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Ageing of juvenile coral grouper (*Plectropomus maculatus*) reveals year-round spawning and recruitment: implications for seasonal closures

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1 **Ageing of juvenile coral grouper (*Plectropomus maculatus*) reveals year-round**
2 **spawning and recruitment: implications for seasonal closures**

3
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23 **Abstract**

24 Temporal patterns in spawning and juvenile recruitment can have major effects on
25 population size and the demographic structure of coral reef fishes. For harvested species,
26 these patterns are crucial in determining stock size and optimising management strategies
27 such as seasonal closures. For the commercially important coral grouper (*Plectropomus*
28 spp.) on the Great Barrier Reef, histological studies indicate peak spawning around the
29 summer new moons. Here we examine the timing of spawning activity for *P. maculatus* in
30 the southern Great Barrier Reef by deriving age in days for 761 juvenile fish collected
31 between 2007 and 2022, and back-calculating settlement and spawning dates. Age-length
32 relationships were used to estimate spawning and settlement times for a further 1002
33 juveniles collected over this period. Unexpectedly, our findings indicate year-round
34 spawning activity generates distinct recruitment cohorts that span several weeks to
35 months. Peak spawning varied between years with no clear association with environmental
36 cues, and little to no alignment with existing seasonal fisheries closures around the new
37 moon. Given the variability and uncertainty in peak spawning times, this fishery may
38 benefit from additional and longer seasonal closures, or alternative measures, in order to
39 maximise the recruitment contribution from periods of greatest reproductive success.

40

41 **Key words:** Seasonal fishing closures; reproductive ecology; coral reef fisheries; age-based
42 demography

43 **Introduction**

44 Marine fish populations are characterised by juvenile recruitment patterns that are highly
45 variable in space and time. For coral reef fishes, considerable attention has been given to
46 understanding spatial variation in recruitment patterns and its impact on the distribution
47 and abundance of a species (Caley et al., 1996; Doherty & Williams, 1988; Wen, et al.,
48 2013a; Williams & Sale, 1981). Recruitment patterns can often vary substantially among
49 locations leading to recruitment hotspots or places that consistently experience reliable

50 levels of recruitment and high population densities (Booth et al., 2000; Eagle et al., 2012;
51 Wen, et al., 2013). Such spatial heterogeneity in the recruitment of reef fishes is often
52 driven by strong habitat preferences at the time of settlement to the reef (Booth & Beretta,
53 1994; Jones, 1991). For exploited species, spatial management strategies such as no-take
54 marine reserves that target recruitment hotspots may be particularly effective in
55 enhancing fish stocks (Wen et al., 2013b).

56 In comparison, there have been fewer studies on temporal variation in the recruitment of
57 coral reef fishes and its management implications. Recruitment is extremely variable
58 among and within years (Williams, 1983; Williams & Sale, 1981; Sponaugle & Cowen,
59 1997a). Such variation can lead to fluctuations in adult population sizes and make fishery
60 stock-recruitment relationships extremely unpredictable (Schindler et al., 2010). There are
61 likely to be multiple causes of temporal variation in recruitment, including the timing of
62 spawning activity (Robertson, 1991), variations in growth and survival of larval stages
63 (Jones, 1991), and temporal variation in larval supply from different source populations
64 (Harrison et al., 2020), all of which can have a large impact on the number of individuals
65 recruiting to the adult population of a given reef. However, in general the causes of
66 temporal variation in recruitment are poorly understood.

67 As most coral reef fishes have a restricted pelagic larval duration (PLD) (Brothers et al.,
68 1983; Victor, 1986a; Wellington & Victor, 1989), temporal patterns in spawning are likely
69 to be a major driver of temporal patterns in recruitment (Robertson et al., 1988; Sponaugle
70 & Cowen, 1996, 1997b). On some low latitude coral reefs, fish spawn and recruit
71 throughout the year (Srinivasan & Jones, 2006). However, most coral reef fishes exhibit
72 distinct spawning seasons, which vary by regions and by latitudes, with shorter breeding
73 seasons at high latitudes (Russell et al., 1977; Doherty, 1983; Robertson, 1990). Distinct
74 spawning seasons are thought to occur during months where environmental conditions
75 maximise the survival and performance of their offspring (Johannes, 1978). The timing and
76 duration of spawning seasonality in coral reef fishes have been linked to temperature
77 cycles (Samoilys, 1997; Zarco-Perello et al., 2022). Other studies have shown weak
78 associations between rainfall and reproductivity, some negative (Srinivasan and Jones,
79 2006; Freitas et al., 2011) and others positive (Abesamis et al., 2015). The effects of

80 temperature and rainfall may be species and location specific. A large proportion of coral
81 reef fishes also exhibit distinct lunar spawning cycles within spawning seasons, often
82 during new or full moon phases (Doherty, 1983; Johannes, 1978; Rankin & Sponaugle,
83 2014). Lunar synchrony may occur at times that reduce predation on larvae or enhance
84 reproductive success, which may enhance recruitment within spawning seasons
85 (Robertson, 1991). Spawning during different lunar phases can have a major influence on
86 pre- and post-settlement growth and survivorship (Jones, 1986, 1987a, Rankin &
87 Sponaugle, 2014; Shima et al., 2020, 2021; Shima & Swearer, 2019). However, the timing of
88 spawning in relation to annual and lunar cycles is not known for the vast majority of reef
89 fish species.

