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3 **Planktonic Larval Duration, Age and Growth of *Ostorhinchus doederleini* (Pisces: Apogonidae) on**
4 **the Southern Great Barrier Reef, Australia**

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25

26 **Abstract**

27 Cardinalfishes (Apogonidae) are abundant on corals reefs, but there are few data on demography to
28 understand trophodynamics and population dynamics. *Ostorhinchus doederleini* is a small and abundant
29 apogonid on the Great Barrier Reef (GBR) and throughout the Western Pacific Ocean. We present key
30 demographic parameters for the entire life history from the southern GBR. Daily deposition of
31 increments in otoliths was validated. Fish had a Planktonic Larval Duration (PLD) of 16 to 26 days.
32 PLD was established from fish collected immediately prior to settlement as no settlement mark was
33 found. Fish grew at about 0.35 mm d⁻¹ for the first 20 d after settlement. Fish reached a maximum
34 standard length at about 200 d and no fish lived longer than 368 d at four reefs separated by kilometers
35 to tens of kilometres. There was no evidence for differences in size at age between sexes. Mortality
36 was very high, for fish greater than 60 days old mortality rates ranged from 2.9 to 4.6% per day. Short
37 lives and high mortality rates makes *O. doederleini*, and potentially other apogonids, vulnerable to
38 recruitment failure. Here we review data on the demographic characteristics of other reef fishes.
39 Although some taxa live to over 50 years, the short lives of apogonids are most aligned with the
40 Gobiidae and Blenniidae (i.e. typically < 1.5 years). Descriptions of fish size, age, longevity, growth
41 and mortality; from hatching to age maxima are very rare for most taxa, even at the level of family.

42

43 **Introduction**

44 Nocturnal fishes are an important trophic group on both coral and temperate reefs (e.g. Marnane and
45 Bellwood 2002; Annesse and Kingsford 2005). Fishes belonging to the Apogonidae, Holocentridae,
46 Nemipteridae and Pempheridae are abundant on reefs and species richness is high (Hobson and Chess
47 1978; Sale and Douglas 1984; Bellwood 1996; Greenfield 2003; Mabuchi et al. 2006; Thacker and Roje

48 2009; Gardiner and Jones 2010; Boaden and Kingsford 2012). These taxa feed at night on a range of
49 invertebrates and fishes (Hiatt and Strasberg 1960; Marnane and Bellwood 2002; Annesse and
50 Kingsford 2005; Barnett et al. 2006) and are the prey of many piscivorous taxa (e.g. Kingsford 1992).

51 Apogonids, and other nocturnal fishes, generally occupy caves and other habitats that provide
52 shelter (e.g. coral Gardiner and Jones 2005) during the day and undergo feeding migrations at night.
53 Movements range from spatial scales of metres to hundreds of metres. In general these fishes feed in
54 habitats that are different from those they occupy during the day (Gladfelter 1979; Marnane 2000;
55 Annesse and Kingsford 2005; Boaden and Kingsford 2012). The trophic importance of these
56 movements to reef ecosystems ~~are~~is potentially substantial in that their feeding behavior and availability
57 to predators are likely to be significant carbon pathways. Furthermore, feeding behavior often varies
58 with size of fish. Many apogonids and other young nocturnal fishes (Annesse and Kingsford 2005) feed
59 in different habitats than large juveniles and adults (Finn and Kingsford 1996).

60 Most apogonids have paternal mouth brooding and a larval phase (Brothers et al. 1983). An
61 exception, the apogonid *Pterapogon kauderni* has paternal mouth brooding and direct development of
62 juveniles with no larval phase (Vagelli and Volpedo 2004). Great attention has been given to filial
63 cannibalism of eggs brooded in the buccal cavity of males *O. doederleini* (Okuda and Yanagisawa 1996)
64 and other species (Okuda et al. 1997; 2003; Kume et al. 2000). Despite their novel reproductive
65 biology, trophic importance and the recognition that there is high local population turnover (e.g. on
66 patch reefs Sale and Douglas 1984), there are few data on demography (but see Okuda et al. 1998). An
67 exception is Longenecker and Langston (2006) who found that *Ostorhinchus rubrimacula* (Apogonidae)
68 lived to a maximum of 274 days at a reef in Fiji. There are some estimates of Planktonic Larval Duration
69 (PLD) for 14 species of apogonids in Japan (mean PLDs ranged from 14 to 31 days, Ishihara and
70 Tachihara 2011), but the generality of these values is unknown.

71 A thorough understanding of population dynamics of any species requires information on growth
72 and mortality at all stages of life history (Hilborn and Walters 1992). The potential for high volatility in
73 population size would be greatest in species that have low age-maxima as there would be little in the
74 way of ‘stored’ year classes from seasons of high recruitment. Great variation in coral reef fish
75 recruitment among seasons is common (Doherty and Williams 1988), but populations persist, often
76 supported by a small number of large peaks in recruitment (Doherty and Fowler 1994; Kingsford 2009).
77 Apogonids are abundant on tropical reefs, but predation on these fishes is known to be very high (e.g.
78 Sale and Ferrell 1984). We have not found any other studies on the growth of apogonids prior to
79 settlement, immediately after settlement and to their age maxima. We hypothesised that age maxima in
80 *Ostorhinchus doederleini* would be low and this would be consistent among reefs. If this were the case
81 it would greatly influence the outcomes of connectivity among reefs and the persistence of population
82 genotypes. Recent evidence suggests that reef-based local populations of *O. doederleini* can be
83 genetically distinct even when the reefs are only separated by kilometers to tens of kilometers. It has
84 been proposed that despite the relatively poor swimming abilities of larval apogonids (Stobutzki and
85 Bellwood 1997), they are capable of detecting olfactory cues from their natal reefs and this combined
86 with larval behavior facilitates reduced dispersal that can create genetically distinct populations (Gerlach
87 et al. 2007), but a knowledge of fish demography is essential for a full understanding of connectivity.

