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REPORT

Fertilisation kinetics among common Indo-Pacific broadcast spawning corals with distinct and shared functional traits

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Abstract Indo-Pacific corals predominantly reproduce using synchronous mass spawning events to maximise fertilisation. However, as disturbances continue to thin population densities, the quantities of gametes released declines and colonies become more isolated, reducing the likelihood of cross-fertilisation. Local hydrodynamic conditions can promote or inhibit gamete contact; thus, the interaction between the abiotic environment and sperm density will determine the amount of time gametes interact. In this study, we investigated the sensitivity of reproduction to manipulations of two key limiting factors of fertilisation: sperm concentration and contact time between gametes. We explored fertilisation kinetics of phylogenetically and functionally similar and diverse coral taxa on the Great Barrier Reef and Western Australia (*Acropora digitifera, A. tenuis*; *Coelastrea aspera, Platygyra daedalea*). Results indicate that fertilisation is optimised at sperm concentrations > 10^3 sperm mL^{-1} and contact times > 30 s, but the extent of these relationships is species-specific. All species showed clear differences in fertilisation success across contact times, although these differences were less distinct for *A. tenuis* and *P. daedalea* at very high sperm concentrations. *Acropora digitifera* and *P. daedalea* exhibited nonlinear trends with steep slopes of increased fertilisation success once sperm concentration surpassed values of 10^4 sperm mL^{-1} and 10^2 sperm mL^{-1}, respectively, followed by slight declines. *Acropora tenuis* and *A. digitifera* had the highest maximum fertilisation success, likely owing to beneficial evolved functional traits like large egg sizes. The present analysis underpins studies of fertilisation kinetics in natural reef populations to help inform management and restoration practices that assist population resilience and recovery.

Keywords Allee effect · Coral reproduction · Density dependence · Sperm limitation

Introduction

Fertilisation is fundamental to sexual reproduction and is a key factor in the facilitation of population growth and recovery in free-spawning invertebrates (Iguchi et al. 2009; Oliver and Babcock 1992). When eggs and sperm are shed into the sea following spawning, the likelihood that they interact and successfully fertilise is dependent on conditions acting on varying scales and intensities including population level dynamics, gametic interactions, and external environmental influences.

Two of the major factors influencing fertilisation success on a population level are the density of fecund individuals in an area and the level of synchrony in spawning within those populations (Himmelman et al. 2008; Levitan et al. 1992). Consequently, reproductive success is highly density dependent, making spawners vulnerable to Allee effects (Allee 1931; Courchamp et al. 1999; Odum and Odum 1955). This can affect sessile organisms such as corals since they cannot aggregate for spawning (Lasker et al. 1996; Oliver and Babcock 1992). Allee effects occur where low population sizes or densities directly influence population growth, thus potentially inhibiting individual fitness

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and local demographics (Gascoigne et al. 2009; Keya et al. 2021; Oliver and Babcock 1992; Stephens et al. 1999). The strength of the relationship is variable across systems, but is generally stronger at low densities of conspecifics, and may lead to reproductive isolation or extinction if severe (Berec et al. 2007; Gascoigne and Lipcius 2004; Keya et al. 2021; Stephens et al. 1999). Pennington (1985) found that fertilisation success of the echinoid *Strongylocentrotus droebachiensis* decreased from 60–95% to 15% when distance between conspecifics was > 20 cm apart. Such declines in reproductive success will directly impact population growth rate, recovery, and persistence.

Mass spawning systems have evolved to maximise fertilisation success of many free spawning invertebrates (Babcock et al. 1986; Harrison et al. 1984) using mechanisms of synchronisation (Coma and Lasker 1997; Levitan et al. 2011), which often combat Allee effects. For example, Coma and Lasker (1997) found that the degree of spawning synchronisation explained 80% of the variation in fertilisation success for the gorgonian *Pseudoplexaura porosa*, with maximum fertilisation occurring at high levels of synchrony. Similarly, Levitan et al. (2004) observed that populations of the scleractinian *Orbicella annularis* achieved optimal fertilisation success with the peak levels of spawning synchrony, while corals that spawned at off-peak times had relatively low fertilisation success. The success of spawning synchronisation as a mechanism to maximise fertilisation is inhibited by large intercolonial distances, which can occur at low population densities (Teo and Todd 2018). Fertilisation of eggs following spawning cannot occur if sperm concentrations are below a certain threshold (Claereboudt 1999), or if there is insufficient time for sperm and eggs to interact (Nozawa et al. 2015).

One of the most notable examples of spawning synchronisation occurs during the annual mass coral spawning event on the Great Barrier Reef (GBR), with over 130 species participating (Babcock et al. 1986; Baird et al. 2009; Harrison et al. 1984; Willis et al. 1985). However, this process likely becomes compromised in disturbed populations as corals experience stress and mortality due to cumulative and intensified disturbances such as cyclones, crown of thorns starfish (CoTS) outbreaks, bleaching events, and coral disease outbreaks (De'Ath et al. 2012; Hughes et al. 2019; Hughes and Tanner 2000; Ortiz et al. 2018; Willis et al. 2004). Such unnatural stress levels can lead to coral cover and density loss following individual events (Condie et al. 2018; Edmunds 2019), and impaired recovery rates in response to the accumulation of disturbances (Doropoulos et al. 2022; Gouezo et al. 2019; Ortiz et al. 2018; Speare et al. 2021). Disturbances can also cause physical or physiological harm which may interfere with gamete production (Kai and Sakai 2008; Ward 1995) and spawning synchrony (Fogarty and Marhaver 2019; Shlesinger and Loya 2019). Thus, it is important to understand the implications of such widespread ecosystem changes on fundamental processes like reproduction.