90 The timing of spawning is particularly important in relation to temporal fisheries
91 management strategies such as seasonal closures. It is surmised that recruitment to the
92 fishery can be enhanced by halting fishing during peak times of the spawning season and
93 lunar cycle (Halliday 1988, Sadovy and Domeier 2005). Although, recent studies have
94 found that seasonal closures implemented on already collapsed stocks may be too little too
95 late (Clarke et al 2015). On this basis, the Queensland Line Fishery (Reef) is subject to short
96 seasonal closures based on the presumption of seasonal and lunar spawning of the
97 common coral grouper *Plectropomus leopardus* (Samoilys, 1997; Fox et al., 2022). The
98 fishery closure applies to both commercial and recreational sectors and covers a range of
99 reef fish species including common coral grouper , bar-cheek coral grouper (*P. maculatus*),
100 and other serranidae, Labridae, Lutjanidae and Lethrindae species (Campbell et al., 2019;
101 Frisch et al., 2016; Department of Agriculture Water and the Environment, 2021; Fox et al.,
102 2022. However, it is not known whether all these species, across all regions of the Great
103 Barrier Reef, exhibit the same seasonal and lunar spawning patterns, and so the
104 effectiveness of the seasonal closure for the whole fishery has not been assessed.

105 Direct observations of spawning activity to define spawning seasons and lunar cycles are
106 not always possible and the histological assessment of seasonal gonad development
107 provides only limited indication of spawning activity and the frequency of spawning events.
108 Even when spawning events are directly observed, knowing where larvae go and
109 successfully settle, and recruit is challenging. Individuals that have already recruited into a

110 population could therefore be considered more demographically relevant to quantify
111 reproductive activity. Direct examination of these individuals and the temporal patterns of
112 their cohorts can be used to hindcast the timing of successful spawning activity, allowing
113 inference of environmental cues for spawning and the best times to apply seasonal closures
114 to enhance recruitment. Here we use age estimates of a large samples of juvenile coral
115 grouper (*P. maculatus*) collected at regular intervals from fringing reefs of a small island
116 archipelago in the Southern GBR to back-calculate the date of spawning of juveniles that
117 have successfully settled and recruited to local reefs. From the age and growth rate of
118 juvenile fish (< 250 mm) we then inferred peaks in spawning activity across multiple years
119 that we could relate to environmental conditions and investigate the effectiveness of
120 seasonal closures for the coral grouper fishery on the Great Barrier Reef.

121 **Methods**

122 **Study site and sample collection**

123 The Keppel Islands are an inshore island archipelago of the southern Great Barrier Reef
124 Marine Park, popular amongst recreational fishers. Prior to 2009, all fishing activity was
125 closed for three nine-day periods during the new moon phases of late spring and early
126 summer (Oct-Dec). Changes in legislation reduced the number and duration of fisheries
127 closures to two five-day periods during the same period.

128 Juvenile *P. maculatus* were sampled from reefs throughout the Keppel Islands (23.18°S,
129 150.95°E) during three multi-year collection periods spanning 15 years (2007-2022), with
130 2-3 sampling trips within each period (Table S1). Individuals up to 250 mm total length
131 were collected on SCUBA using either spearguns or hand spears, with some smaller fish up
132 to 50 mm collected using clove oil and hand nets. In total, 1763 juveniles were collected
133 and the fork length (FL) and total length (TL) of each fish was measured to the nearest
134 millimeter and weighed to the nearest 0.1 gram.

135 **Otolith preparation and age determination**

136 The sagittal otoliths were extracted from a subset of individuals from each collection
137 period (Table S2) to estimate age and growth rates. The preparation of otoliths followed
138 the methods described in Taylor et al. (2016) and is consistent with previous studies of
139 early life history growth in *P. maculatus* from the southern GBR (Mannering, 2008;
140 Williamson et al., 2016; Harrison et al., 2020). Briefly, one otolith from each juvenile fish
141 was affixed to a glass microscope slide using thermoplastic glue (Crystalbond 509), with
142 the primordium (nucleus) on the inside edge of the slide and sulcus ridge perpendicular to
143 the slide edge to obtain a transverse section of the sagittal otolith. Each otolith was ground
144 to the edge of the slide using a GEMMASTA lapping wheel with a 1200 grit diamond
145 sanding wheel. The otoliths were then removed and affixed to a clean labelled slide, with
146 the ground surface down, and polished using the same grit to a thin ($\approx 150 \mu\text{m}$) transverse
147 section that intercepts the nucleus. Successive polishing was then carried out with 9, 3, and
148 0.3 micron lapping film until daily growth increments (DGIs) were of optimal clarity.
149 Sectioned otoliths were then coated in immersion oil and photographed under 200x and
150 400x magnification.