88 The objective of the present study was to describe the growth and mortality of *Ostorhinchus*
89 *doederleini* (Jordan and Snyder 1901) at four sites within the southern Great Barrier Reef. We
90 examined otolith microstructures to (1) validate the aging technique, and (2) determine the Planktonic
91 Larval Duration (PLD), the duration of the presettlement phase. We also, (3) describe the early growth
92 characteristics in presettlement and newly settled fish and (4) potential differences in the growth rates
93 and demographics of fish at multiple reefs. We also provide information on (5) mortality rates based

94 upon length-at-age estimates of post-settlement fishes. Finally, we (6) review and compare the
95 demographic characteristics of apogonids with other reef fishes.

96

97

98 **Materials and methods**

99 Study sites and fish sampling

100 *Ostorhinchus doederleini* were sampled at multiple sites on four reefs of the Capricorn Bunker group,
101 southern Great Barrier Reef: Heron Island, One Tree Island, Lamont and Fitzroy reefs (Fig. 1).

102 Presettlement fish were only collected at One Tree Island. Channel nets were set to sample fish on the
103 flood tides only at night in January 1994, February 1995 and February 2009 (Table 1). The net was
104 square mouthed (0.75 x 0.75 m), the mesh was 500 μm , organized as a box/pyramid with an efficiency
105 of 1:12 (mouth area: open sifting surface; full procedures see Kingsford and Finn 1997). To preserve
106 the calcium carbonate of otoliths, subsamples of collections from nets were preserved in ethanol.

107 Samples were then rinsed in alcohol to reduce the seawater content, the final percentage ethanol was
108 80%. *Ostorhinchus doederleini* entering the lagoon to settle were easily identified by morphology and
109 pigmentation (e.g. a black dot on the caudal peduncle).

110 Newly settled *O. doederleini* (10 to 18 mm SL) settle on sand and often away from continuous
111 reef (Finn and Kingsford 1996). We constructed six peaked patch reefs on sand (diameter ~ 1.5 m by 0.
112 5 m maximum height) 20 to 60 m from continuous reef. Patch reefs were monitored on a daily basis and
113 all newly settled fish were collected with fine-meshed hand nets and a wide size range was preserved in
114 80% ethanol for ageing. Some fish that colonized patch reefs were larger than new settlers (18 to 27
115 mm SL), but were collected for a description of early post-settlement growth (Table 1).

116 Juvenile and adult *O. doederleini* were collected at four reefs during January and February of
117 2009, 2010 and two large individuals in 2013 (Table 1). At each reef we sampled at multiple sites
118 separated by hundreds of metres to tens of kilometers to obtain a representative sample, and fish were
119 pooled for analyses. Juveniles and adults were collected from caves or branching coral, (especially
120 *Porites cylindrica* and branching *Acropora* spp.) and preserved in 80% ethanol. A wide size-range of
121 fish were collected using a mix of 5:1 ethanol: clove oil. At Heron Island and Lamont reef, we sampled
122 all fish from some large patch reefs and this allowed us to estimate mortality rates (see below). Great
123 care was taken to obtain all size classes of fish, especially large individuals that can be missed because
124 they are the most secretive in the backs of caves. Because *O. doederleini* were potentially short-lived
125 (e.g. Longenecker and Langston 2006) we also sampled fish in October 2010 in case the time of
126 sampling altered our estimates of age maxima; these samples did not allow estimates of mortality as
127 only large fish were selected. All fish collected in October 2010 were sexed macroscopically (ie the
128 presence of oocytes in females or fine-grain spermatogenic tissue in males) to determine size and age
129 versus sex relationships.

130

131 Otolith preparation

132 Increments in otoliths were used to obtain estimates of the age and growth of *O. doederleini*. All fish
133 were weighed (± 0.01 g) and then measured (standard length [SL] ± 1 mm). Sagittal otolith pairs were
134 dissected, rinsed in water, and dried overnight. One otolith from each pair was randomly selected,
135 embedded to the edge of a glass microscope slide using Crystal Bond thermoplastic glue. The sulcal
136 groove of the otolith was orientated perpendicular to the surface of the slide and outer edge of the
137 primordium was flush with the inside edge of the slide. Slides were then held vertically and ground to
138 the transverse mid-plane using a Gemmasta GF4 Faceting Machine with a 3000 μ diamond encrusted

139 steel disc. The glue was then reheated and otoliths were remounted with the newly ground surface
140 placed face down in the centre of the glass slide. Otoliths were ground until a thin section (20 μm thick)
141 was obtained which included the primordium.

142

143 Analysis of growth increments

144 The opaque zones visible in the internal structure of the otolith were counted along a radius from the
145 primordium to the outer edge of the otolith from an image taken with a compound microscope (Leica
146 DMLB using a Leica DC300 digital camera); a white incident light source was used. Alternating
147 translucent and opaque increments were interpreted as daily rings; no annuli were observed, even in the
148 largest fish. The counting of increments began from the first clear increment closest to the primordium.
149 Sections were coded and examined in random order and the opaque increments counted on two
150 occasions by the same observer separated by at least seven days. Counts of daily rings were compared
151 between these two occasions in order to assess the confidence that could be placed in the interpretation
152 of otolith structure. If increment counts differed by more than 10% between counting occasions, then the
153 otoliths were re-examined. If, following a third reading, agreement between the third and one of the two
154 other counts was not reached (only closely matching counts were used in analyses), then the otolith was
155 not included in the analysis. To calculate the age, an average of the two closest age estimates was used.
156 Rejection rate over the entire sample was 2.8%, leaving a total sample of $n=581$ for aging.

