SOI predictors were not highly correlated to each other (Pearson's

204   correlation = < 0.7) and all showed inter-annual variation, with temperature (growth year and spawning

205   season) showing temporal linear trends (Fig S3).

206

207   Three random effect predictors were included in the analysis, *FishID*, *Year* and *Year Class*, which were

208   seen as a random sample from all possible fish, years, and year classes respectively. Fitting a random

209   intercept for *FishID* generated a correlation among increment measurements (*Growth*) within an

210   individual, allowing each individual to have above or below average growth relative to the model's

211   intercept (average growth) (Morrongiello and Thresher 2015). This accounts for the inherent repeated

212   increment measures within the growth data and the likelihood that increment measures are more likely

213   correlated within than among individuals (Morrongiello et al. 2011). Similarly, including a random

214   intercept for *Year* and *Year Class* generated a correlation among increments formed in the same year

215   and a correlation among increments from fish born in the same year respectively. The former predictor

216   is particularly relevant to sclerochronological analyses as it provides an estimate of above or below

217   average growth for a given calendar year after the effects of intrinsic 'nuisance' variables (e.g. *Age* and

218   *Age-at-capture*) are accounted for (Morrongiello and Thresher 2015). A random *Age* slope for each

219   individual (*Age|FishID*) was also included as it allows each individual to have unique *Growth ~ Age*

220   relationships and is akin to the 'dendrochronological method' of detrending age-related trends for each

221   individual prior to analysis (Morrongiello and Thresher 2015; Morrongiello et al. 2014). For Tasmania,

222   *FishID* was nested within *Estuary* to account for potential growth variation among estuaries.

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223

Mixed modelling

Inter-annual variation in *Growth* was analysed separately for each region using a two stage process (Morrongiello and Thresher 2015; Morrongiello et al. 2014). All mixed modelling analyses were performed using the *lme4* (Bates et al. 2013) and *MuMIn* (Barton 2013) packages in R (version 3.0.2) (R Development Core Team 2008)**.** *Growth*, *Age* and *Age-at-capture* were natural log-transformed to meet model assumptions and all fixed effect variables were mean-centred to facilitate model convergence and interpretation of random slopes (Morrongiello et al. 2014).

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The first stage of analysis involved building a base set of linear mixed models that included a range of random effect and fixed intrinsic effect structures. The first base model (1) considered just a random intercept for *FishID* and the second base model (2) considered *FishID* and a random *Age* slope for *FishID*, with additional Tasmanian models including *FishID* nested within *Estuary* (models 3 and 4) (Table 3). These models were fitted using restricted maximum likelihood estimation (REML) (Zuur et al. 2009) and ranked using Akaike's Information Criterion corrected for small sample sizes (AIC$_C$) rescaled as the difference between the model with the lowest AIC$_C$ (or optimal model) and each other model (ΔAIC$_C$) (Burnham and Anderson 2004). Random intercepts for *Year* and *Year Class*, and a combination of both, were added individually to the optimal model and then fitted and ranked as above (Table 3). At this stage all models included the maximum intrinsic fixed effect structure (*Age* and *Age-at-capture*) (Zuur et al. 2009). To determine if *Age-at-capture* improved model fit the optimal random effects model was re-analysed with and without the *Age-at-capture* term (Table 3). These models were initially fitted using maximum likelihood estimation (ML) with the best ranked model refitted with REML to produce unbiased parameter estimates (Zuur et al. 2009).

246

To investigate how environmental variables influence *Growth*, the second stage of the analysis involved extending the optimal base model for each region to include different environmental covariates, which were fitted individually (Table 2). Additional models were also explored that included the two highest ranked environmental covariates in combination. It was deemed that there was substantial support for

251 a model if the difference in ΔAIC_C between the highest and second highest ranked model was < 2

252 (Burnham and Anderson 2004). The ratio of evidence for the highest ranked 'environmental model'

253 against the base model was also calculated by dividing the AIC_C weight ($wAIC_C$) of the environmental

254 model by the $wAIC_C$ of the optimal base model. *Year*, as a fixed effect, was also added to the optimal

255 model to test for linear and curvilinear temporal growth trends (Morrongiello and Thresher 2015). As

256 above, these models were initially fitted using ML, with the best ranked model refitted with REML.

257 Age-dependent, environmental effects on growth were also initially explored for the highest ranked

258 covariates, but were found to be negligent and, therefore, not presented.