On a gametic level, sperm limitation is the major restrictive factor during fertilisation (Benzie and Dixon 1994; Levitan 1998; Levitan and McGovern 2005; Levitan et al. 1991), due to sperm dilution (Lasker et al. 1996; Levitan and Petersen 1995). Low sperm concentrations generally occur when densities of fecund adults are reduced (Oliver and Babcock 1992), or when sperm is mixed by the hydrodynamic environment (Crimaldi and Browning 2004), causing lack of adequate contact between sperm and eggs (Benzie and Dixon 1994) during the period of time that the gametes are viable. Fertilisation rates in corals generally follow a positive relationship with increasing sperm concentration (Chui et al. 2014; dela Cruz and Harrison 2020; Nozawa et al. 2015; Willis et al. 1997); however, the intricacies of these relationships appear to be species-specific. For example, Nozawa et al. (2015) found that *Acropora gemmifera* and *A. hyacinthus* each had fertilisation success of < 30% at sperm concentrations of around 10^4 sperm mL^{-1} and increased steadily to > 75% fertilisation success at > 10^5 sperm mL^{-1}. While dela Cruz and Harrison (2020) found similar trends of increased fertilisation with greater sperm concentrations for *A. millepora* and *A. tenuis*, a lower sperm concentration was required (~ 10^3 mL^{-1}) to achieve fertilisation success rates > 50%.

The degree to which gamete contact time influences fertilisation is likely variable across sperm concentrations. In other words, reproduction can be effective at lower sperm concentrations if eggs are exposed to sperm for longer periods, thus ensuring more opportunities for fertilisation to occur. This has been quantified for some spawning invertebrates (Babcock and Keesing 1999; Gribben et al. 2014), but has not been examined in corals. For the geoduck, *Panopea zelandica*, Gribben et al. (2014) reported significantly higher fertilisation success at lower sperm conditions when gametes were exposed for 30 min, compared to shorter interactions of 1 min and 10 min. As in other free spawners, coral gametes have a specific amount of time to mix and fertilise before they become too diluted to interact (Omori et al. 2001) or they are no longer viable (Chui et al. 2014; dela Cruz and Harrison 2020). Nowaza et al. (2015) found that at a constant sperm concentration, fertilisation success increased as contact time increased from 10 to 30 to 60 min for four of their study species, *A. gemmifera*, *Favites abdita*, *F. pentagona*, and *F. valensiennesi*, but had no influence on fertilisation success for *A. papillare* and *Platygyra ryukyuensis* (Nozawa et al. 2015). There is capacity for fertilisation success at shorter contact times, but this is variable across species (Nozawa et al. 2015). Contact time thresholds are likely a function of the distance between spawning colonies and the degree

of water flow experienced to mix the gametes (Denny and Shibata 1989; Nozawa et al. 2015). Quantification of adequate contact times is needed to understand fertilisation kinetics and to develop and parameterise mechanistic models of sperm-egg interactions across a range of ecological contexts.

The goal of this study was to fill key knowledge gaps about how two main limiting factors of fertilisation, sperm concentration and gamete contact time, interact to influence coral reproduction. Previous studies have evaluated relevant parameters in isolation (dela Cruz and Harrison 2020; Morita et al. 2006; Nozawa et al. 2015; Oliver and Babcock 1992), but it is important to gather more comprehensive results that highlight their collective influences on fertilisation kinetics. Trials were conducted using four species of spawning corals: two branching Acroporidae—*Acropora digitifera* and *A. tenuis*—and two submassive Merulinidae—*Platygyra daedalea* and *Coelastrea aspera*. Results have improved understanding of fertilisation kinetics across diverse and functionally distinct species. Further, knowledge gained from this study will inform management and restoration decisions aiming to safeguard natural recovery processes that are under threat as coral densities across the GBR continue to decline (Dietzel et al. 2020).

Materials and methods

Study sites

Laboratory trials for *Acropora* cf. *digitifera* were conducted in Western Australia in 2017 at Coral Bay Research Station. Five colonies of *A.* cf. *digitifera* were collected from shallow reef flat in Coral Bay (23.1423° S, 113.7723° E). Trials for *A.* cf. *tenuis* and *Coelastrea* cf. *aspera* were conducted in October 2021 at the National Sea Simulator (SeaSIM) facility in Townsville, Australia. Six *A.* cf. *tenuis* and six *C.* cf. *aspera* colonies were collected from reefs surrounding Magnetic Island (19.1385° S, 146.8339° E) in the central GBR, implying that the *A.* cf. *tenuis* individuals used were genetically distinct from others known by the same name in different regions of the Indo-Pacific (Cooke et al. 2020). Work with *Platygyra* cf. *daedalea* was conducted in November 2021 at Heron Island Research Station (HIRS). Six colonies were collected from the reefs on the southern side of Heron Island (23.4423° S, 151.9148° E) in the southern GBR. For all corals, while species were identified using Veron (2000) and Wallace (1999), we recognise the cf. nomenclature to note uncertainty in species identification due to the constant revision and changes in Indo-Pacific coral taxonomy (Bridge et al. 2023; Huang et al. 2011), but do not apply it in the text from hereon for simplicity.