157

158 Validation of aging technique

159 To determine the periodicity of increment deposition in *O. doederleini* otoliths, a validation experiment
160 (using tetracycline) was completed at One Tree Island Research Station in January 1994. Fish were
161 treated with tetracycline, it is transported to the endolymph of the inner ear via the blood and deposited

162 in the otoliths and other bony tissues as a mark (Odense and Logan 1974). The tetracycline mark can be
163 viewed as a fluorescent line under ultraviolet light. The otoliths of 20 untreated fish were examined for
164 autofluorescence.

165 Newly settled and other juvenile *O. doederleini* between 16.2 and 32.0 mm SL were collected
166 from isolated patch reefs. Fish were collected with a small hand net and transferred to buckets filled with
167 seawater for transport back to the laboratory. They were immersed in tetracycline-treated seawater (0.25
168 g L⁻¹) for 18 hours in the laboratory in order to mark their otoliths (higher concentrations killed small
169 fish). Fish were transferred to 25 L buckets with one mm mesh windows in the lagoon after removal
170 from the tetracycline solution. Treated fish, therefore, were exposed to the natural cycle of day and night
171 and to normal levels of salinity and water temperature. Fish were fed on wild zooplankton and *Artemia*
172 *nauplii* that were reared in the laboratory. Fish of a range of sizes were euthanased after five, 10 and 15
173 d; fish were then preserved in 98% ethanol. Sagittal otoliths were removed, processed and viewed under
174 transmitted and fluorescent light using a compound microscope. Under fluorescent light an ocular
175 marker was aligned with the fluorescent band if present. The otolith was then viewed under natural light
176 and increments counted between the ocular marker and the otolith margin. Processed otoliths from a
177 similar size range of untreated *O. doederleini* were also examined for the presence of auto fluorescence.
178 All otoliths were examined without knowledge of size or treatment.

179

180 Spacing of otolith increments

181 Most reef fish have a mark in otoliths that corresponds with the time of settlement (Brothers et al. 1983).
182 Settlement marks are an abrupt change in increment spacing, usually from wide to narrow (Victor 1986;
183 Kingsford et al. 2011). Our initial observation of otoliths in recently settled fish failed to detect a
184 settlement mark. We tested this more critically by measuring the spacing of increments in eight

185 randomly selected juvenile *O. doederleini* to determine how the increment pattern changed with distance
186 from the primordium. Transverse sections of the sagittal otolith were prepared. In the first group of
187 fish increment widths were measured from the primordium to the otolith margin (n = 4 fish) and in the
188 second group of fish, from sulcal groove along the longest axis of the otolith to the ventral edge (n = 4
189 fish) were measured. Increment widths were measured using a calibrated video-analysis system (Leica
190 IM50) linked to a compound microscope (Leica DMLB).

191

192 Age and Growth

193 Growth was described using the von Bertalanffy growth function (VBGF) which provided the best fit to
194 size-at-age data when compared with estimates of the Schnute growth function (Schnute 1981). The von
195 Bertalanffy expression for length at age t (L_t), as a function of time was calculated using equation (1):

$$196 \quad L_t = L_\infty [1 - e^{-K(t-t_0)}] \quad (1)$$

197 where L_t = length at age t (*days*), L_∞ = the mean asymptotic standard length, K = the rate at which the
198 growth curve approaches L_∞ , and t_0 = the age at which the fish have a theoretical length of zero. The
199 growth function was run by solver (Microsoft Excel) which minimizes the sum of squares by changing
200 L_∞ , K and t_0 . Some of our demographic comparisons use ‘Age max’ = maximum age of an individual
201 within a sample; and adapted from the convention of Choat and Robertson (2002), max 5% refers to the
202 average age of fish from the 95th to 100th percentile, max 10% the average age from the 90th to the 100th
203 percentile of the sample.

204

205

206 Mortality

207 The instantaneous rate of mortality (Z) was calculated using log-linear regression analyses of age-
208 frequency data sets for *O. doederleini* populations from two reefs where all fish from new recruits to
209 large adults were collected. This method assumes that recruitment is consistent over time at each reef
210 (Haddon 2001). Year classes to the left of the age-frequency mode were excluded from the analysis
211 because our sampling technique was biased against small fish. Mortality was only estimated where fish
212 (over 45 mm SL) were collected representatively (i.e. Heron Island and Lamont reef). The slope of the
213 regression line for each reef provided an estimate of daily instantaneous mortality (Z); equation (2),
214 when expressed as a percentage = loss of individuals per day.

215
$$Z = F + M \quad (2)$$

216 where F is fishing mortality and M is natural mortality (Gust et al. 2002). Since there is not a fishery for
217 *O. doederleini* on the GBR, F equals zero and therefore Z estimates natural mortality only. Daily
218 survival rate estimates (S) were then calculated (i.e. percentage surviving per day, Ricker 1975)
219 according to the equation (3).

220

221
$$S = e^{-Z} \quad (3)$$

222

223 Data from each site were pooled for each reef. Similarities in mortality rates among replicate reefs
224 allowed comparisons of mortality between reefs.

225 **Results**

226 Validation of aging

227 The otoliths of most *Ostorhinchus doederleini* (75%) immersed in tetracycline showed a bright
228 fluorescent band close to the otolith edge (Fig. 2b). Twenty untreated *O. doederleini* otoliths were
229 checked for autofluorescence and showed no fluorescent band ($n = 20$). There was close agreement
230 between the number of increments laid down from the time of immersion in tetracycline and known
231 number of days since treatment; this was true of fish sampled at 5, 10 and 15 days (Table 2).