259

260 Furthermore, to investigate the level of correlation or temporal synchrony among growth increments

261 from individuals living in the same *Year* and born in the same *Year Class*, an intraclass correlation

262 coefficient (ICC) was calculated using the variance estimates from models 4a and 4b (Tasmania) and

263 models 2a and 2b (South Australia) (Table 3) (Morrongiello and Thresher 2015). To examine temporal

264 patterns in growth, *Year* random effect plots were generated by extracting best linear unbiased

265 predictors (BLUPs) from models 4a and 2a. Predicted effects of the most influential fixed effect

266 predictors on growth were also estimated using the *effects* (Fox 2003) package in R.

267

268 **Results**

269

270 *Sources of growth variation*

271 Otolith growth chronologies generated a record of black bream growth over a 13 (1997 to 2009) and 21

272 (1988 to 2008) year period for South Australia and Tasmania respectively. Calculation of AIC_c for the

273 initial base models showed that the incorporation of a random *Age* slope for *FishID* was

274 overwhelmingly supported in both Tasmanian and South Australian datasets, indicating that *Growth ~*

275 *Age* relationships varied among individuals (Tables S1, S2). The addition of *Estuary* in the Tasmanian

276 base models improved model fit, indicating that growth trends varied among estuaries (Table S1).

277 For both regions, the random effects model was significantly improved through the addition of *Year*,

278 but not *Year Class* (Tables S1, S2). Comparison of variance components for random effects among the

279   two regions show that *Age/FishID* explained a relatively high proportion of growth variance in South

280   Australia and *Year* explained a relatively high proportion of variance in Tasmania, although Tasmania

281   also had a higher level of unexplained variance (*Residual*) (Table 4). For Tasmania, *Year* explained a

282   higher proportion of the variance than *Estuary*. Furthermore, among-individual correlation of growth

283   increments for a given *Year* and *Year Class* was significantly higher in Tasmania than South Australia,

284   with *Year* having significantly higher levels of growth synchrony than *Year Class* overall (ICC for

285   Tasmania: 0.138 [Year], 0.016 [Year Class]; ICC for South Australia: 0.030 [Year], 0.003 [Year

286   Class]).

287

288   *Age*, as anticipated, had a significant negative influence on growth for both regions (Table 5). *Age-at-*

289   *capture* also had a negative, though much weaker, influence on growth in both regions, which suggests

290   that fast growers were more likely to be captured at a relatively young age (Table S3, Table 5).

291

292   *Temporal patterns in growth variation*

293   *Year* random effect plots revealed significant long-term inter-annual variation in fish growth. This was

294   particularly evident for Tasmania, with strong growth years in 1993/1994 and 1997/1998, followed by

295   an overall marked decline in growth from 2000 to 2008 (Fig 3). Years with especially poor growth were

296   1988, 2003, 2005 and 2008. South Australia also showed inter-annual variability through time, but at a

297   lower magnitude than Tasmania (Fig 3). There were relatively good growth years in 2004/2005, and

298   relatively poor growth years in 2001 and 2006/2007. The addition of *Year* as a fixed effect to the optimal

299   base model markedly improved model fit for Tasmania, but not South Australia (Table S4). The *Growth*

300   *~ Year* relationship was negative and curvilinear for Tasmanian fish, with a predicted decline in growth

301   over the chronology time series of 1% year^{-1} (Table 5, Fig 4A).

302

303   *Attributing growth variation to environmental variation*

304   The addition of fixed effect environmental predictors to the optimal base models for Tasmania and

305   South Australia revealed significant correlative relationships to growth. For Tasmania, including

306   *Temperature (spawning season)* improved model fit relative to the base model, albeit weakly, and was

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307　　1.3 times more likely to explain growth variation (Table S5). *Temperature (spawning season)* was

308　　negatively correlated to growth, with a predicted effect on growth rate of -7.0% $°C^{-1}$ (within the

309　　environmental range experienced by the fish) (Fig 4B, Tables 5, 6). For South Australia, including both

310　　*Rainfall (summer)* and *Temperature (spawning season)* improved model fit relative to the optimal base

311　　model (Tables S6, S7), with the ratio of evidence indicating that it was 2.6 times more likely to explain

312　　growth. *Temperature (spawning season)* and *Rainfall (summer)* were both positively correlated to

313　　growth, with a predicted effect on growth rate of 3.7% $°C^{-1}$ and 6.0% mm^{-1} respectively (Fig 4C,D;

314　　Tables 5, 6).

315

316　　**Discussion**

317

318　　Otolith growth chronologies provided a continuous, reconstructed record of black bream growth over a

319　　13 and 21 year period in South Australia and Tasmania respectively. Temporal growth variation across

320　　years and sources and drivers of such variation were markedly different between the two regions.

