**Ageing of juvenile coral trout (*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 trout (*Plectropomus* spp.) on the Great Barrier Reef, histological studies have previously indicated peak spawning around the summer new moons. Here we examined this hypothesis and the efficacy of seasonal closures for *P. maculatus* by deriving age in days for 761 juveniles (<250mm) collected from the Keppel Islands 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. While spawning activity was greater in summer, peak spawning varied between years with no clear association with lunar phases, sea surface temperature, or rainfall. The existing short seasonal fisheries closures around the new moon often miss peak spawning activity, with the vast majority of juveniles spawned outside closure periods. 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 known to be 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 fisheries stocks 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 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 on new or full moons (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 trout *Plectropomus leopardus* (Samoilys, 1997; Fox et al., 2022). The fisheries closure applies to all commercial and recreational coral trout fisheries, comprising of not only the common coral trout (*P. leopardus*) but also the bar-cheek coral trout (*P. maculatus*), and other Serranids (Campbell et al., 2019; Frisch et al., 2016). The seasonal closures also apply to many other fishery species that form part of the Queensland Line Fishery (Reef) (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 GBR, 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. However, temporal patterns in recruitment and the timing of strong juvenile cohorts can be used to hindcast the timing of successful spawning activity, providing information on environmental cues for spawning and the best times to apply seasonal closures to enhance recruitment. Here we use age estimates of large samples of juvenile coral trout (*P. maculatus*) collected at regular intervals from the Keppel Island 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 identified peaks in spawning activity across multiple years that we could relate to environmental conditions and investigate the effectiveness of seasonal closures for coral trout fisheries on the Great Barrier Reef. It’s important to note our estimates of 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.

**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 (≃150 μm) 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 ± 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.

**Temporal spawning patterns**

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

𝑦=𝛽0+𝑓(5 𝑑𝑎𝑦 𝑤𝑖𝑛𝑑𝑜𝑤)+𝜖,       𝜖∼𝑇𝑤𝑝(𝜇,𝜎2)

Where 0 is the average number of individuals spawned in a 5-day period and fSpawning counts indicate the additive smoothing functions of the annual trends in spawning. DHARMa residuals were checked for homogeneity of variance, dispersion, and outliers. Additional tests for zero inflation, overdispersion, and over-smoothing were performed to satisfy model fit. Model selection was informed from the Akaike information criterion (AICc) with the lowest score (Burnham and Anderson 2002). Spawning peaks were identified from model derivatives and plotted with partial residuals. The model predictions were used to identify peaks in spawning activity, the duration between peaks, and to quantify the likely contribution of spawning closures between October - December of each year.

**Environmental drivers of spawning activity**

We also explored the environmental conditions associated with spawning activity using GAMs that included lunar illumination, Sea Surface Temperature (SST), local rainfall and flood gauge data from the Fitzroy River as covariates. The number of individuals spawned were summed over 5-day periods to minimise the influence of zero-values in the data. Lunar illumination values were averaged over the same 5-day period using the *lunar* 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=𝛽0+𝑓(*SST*|*Month*)+γ*year*+𝜖*,*∼𝑇𝑤𝑝(𝜇,𝜎2)

Where 0 is the average number of individuals spawned in a 5-day period, fSST|Month indicate the additive smoothing functions of the interaction between sea surface temperature and time of year (month), and γ*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 concurvivity with SST and month (0.77). DHARMa residuals were checked for homogeneity of variance, dispersion, and outliers. Additional tests for zero inflation, overdispersion, concurvity, 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 wiggliness (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.

Chart

Description automatically generated

*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 in 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 other unknown factors not considered here may be influencing 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 summer conditions.

Histogram

Description automatically generated with medium confidence

*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 provide an overall net benefit beyond what would be expected for the duration of the closures and multiple closures may be more important to mitigate against the annual and monthly volatility in spawning activity by increasing the likelihood of capturing peaks in successful spawning activity.

Chart, scatter chart

Description automatically generated

*Figure 3. The effectiveness of spawning closures depends on the timing and duration of spawning activity. 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 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 year-round for periods of 2-3 months to generate distinct cohorts in the juvenile population. 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 few 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. However, these results may only be applicable for *P. maculatus* on the southern GBR and should not be taken as typical for other geographic locations or species.