151

152 **Calculating date of spawning for aged juveniles**

153 The post-settlement age of each aged juvenile was estimated through three independent
154 counts of the DGIs, from the settlement mark to the outer edge along the ventral surface,
155 following the longest plane. The final post-settlement age was taken from the mean of the
156 three counts, when each of the three counts were within 10% difference of the median.
157 Samples with counts greater than 10% of the median were excluded from the analysis. To
158 reduce the possibility of potential observer effects in counts, a sub-sample of 50 otoliths
159 across sampling periods were cross-validated and verified by the same observer (BMT)
160 and found to be consistent between observers.

161 In total, 761 juvenile *P. maculatus* were aged, ranging from 23 mm to 248 mm in total
162 length with a mean length of 116.6 mm (Table S2, Fig S1a). The pelagic larval durations
163 (PLDs) were estimated for 70 individuals by counting daily age increments from the
164 primordium to the settlement mark of the otolith (Fig S1b), with a mean PLD of 27.9 days \pm

165 1.6 SD. We calculated the date of hatching of aged juveniles by subtracting their measured
166 post-settlement age and mean PLD from the date of collection. Approximately 43% of
167 juvenile fish were aged across all sampling periods (Fig S2) to account for variation in early
168 growth between years.

169

170 **Estimating date of spawning for non-aged juveniles**

171 Six discrete cohorts were visually identified from the distribution of spawning times (Fig
172 S3) to estimate growth rates and the time of spawning of un-aged juvenile fish up to 250
173 mm in total length. A generalised linear mixed effects model with a third order polynomial
174 structure was used to model post-settlement age against total length with a Gaussian error
175 structure controlling for pre-defined cohorts (random effect) using the *glmmTMB* package
176 in R (Brooks et al., 2017). The data fit the assumptions of the model with homogeneity of
177 variance and no dispersion or outliers. To control heteroscedasticity in the residuals plots
178 due to decreasing ageing precision with total length, we included a dispersion factor for
179 length and cohort to minimise its effect on the model predictions. We used the modelled
180 relationships for each cohort to predict the time of settlement of un-aged juvenile fish up to
181 250 mm in total length that were collected from the same cohorts (57% of the data). The
182 time of settlement of individuals that were collected outside of the modelled cohorts was
183 estimated from the marginalised mean of all cohorts (Fig S4). Finally, we subtracted the
184 mean PLD from the time of settlement to estimate the time of hatching of each juvenile fish
185 that successfully recruited to the island group.

186 For all GLMMs, model residuals were inspected in the package *DHARMA* (Hartig, 2022) and
187 checked for homogeneity of variance, dispersion, and outliers. Model predictions were
188 performed and visualised with *emmeans* (Lenth, 2021) and *tidyverse* (Wickham et al.,
189 2019), and summarised with *broom.mixed* (Bolker and Robinson, 2020). All models and
190 graphics were conducted within the R (R Core team 2022) statistical and graphical
191 environment. Where relevant, confidence intervals were based on a 95% significance level.

192

193 **Temporal spawning patterns**

194 We used Generalised Additive Models (GAMs) within the package *mgcv* (Wood, 2006) to
195 identify peak spawning times of juveniles *P. maculatus* at the Keppel islands for five austral
196 years (July-June) that had sufficient data (83 individuals were removed). The number of
197 fish spawned in 5-day windows were used as the response variable that assumed a
198 Tweedie error distribution with a logarithmic link-function to account for over-dispersion
199 caused by periods with no spawning activity. The GAMs were tested for each austral year
200 based on the following formula:

$$201 \quad y = \beta_0 + f(5 \text{ day window}) + \epsilon, \quad \epsilon \sim Tw_p(\mu, \sigma^2)$$

202 Where β_0 is the average number of individuals spawned in a 5-day period and f Spawning
203 counts indicate the additive smoothing functions of the annual trends in spawning.
204 DHARMA residuals were checked for homogeneity of variance, dispersion, and outliers.
205 Additional tests for zero inflation, overdispersion, and over-smoothing were performed to
206 satisfy model fit. Model selection was informed from the Akaike information criterion
207 (AICc) with the lowest score (Burnham and Anderson 2002). Spawning peaks were
208 identified from model derivatives and plotted with partial residuals. The model predictions
209 were used to identify peaks in spawning activity, the duration between peaks, and to
210 quantify the likely contribution of spawning closures between October – December of each
211 year.