232 Settlement marks were not found in *O. doederleini* regardless of the orientation of counts with
233 respect to the otolith primordium (Fig. 3a & c). There were no rapid changes in increment width that
234 could be attributed to settlement. The approximate age at settlement could be estimated from the average
235 age that potential settlers entered the lagoon to settle (Fig. 3a & b, Table 3). Although increment width
236 varied across the otolith, they did not relate to settlement. Increments close to the primordium ranged
237 from 2 to 4 μm in width and at approximately the 5 to 8 day mark increments rapidly became wider (5 to
238 7 μm); Fig. 3a. The rapid increase in increment widths at the 5 to 8 day mark was not related to
239 settlement as the mean number of increments in *O. doederleini* caught just prior to settlement was 19.5
240 (SE = 0.38, $n = 34$; Table 3). Similar patterns were found in separate profiles, but increments were
241 generally wider (5 to 18 μm) across the profile (Fig.3b).

242

243 Age and size of presettlement and recently settled *Ostorhinchus doederleini*

244 The age of presettlement *O. doederleini* caught in the channel nets ranged from 15.7 to 26.0 days (mean
245 = 19.9; $n = 34$) and SL ranged from 7.5 to 13.8 mm (mean 10.7; $n = 34$); Table 3. The age of recently
246 | settled *O. doederleini* collected from experimental patch reefs ranged from 16 to 42 days (mean = 25.0;
247 | $n = 232$) and SL ranged from 8.6 – 18.0 mm (mean 12.7; $n = 677$); Table 3.

248 There was great overlap in the age and size of presettlement fish entering the lagoon and that of
249 recently settled fish. Youngest fish on patch reefs were 16 to 17 days old and were as small as 8.6 mm
250 SL. Older and larger fish were found on patch reefs, but many of them would have been associated with
251 the reef for days as some recently settled fish move between patch reefs (Finn and Kingsford 1996).
252 There was a strong linear relationship between age and standard length in presettlement fish over the
253 first 20 days and recently settled fish and growth was rapid at about 0.~~35~~26 mm per day (Fig. 4).

254 255 Variation in growth and sizes among reefs

256 The maximum age of *O. doederleini* among all reefs was 368 days ~~old~~ and at most reefs few fish were
257 older than 200 days old (Fig. 5; Table 4). Time of sampling did not affect estimates of age maxima. The
258 oldest fish caught in January to February at One Tree Island was 284 days and 59 mm long (SL), while in
259 October it was 263 days and 62 mm long (SL). When the average age of the top 5 and 10% of fish was
260 considered at each reef, fish were 150 to 250 days old (Table 4). All von Bertalanffy relationships were
261 well anchored with small fish around 15 to 20 mm SL. Best estimates of asymptotic length were
262 obtained from One Tree Island, where fish grew little in length from 150 to 200 days old. Although there
263 were no significant differences in the size of fish among reefs in the age range of 90 to 110 days
264 (ANOVA, $F_{(3, 60)} = 0.568$, $P = 0.63$), the maximum size of fish did vary. By reef the average size for the
265 top 5% of fish and the maximum SL was (average, max): One Tree Island (61.0, 66 mm), Heron (57.0,
266 65 mm); Lamont (62.6, 74 mm) and Fitzroy (65.5, 68 mm). . The largest fish caught at Heron Island,
267 One Tree Island and Fitzroy reef were 65 to 70 mm SL (= ~80 to 85 Total Length). The two largest and
268 oldest fish ever collected (days/SL, mm: 246/69, 368/74) were from Lamont reef, January 2013. The
269 mean and range of lengths (SL) and ages differed little between males and females (Table 5).

270

271 Mortality

272 Instantaneous mortality rates calculated from catch-curves indicated that mortality rates were high for
273 Lamont and Fitzroy reefs(2.9 to4.6 % per day, Fig.6). Further, mortality rates were highest at Lamont
274 where large fish were rare. Survival (S) rates ranged from 0.971 to 0.955 d⁻¹.

275 **Discussion**

276 *Ostorhinchus doederleini* had a short PLD and once they settled, grew fast and died young. High
277 mortality rates within days of settlement are common for reef fishes (Sale and Ferrell 1988) and low age
278 maxima have been found in other apogonids (Longenecker and Langston 2006). Our study has
279 demonstrated that *O. doederleini* has a high mortality (2.9 to 4.6% per day) and a low age-max. Ages of
280 one year or less clearly put these tropical apogonids at the lower end of the longevity spectrum for
281 tropical fishes along with the Gobiidae and Blenniidae (Table 6). Although some taxa such as gobies
282 may live for less than a year and have high mortality rates (e.g. *Eviota silligata* has an age max of 59
283 days, mortality rate 7.8% per day; Depczynski and Bellwood 2005), species from families of common
284 reef fishes such as the Pomacentridae (e.g. Doherty and Fowler 1994; Kingsford and Hughes 2005),
285 Labridae (Choat et al. 2006), Scaridae (Choat et al. 1996; Gust et al. 2002), Serranidae, Lutjanidae
286 (Kingsford 2009) and Acanthuridae (Choat and Axe 1996) live for years and sometimes decades
287 (Munday and Jones 1998; Fowler 2009) Table 6. Fishes with the lowest age-max were generally small
288 and represented three different trophic groups: nocturnal planktivores, micro/meso carnivores and
289 herbivores/detrital feeders. Although short-lived reef fish appear to be small, not all small fish are short
290 lived (e.g. *Pomacentrus mollucensis* SL max 90 mm (TL) and age max 18 years; Doherty and Fowler
291 1994).