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 combine histological studies of seasonal gonad development, 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. Alternatively, supplementing other management strategies such a no-take marine reserve and minimum size-limits may provide other benefits beyond what seasonal spawning closures can achieve.

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**Author contribution**

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

**References (BEN AND LACHY)**

1. Booth DJ, Beretta GA. Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs 1994 132 [Internet]. 1994 May [cited 2022 May 30];13(2):81–9. Available from: https://link.springer.com/article/10.1007/BF00300765

2. Booth DJ, Kingsford MJ, Doherty PJ, Beretta GA. Recruitment of damselfishes in One Tree Island lagoon: persistent interannual spatial patterns. Mar Ecol Prog Ser [Internet]. 2000 Aug 28 [cited 2022 May 23];202:219–30. Available from: https://www.int-res.com/abstracts/meps/v202/p219-230/

3. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. (glmmTMB) Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J [Internet]. 2017 [cited 2022 May 19];9(2):378–400. Available from: https://journal.r-project.org/archive/2017/RJ-2017-066/index.html

4. Brothers EB, Williams DMB, Sale PF. Length of larval life in twelve families of fishes at “One Tree Lagoon”, Great Barrier Reef, Australia. Mar Biol [Internet]. 1983 Nov [cited 2022 May 22];76(3):319–24. Available from: https://link.springer.com/article/10.1007/BF00393035

5. Burnham KP, Anderson DR. Model Selection and Multimodel Inference. Burnham KP, Anderson DR, editors. New York, NY: Springer New York; 2004.

6. Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA. Recruitment and the Local Dynamics of Open Marine Populations. Annu Rev Ecol Syst [Internet]. 1996 Nov 28 [cited 2022 May 22];27:477–500. Available from: https://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.27.1.477

7. Campbell A, Leigh G, Bessell-Browne P, Lovett R. Stock assessment of the Queensland east coast common coral trout (Plectropomus leopardus) fishery [Internet]. 2019 [cited 2022 Jan 17]. Available from: www.reeflifesurvey.com,

8. Colin PL, Clavijo IE. Spawning Activity of Fishes Producing Pelagic Eggs on a Shelf Edge Coral Reef, Southwestern Puerto Rico. Bull Mar Sci. 1988;43(2):249–79.

9. Cushing DH. Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. Adv Mar Biol. 1990 Jan 1;26(C):249–93.

10. Department of Agriculture Water and the Environment. Assessment of the Queensland Line Fishery (Reef) [Internet]. 2021 [cited 2022 May 9]. Available from: https://www.environment.gov.au/system/files/pages/c8f3f7b7-fd3b-4cac-b4c9-c26cd0afd2d5/files/qld-line-reef-assessment-2021.docx

11. Doherty PJ. Diel, lunar and seasonal rhythms in the reproduction of two tropical damselfishes: Pomacentrus flavicauda and P. wardi. Mar Biol. 1983;75:215–24.

12. Doherty PJ, Fowler AJ, Samoilys MA, Harris DA. Monitoring the Replenishment of Coral Trout (Pisces: Serranidae) Populations. Bull Mar Sci. 1994;54(1):343–55.

13. Doherty PJ, Williams DM. The Replenishment of Coral Reef Fish Populations. Oceanogr Mar Biol An Annu Rev [Internet]. 1988 [cited 2022 May 12];26:487–551. Available from: https://books.google.com.au/books?hl=en&lr=&id=dUNZDwAAQBAJ&oi=fnd&pg=PA422&dq=the+replenishment+of+coral+reef+populations&ots=u3XCBRjay-&sig=uAsu6Ou4gyg0tGXdBsCBh\_BDqiU#v=onepage&q=the replenishment of coral reef populations&f=false

14. Domeier ML, Colin PL. TROPICAL REEF FISH SPAWNING AGGREGATIONS: DEFINED AND REVIEWED. Bull Mar Sci. 1997;60(3):698–726.

15. Eagle J V, Baird AH, Jones GP, Kingsford MJ. Recruitment hotspots: consistent spatial patterns in the relative abundance of coral recruits at One Tree Island, Australia. Galaxea, J coral reef Stud. 2012;5–22.