212

213 **Environmental drivers of spawning activity**

214 We also explored the environmental conditions associated with spawning activity using
215 GAMs that included lunar illumination, Sea Surface Temperature (SST), local rainfall and
216 flood gauge data from the Fitzroy River as covariates. The number of individuals spawned
217 were summed over 5-day periods to minimise the influence of zero-values in the data.
218 Lunar illumination values were averaged over the same 5-day period using the *lunar*
219 package (Lazardis 2014) with a +10-hour shift to account for Australian Eastern Standard

220 Time. SST values were generated by the Giovanni online data system, developed and
 221 maintained by the NASA GES DISC (Acker and Leptoukh 2007), which generates an 8-day
 222 average of night-time SST collected by the MODIS-Aqua satellite sensing system. Rainfall
 223 and flood data were generated from the Australian Government Bureau of Meteorology
 224 data portal.

225 The number of individuals spawned in a 5-day period were used as the response variable
 226 for GAMs that assumed a Tweedie error distribution with a logarithmic link-function to
 227 account for overdispersion caused by periods with no spawning activity. We explored
 228 models with a spline fitted to each covariate and the possible interaction between lunar
 229 phase and SST. Model selection was informed from the Akaike information criterion (AICc)
 230 and model fit. The best model included an interaction between SST and month,
 231 marginalised over years and was based on the following formula:

$$232 \quad y = \beta_0 + f(SST|Month) + \gamma_{year} + \epsilon, \quad \sim Tw_p(\mu, \sigma^2)$$

233 Where β_0 is the average number of individuals spawned in a 5-day period, $f(SST|Month)$
 234 indicate the additive smoothing functions of the interaction between sea surface
 235 temperature and time of year (month), and γ_{year} indicates the random smoothing term of
 236 year. *Rainfall*, and *Lunar illumination* were not important explanatory variables and were
 237 excluded from the model. *Flood Height* had a significant effect though showed high
 238 concurrency with SST and month (0.77). DHARMA residuals were checked for homogeneity
 239 of variance, dispersion, and outliers. Additional tests for zero inflation, overdispersion,
 240 concurrency, and over-smoothing were performed to satisfy model fit.

241

242 **Assessing the effectiveness of seasonal closures**

243 Finally, we assessed whether the number and duration of spawning closures from October
 244 to December increases the likelihood of capturing a peak in spawning activity. For each
 245 year, we calculated the number of successful spawning counts during 5-day and 9-day
 246 closures around the new moon, rounded to the nearest integer. A generalised linear mixed
 247 effects model was used to model spawning activity against the duration and number of

248 seasonal closures with a Poisson error structure controlling for the number of closures
249 nested in years (random effect) using the *glmmTMB* package in R (Brooks et al., 2017). The
250 data fit the assumptions of the model with homogeneity of variance and no dispersion or
251 outliers. We used the modelled relationship to predict and compare the spawning activity
252 captured by each seasonal closure.

253 **Results**

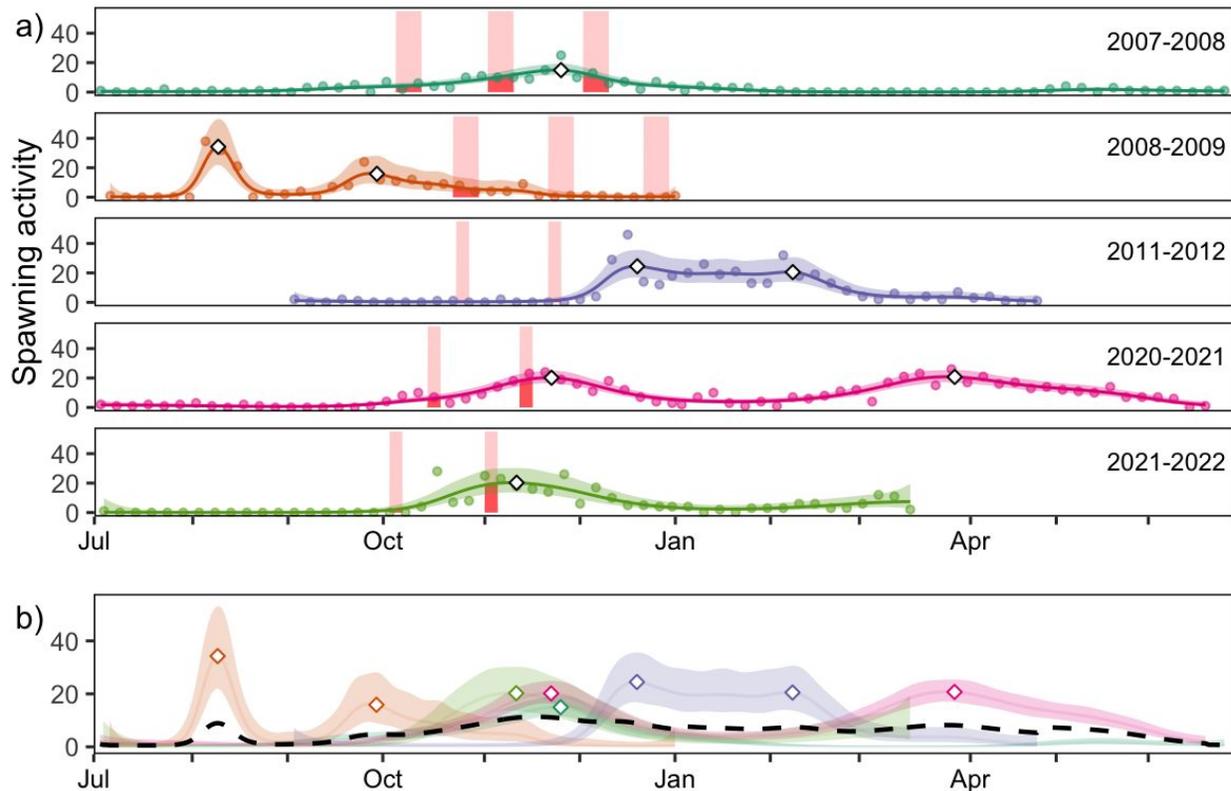
254 **Temporal patterns in spawning activity**