Gamete collection

At all locations, gravid adult colonies were collected using a hammer and chisel in the days prior to the full moon during the anticipated spawning month (12 March 2017 at Coral Bay, 21 October 2021 at SeaSIM, 19 November 2021 at HIRS). Gravid colonies were assessed in the field by taking a sample and examining whether pigmented eggs were present (Harrison et al. 1984) and colonies > 5–10 m apart were collected to minimise the likelihood of selecting clonemates (Ayre and Hughes 2000). At Coral Bay, *A. digitifera* colonies were transported to the local jetty, isolated in 60-L containers at sunset, and spawned at 21:45–22:15 on the 22nd of March. At SeaSIM and HIRS, colonies were collected and housed in large, free flowing laboratory aquaria with ambient lighting for the duration of the spawning period. On spawning nights, colonies were isolated into individual 60-L containers with no flowing water and observed for setting and spawning (Babcock et al. 1986). At SeaSIM, *A. tenuis* spawned at 18:20–18:45 on the 22nd of October and *C. aspera* spawned at 21:20–21:55 on the 24th of October. At HIRS, *P. daedalea* spawned at 18:39–18:46 on the 24th of November. Once spawning occurred, egg-sperm bundles were collected from four colonies, separated into their egg and sperm components using a 125 µm mesh sieve, and kept isolated to prevent cross-contamination. Eggs from two of the four colonies were used for experimentation and were separated into clusters of 200 eggs to prepare for each treatment. Sperm is the major limiting factor of fertilisation and egg-sperm incompatibility is common. Therefore, sperm from each of the four donor colonies was pooled to maximise the functional interactions across gametes (6 total: 3 sperm donors for each egg donor) while minimising bias from biological factors like individual variability (Johnson et al. 2013) or conspecific incompatibilities (Willis et al. 1997). Homogenised sperm samples were counted using a haemocytometer (Babcock and Keesing 1999; Oliver and Babcock 1992; Willis et al. 1997); then, a serial dilution was performed to obtain a 200 mL sample of each sperm concentration.

Trials included eight sperm concentrations (0, 10^2–10^8 sperm mL^{-1}) for *A. digitifera*, seven (0, 10^2–10^7 sperm mL^{-1}) for *A. tenuis* and *C. aspera*, and six (0, 10^2–10^6 sperm mL^{-1}) for *P. daedalea*, but these concentration values were reduced by 25% when reporting the results to remove each individuals own sperm from the comparison, assuming no self-fertilisation occurred. Despite some evidence of self-fertilisation in *Platygyra* spp. (Willis et al. 1997), it is unlikely that this would occur in the presence of other conspecific sperm, or on such short time scales (Miller 1994). Therefore, values were shifted with the other taxa that have little evidence of self-fertilisation (Hatta et al. 1999; Willis et al. 1997), to maintain consistency because there were

no self-fertilisation controls to explicitly test otherwise. All sperm concentrations were tested at five contact times (10 s, 30 s, 1 min, 10 min, 30 min). The maximum sperm concentration used for each species varied based on the gamete quantity during spawning and gamete separation processing.

Experimental methods

Conditions and methodologies throughout the gamete collection, preparation, experimentation, and fixation process were standardised as much as possible despite the apparent spatial and temporal variability across assays for each species. Gamete viability and compatibility vary with time after spawning (dela Cruz and Harrison 2020; Miller and Babcock 1997), so experiments for all species commenced < 2 h since the beginning of spawning and were completed within 4 h to ensure that gametes remained viable. Salinity, and water and air temperatures, were maintained to mimic ambient conditions of the natal reef in each region (25 °C at Coral Bay and HIRS, 27 °C at SeaSIM). All seawater was filtered to prevent external influences on fertilisation dynamics; however, the degree of filtration was dependent on the capacity of each research facility and the water quality at each intake site, ranging from 0.2 µm to 5.0 mm. At all locations, seawater was collected in the afternoons prior to anticipated spawning nights to remove any possibility of sperm contamination in the water.

Coral eggs were exposed to each sperm concentration in respective sperm baths of 200 mL for a precise contact time. The order that each contact time was tested was randomised for each trial to minimise bias. Following exposure, eggs were rinsed with a sodium lauryl sulphate (SLS) solution of 0.01 g L^{-1} filtered seawater (FSW) to deactivate sperm and prevent additional interactions, then were rinsed twice with FSW. SLS is a detergent and surfactant that can be used to denature proteins such as those in sperm (Allen and Hagström 1955). Six replicates, three from each egg donor colony, were conducted simultaneously per sperm concentration and contact time interaction by attaching replicate groups to an apparatus which allowed movement in and out of their respective sperm baths at once (Fig. 1). Following experimentation, samples were fixed at the ~ 4-cell stage, 3–4 h after exposure to sperm, using a 4% buffered formalin solution in filtered seawater containing 10 g L^{-1} sodium β-glycerophosphate at a ratio of 1:4 fixative to sample, to prevent further embryogenesis. All samples were counted using a dissecting microscope to assess the proportion of fertilisation success at each level of interaction.

Statistical analyses

In the experiment, we used multiple replicates across a range of sperm concentrations, which were examined using replicated regressions in the statistical analyses (Cottingham et al. 2005). To estimate the relationships between proportional fertilisation success and sperm concentration and contact time, binomial generalised linear mixed models (GLMMs) were applied to each species, with the corrected sperm concentration treated as a continuous numeric predictor and contact time as a categorical predictor. Individual egg donor colony number and observation number were each included as random variables to account for any additional variability caused by differences in individual reproductive capabilities, or individual treatment meshes used in the experiment. Fertilisation success was examined as proportion data by binding the number of successes—i.e. fertilised eggs—and failures—i.e. unfertilised eggs (Crawley 2007). Each species was analysed separately to evaluate any species-specific gamete interactions during reproduction. Models were conducted in RStudio version 2022.07.2 (RStudio 2022) under R version 4.2.2 (RCoreTeam 2022). The *glmmTMB* function was used from the glmmTMB package (Brooks et al. 2022) with diagnostics examined using the DHARMa package (Hartig and Lohse 2022).

