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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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**Abstract**

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

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

**Introduction**

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

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

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

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

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

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

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

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

## Methods

### Study site and sample collection

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

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

### Otolith preparation and age determination

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

### Calculating date of spawning for aged juveniles

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

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



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

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

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

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

## 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 0 is the average number of individuals spawned in a 5-day period and fSpawning  
 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

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

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

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

Where 0 is the average number of individuals spawned in a 5-day period,  $f(SST|Month)$  indicate the additive smoothing functions of the interaction between sea surface temperature and time of year (month), and  $\gamma_{year}$  indicates the random smoothing term of year. *Rainfall*, and *Lunar illumination* were not important explanatory variables and were excluded from the model. *Flood Height* had a significant effect though showed high concavity with SST and month (0.77). DHARMA residuals were checked for homogeneity of variance, dispersion, and outliers. Additional tests for zero inflation, overdispersion, concavity, and over-smoothing were performed to satisfy model fit.

## Assessing the effectiveness of seasonal closures

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

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

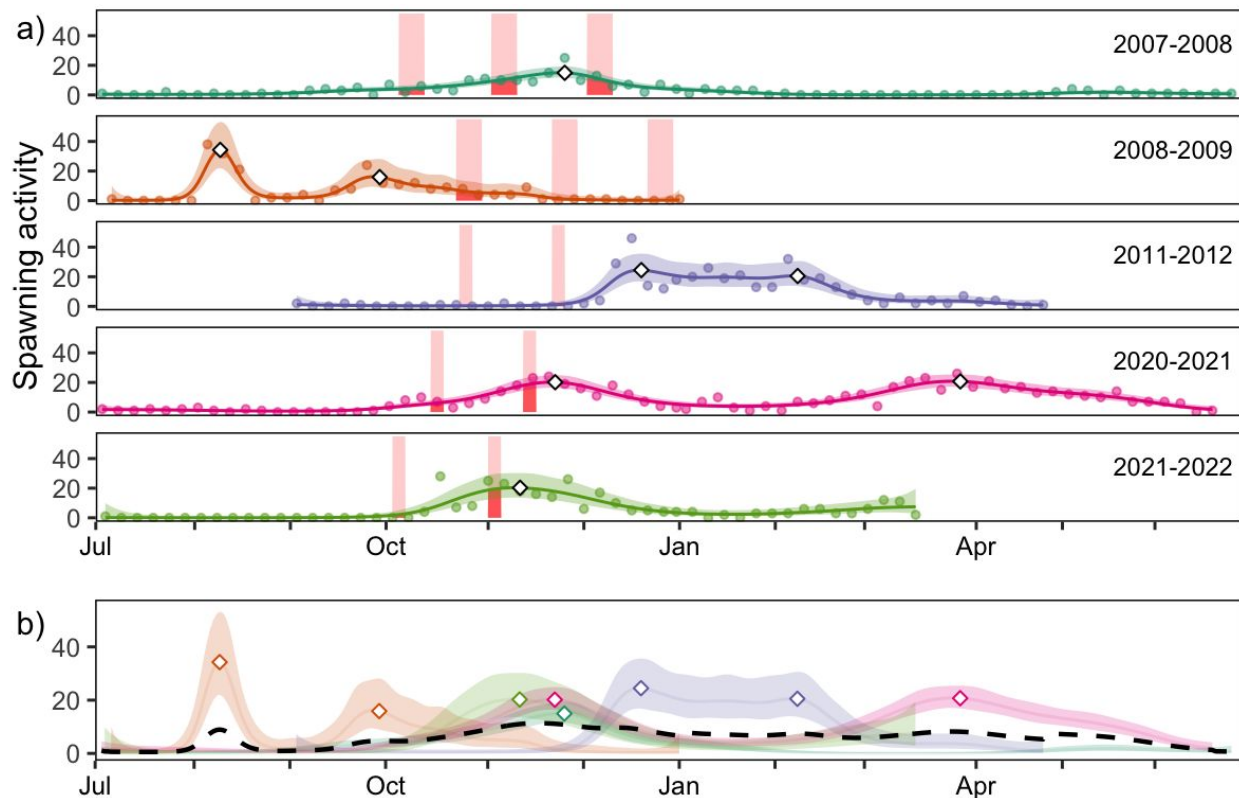
## Results

### Temporal patterns in spawning activity

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

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

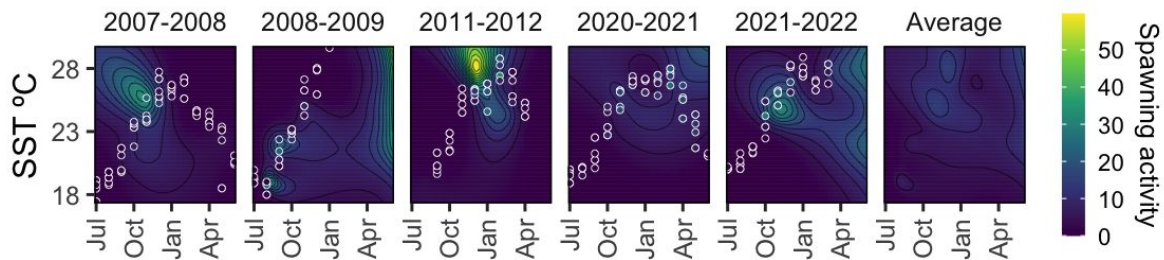
in spawning activity between October-December, the spawning patterns were too variable to confidently differentiate spawning activity between seasons.



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

**Environmental drivers of spawning activity**

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



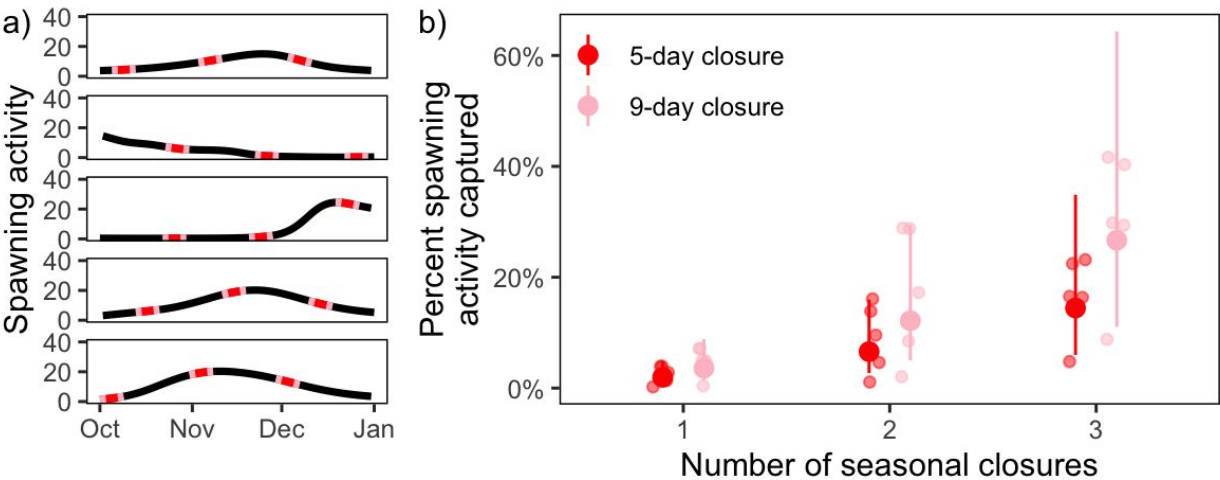
**Figure 2.** Spawning activity of *P. maculatus* at the Keppel Islands was strongly associated with sea surface temperature (SST) and time of year, though trends were inconsistent between years. Shaded areas and contour lines indicate the predicted spawning activity (in 5-day windows) of *P. maculatus*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

### **Aligning seasonal fishing closures with spawning times**

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

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

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



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

## Discussion

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



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

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

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

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

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

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

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

## Conclusion

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

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

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## Author contribution

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

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