255 By ageing 761 juvenile *P. maculatus* under 250 mm (TL) collected from the Keppel Islands,
256 we were able to hindcast the date of spawning for an additional 1002 juvenile fish that
257 successfully settled to the island group. Over the course of three sampling periods between
258 2007-2022, we found spawning activity occurred year-round in distinct cohorts spanning
259 periods of 1-4 months (Fig S5). However, the timing of peak spawning activity was not
260 consistent in each year indicating temporal fluctuations in successful spawning (Fig 1). This
261 provided the basis to investigate temporal patterns in spawning activity, the environmental
262 conditions that may trigger spawning, and the effectiveness of spawning closures for *P.*
263 *maculatus* at the Keppel Islands.

264 Generalised Additive Models, centred on the austral summer, were fitted separately to the
265 date of spawning of juvenile *P. maculatus* in each of 5 years. The best fit GAMs yielded
266 robust diagnostics and explained at least 80 % of the null deviance depending on the year,
267 indicating good model fits. All years showed evidence of a long-term non-linear trend in
268 spawning and of similar and significant wiggleness (Table S4). The timing of peak spawning
269 varied between years and ranged from August through to March. Each year presented one
270 to three peaks in spawning, with distinct peaks separated by 50 to 127 days (Fig 2a). Peaks
271 in spawning were of similar strength ranging from 15 to 34 juveniles successfully spawned
272 in a 5-day window (mean: 21.4 95 % CI [15.0-30.9]) though ranged in their duration and
273 thus their contribution to local recruitment at the Keppel Islands. Averaged across the five
274 years (Fig 2b), spawning occurred year-round and although there appears to be an increase

275 in spawning activity between October-December, the spawning patterns were too variable
 276 to confidently differentiate spawning activity between seasons.

277



278

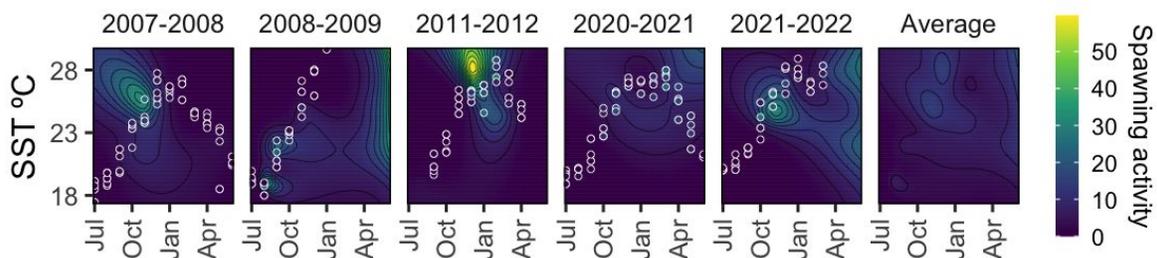
279 **Figure 1.** Annual variation in spawning activity of *P. maculatus* at the Keppel Islands
 280 inferred from hatching dates of 1763 juveniles. a) Spawning activity that led to the
 281 successful recruitment of juveniles *P. maculatus*. In each 12-month period, lines and shaded
 282 areas represent the predicted number of individuals spawned in a 5-day window with 95%
 283 confidence intervals. Points represent the observed data and white diamonds identify
 284 peaks in spawning activity. Red bars indicate seasonal spawning closures. b) Predicted
 285 spawning activity overlaid for each year with the dashed line representing the yearly
 286 average number of juveniles spawned in a 5-day window that successfully recruited to
 287 reefs at the Keppel Islands.