Acropora digitifera and *P. daedalea* exhibited signs of nonlinearity which resulted in poor fits under the glmmTMB model framework. Therefore, binomial generalised additive mixed models (GAMMs) were applied to each with the corrected sperm concentration as a continuous numeric predictor, contact time as a categorical predictor, and a t2 smooth function to account for the interaction between them. Knot values were determined based on sensitivity analyses of model fit and smoother accuracy compared to the observed data. Individual egg donor colony number and observation number were included as random variables. The *gamm4* function was used from the gamm4 package (Wood and Scheipl 2022) with diagnostics examined using the *gam.check* function from the mgcv package (Wood 2023).

Mean values of GLMM and GAMM model fits and upper and lower limits were derived using the *predict* function for each species across the five contact time treatments. Effective Concentration values are commonly used in concentration–response modelling and were used to predict the sperm concentration that promoted fertilisation success of absolute 50% (EC50) (Albright and Mason 2013; Nozawa et al. 2015). EC50s and 95% confidence intervals were derived from the predicted data by interpolation to aid in comparisons within and between species. Replicated regressions were preferred because they provided more quantitative output metrics, such as EC50s,

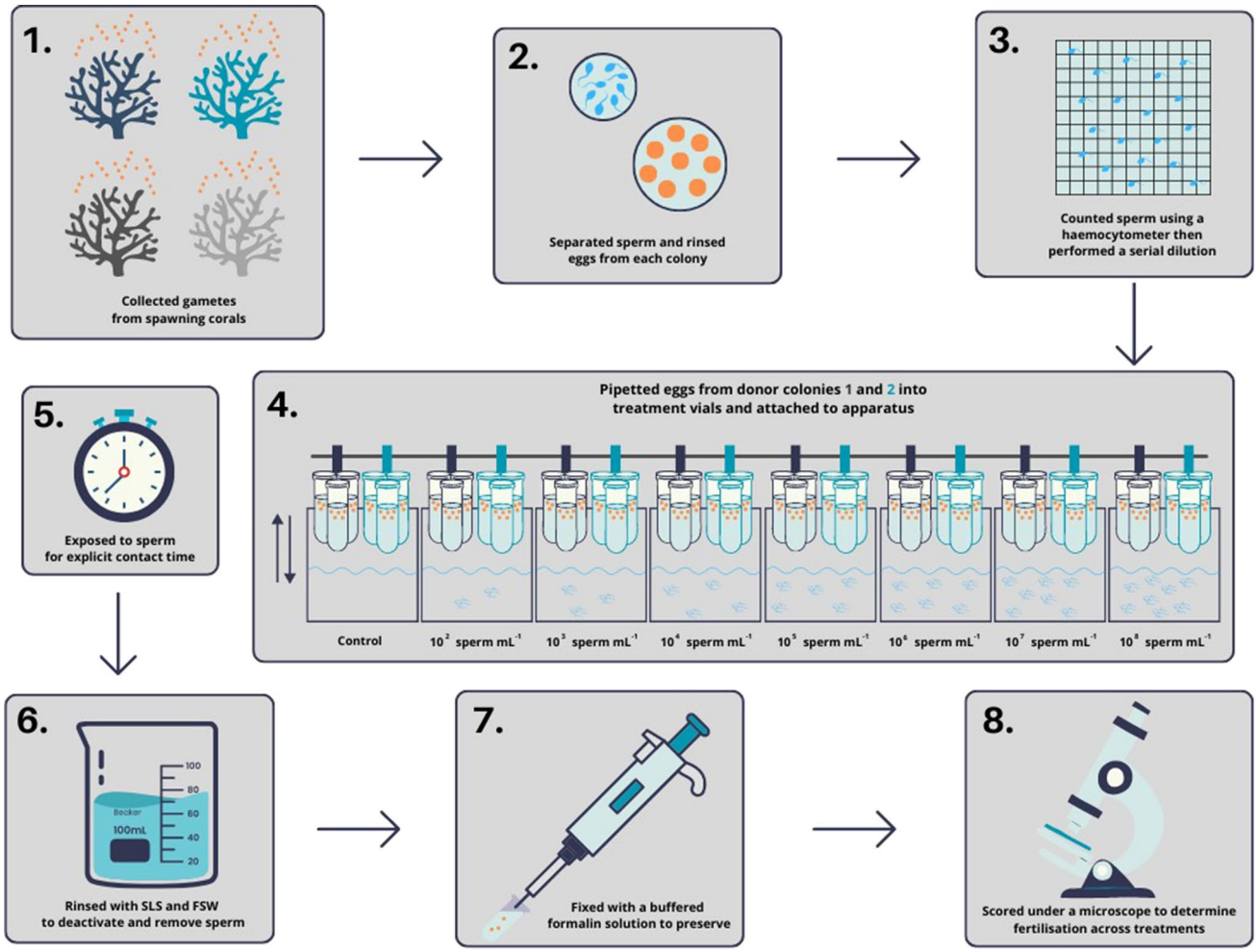

Fig. 1 Procedural flow chart outlining the spawning protocol and experimental design. Gamete bundles were first collected from the four spawning corals (1), then separated and rinsed (2). Sperm was counted using a haemocytometer and a serial dilution was performed to prepare treatments (3). Eggs from two donor colonies were pipetted into treatment vials and attached to an experimental apparatus (4) where they were exposed to sperm for an explicit contact time (5). Following treatment, eggs were thoroughly rinsed with sodium lauryl sulphate (SLS), then twice with filtered seawater (FSW), to deactivate and remove sperm (6). Samples were fixed with a buffered formalin solution to preserve gametes and prevent additional cell division (7), then counted using a dissecting microscope to evaluate fertilisation success across treatments (8)

that can also be used later downstream in ecological and risk-assessment modelling (Cottingham et al. 2005).