16. Fox AR, Campbell AB, Zieth JD. Stock assessment of Queensland east coast common coral trout (Plectropomus leopardus), Australia, with data to December 2021 [Internet]. Department of Agriculture and Fisheries. 2022 [cited 2022 May 9]. Available from: https://era.daf.qld.gov.au/id/eprint/8618/1/Stock assessment of Queensland east coast common coral trout 2022.pdf

17. Frisch A, Van Herwerden L. Field and experimental studies of hybridization between coral trouts, Plectropomus leopardus and Plectropomus maculatus(Serranidae), on the Great Barrier Reef, Australia. J Fish Biol [Internet]. 2006 Apr 1 [cited 2022 Jan 18];68(4):1013–25. Available from: https://onlinelibrary.wiley.com/doi/full/10.1111/j.0022-1112.2006.00977.x

18. Frisch AJ, Cameron DS, Pratchett MS, Williamson DH, Williams AJ, Reynolds AD, et al. Key aspects of the biology, fisheries and management of Coral grouper. Rev Fish Biol Fish 2016 263 [Internet]. 2016 Mar 23 [cited 2022 Jan 12];26(3):303–25. Available from: https://link.springer.com/article/10.1007/s11160-016-9427-0

19. Gladstone’ W, Westoby M. Growth and reproduction in Canthigaster valentini (Pisces, Tetraodontidae): a comparison of a toxic reef fish with other reef fishes. Environ Biol Fishes. 1988;21(3):207–21.

20. Greenwell B, Boehmke B, Cunningham J, GBM Developers. gbm: Generalized Boosted Regression Models. 2022;

21. Harrison HB, Bode M, Williamson DH, Berumen ML, Jones GP. A connectivity portfolio effect stabilizes marine reserve performance. Proc Natl Acad Sci U S A [Internet]. 2020 Oct 13 [cited 2022 Feb 10];117(41):25595–600. Available from: https://www.pnas.org/content/117/41/25595

22. Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, et al. Larval export from marine reserves and the recruitment benefit for fish and fisheries. Curr Biol. 2012 Jun 5;22(11):1023–8.

23. Hartig F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [Internet]. R package version 0.4.5. 2022. Available from: https://cran.r-project.org/package=DHARMa

24. Hempson TN, Graham NAJ, MacNeil MA, Williamson DH, Jones GP, Almany GR. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecol Evol [Internet]. 2017 Apr 1 [cited 2022 Sep 15];7(8):2626–35. Available from: https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.2805

25. Heupel MR, Williams AJ, Welch DJ, Davies CR, Adams S, Carlos G, et al. Demography of a large exploited grouper, Plectropomus laevis: Implications for fisheries management. Mar Freshw Res [Internet]. 2010 Feb 25 [cited 2022 Jan 18];61(2):184–95. Available from: https://www.publish.csiro.au/mf/MF09056

26. Johannes RE. Reproductive strategies of coastal marine fishes in the tropics. Environ Biol Fishes 1978 31 [Internet]. 1978 Mar [cited 2022 Jan 18];3(1):65–84. Available from: https://link.springer.com/article/10.1007/BF00006309

27. Jones GP. Food availability affects growth in a coral reef fish. Oecologia 1986 701 [Internet]. 1986 Aug [cited 2022 May 23];70(1):136–9. Available from: https://link.springer.com/article/10.1007/BF00377123

28. Jones GP. Some interactions between residents and recruits in two coral reef fishes. J Exp Mar Bio Ecol. 1987 Jan 28;114(2–3):169–82.

29. Jones GP. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale PF, editor. The Ecology of Fishes on Coral Reefs. San Diego: Academic Press; 1991. p. 294–328.

30. Lavin CP, Jones GP, Williamson DH, Harrison HB. Minimum size limits and the reproductive value of numerous, young, mature female fish. Proc R Soc B [Internet]. 2021 Mar 10 [cited 2022 May 23];288(1946). Available from: https://royalsocietypublishing.org/doi/full/10.1098/rspb.2020.2714

31. Lazaridis E. lunar: Lunar Phase & Distance, Seasons and Other Environmental Factors. 2022;

32. Lenth R V. emmeans: Estimated Marginal Means, aka Least-Squares Means [Internet]. R package version 1.5.4. 2021. Available from: https://cran.r-project.org/package=emmeans

33. Mannering TD. Benefits of marine protected areas beyond boundaries : an evaluation for two coral reef fishes. James Cook University; 2008.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