292 To the best of our knowledge, this is the first study to report information on the growth rates of *O.*
293 *doederleini* prior to settlement and immediately after settlement. Further, it is the first to provide data

294 on longevity (age maxima) of the species in the tropics..Some families had data on multiple stages of life
295 history when multiple species were pooled (e.g. omnivorous/herbivorous damselfishes), but given the
296 differences in demographic characteristics within a family general patterns would be crude or simply
297 inaccurate. There was an abundance of data on age, growth and mortality of representatives of families
298 that are the focus of fisheries, especially macrocarnivores and piscivores such as lutjanids, serranids and
299 carangids. However, data on presettlement growth, PLDs and post-settlement growth was
300 comparatively rare. In other families the focus has only, or primarily, been on early life history stages
301 (e.g. Holocentridae, Pomacentridae). For many important families, we found no data at all on age and
302 growth (e.g. Holocentridae, Pempheridae, Caesionidae and Pomacanthidae). The paucity of data is due
303 in part to a relatively recent understanding that the otoliths of tropical species can provide reliable
304 estimates of age (Meekan et al. 2001). Despite this there is a clear need to increase knowledge in this
305 area for the management reef assemblages and tropical fisheries

306

307 We concluded that accurate estimates of age could be obtained from daily increments. Evidence
308 that counts were accurate included the following: the technique was validated, daily increments were
309 easily observed (Fig. 2), the asymptote for age/length relationship for all reefs was beyond 200 days and,
310 adult fish were collected from a size of 49 mm and 132 days or older (based on brooding fish and
311 macroscopic examination of gonads).

312

313 The oldest fish we found was 368 days (n=581); at 23°35' S) and, unpublished data by Michael
314 Marnane at One Tree Island also indicated that some *O. doederleini* can reach an age of over one year.
315 Similar to our study, Longenecker and Langston (2006) found that *Ostorhinchus rubrimacula*
316 (Apogonidae) lived to a maximum of 280 days in Fiji (17°15' S). However, there are great differences

317 between our results for *O. doederleini*, and other data from temperate waters in Japan. Okuda et al.
318 (1998) concluded age estimates of up to seven years in at Shikoku Island, Japan (33° 40" N). The fish
319 sampled in Japan grew to a maximum SL of 86 mm SL whereas we only found fish to a size of 74 mm
320 (93 mm TL). The maximum size of *O. doederleini* recorded for the GBR is 90 mm TL ~ 74 mm SL, but
321 no location is given by Randall et al. (1990) for this specimen. Okuda et al. (1998) had few data on fish
322 less than one year for us to make comparisons of age versus a fish of known size. There are three
323 possibilities to explain latitudinal variation in *O. doederleini* age and growth: (1) there are great
324 differences in age over 10 degrees of latitude, which is partly reflected by differences in size max; (2) a
325 methodological issue where the accuracy of aging techniques varies; Okuda et al. (1998) used scales,
326 whereas we used daily increments in otoliths; (3) mortality rates vary greatly between latitudes. With
327 respect to options one and two, we favour option one as latitudinal variation in growth and age maxima
328 are common in fishes (growth, Conover et al. 1997; age-max, Boehlert and Kappenman,1980)
329 Furthermore, scales tend to underestimate not overestimate ages. In Japan Okuda et al. (1998) fin
330 clipped some fish that were monitored for up to two years, so they clearly get older than their tropical
331 conspecifics. The apogonid *Apogon ruepillei* found in estuaries near Perth (~ 32°S) were over a year old
332 (Chrystal et al. 1985). All of the evidence from tropical waters indicates that small *O. doederleini* have
333 age maxima of a year or less. Estimates of L_{∞} would be most reliable for all reefs combined (Table 4)
334 as very large fish were rare. Our comparisons of the size/age of fish among reefs in the 80to 90 mm SL
335 range would be robust, but beyond 200 days would be weak. Latitudinal gradients in growth and life
336 span would be interesting to examine. Conover et al. (1997), for example, demonstrated a strong
337 positive correlation between the latitude of origin of *Morone saxatilis* and growth. Further, it is
338 common for there to be positive relationships between life-span and latitude in ectotherms, including
339 fishes (Boehlert and Kappenman,1980; review, Munch and Salinas 2009). At present there are no

340 comparative data on growth by latitude for *O. doederleini*. The presettlement phase of *O. doederleini*
341 was 16 to 26 days and fish settled at 9.5 to 13 mm SL. Settlement marks were not observed and the age
342 of settling fish was determined from potential settlers collected in nets at night and new arrivals to patch
343 reefs. Ishihara and Tachihara (2011) estimated the PLDs of six *O. doederleini* in Japan at ~ 16 to 24
344 days and 10 to 11.5 mm SL, which fell within the ranges of values we had from the southern GBR; these
345 authors also collected fish in channel nets. The range of ages over which fish settled was 38% of the
346 maximum age at settlement, a little less than that recorded for the damselfish *Pomacentrus coelestis*
347 (45%; Kingsford et al. 2011). Although many damselfishes spend a similar time in the plankton to
348 *O. doederleini*, there are many other taxa that have longer PLDs. For example, scarids have PLDs of 34
349 to 58 days; chaetodonts 25 to 40 and acanthurids 80+ days (Brothers et al. 1983).

350 *Ostorhinchus doederleini* have strong olfactory senses and can respond to the presence of
351 lagoonal waters (Atema et al. 2002). Presettlement fish swim and/or are carried over the reef crest at
352 night (Kingsford 2001) into One Tree lagoon where they find suitable settlement habitat to settle.
353 *Ostorhinchus doederleini* commonly settle away from continuous reef on sections of substratum,
354 potentially to avoid predatory parents (Finn and Kingsford 1996). We demonstrated that during this
355 phase fish had linear growth, this is typical of other fishes during the early juvenile phase (Kingsford &
356 Milicich).