Results

For each species, fertilisation success significantly increased as sperm concentration and contact time increased (Fig. 2, Online Resource 1,2). Yet, the degree of change varied among species, denoted by the different slopes and functional forms of each set of curves. In general, *A. digitifera* (Fig. 2c) and *P. daedalea* (Fig. 2d) had more nonlinear trends exhibited by steep slopes of increased fertilisation success once sperm concentration surpassed threshold values of 10^4 sperm mL^{-1} and 10^2 sperm mL^{-1}, respectively. Fertilisation success increased predictably as contact times increased across all sperm concentrations in *C. aspera* (Fig. 2b) and *A. digitifera* (Fig. 2c). Similar trends in fertilisation success were observed in *A. tenuis* (Fig. 2a) and *P. daedalea* (Fig. 2d) as contact times increased, although in most cases, fertilisation success converged on a similar range of values at sperm concentrations $> 10^5$ sperm mL^{-1} and $> 10^4$ sperm mL^{-1}, respectively.

For *A. digitifera*, fertilisation was minimal across the lower sperm concentrations $< 10^4$ sperm mL^{-1}, increased slightly from 10^4 sperm mL^{-1} and peaked at $< 10^5$ sperm mL^{-1} with > 95% fertilisation success in the longest contact time of 30 min (Fig. 2c). *A. digitifera* also exhibited gradual declines in fertilisation success at the highest sperm concentration (10^6 sperm mL^{-1}) and longer contact times

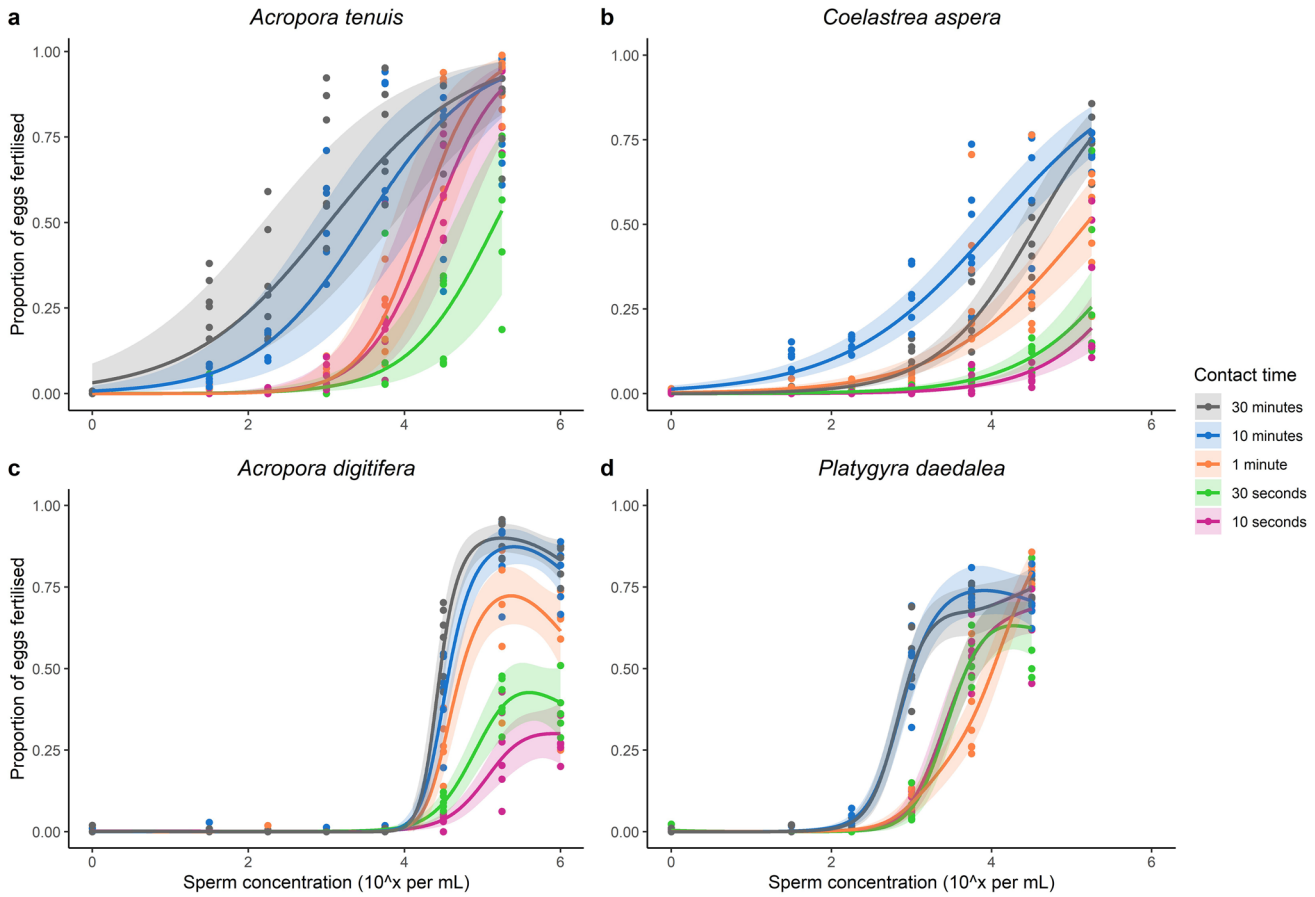

Fig. 2 Fertilisation success as a function of the interaction between sperm concentration and contact time for the four study species: (**a**) *A. tenuis*, (**b**) *C. aspera,* (**c**) *A. digitifera* and (**d**) *P. daedalea*. Each point signifies one replicate of the treatment at each level of interaction ($n = 6$ per sperm concentration and contact time cross). The solid lines represent the mean of generalised linear mixed model fits at each contact time for (**a**) and (**b**), and the mean of generalised additive mixed model fits at each contact time for (**c**) and (**d**). Confidence intervals of 95% are visualised by the shaded regions