321　　Notably, the level of temporal growth synchrony among Tasmanian fish, which were sampled across

322　　nine estuaries, was four times higher than South Australian fish, which were sampled from a single

323　　estuary. Furthermore, in Tasmania, a much higher proportion of growth variation was attributed to year-

324　　to-year fluctuations rather than differences among estuaries. This is surprising given that estuarine black

325　　bream populations are largely independent from one another, with only low levels of gene flow

326　　occurring among proximate estuaries (Burridge et al. 2004; Burridge and Versace 2007).　These

327　　findings suggest that regional climatic variation exerts a greater influence on black bream growth than

328　　population-level, estuary-scale factors such as density-dependent effects, population genotype, and

329　　geomorphological and land use attributes of the estuary and catchment, with the latter known to vary

330　　among Tasmanian estuaries (Edgar et al. 1999, Table 1).

331

332　　For South Australian fish, a much higher proportion of growth variation was attributed to individual

333　　variation in growth-age relationships rather than year. Although the South Australian growth

334　　chronology was shorter, differences in the patterns and magnitude of growth variation were still

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335   apparent in years overlapping with Tasmania (1998 – 2009). Additionally, the number of fish sampled

336   from the Murray River estuary was greater than the number of fish sampled from any one estuary in

337   Tasmania. Yet, the Murray River estuary is a relatively large and physically complex system (see Table

338   1), which may explain differences in growth synchronicity among the two regions. Furthermore, an

339   otolith chemistry study on black bream demonstrated the presence of partial migration (i.e. populations

340   consist of both resident and migratory individuals) within the Murray River estuary, with each

341   migratory contingent having different growth histories (Gillanders et al. in press). Although, the

342   presence of partial migration has not been investigated in Tasmanian populations, this suggests that

343   South Australian populations may be exposed to a broader range of environmental conditions

344   throughout their life cycle. Differences in fishing pressure may also be driving growth differences

345   among the two regions. In Tasmania, black bream are fished recreationally, with a high proportion of

346   catch-and-release (Lyle et al. 2009), while in the Murray River estuary, they are fished both

347   commercially and recreationally with evidence of fishing-induced age truncation (Ferguson et al. 2013).

348   Our results suggest that age-at-capture influenced temporal growth variation, particularly in South

349   Australia, with younger fish having relatively faster growth. Therefore, it is plausible that the depletion

350   of longer-lived, potentially slower-growing, individuals from the South Australian population has

351   affected long-term growth patterns.

352

353   Nonetheless, the level of growth synchrony even among Tasmanian black bream was still relatively low

354   (0.13) compared to other fish species, including red snapper (*Lutjanus campechanus*; 0.54), gray

355   snapper (*Lutjanus griseus*; 0.76) (Black et al. 2011), rock flathead (*Platycephalus laevigatus*; 0.64),

356   longhead flathead (*Leviprora inops*; 0.62) (Coulson et al. 2014), and parore (*Girella tricuspidata*; 0.51)

357   (Gillanders et al. 2012), all of which are marine. Movement of individuals across dynamic,

358   heterogeneous estuarine environments, even within small enclosed systems, may explain the relatively

359   low levels of temporal synchronicity among individuals. Yet, low levels of growth synchronicity have

360   also been observed in western blue groper (*Achoerodus gouldii*, 0.11), a site-attached marine reef fish

361   (Rountrey et al. 2014), suggesting that other factors, aside from environmental heterogeneity, may drive

362   high individual growth variation. It is interesting to note, also, that all of the aforementioned studies are

363 based on a 'dendrochronological', rather than a mixed modelling, approach, which is designed to

364 maximise environmental-growth relationships and reduce ecological 'noise' and typically entails

365 sampling the longest-lived individuals from a population. Thus, synchronicity coefficients derived from

366 mixed modelling approaches may be more ecologically relevant.