288

289 Environmental drivers of spawning activity

290 We investigated the environmental conditions associated with spawning activity of *P.*
 291 *maculatus* at the Keppel Islands and identified an important interaction between SST and
 292 time of year (month). Neither lunar illumination or rainfall captured variation in spawning
 293 activity whereas flood height was highly correlated with SST and time of year and was
 294 therefore excluded from the model (Fig S6). The best fit GAM included an interaction
 295 between SST and month marginalised over years (Table S5), which yielded robust
 296 diagnostics and explained at least 80 % of the null deviance, indicating a good model fit. All
 297 years showed evidence of a long-term non-linear trend in spawning activity associated
 298 with SST throughout the year (Table S5). When predicting spawning activity throughout
 299 the range of SST recorded at the Keppel Islands it is possible to identify clear peaks in
 300 spawning activity (Fig 3). However, the results were not consistent between years
 301 suggesting that additional unknown factors not considered here may influence the timing
 302 of spawning activity or survival of juvenile *P. maculatus* at the Keppel Islands. When
 303 averaged across all years, the conditions associated with spawning activity are only very
 304 broadly associated with the Austral summer conditions.

305



306

307 **Figure 2.** Spawning activity of *P. maculatus* at the Keppel Islands was strongly associated
 308 with sea surface temperature (SST) and time of year, though trends were inconsistent
 309 between years. Shaded areas and contour lines indicate the predicted spawning activity (in
 310 5-day windows) of *P. maculatus* at the Keppel Islands. Estimates of spawning activity are
 311 overlaid in open circles for each year.

312

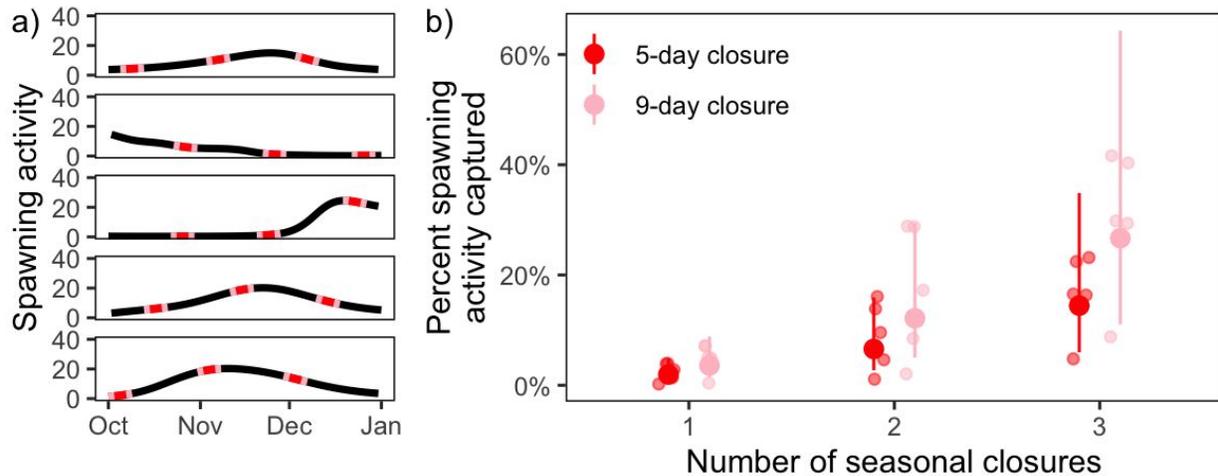
313 Aligning seasonal fishing closures with spawning times

314 Using the predicted spawning activity in each year (Fig 1), we explored how spawning
315 activity aligned with seasonal closures. In 2007 and 2008, there were 27-days of closures
316 and 10-days in subsequent years – assuming an equal daily probability of spawning, we
317 would expect seasonal closures to capture 29 % and 11 % of all spawning activity between
318 October and December, respectively. However, temporal spawning patterns were highly
319 variable during these periods (Fig 3a). In 2007 and 2008, three 9-day spawning closures
320 captured 41.5% and 20.9% of spawning activity, respectively. In 2011, 2020 and 2021, two
321 5-day spawning closures captured 1.2 %, 13.5 %, and 10.0 % of spawning activity,
322 respectively. Spawning closures were not effective at capturing peak spawning activity
323 between October - December, which represents only a fraction of all spawning that occurs
324 year-round.