(1 min, 10 min, 30 min). Similar trends were observed for *P. daedalea* with very low fertilisation at the lowest sperm concentrations, increasing from ~ 10^3 sperm mL^{-1}, and reaching maximum fertilisation success at $10^{4.5}$ sperm mL^{-1} with > 75% fertilisation success observed in long and short contact times (Fig. 2d). At concentrations < 10^4 sperm mL^{-1}, there is a clear distinction in fertilisation success between the shorter (≤ 1 min) and longer (≥ 10 min) contact times. There also appears to be a slight declining trend of fertilisation developing at higher sperm exposure for *P. daedalea,* but there is insufficient data at the upper sperm concentrations to disentangle this.

Acropora tenuis achieved the most fertilisation across contact times and had the largest variation in fertilisation values at each treatment (Figs. 2a, 3a). At shorter contact times, higher sperm concentrations (> 10^3 sperm mL^{-1}) were required to promote fertilisation success, but greater increases in fertilisation were also observed as sperm concentrations increased. At the longest contact times, fertilisation success of 10–30% occurred at very low sperm concentrations, < 10^2 sperm mL^{-1}, and steadily increased and stabilised at higher sperm concentrations of > 10^4 sperm mL^{-1} (Fig. 2a). For *C. aspera*, fertilisation was low at lower sperm concentrations and accelerated once sperm concentration surpassed ~ 10^3 sperm mL^{-1}. However, a more linear trend was observed during the 10 min contact time with roughly 5–10% fertilisation success at the lowest sperm concentration < 10^2 sperm mL^{-1}, and marginally increasing in a cumulative fashion as sperm concentration increased. Maximum fertilisation was achieved at the highest sperm concentration tested, ~ 10^5 sperm mL^{-1}, reaching a maximum of > 75% success in the longest two contact times of 10 min and 30 min (Fig. 2b).

When comparing EC50 values across species, *A. tenuis* and *P. daedalea* required the least sperm to fertilise eggs, only requiring 10^3 sperm mL^{-1} to reach 50% fertilisation success at their longest contact times (Fig. 3a, d, Online Resource 3). *Coelastrea aspera* and *A. digitifera* both

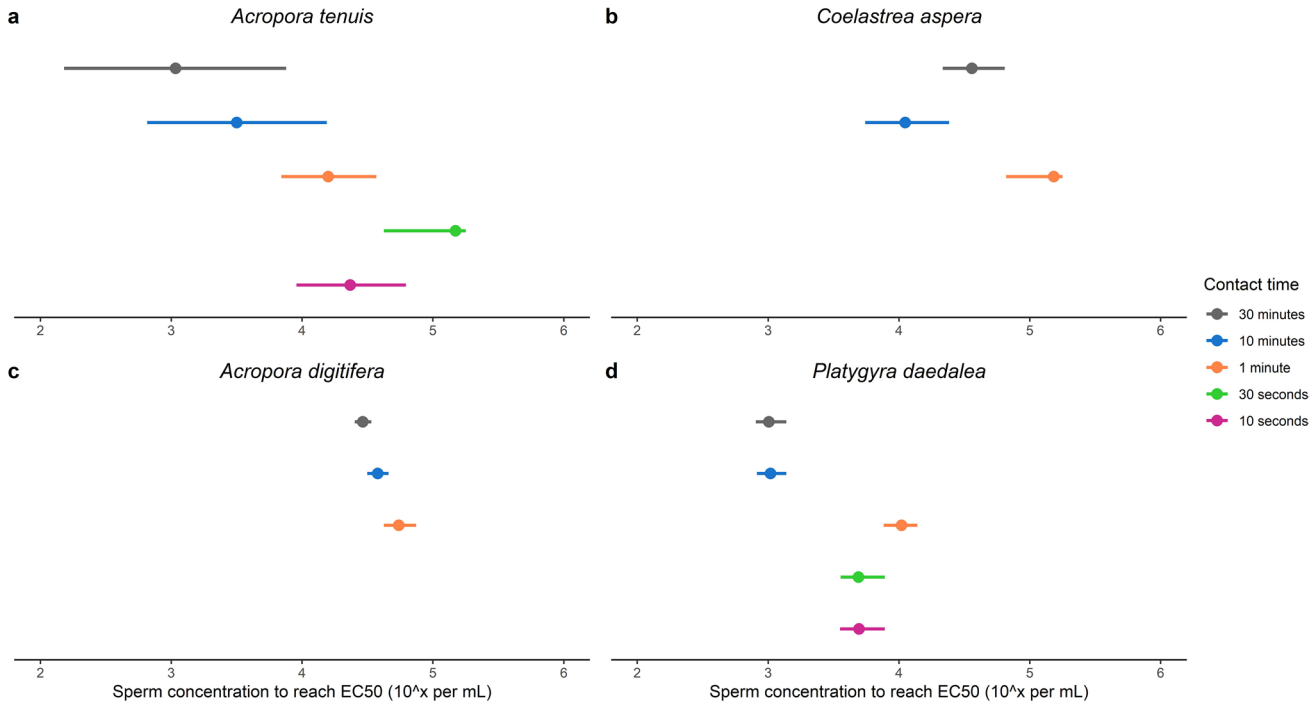

Fig. 3 The effective concentration (EC50) values at each contact time for the four study species: (**a**) *A. tenuis*, (**b**) *C. aspera*, (**c**) *A. digitifera* and (**d**) *P. daedalea*. Points represent the mean EC50 value and line length signifies the 95% confidence intervals for each estimate derived from model predictions based on the corresponding generalised linear mixed model fits at each contact time for (**a**) and (**b**) and the generalised additive mixed model fits at each contact time for (**c**) and (**d**)

required more sperm, > 10^4 sperm mL^{-1}, to reach the 50% threshold at longer contact times and failed to reach this critical point at their shortest contact times of 10 and 30 s (Fig. 3b, c).