367

368 Growth variation in Tasmanian black bream showed a negative, albeit weak, correlation with air

369 temperature, which is also reflected in the marked decline in growth over the chronology time series

370 (1988 to 2008), with growth variation in South Australian showing a positive correlation. These

371 correlative relationships are unexpected given that Tasmania represents the cooler, southern range edge

372 for black bream. In contrast, growth of banded morwong (*Cheilodactylus spectabilis*), a marine reef

373 fish, was positively correlated to temperature in the middle and southern end of the species range (south-

374 east Australia) and negatively correlated to growth in the extreme northern edge of the species range

375 (northern New Zealand) (Neuheimer et al. 2011). Similar correlative relationships with temperature

376 have also been observed in tiger flathead (*Platycephalus richardsoni*), a demersal marine fish also

377 native to south-east Australia (Morrongiello and Thresher 2015). These predictable patterns coincide

378 with the theorised and known physiological effects of temperature increase on ectotherms, whereby

379 growth increases with increasing temperature to a point where metabolic demand can no longer be

380 sustained and growth declines (Neuheimer et al. 2011; Pörtner and Farrell 2008). One explanation for

381 our contrasting result in black bream is intra-specific variation in thermal tolerance, where the pejus

382 temperature (the point at which further temperature increases result in decreased growth) has been

383 already reached for Tasmanian fish, but not South Australian fish. Intra-specific variation in thermal

384 tolerance has been observed in estuarine fish species, including Australian barramundi (*Lates*

385 *calcarifer*) and North American killifish (*Fundulus heteroclitus*), whereby lower latitude sub-

386 populations had higher critical thermal maxima than their higher latitude counterparts (Fangue et al.

387 2006; Newton et al. 2010). Localised thermal adaptation is plausible for black bream particularly given

388 their restricted movement patterns, tendency to form distinct genetic sub-populations, and dependence

389 on estuarine systems, however, physiological tests should be conducted to further corroborate this

390 hypothesis. An alternative explanation is that temperature increase may lead to a more prolonged

391   spawning season, resulting in greater investment in reproduction than somatic growth. As temperature

392   averaged across the spawning season was more strongly associated with growth than the other two time

393   periods, it also suggests that growth is more responsive to temperature during this time. *Acanthopagrus*

394   hybrid complexes in southern New South Wales, composed of black bream and yellowfin bream

395   (*Acanthopagrus australis*), also appear to have a more prolonged spawning season (August to January)

396   relative to higher-latitude hybrid and pure black bream populations (Ochwada-Doyle et al. 2012).

397   Although the reason for this is unknown, it may relate to geographical differences in temperature, which

398   plays an important role in the onset and cessation of spawning in the species (Haddy JA, unpublished

399   data). Physiological impacts aside, temperature may also influence estuarine attributes, such as water

400   quality and salinity stratification, as well as population-level (e.g. density dependent effects) and

401   ecosystem-level processes (e.g. trophic interactions) (Pörtner and Peck 2010), which, in turn, may

402   indirectly impact fish growth. Regardless of the underlying mechanisms, however, a decline in somatic

403   growth as a consequence of temperature increase may have significant implications for a species' ability

404   to persist in the face of global warming and may result in localised shifts in distribution, abundance and

405   productivity (Sorte et al. 2011). As air temperature and sea surface temperature are both currently

406   increasing at a relatively rapid rate in eastern Tasmania (Lough and Hobday 2011), black bream may

407   be more vulnerable to climate change in the region.

408

409   Summer rainfall was also positively correlated to growth in South Australian fish, although freshwater

410   inflow, surprisingly, was poorly related to growth. The disconnect between rainfall and flow in the

411   Murray River estuary is the likely product of water abstraction and regulation, as well as prolonged

412   drought, with the growth chronology encompassing the worst dry period (the Millennium Drought,

413   2001 – 2009) ever recorded in southern Australia (van Dijk et al. 2013). In a drought-stressed,

414   hypersaline system where inflow is negligible, rainfall could have a positive influence on growth by

415   reducing salinity and thus osmotic stress to the fish. Although black bream is tolerant of a wide range

416   of salinities (Partridge and Jenkins 2002), increased osmoregulation can affect basal metabolic rate and

417   energy requirements (Gillanders et al. 2011). This result further supports the widely held belief that

418   freshwater inflows are a key driver of biological processes in estuarine systems (Gillanders et al. 2011;

419   Morrongiello et al. 2014), but, conversely, the results also indicate that temperature is an important

420   driver. This aligns with another otolith chronology study that showed that temperature was a dominant

421   driver of growth in estuary perch (*Percalates colonorum*), an estuarine-dependent species native to

422   south-east Australia (Morrongiello et al. 2014). It should be noted that the environmental predictors

423   explored herein only explained a small proportion of the growth variation observed, and that other

424   environmental and biological factors may be influencing growth to a greater extent. Yet, given the

425   complex and dynamic nature of estuarine environments, it is likely that a synergistic interplay of several

426   factors is driving growth; such as in South Australia, for example, whereby temperature and rainfall

427   combined explained more growth variation than just rainfall or temperature alone.