34. Rankin TL, Sponaugle S. Characteristics of Settling Coral Reef Fish Are Related to Recruitment Timing and Success. PLoS One [Internet]. 2014 [cited 2022 May 22];9(9). Available from: www.plosone.org

35. Robertson DR. The Role of Adult Biology in the Timing of Spawning of Tropical Reef Fishes Electronic guides and information systems for Neotropical Shorefishes View project. In: Sale PF, editor. The Ecology of Fishes on Coral Reefs [Internet]. San Diego: Academic Press; 1991 [cited 2022 Jan 19]. p. 356–86. Available from: https://www.researchgate.net/publication/280557683

36. Robertson DR, Green DG, Victor BC. Temporal Coupling of Production and Recruitment of Larvae of a Caribbean Reef Fish. Ecology [Internet]. 1988 Apr 1 [cited 2022 May 23];69(2):370–81. Available from: https://onlinelibrary.wiley.com/doi/full/10.2307/1940435

37. Ross Robertson D. Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. J Exp Mar Bio Ecol. 1990 Nov 27;144(1):49–62.

38. Russell BC, Anderson GRV, Talbot FH. Seasonality and recruitment of coral reef fishes. Mar Freshw Res [Internet]. 1977 [cited 2022 Jan 25];28(4):521–8. Available from: https://www.publish.csiro.au/mf/mf9770521

39. Samoilys MA. Periodicity of spawning aggregations of coral trout Plectropomus leopardus (Pisces: Serranidae) on the northern Great Barrier Reef. Mar Ecol Prog Ser [Internet]. 1997 Dec 15 [cited 2022 Jan 17];160:149–59. Available from: <https://www.int-res.com/abstracts/meps/v160/p149-159/>

Schindler, D., Hilborn, R., Chasco, B. *et al.* Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612 (2010)

40. Shima JS, Osenberg CW, Alonzo SH, Noonburg EG, Mitterwallner P, Swearer SE. Reproductive phenology across the lunar cycle: parental decisions, offspring responses, and consequences for reef fish. Ecology [Internet]. 2020 Aug 1 [cited 2022 May 23];101(8):e03086. Available from: https://onlinelibrary.wiley.com/doi/full/10.1002/ecy.3086

41. Shima JS, Osenberg CW, Noonburg EG, Alonzo SH, Swearer SE. Lunar rhythms in growth of larval fish. Proc R Soc B [Internet]. 2021 Jan 13 [cited 2022 Jan 27];288(1942). Available from: https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2020.2609

42. Shima JS, Swearer SE. Moonlight enhances growth in larval fish. Ecology [Internet]. 2019 Jan 1 [cited 2022 Jan 29];100(1):e02563. Available from: https://onlinelibrary.wiley.com/doi/full/10.1002/ecy.2563

43. Sponaugle SU, Cowen RK. EARLY LIFE HISTORY TRAITS AND RECRUITMENT PATTERNS OF CARIBBEAN WRASSES (LABRIDAE). Ecol Monogr. 1997;67(2):177–202.

44. Sponaugle SU, Cowen RK. Larval Supply and Patterns of Recruitment for Two Caribbean Reef fishes Stegastes partitrus. Mar Freshw Res [Internet]. 1996 [cited 2022 May 23];47(2):433–47. Available from: https://www.publish.csiro.au/mf/mf9960433

45. Srinivasan M, Jones · G P. Extended breeding and recruitment periods of fishes on a low latitude coral reef. Coral Reefs. 2006;25:673–82.

46. Taylor BM, Gourley J, Trianni MS, Taylor BM, Gourley J, Trianni MS. Age, growth, reproductive biology and spawning periodicity of the forktail rabbitfish (Siganus argenteus) from the Mariana Islands. Mar Freshw Res [Internet]. 2016 Aug 31 [cited 2021 Dec 14];68(6):1088–97. Available from: https://www.publish.csiro.au/mf/MF16169

47. Victor BC. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar Biol [Internet]. 1986 Feb [cited 2022 May 23];90(3):317–26. Available from: https://link.springer.com/article/10.1007/BF00428555

48. Walsh WJ. Patterns of recruitment and spawning in Hawaiian reef fishes. Environ Biol Fishes 1987 184 [Internet]. 1987 Dec [cited 2022 Jan 31];18(4):257–76. Available from: https://link.springer.com/article/10.1007/BF00004879