Discussion

Our analysis examined the complex interactions between sperm concentration and contact time on fertilisation success across four coral species common to the Indo-Pacific. Sperm concentration and contact time are critical factors which drive fertilisation success in corals, yet there is little previous information on how they collectively influence fertilisation kinetics across species. As predicted, our results show that when sperm concentration is low, more time is required for sperm to find eggs and fertilise successfully. Conversely, when sperm concentrations are higher, fertilisation is more likely to occur at shorter contact times due to the higher likelihood of gamete interactions at higher densities. However, reproductive relationships were nonlinear in some cases and differed across taxa, demonstrating species-specific nuances. Thus, the complex functional relationships defined will improve the overall understanding of fertilisation kinetics across taxa and help inform in situ spawning outcomes to establish species-specific management and out-planting strategies (Boström-Einarsson et al. 2020), as well as ex situ spawning and nursery facilities (O'Neil et al. 2021), which promote coral resilience and conservation. Specialised management plans can be developed based on the coral density of a given reef or the target density of a proposed restoration project with the local hydrodynamic conditions to safeguard reproductive success and combat Allee effects.

Current findings for *A. tenuis* suggest that the species is more fertile than the other species examined due to higher fertilisation across contact times. Further, our results echoed previous observations in the literature (Albright and Mason 2013; dela Cruz and Harrison, 2020; Ricardo et al. 2015), with EC50 values ranging from $10^{3–3.8}$ sperm mL^{-1}. However, our results for *A. tenuis* had less drastic sigmoidal shaped curves at longer contact times compared to previous studies. One study has previously examined fertilisation of *P. daedalea*, and observed fertilisation success > 50% at 10^3 sperm mL^{-1}, similar to what was observed at 10 and 30 min contact times in our study, but specific EC50 thresholds are unknown due to different experimental methods (Miller and Babcock 1997). Others using *P. ryukyuensis* (Nozawa et al. 2015), *P. sinensis* (Oliver and Babcock 1992), and *P. acuta* (Chui et al. 2014; Lam et al. 2015), observed similar overall trends, but variable EC50 values and higher maximum fertilisation success compared to this study. *P. acuta* from Hong Kong had low EC50 values of $10^{2.5–3.8}$ sperm

mL^{-1} (Chui et al. 2014; Lam et al. 2015), similar to *P. daedalea* studied presently. *Platygyra sinensis* from the central GBR had a higher EC50 value of 10^4 sperm mL^{-1} (Oliver and Babcock 1992), while *P. ryukyuensis* from Taiwan had the highest EC50 value of $10^{5.6}$ sperm mL^{-1} (Nozawa et al. 2015) suggesting lower reproductive potential. However, it is important to note that few of the preceding studies have documented the explicit time that sperm and eggs were in contact prior to reporting, and it is likely that most interactions were longer than our maximum exposure time. The longest contact time of 30 min from the present study was used to standardise the comparisons, but different methodologies across studies may contribute to apparent variation among species.

Similar to previous studies, our results indicate apparent species-specific differences in fertilisation kinetics (dela Cruz and Harrison 2020; Nozawa et al. 2015). Differences in fertilisation kinetics across species are likely caused by varied traits that contribute to overall fecundity (Harrison and Wallace 1990; Kojis and Quinn 1984; Ward and Harrison 2000). For example, egg traits like size (Levitan 1993; Marshall et al. 2000) and quantity (Hall and Hughes 1996), sperm characteristics, like swimming speed (Morita et al. 2006) and quantity (Teo et al. 2016) per bundle, and gamete longevity (Chui et al. 2014; dela Cruz and Harrison, 2020), are parameters known to influence fertilisation success and vary across species. Levitan (1993) found that species of sea urchins that produced larger eggs had higher fertilisation success at a given sperm concentration, but trade-offs existed because larger eggs require more energy, thus fewer can be produced. This trend is also observed in spawning corals when comparing acroporids to merulinids, where the former produce fewer eggs ($n = 3$–20 per egg-sperm bundle) that are larger (400–800 µm), while the latter produce significantly more ($n = 30$–250 per egg-sperm bundle) smaller eggs (200–400 µm) (Álvarez-Noriega et al. 2016; Babcock et al. 2003; Madin et al. 2016). Such a dichotomy has likely evolved to benefit each group, respectively, while also delineating their fertilisation kinetics and reproductive potential.

Our results suggest that larger egg sizes may promote higher fertilisation success in corals, since the acroporids *A. tenuis* and *A. digitifera* had higher maximum observed fertilisation success compared to the merulinids *C. aspera* and *P. daedalea*. However, the relationship between egg size and sperm concentration is complex and heavily reliant on many other interacting parameters, which likely explain more nuanced differences in fertilisation between the congeners *A. tenuis* and *A. digitifera* at lower sperm concentrations. For example, such divergence in reproductive capacity of *A. tenuis* and *A. digitifera* may be a result of differences in evolved gamete compatibility or recognition faculties at low sperm concentrations. Similar congeneric variation has been observed among three sympatric species of sea urchins where gamete traits, species density and spatial distribution, seawater advection, and historical demographic traits all influenced fertilisation success (Levitan 1993). Under conditions of sperm limitation and sperm competition, fertilisation kinetics and gamete traits in these species are likely to have evolved in response to demographic and ecological factors (Levitan et al. 2004). A more complete understanding of how gamete traits such as egg size affect fertilisation will require both modelling and in situ studies of fertilisation in corals (Levitan 2006).