428

429   Otolith growth chronologies do not reflect absolute changes in somatic growth of individual fish, but

430   rather relative changes in inter-annual rates of growth averaged across a population (i.e. growth

431   anomalies) (Black et al. 2013). The significant otolith growth trends observed in Tasmanian bream

432   particularly (e.g. - 1% year^{-1}), however, should be observable at a somatic scale relevant to ecological

433   processes and fisheries management (see also Morrongiello and Thresher 2015 for comparison).

434   Furthermore, as the first two years of growth were not included in our analysis, growth trends, in reality,

435   may be even more pronounced as early life history stages are typically more responsive to the

436   environment. One otolith chronology study has also directly related otolith size to fish size in western

437   blue groper, with modelled predictions suggesting that a 10% increase in otolith size would result in a

438   5% increase in somatic growth (Rountrey et al. 2014). Although these changes may appear small,

439   seemingly minor changes in fish growth can have disproportionately large ramifications. For instance,

440   a recent modelling study on five marine fish species in south-east Australia predicted that a 4% decline

441   in length-at-age over 50 years would result in a 1 to 35% decline in biomass (Audzijonyte et al. 2013).

442

443   This study further validates the use of calcified tissues as valuable tools for retrospectively generating

444   long-term ecologically-relevant datasets in aquatic systems, which would otherwise be logistically

445   difficult and costly to produce. The comparison of growth patterns among two geographically and

446   climatically distinct regions is inherently confounded due to differences in a range of other factors, such

447 as estuary characteristics, habitat modification, fishing pressure and sampling regimes; yet, with careful

448 model selection and robust statistical analyses, valuable insights into the underlying drivers of growth

449 variation at an intra-specific level can still be gleaned. Overall, the results showed that fish from one

450 region were more responsive to regional-scale changes in the environment than the other, and that the

451 environmental variables examined influenced growth in different ways. This highlights the importance

452 of considering how populations respond to environmental change at the intra-specific level to make

453 more accurate predictions of how they may change in the future.

454

461

462 **Statement of Animal Rights**

463 All applicable institutional guidelines for the care and use of animals were followed.

464

465 **Conflict of Interest**

466 The authors declare that they have no conflict of interest.

467

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Table 1. Details of black bream otolith samples used to develop biochronologies. Tasmanian estuaries are listed from north to south.

Region	Estuary	Estuary type	Estuary area (km²)	Latitude, longitude	# sampling years	# fish	age range (years)	# year classes	year range
South Australia	Murray River	Open (dredged)	73	-35.532720, 138.842654	4	82	7-13	9	1998-2010
Tasmania	Ansons Bay	Open	4.9	-41.044480, 148.278539	2	23	9-21	10	1991-2009
	Grants Lagoon	Closed	0.5	-41.252038, 148.295832	1	7	12-22	6	1990-2009
	Diana's Basin	Closed	0.8	-41.371621, 148.285279	1	2	11-20	2	1992-2009
	Scamander River	Seasonally closed	1.6	-41.460404, 148.243077	2	68	8-23	12	1989-2009
	Four Mile Creek	Seasonally closed	0.01	-41.557944, 148.290112	1	16	8-19	9	1999-2009
	Swan River	Open	22	-42.087191, 148.224845	3	43	7-17	11	1991-2005
	Meredith River	Seasonally closed	0.1	-42.112600, 148.068193	1	11	8-13	4	1989-2005
	Little Swanport	Open	4.8	-42.338567, 147.955257	3	20	9-16	8	1990-2009
	Prosser River	Open	0.4	-42.557806, 147.867426	1	11	9-21	6	1990-2009
	all Tas estuaries				4	197	7-23	16	1989-2009

Table 2. Details of predictor variables used in the analysis of annual black bream growth. Type refers to whether the predictors were defined as random (R) or fixed (F) effects. Environmental predictor variables were calculated for three time periods: annual growth year (October to September), spawning season (August to December) and summer (December to February).

Predictor	Type	Description
FishID	R	Unique value to identify each individual fish
Estuary	R	Tasmanian estuaries listed in Table 1
Year	R, F	Annual growth year for black bream (October to September)
Year class	R	Cohort of individuals born in the same year
Age	F	Age in years when each growth increment formed
Age-at-capture	F	Age in years at time of capture
Temperature	F	Mean daily air temperature derived from daily minimum and maximum values (°C)
Rainfall	F	Mean daily rainfall values (mm)
SOI	F	Mean Southern Oscillation Index derived from monthly values
Flow	F	Mean monthly inflows through the Murray River estuary (GL)

Table 3. Description of base models used in the first stage of mixed modelling analysis. | = denotes random *Age*

slopes for each random *FishID* intercept, parentheses = nested term, AAC = Age-at-capture.

