Allee effects in corals during fertilisation

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Abstract

Allee effects – where individual fitness declines at low population densities or sizes – are pivotal in shaping the reproductive ecology of broadcast-spawning corals. In these species, successful external fertilisation requires that gametes remain at sufficiently high concentrations for long enough periods before turbulent water movement disperses them below fertilisable levels. As reefs degrade and coral populations fragment, this inverse density dependence can severely limit reproductive success, undermining reef resilience and recovery. This review explores Allee effects in corals during fertilisation, highlighting how spatial configuration, colony size, and hydrodynamics influence gamete encounters. We synthesise empirical and modelling studies that quantify fertilisation under varying densities and spatial arrangements, revealing the threshold conditions essential for reproductive viability. We also evaluate the roles of water flow, turbulence, and spawning synchrony in shaping fertilisation rates, with direct implications for coral recruitment. Methodological challenges, particularly *in situ* sampling biases and complex hydrodynamic conditions, are discussed, underscoring the difficulty of accurately measuring fertilisation success. We address how Allee effects inform coral restoration strategies, particularly outplanting design for fertilisation and genetic diversity, and identify equivalent implications for harvest management frameworks where selective removal of large, aggregated colonies may erode reproductive viability. Understanding these processes is crucial for predicting coral reproductive outcomes under changing environmental conditions and guiding effective conservation of degraded reef systems.

What are Allee effects?

Allee effects, also referred to as *inverse density-dependence*, are decreases in fitness (e.g., survival, reproduction) at low population densities or sizes (Courchamp et al. 1999, Stephens et al. 1999), and feature throughout the life stages of corals. Perhaps the most critical Allee effect occurs during external fertilisation in broadcast-spawning species where small population densities or sizes can decrease the overall output of eggs as well as the proportion of eggs fertilised resulting in fewer larvae.

While typically lower than internal fertilisers, broadcast-spawning corals generally require greater than ~10^3 sperm mL^{-1} to fertilise the egg, depending on species and environmental conditions (Rodriguez-Martinez 2003, Nozawa et al. 2015). The sperm concentration reflects the number of adult spawning colonies in close enough proximity that their gametes mix, before wind, waves and currents dilute the gametes to low concentrations. While Allee effects strictly relate to spatial population parameters such as population density and size, other factors such as colony size similarly influence gamete concentrations and are thus included in this review. This paper examines the reproductive biology of broadcast-spawning corals in the context of Allee effects, and their relevance to restoration and marine ornamental harvesting activities.

Allee effects can be categorised as either component (affecting only a specific aspect of fitness) or demographic (influencing overall population dynamics) (Kramer et al. 2009) (Gascoigne & Lipcius 2004, Kramer et al. 2009). Fertilisation-related Allee effects fall into the component category, as reduced gamete concentrations diminish fertilisation success, thereby reducing embryo and subsequently larval production. However, lower fertilisation success may not necessarily limit recruitment at downstream or sink reefs. Recruitment may be governed more strongly by negative density-dependent processes, such as competition among settlers, rather than by fertilisation rates per se (Caley et al. 1996, Kramer et al. 2009). Additionally, if the initial egg pool is sufficiently large, low fertilisation rates may still yield high absolute numbers of larvae. Setting aside other larval processes such as predation, whether fertilisation success is a limiting factor at the metapopulation scale therefore depends on both the size of the egg pool and the availability of suitable substrate for recruitment. In this context, Levitan (1995) notes that 100% fertilisation success should not be expected in mass-spawning taxa. Corals have likely evolved a level of fertilisation efficiency that is sufficient to sustain populations, with further increases in reproductive capacity potentially constrained by trade-offs between energetic costs and other life-history processes such as somatic growth.

A series of reviews in the 1990s and early 2000s explored Allee effects in externally spawning marine invertebrates (Levitan 1995, Levitan & Petersen 1995, Levitan 1998, Yund 2000, Gascoigne & Lipcius 2004), with much of the focus on echinoderms and chordates. However, little attention has been given to broadcast-spawning corals, and there has been limited synthesis of this topic in the decades since. Moreover, corals can present additional complexities, including surface water fertilisation, mass spawning, hybrid embryo formation, and reproduction under complex hydrodynamic processes. This review first summarises reproductive properties of corals relevant to assessing Allee effects in broadcast-spawning corals, with key terminology defined in Table 1. Hydrodynamic and physical considerations are discussed alongside biophysical models and methodological approaches, followed by future opportunities for addressing these challenges. As coral reefs undergo extensive degradation, primarily due to climate change, understanding Allee effects in thinning and declining populations has never been more urgent. Restoration activities that aim to create enduring local populations will also have to contend with small population effects.

Table 1. Glossary of the key terms used throughout the review.

TERM	NOTES/EXPLANATION
ALLEE EFFECT	A phenomenon where individual fitness (e.g., survival, reproduction) decreases with declining population density or size. Also referred to as 'inverse density-dependence'.
BROADCAST SPAWNING	A reproductive strategy where organisms release eggs and sperm into the water column for external fertilisation.
BUNDLE DISSOCIATION	The process by which egg-sperm bundles rupture, releasing gametes for fertilisation.