Gamete recognition factors further complicate understanding of patterns in coral fertilisation among different species. Intra-specific sperm chemoattraction has been observed in several species, promoting the movement of sperm in the presence of conspecific eggs (Morita et al. 2006). Sperm-egg recognition and binding abilities likely evolved across species in parallel based on localised conditions (Levitan et al. 2004; Willis et al. 1997); thus, the efficiency of such mechanisms to promote fertilisation is expected to be variable.

Our results also demonstrate reproductive variability within species and treatments. This was most evident for *A. tenuis*, with high variability in fertilisation success at each contact time and sperm concentration interaction. Previous studies have observed high variability within *P. daedalea* (Miller and Babcock 1997), *A. gemmifera*, *A. hyacinthus*, *F. abdita*, and *F. valensiennesi* (Nozawa et al. 2015). Intra-species differences in fertilisation are likely driven by variability in key gamete properties like egg size, sperm swimming speed, and sperm binding capabilities (Babcock et al. 2003; Morita et al. 2006; Moy et al. 2008). For example, the ranges of conspecific egg diameters have been observed to vary by > 100 µm for many species (Babcock et al. 2003) and similar variability has been observed for sperm swimming speed (Morita et al. 2006). Such differences across individuals are expected to influence gamete interactions and fertilisation outcomes.

Declines in fertilisation success at the highest sperm concentrations observed for *A. digitifera* and *P. daedalea* are likely a result of polyspermy (dela Cruz and Harrison 2020; Ritson-Williams et al. 2009) or low dissolved oxygen (Oliver and Babcock 1992). Polyspermy occurs when multiple sperm fertilise an egg, resulting in developmental abnormalities or death (Brawley 1987; Fogarty et al. 2012; Gribben et al. 2014; Levitan et al. 2007). Polyspermy is less likely in acroporids due to specialised polyspermy blocks in eggs (Morita et al. 2006), therefore low dissolved oxygen may be a more probable explanation for the declines in fertilisation in *A. digitifera* due to the high maximum sperm concentration examined in the respective trials. Polyspermy has been observed in the literature for *P. sinensis*, with declining fertilisation success starting > 10^6 sperm mL^{-1} (Oliver and Babcock 1992), so a similar trend may exist in *P. daedalea*.

More data at higher sperm concentrations and direct demonstrations of polyspermy are required to establish the robustness of these observations.

It is also well documented that fertilisation is particularly vulnerable to external pressures like changes in pH (Leuchtenberger et al. 2022), thermal stress (Albright and Mason 2013; Bouwmeester et al. 2022; Henley et al. 2022; Humanes et al. 2017), nutrients (Harrison and Ward 2001; Lam et al. 2015; Ward and Harrison 2000), sedimentation (Erftemeijer et al. 2012; Humanes et al. 2017; Ricardo et al. 2015), and local hydrodynamic mixing (Babcock 1995; Teo and Todd 2018). For ease of comparisons across study sites and species, some parameters, like pH, temperature, and salinity, have been controlled for by mimicking natal reef conditions. While others, like hydrodynamic mixing and water quality, have been eliminated by conducting experiments in controlled laboratory settings. However, due to the spatial and temporal variability in natal reef characteristics, there were likely some minor differences across sites and spawning months that could influence reproduction and reef recovery in wild populations, thus potentially affecting outcomes of laboratory trials.

At the population level, reproduction is highly sensitive to different types of disturbances and external influences, which can act on varying scales. Disturbances, like coral bleaching, can lower fecundity by reducing egg size and quantities and testes volume per polyp, as well as reducing the number of gravid, gamete-producing polyps in adult corals (Baird and Marshall 2002; Levitan et al. 2014; Ward et al. 2000). The latter could cause partial mortality that may force re-allocation of resources away from gamete production (Kai and Sakai 2008), or full mortality across individuals during more serious events (Harriott 1985). Such circumstances have been observed on the GBR in the past four decades, owing to unprecedented disturbance regimes. Specifically, over 50% of coral cover has been lost between 1985 and 2012 (De'Ath et al. 2012; Hughes et al. 2015), and coral recovery rates have fallen by an average of 84% from 1992 to 2010 (Ortiz et al. 2018). Recent reports by the Australian Institute of Marine Science (2022) highlight rapid post-bleaching recovery at many reef sites. Yet, this has been primarily observed from fast-growing acroporids (AIMS 2022), which suggests that species diversity and structural complexity may still be affected long term at many sites. Coral size frequency and density distributions have also been affected, which has significant repercussions for coral demographics (Dietzel et al. 2020; Edmunds and Riegl 2020; Pisapia et al. 2020), specifically relating to reproduction and Allee effects.

Understanding the processes that promote and limit successful reproduction is crucial for informing management decisions and potential restoration strategies that aim to maximise reef recovery. Informed metrics like optimal sperm concentrations and time required for insemination to occur are important for developing and optimising mass larval culturing methods and laboratory systems that promote fertilisation (dela Cruz and Harrison 2020). These data are also required for the parameterisation of fertilisation kinetics models (Vogel et al. 1982) and larger scale coral spawning models (Teo and Todd 2018), which act as useful predictors of reproductive processes that are generally difficult to measure in situ. Further, upscaling these findings to determine a projected coral density that may optimise reproduction in situ could also act as a guide for restoration out-planting strategies to combat detrimental Allee effects.

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Data availability The datasets used for this study are deposited in the CSIRO Data Access Portal https://data.csiro.au/collection/csiro:58707 and will be made fully available following publication.

Declarations

Competing interests The authors declare no competing interests that interfered with the completion of this work.

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