Model #	Random effects	Fixed effects
Tasmania		
1	FishID	Age, AAC
2	age|FishID	Age, AAC
3	Estuary(FishID)	Age, AAC
4	Age|Estuary(FishID)	Age, AAC
4a	Age|Estuary(FishID), Year	Age, AAC
4b	Age|Estuary(FishID), Year Class	Age, AAC
4c	Age|Estuary(FishID), Year, Year Class	Age, AAC
4a1	Age|Estuary(FishID), Year	Age
4a2	Age|Estuary(FishID), Year	Age, AAC
South Australia		
1	FishID	Age, AAC
2	Age|FishID	Age, AAC
2a	Age|FishID, Year	Age, AAC
2b	Age|FishID, Year Class	Age, AAC
2c	Age|FishID, Year, Year Class	Age, AAC
2a1	Age|FishID, Year	Age
2a2	Age|FishID, Year	Age, AAC

Table 4. The estimate of variance associated with each random effect (variance components ± SD) for optimal base models 4a2 and 2a2 for Tasmania and South Australia respectively. | = denotes random *Age* slopes for each random *FishID* intercept, corr = correlation statistic.

Random effects	Tasmania	South Australia
Estuary(FishID)	0.012 (0.110)	-
FishID	-	0.010 (0.100)
Age|Estuary(FishID)	0.005 (0.073) corr =0.10	-
Age|FishID	-	0.018 (0.133) corr = 0.28
Year	0.006 (0.081)	0.001 (0.038)
Estuary	0.001 (0.038)	-
Age|Estuary	0.004 (0.063) corr = 0.83	-
Residual	0.022 (0.149)	0.017 (0.129)

Table 5. Fixed effect parameter estimates (±SE) and test statistics for optimal models describing intrinsic, temporal and environmental effects on growth (see Table 3 for base model details). Spawning = spawning season (August to December); and summer = period of maximum otolith growth (December to February).

Fixed effects parameter	Tasmania			South Australia		
	Model	**Estimate**	**t-value**	**Model**	**Estimate**	**t-value**
Intrinsic effects						
Intercept	4a2	-2.636 (0.025)	-106.44	2a2	-2.509 (0.017)	-149.89
Age	4a2	-0.404 (0.024)	-16.51	2a2	-0.436 (0.020)	-22.09
Age-at-capture	4a2	-0.035 (0.041)	-0.84	2a2	-0.140 (0.068)	-2.05
Temporal effects						
Year (Y)	4a2+Y	-0.015 (0.004)	-3.7	-	-	-
Environmental effects						
Rainfall (summer) (R)	-	-	-	2a2+R+T	0.056 (0.034)	1.65
Temperature (spawning) (T)	4a2+T	-0.071 (0.044)	-1.96	2a2+R+T	0.038 (0.023)	1.64

Table 6. Predicted effect of significant environmental predictors on growth rate. * 1 unit is defined as 1 °C or 1 mm.

Environmental predictor	Predictor range	Predicted effects (% change)	
		across range	per unit*
Tasmania			
Temperature (spawning)	12.4 – 13.9 °C	-10.5	-7.0
South Australia			
Temperature (spawning)	14.3 – 16.0 °C	6.6	3.7
Rainfall (summer)	0.3 – 1.3 mm	6.0	6.0

Figure Captions

Fig 1. Map of study region (X = black bream collection sites). Dashed lines on smaller map represent black bream distribution

Fig 2. Number of otolith increment measurements representing each growth year. Grey columns = Tasmanian samples; black columns = South Australian samples

Fig 3. Predicted inter-annual variation in growth of black bream for Tasmania (grey line; n = 197) and South Australia (black line; n = 82) based on *Year* random effect estimates (± SE) from model 4a (Tasmania) and 2a (South Australia). Dashed line represents average growth across the time periods examined

Fig 4. Predicted effects of A) *Year* and B) *Temperature (spawning season)* on the growth of Tasmanian fish (grey plots; n = 197), and predicted effects of C) *Rainfall (summer)* and D) *Temperature (spawning season)* on the growth of South Australian fish (black plots; n = 82). Dashed lines represent 95% CI