357 Although reef fishes often have a mark in their otoliths related to settlement from pelagic to
358 benthic environments (Brothers et al. 1983; Kingsford et al. 2011), 'settlement marks' were absent in the
359 otoliths of *O. doederleini*. Brothers et al. (1983) also concluded that *O. doederleini* settle at 16 to 27
360 days (n=5) and did not mention a settlement mark (= 'transition'). Settlement marks are not found in all
361 fishes and, it has been speculated that the eco-behavioral transitions are less traumatic in these
362 circumstances (e.g. monacanthids settling from drift algae to algae attached to the substratum, Kingsford

363 and Milicich 1987). *Ostorhinchus doederleini* may experience less post-settlement trauma by not
364 settling on continuous reef, where the risk of predation (and stress) is high. Further, they usually settle
365 with conspecifics (pers. obs.) and they already have an established ability to feed in low light (Job and
366 Bellwood 2000).

367 There is strong evidence that population structure within a metapopulation of *O. doederleini* can
368 be complex at spatial scales of kilometers to tens of kilometers. Despite having a PLD of 16 to 26 days,
369 a combination of favorable oceanography and larval behavior means that a disproportionately high
370 number of fish return to natal reefs and this can result in significant genetic differences among reefs
371 (Gerlach et al. 2007). The robustness of population structures through time is likely to depend on larval
372 survival, physical forcing (Sissenwine 1984), post-settlement processes (Jones 1991; Almany and
373 Webster 2006) and demographic characteristics. It is critical to consider age for numerical modeling of
374 ecological variation in population size and genetic robustness. For short-lived species such as
375 *O. doederleini*, there is a great vulnerability to recruitment failure, especially if they do not have a
376 prolonged spawning season. This in turn could compromise the resistance and resilience of a local
377 genotype to change. Information on the timing and duration of spawning of *O. doederleini* is largely
378 anecdotal, but does suggest a prolonged spawning season. Mouth brooding fish have been observed in
379 October and January-February and peak recruitment is in January to February (i.e. from spawning in
380 December and January), Further, the collection of *O. doederleini* larvae, in June by Kingsford (2001)
381 indicates that at least some spawning occurs in winter and backdating the age of fish collected in
382 January and February puts many birthdates in the Austral winter to spring.

383 In conclusion, *O. doederleini* have a short PLD, they settle onto sand and rubble away from
384 continuous reefs and grow quickly. They reach asymptotic size beyond 200 days, but few fish reach 200
385 days old and the age maximum we found at four reefs was 368 days. These small fish were

386 characterized by high mortality rates and presumably have a high population turn over; this should be
387 considered in models relating to the trophodynamics of reefs and the population biology of
388 *O. doederleini*. A review of the literature indicated that other fishes with similar demographic
389 characteristics are small gobies and blennies.

390

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396

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614

615 **Table 1** Collection details for *Ostorhinchus doederleini* specimens, 1994 to 2013. OTI- One Tree Island;
 616 H- Heron Reef; F- Fitzroy Reef; and L= Lamont.

617

Dates Sampled	Methods used	Reefs	Life stage
Jan 1994	Channel nets; Patch Reefs	OTI	Presettlement and early post-settlement
Feb 1995	Channel nets; Patch Reefs	OTI	Presettlement and early post-settlement
Feb 2009	Channel nets, Hand nets; clove oil	OTI, H, F, L	Juveniles and adults
Jan-Feb. 2010	Hand nets; clove oil	OTI, H, F, L	Juveniles and adults
Oct 2010	Hand nets; clove oil	OTI	Juveniles and adults
Jan 2013	Hand nets; clove oil	L	Adults

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620

621 **Table 2** Results of validation marking experiments for *Ostorhinchus doederleini*. No. of days = number

622 of days since fish were immersed in tetracycline.

623

No. of days	<i>n</i>	SL range (mm)	Mean of counts (SE)
5	42	17.0 - 25.2	4.95 (0.07)
10	16	17.4 - 34.0	10.06 (0.11)
15	11	16.2 - 25.0	14.82 (0.23)

624

625 **Table 3** Age (days) and size (mm; SL) of presettlement and recently settled *Ostorhinchus doederleini* in
 626 two recruitment seasons. Data shown are the mean (range) and total n is given by row. For recently
 627 settled fish n varied for size and age, more fish were collected for measurements of size and were not
 628 preserved in ethanol (Kingsford and Finn 1997).
 629

	1994	1995	<i>n</i>
Presettlement fish			
SL	10.7 (7.5 - 13.0) 4	10.6 (9.0 - 13.8) 30	34
Age	18 (15.7 - 19.7) 4	19.7 (16.0 - 26.0) 30	34
Recently settled fish			
SL	14.1 (9.8 - 18.0) 299	11.23 (8.6 - 18.0) 378	677
Age	28.2 (17.0 - 41.5) 113	22.5 (16.0 - 40.0) 119	232

630

631

632 **Table 4** von Bertalanffy growth parameters for four reefs and estimates of age maxima for individual
633 fish from samples at each location and average age of the oldest five and 10 percent of fish (i.e. Max %).

634

Reef	n	L_{∞}	K	r^2	Age Max	Max 5% (n) SE	Max10% (n) SE
Heron	122	76.24	0.008	0.86	215	173 (6) 13	144 (12) 11
One Tree Island	257	60.76	0.012	0.88	284	255 (13) 4	240 (26) 4
Lamont	91	83.84	0.006	0.82	368	213 (5) 6	176 (9) 27
Fitzroy	123	70.48	0.009	0.77	282	224 (6) 12	207 (12) 8
All reefs	593	65.04	0.010	0.89	368	249 (30) 5	226 (59) 4

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639

640 **Table 5** Size, age and sex differences for *Ostorhinus doederleini* collected at One Tree Island, October
641 2010.