325 We investigated whether increasing the number and duration of spawning closures
326 between October - December increases the likelihood of capturing a spawning event,
327 thereby increasing the proportion of spawning activity protected by spawning closures in
328 each year. The interaction between the duration and the number of closures was not
329 important, indicating that the effect of duration did not depend on the number of closures,
330 and vice versa. When averaged across years, we found that 9-day closures around the new
331 moon captured 1.85 times more spawning activity than 5-day closures (Tukey's: $df = 28$, $t =$
332 16.3 , $p < 0.0001$, Table S6). Although the difference is significant, it is no more than the
333 expected increase in spawning activity for the additional days of closure ($9/5 = 1.8$). The
334 number of closures had a larger effect on capturing spawning activity (Fig 3a, Table S6). On
335 average, a single 5-day and 9-day closure in October captured 2.0% (95% CI [0.8-4.7]) and
336 3.6% (95% CI [1.4-8.8]) of all spawning activity between October-December, respectively.
337 The spawning activity captured by closures increased by 237% with an additional closure
338 in November (Tukey's: $t = 2.52$, $p = 0.046$) and by a further 119% with an additional
339 closure in December (Tukey's: $t = 1.65$, $p = 0.24$). Collectively, longer 9-day closures may
340 not yield an overall net benefit beyond what would be expected for the duration of the

341 closures and multiple closures may be more effective in mitigating the annual and monthly
 342 volatility in spawning activity by increasing the likelihood of capturing peaks in successful
 343 spawning activity.

344



345

346 **Figure 3.** The effectiveness of spawning closures depends on the timing and duration of
 347 spawning activity of *P. maculatus* at the Keppel Islands. a) The timing of five-day (red) and
 348 nine-day (pink) seasonal closures capture different periods of spawning activity from
 349 October to December in each year. b) We asked whether increasing the number and
 350 duration of spawning closures between October - December increases the likelihood of
 351 capturing a spawning event, thereby increasing the proportion of spawning activity
 352 protected by spawning closures in each year and reducing the volatility in their
 353 effectiveness.

354

355 Discussion

356 High-resolution age and size estimates of juvenile *Plectropomus maculatus* at the Keppel
 357 Islands over a 15-year period revealed several unexpected temporal patterns in spawning
 358 activity. Despite being a high latitude reef fish population, spawning occurred in all months
 359 of the year, with each sampling period showing broad summer and winter cohorts that

360 varied in terms of their exact timing and duration. Unexpectedly, there was no effect of
361 lunar patterns on spawning activity, and we found no clear environmental cue at the onset
362 of spawning peaks. Such lack of seasonality and asynchrony with lunar cycles in the
363 spawning activity of *P. maculatus* suggest the current timing and duration of spawning
364 closures, which are based on spawning observations for *P. leopardus*, are of limited benefit
365 to *P. maculatus* in this region.

366 It is evident that spawning in *P. maculatus* at the Keppel Islands is occurring in periods of 2-
367 3 months to generate distinct cohorts in the juvenile population than can occur at any time
368 of the year. This was unexpected given that histological assessments of seasonal gonad
369 development suggest most coral reef fishes on the GBR have distinct spawning seasons,
370 usually late spring to early summer (Robertson, 1991; Russell et al., 1977; Samoily, 1997).
371 The spawning patterns found in this study indicate *P. maculatus* contrasts with other reef
372 fishes with restricted summer recruitment periods (Russell et al., 1977; Walsh, 1987;
373 Williams, 1983; Williams & Sale, 1981) and other *Plectropomus* spp on the GBR. For
374 example, *P. leopardus* and *P. laevis* both exhibit clear seasonal spawning in late spring and
375 early summer on the central and northern GBR (Heupel et al., 2010; Samoily, 1997). While
376 our results were not corroborated with histological assessments of seasonal gonad
377 development, we are confident the large majority of juvenile fish that successfully recruit to
378 the Keppel Islands originate from local reefs (Harrison et al. 2012, 2020), and are therefore
379 representative of spawning activity throughout the year.

380 Year-to-year variation in spawning activity with only a weak association with SST and the
381 time of year indicates other mechanisms not captured in our model may be responsible for
382 the temporal variation in spawning activity of *P. maculatus*. For example, survivorship of
383 pre- and post- settlement larvae (Robertson, 1991) and fluctuations in the abundance of
384 prey abundance throughout the year may lead to differential fitness of juvenile fish (Jones,
385 1986, 1987a). Juvenile *P. maculatus* consume small crustaceans and gobies (Wen et al.,
386 2012; Wen et al., 2016), which may also fluctuate in abundance. Equally, adult
387 *Plectropomus* spp are piscivorous (Hempson et al. 2017) and fluctuations in the availability
388 of prey species for breeding female fish may lead to fluctuation in the timing and duration
389 of spawning peaks.