49. Wellington GM, Victor BC. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar Biol [Internet]. 1989 Dec [cited 2022 May 23];101(4):557–67. Available from: https://link.springer.com/article/10.1007/BF00541659

50. Wen CKC, Pratchett MS, Almany GR, Jones GP. Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. Coral Reefs [Internet]. 2013 Jun 1 [cited 2022 Jun 2];32(2):389–98. Available from: https://link.springer.com/article/10.1007/s00338-012-0985-x

51. Wen CKC, Bonin MC, Harrison HB, David •, Williamson H, Jones GP. Dietary shift in juvenile coral trout (Plectropomus maculatus) following coral reef degradation from a flood plume disturbance. Coral Reefs. 2016;35.

52. Wen CKC, Almany GR, Williamson DH, Pratchett MS, Mannering TD, Evans RD, et al. Recruitment hotspots boost the effectiveness of no-take marine reserves. Biol Conserv. 2013 Oct 1;166:124–31.

53. Wen CK, Almany GR, Williamson DH, Pratchett MS, Jones GP. Evaluating the effects of marine reserves on diet, prey availability and prey selection by juvenile predatory fishes. Mar Ecol Prog Ser [Internet]. 2012 Nov 26 [cited 2022 Jun 3];469:133–44. Available from: https://www.int-res.com/abstracts/meps/v469/p133-144/

54. Wickham H, Averick M, Bryan J, Chang W, D’ L, Mcgowan A, et al. Welcome to the Tidyverse. J Open Source Softw [Internet]. 2019 Nov 21 [cited 2022 May 17];4(43):1686. Available from: https://joss.theoj.org/papers/10.21105/joss.01686

55. Williams DM. Daily, Monthly and Yearly Variability in Recruitment of a Guild of Coral Reef Fishes. Mar Ecol Prog Ser [Internet]. 1983 [cited 2022 May 23];10:231–7. Available from: https://www.int-res.com/articles/meps/10/m010p231.pdf

56. Williams DM, Sale PF. Spatial and Temporal Patterns of Recruitment of Juvenile Coral Reef Fishes to Coral Habitats Within “One Tree Lagoon”, Great Barrier Reef. Mar Biol. 1981;65:245–53.

57. Williamson DH, Harrison HB, Almany GR, Berumen ML, Bode M, Bonin MC, et al. Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. Mol Ecol [Internet]. 2016 Dec 1 [cited 2022 Feb 10];25(24):6039–54. Available from: https://onlinelibrary.wiley.com/doi/full/10.1111/mec.13908

58. Wood SN, Pya N, Säfken B. Smoothing Parameter and Model Selection for General Smooth Models. J Am Stat Assoc. 2016 Oct 1;111(516):1548–63.

Zarco-Perello S, Fairclough D, Dowling C, DiBattista J, Austin R, Wernberg T, Taylor B. (2022). Maximization of fitness by phenological and phenotypic plasticity in range expanding rabbitfish (Siganidae). Journal of Animal Ecology 91: 1666-1678. (doi: 10.1111/1365-2656.13739)

Abesamis, Rene A., Claro Renato L. Jadloc, and Garry R. Russ. “Varying Annual Patterns of Reproduction in Four Species of Coral Reef Fish in a Monsoonal Environment.” Marine Biology 162, no. 10 (October 1, 2015): 1993–2006. <https://doi.org/10.1007/s00227-015-2725-6>.

Oliveira Freitas, Matheus, Rodrigo Leão de Moura, Ronaldo Bastos Francini-Filho, and Carolina Viviana Minte-Vera. “Spawning Patterns of Commercially Important Reef Fish (Lutjanidae and Serranidae) in the Tropical Western South Atlantic.” Scientia Marina 75, no. 1 (March 30, 2011): 135–46. <https://doi.org/10.3989/scimar.2011.75n1135>.

Srinivasan, M., and G. P. Jones. “Extended Breeding and Recruitment Periods of Fishes on a Low Latitude Coral Reef.” Coral Reefs 25, no. 4 (September 2006): 673–82. <https://doi.org/10.1007/s00338-006-0153-2>.

J. Clarke, D. M. Bailey, P. J. Wright, Evaluating the effectiveness of a seasonal spawning area closure, ICES Journal of Marine Science, Volume 72, Issue 9, November/December 2015, Pages 2627–2637, <https://doi.org/10.1093/icesjms/fsv144>