	Female	Male
n	55	70
Mean (SL)	53.27 mm	52.09 mm
SE	0.535	0.596
Min (SL)	43 mm	41 mm
Max (SL)	60 mm	66 mm
Mean (Age)	191 days	190 days
Min (Age)	139 days	132 days
Max (Age)	258 days	263 days

642

643

Table 6 A comparison of with examples of demographic characteristics among multiple families of tropical reef fishes, by trophic groups (adapted from Randall et al. 1990); in some cases we found more references than listed, but the age range was within the other publication listed. A Yes (Y) indicates that some information is available; ND- no data, y- years, d- days. Brothers et al. (1983) provided estimates of PLD for many of the groups listed, but they relied on the presence of settlement marks which are not found in some families such as apogonids. Some families appear in more than one trophic group (e.g. Pomacentridae). Data from temperate regions are not included.

Family	Species	Presettlement growth	PLD (range)	Settlement mark	Early Post-settlement growth	Life time growth	Age maxima	Estimates of mortality	Country	Source
Nocturnal planktivores/piscivores										
Apogonidae	<i>Apogon cyanosoma</i>	N	18-19d	ND	ND	ND	ND	ND	GBR, Australia	Brothers et al. 1983
	<i>Cheilodipterus quinquelineatus</i>	N	17-29d	ND	ND	ND	ND	ND	GBR, Australia	Brothers et al. 1983
	<i>Ostorhinchus doederleini</i>	Y	16-26d	ND	Y	Y	< 1 year	Y	GBR, Australia	This study
	<i>Ostorhinchus rubrimacula</i>	N	N	ND	Y	Y	< 1 year	ND	Fiji	Longenecker and Langston 2006
Holocentridae	Multiple (7)	Y	32-56d	ND	ND	ND	ND	ND	Western Atlantic	Tyler et al. 1993
Pempheridae		ND	ND	ND	ND	ND	ND	ND		
Diurnal planktivores										
Caesionidae		ND	ND	ND	ND	ND	ND	ND		
Pomacentridae	Multiple (8)	ND	8-32d	Y	Y	ND	ND	ND	GBR, Australia	Bay et al. 2006; Green and McCormick 2005
Acanthuridae	<i>Naso sp</i> (6)	ND	ND	ND	ND	Y	9-30y	ND	GBR, Australia	Choat and Robertson 2002

Serranidae	e.g. <i>Anthias</i> spp. and <i>Pseudoanthias</i> spp	ND	ND	ND	ND	ND	ND	ND	ND		
Micro-Meso carnivores											
Balistidae	Multiple (2)	ND	ND	ND	ND	Y	11-14y	Y	Brazil	de Albuquerque et al. 2011;	
Chaetodontidae	Multiple (8)	Y	23-45d	Y	Y	Y	6-20y	Y	GBR, Australia	Bernardes 2002 Fowler 1989; Berumen 2005; Berumen et al. 2012	
Gobiidae	Multiple (3)	ND	24-26d	Y	Y	Y	59-100d	Y	GBR, Australia	Depczynski and Bellwood 2006	
	<i>Coryphopterus kuna</i>	ND	45-74d	Y	Y	Y	120d	Y	Caribbean	Victor et al. 2010	
	<i>Eviota sigillata</i>	ND	23-27d	Y	Y	Y	59d	Y	GBR, Australia	Depczynski and Bellwood 2005	
Labridae	Multiple (9)	ND	21-50d	Y	ND	Y	15-36y	Y	GBR, Australia	Brothers et al. 1983; Choat et al. 2006	
	<i>Thalassoma bifasciatum</i>	Y	40-72d	Y	Y	ND	ND	ND	Caribbean	Victor 1982	
Nemipteridae	<i>Scolopsis bilineatus</i>	ND	ND	ND	ND	Y	16	Y	GBR, Australia	Boaden and Kingsford 2012	
Pomacanthidae	<i>Pomacanthus imperator</i>	ND	ND	ND	ND	Y	16	ND	China	Chung and Woo 1999	
Macrocarivore/ piscivore											
Carangidae	Multiple (2)	ND	ND	ND	ND	Y	6-10y	ND	Hawaii	Sudekum et al. 1991	
	<i>Caranx bucculentus</i>	ND	ND	ND	ND	Y	ND	Y	Northern Australia	Brewer et al. 1994	
Lethrinidae	Multiple (7)	ND	ND	ND	ND	Y	15-36y	Y	GBR, Australia	Currey et al. 2013; Brown and Sumpton 1998	
Lutjanidae	Multiple (11)	ND	ND	ND	ND	Y	12-55y	Y	Northern Australia, Indonesia	Marriott et al. 2007; Newman et al. 1996; Newman et al. 2000; Heupel et al. 2010	
	<i>Lutjanus carponotatus</i>	ND	ND	ND	ND	Y	18y	Y	GBR, Australia	Kingsford 2009	
Scorpaenidae	<i>Pterois volitans</i>	ND	20-35d	ND	ND	ND	ND	ND	Bahamas	Ahrenholz and Morris 2010	
Serranidae	<i>Cephalopholis cyanostigma</i>	ND	ND	ND	ND	Y	45y	Y	GBR, Australia	Mosse et al. 2002	
	<i>Cromileptes altivelis</i>	ND	ND	ND	ND	Y	19y	Y	GBR, Australia	Williams et al. 2009	