390 While spawning and recruitment of coral reef fishes often follow a lunar cycle (Doherty,
391 1983; Doherty et al., 1994; Johannes, 1978; Rankin & Sponaugle, 2014), this was clearly not
392 the case for *P. maculatus* at the Keppel Islands. Lunar spawning offers a strong set of
393 environmental cues for synchronising spawning across a population (Robertson, 1991),
394 which has been documented for the closely related *P. leopardus* at Scott Reef on the GBR
395 (Samoilys, 1997) and extended to *P. maculatus* (Frisch & Van Herwerden, 2006; Frisch et
396 al., 2016). This assumption likely stems from the observation that *P. maculatus* occasionally
397 appears in lunar spawning aggregations of *P. leopardus* (Frisch & van Herwerden, 2006).
398 One hypothesis for the lack of lunar spawning may be due to the increased cost of
399 spawning migrations for lunar cyclic spawning (Colin & Clavijo, 1988; Domeier & Colin,
400 1997). There have been no observations of spawning aggregations of *P. maculatus* at the
401 Keppel Islands or movement between reefs. Individuals are likely to be spawning in small
402 groups that would lead to the more continuous and unsynchronized spawning we
403 observed. Another factor could be geographic variation in the propensity to exhibit lunar
404 spawning patterns. Studies have demonstrated intraspecific variation in lunar spawning
405 patterns in different areas (Doherty & Williams, 1988; Williams, 1983; Williams & Sale,
406 1981). Hence, the lack of lunar spawning in *P. maculatus* on the southern GBR may be
407 atypical and does not necessarily apply to populations at lower latitudes.

408 Temporal volatility in spawning activity has two clear implications for fisheries
409 management. In the case of *P. maculatus* at the Keppel Islands, seasonal spawning closures
410 did not effectively protect spawning activity due to the lack of synchrony with the new
411 moon and year-to-year variation in the timing of peak spawning activity. Seasonal closures
412 are implemented with the primary objective of protecting spawning aggregations
413 vulnerable to overfishing yet are likely too short or too infrequent to effectively capture
414 spawning activity. This suggests that the current temporal closures are too narrow or too
415 few and it is likely that other species managed under the Queensland Line Fishery (Reef)
416 will exhibit similar variation in spawning, which needs to be investigated as a high priority.
417 Given the volatility in spawning activity, we show that increasing the number of spawning
418 closures may provide greater benefits than increasing their duration in order to increase
419 the likelihood of capturing peaks in spawning activity. While these findings may be useful

420 in guiding revisions for the management plan of *P. maculatus* on the southern GBR, we
421 caution that complex ecological traits such as spawning activity may not be transferable
422 across species, even conspecifics. It's important to note the Queensland Reef Line Fishery is
423 supplemented by the GBR Marine Park no-take marine reserve network, and directly
424 managed via a range of additional catch and effort controls including minimum size-limits,
425 recreational possession limits, limited entry licencing and total allowable catch quotas.

426 Ageing of juvenile *P. maculatus* at the Keppel Islands indicates strong variation in the
427 timing of spawning beyond what was previously understood for coral reef fishes. To
428 investigate these patterns further, consideration should be given to the experimental
429 design to accurately assess spawning times of juvenile coral trout, the potential causes of
430 temporal variation in spawning peaks, and whether the patterns observed at the Keppel
431 Islands are consistent throughout the GBR and for other congeners. An important caveat to
432 this study is that our estimates of peak spawning activity are based on juvenile fish that
433 successfully settled and recruited to the island group and may not be representative of all
434 spawning in the region, particularly spawning that leads to unsuccessful recruitment.
435 Although we are confident that our sampling design identified recruitment cohorts for the
436 period that we investigated, there may have been additional cohorts in some years. Ideally,
437 future studies would employ a combination of histological studies of seasonal gonad
438 development and direct observations of spawning behaviour, followed by recruitment
439 surveys, and matched with parentage to provide a direct link between spawning and
440 recruitment. On their own, each approach has offered insights into the behaviour (Samoilys
441 et al. 1997), dispersal patterns (Harrison et al. 2012) and reproductive success (Lavin et
442 al. 2021) of coral trout. When combined, these methods may offer important new insight
443 into reproductive strategies and the ability to predict peak spawning periods in coral reef
444 fish.

445 **Conclusion**

446 Our findings highlight several unexpected temporal patterns in the spawning activity of *P.*
447 *maculatus* at the Keppel Islands. In each year, recruitment originated from several distinct

448 cohorts with no consistent timing or environmental trigger. These patterns suggest a
449 mismatch with management strategies that aim to protect peak spawning activity on the
450 GBR. If species on the GBR have a bet-hedging reproductive strategy or environmental
451 conditions create volatility in their reproductive success, then fisheries management must
452 adopt strategies that mitigate these uncertainties. In the case of *P. maculatus* at the Keppel
453 Islands, the current two-times 5-day spawning closures were ineffective at protecting
454 successful spawning activity and may need to be extended and/or multiplied to ensure
455 adequate protection of spawning biomass. Our findings demonstrate that there is scope to
456 refine seasonal spawning closures in the Reef Line Fishery to maximise their effectiveness
457 and provide additional complementarity to existing fishery controls and marine park
458 management actions.

459

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471

472 **Author contribution**

473 All authors contributed to the study design, data collection, analysis and writing.

474 **References**

475 (intentionally alphabetical for review)

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