	<i>Epinephelus fuscoguttatus</i>	ND	ND	ND	ND	Y	42y	Y	GBR, Australia	Pears et al. 2006
	<i>Plectropomus laevis</i>	ND	ND	ND	ND	Y	16y	Y	GBR, Australia	Heupel et al. 2010
	<i>Plectropomus leopardus</i>	ND	ND	ND	ND	Y	15y	Y	GBR, Australia	Kingsford 2009
Omnivores/herbivores/ scrapers and detrital feeder										
Acanthuridae	Multiple (5)	ND	84d	Y	ND	Y	21-70y	ND	GBR, Australia	Choat and Axe 1996
Blenniidae	Multiple (3)	ND	12-33d	Y	ND	ND	ND	ND	GBR, Australia	Beldade et al. 2007; Brothers et al. 1983
	<i>Salarias patzneri</i>	ND	ND	Y	Y	ND	350d	ND	GBR, Australia	Wilson 2004
Pomacentridae	Multiple (100)	Y	12-39d	Y	ND	ND	ND	ND	GBR, Australia; Pacific, Atlantic	Bay et al. 2006; Wellington and Victor 1989
	<i>Acanthochromis polyacanthus</i>	ND	ND	Y	Y	N	9-11y	Y	GBR, Australia	Kingsford and Hughes 2005
	<i>Pomacentrus amboinensis</i>	Y	15-23d	ND	ND	ND	ND	ND	GBR, Australia	Kerrigan 1996
	<i>Pomacentrus coelestis</i>	Y	15-27d	Y	Y	ND	ND	ND	GBR, Australia	Kingsford et al. 2011
	<i>Pomacentrus moluccensis</i>	ND	ND	ND	Y	Y	18y	Y	GBR, Australia	Doherty and Fowler 1994
	<i>Stegastes acapulcoensis</i>	ND	ND	ND	ND	Y	12-32y	Y	Panama, Galapagos	Meekan et al. 2001
Scaridae	Multiple (7)	Y	30-50d	Y	ND	Y	5-20y	Y	GBR, Australia	Brothers et al. 1983; Gust et al. 2002; Choat et al. 1996
	<i>Sparisoma viride</i>	ND	ND	ND	ND	Y	7-9y	Y	Caribbean	Choat et al. 2003

644

645

646 **Figure Captions**

647

648 **Fig. 1** Map showing the location of the four reefs in the Capricorn-Bunker Group, southern Great
649 Barrier Reef, Australia where *Ostorhinchus doederleini* was collected.

650

651 **Fig. 2** (a) Sagittal otolith section of a 21 day old *Ostorhinchus doederleini*. Width of otolith section is
652 1500 μm . Initial measurement made at first visible increment (Insert showing enlargement of
653 300 μm long); (b) Otolith of a fish euthanised 10 days after immersion in tetracycline viewed under UV
654 light, scale bar = 100 μm ; (c) A section of an 90 day old fish (from OTI; 34 mm SL) showing track used
655 for aging, which extended from the primordium to the outer edge of the otolith along the longest axis
656 (Section is 2100 μm long).

657

658 **Fig. 3** Otolith increment widths plotted as a function of increment number for a subset of four post-
659 settlement *Ostorhinchus doederleini*, (a) 1994 and 1995; (b) 2010 from One Tree Island, Great Barrier
660 Reef, Australia. The dotted vertical line indicates the mean no. of increments deposited by presettlement
661 apogonids caught just prior to settlement measured from the primordium to along the sulcal groove;
662 from the primordium to the ventral edge of the otolith. Initial measurement made at first visible
663 increment.

664

665 **Fig. 4** Relationship between standard length and age (days) of presettlement versus newly settled
666 recruits *Ostorhinchus doederleini* in 1994 and 1995 together with fitted regression lines and summary
667 statistics.

668

669 **Fig. 5** von Bertalanffy growth curves for *Ostorhinchus doederleini* for the four reefs in the Capricorn
670 Bunker group, Great Barrier Reef, Australia.

671

672 **Fig 6** Age-based ‘catch-curves’ that provide estimates of mortality for *Ostorhinchus doederleini* for
673 Heron and Lamont reefs in the Capricorn Bunker group, Great Barrier Reef, Australia; each data point
674 indicates Log_e frequency of each age class.

675

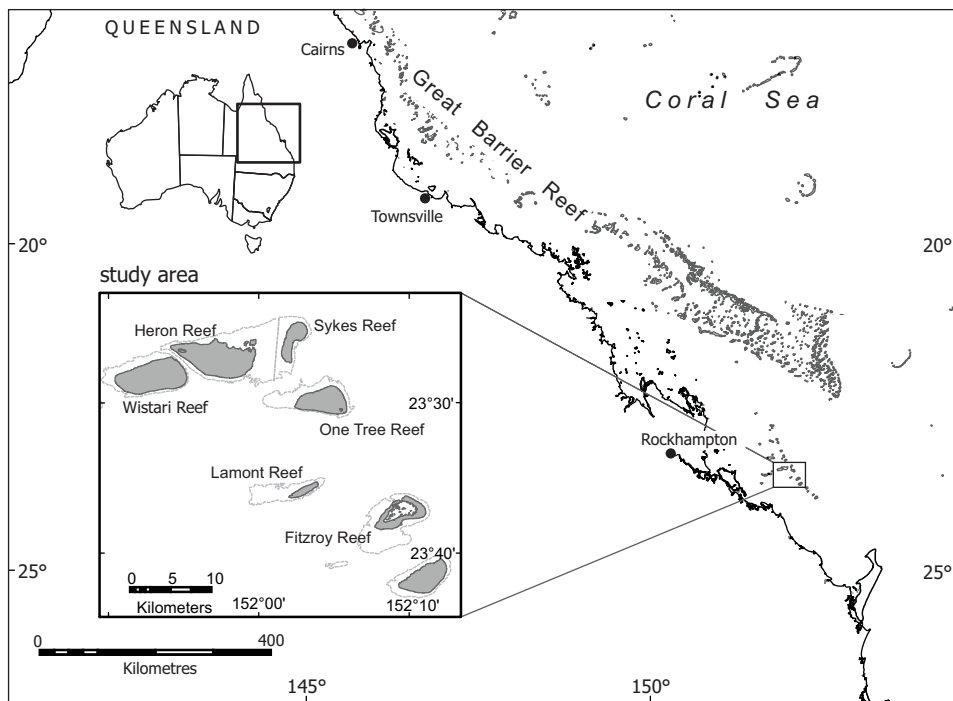


Figure 2