CHEMOTAXIS	The movement of sperm toward eggs in response to chemical signals, enhancing fertilisation success in certain marine organisms, including corals.
CONVERGENCE ZONES	Areas in the ocean where hydrodynamic forces cause gametes to accumulate, potentially increasing local fertilisation rates.
DEMOGRAPHIC ALLEE EFFECT	A type of Allee effect where reduced population density directly limits population growth.
DENSITY-DEPENDENT FERTILISATION	The relationship between coral colony density and fertilisation success, where higher densities often result in higher gamete concentrations and fertilisation rates.
EGG-SPERM BUNDLE	A mucous-bound cluster of eggs and sperm released by hermaphroditic corals, which ascends to the water's surface before dissociating.
EGG-SPERM ENCOUNTER RATE	The rate at which eggs and sperm encounter each other, influenced by turbulence, gamete concentration, and swimming speeds.
FERTILISATION EFFICIENCY	The proportion of gamete encounters that result in successful fertilisation, influenced by sperm motility, chemotaxis, and hydrodynamic conditions.
GAMETE DILUTION	The reduction of gamete concentration due to dispersal by water currents, leading to lower fertilisation rates.
GAMETE VIABILITY	The functional lifespan of eggs and sperm, beyond which fertilisation success declines, often reported as a half-life.
INVERSE DENSITY DEPENDENCE	See Allee effect.
LANGMUIR CIRCULATION	A type of surface water motion driven by wind causing secondary circulation that can cause streaks on the water's surface aligned with the wind direction.
MASS SPAWNING	The simultaneous release of gametes into the water column by multiple species.
MICROAGGREGATES	Small-scale clumping of gametes due to mucus or hydrodynamic interactions.
NEAREST-NEIGHBOUR DISTANCE	A spatial population parameter by measuring the shortest distance between two individuals.
POLYSPERMY	A condition where multiple sperm fertilise a single egg, often leading to embryo inviability; some corals have mechanisms to block polyspermy.
SELF-FERTILISATION	The fertilisation of eggs by sperm from the same individual.
SPAWNING SYNCHRONY	The degree to which individuals within a population release gamete simultaneously, influencing fertilisation success.
SPERM COMPETITION	The interaction between sperm from different individuals competing to fertilise available eggs, which can influence genetic diversity.
SPERM DILUTION	The rapid decline in sperm concentration due to water column mixing, reducing fertilisation probability at low population densities.
SPERM LIMITATION	A reduction in fertilisation success caused by insufficient sperm concentrations in the water column, preventing adequate contact between sperm and eggs.
SURFACE TURBULENCE	The chaotic motion at the ocean surface caused by wind and waves, influencing gamete distribution and fertilisation outcomes.
TURBULENT DIFFUSION	The spread of water and particles through turbulent water motion.
VERTICAL MIXING	The movement of water and particles between different depths.

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Challenges in investigating Allee effects in external reproduction

To date, there has been a paucity of studies attempting to quantify *in situ* fertilisation success, remarkably fewer than those documenting *in situ* spawning observations. For example, Baird et al. (2021), as reported in the Coral Spawning Database (CSD), comprises 6,178 observations of species-specific spawning times or dates. This is compared with 10 studies reporting species-specific *in situ* coral gamete concentrations and fertilisation, with even fewer reporting population characteristics (Table 2). This disparity is primarily attributable to the inherent difficulty in distinguishing spawn of target species from those of non-target species that concurrently spawn during multispecies events. Additionally, the ephemeral and typically nocturnal nature of these spawning events imposes substantial logistical constraints, often involving sizeable field teams to dive to make observations, collect gametes, and track spawn on the water surface from vessels, thereby limiting experimental opportunities. Consequently, research on Allee effects during fertilisation has predominantly concentrated on species that are easier to study by being reproductively or spatially isolated – i.e., those that spawn at distinct times or locations separate from co-occurring allospecific counterparts.

Sampling biases are readily introduced in most experimental designs aiming to understand *in situ* fertilisation success, including survivorship bias, inflated estimates resulting from self-fertilisation, spawn contamination by gametes from non-target conspecific or heterospecific spawners (hybridisation)(Fig. 1). An ideal random sampling approach of a natural gamete plume would necessitate collecting samples from the spawn within the top metre of water across the full extent of the reef. However, this methodology would likely yield very low concentrations of gametes in most samples. Instead, researchers often target visible concentrations of gametes (slicks), which may not accurately represent the entire reef ecosystem and may preferentially sample convergence zones where fertilisation rates are often high and likely inflated (Langley et al. 2024). The extent to which reproductive output is concentrated in these convergence zones, particularly during the fertilisation time-window, remains uncertain. Furthermore, sampling spawn slicks during daylight hours following nocturnal spawning introduces additional biases, as unfertilised eggs and non-viable embryos begin to decompose (Oliver & Willis 1987), possibly resulting in survivorship bias.

To prevent spawn from non-target colonies interfering and contaminating the target patch, various isolation controls have been employed. Temporal isolation – selecting species that spawn outside of multispecific events – substantially reduces the risk of contamination. However, this approach is often constrained by the limited number of temporally isolated species, and the frequently inadequate understanding of their spawning cues. Spatial isolation involves the manipulative relocation of corals to areas distant from conspecifics, ensuring that the hydrodynamic and environmental conditions remain realistic and controlled, albeit simplified. The relocation distance must be sufficient to minimise the likelihood of natural spawn gametes reaching the experimental site during the sampling period. This approach affords researchers the flexibility to choose species whose reproductive timing is well characterised. Lastly, physical isolation exploits natural barriers to prevent slick convergence, such as using exposed reef flats that inherently block the interaction between natural and experimental slicks.

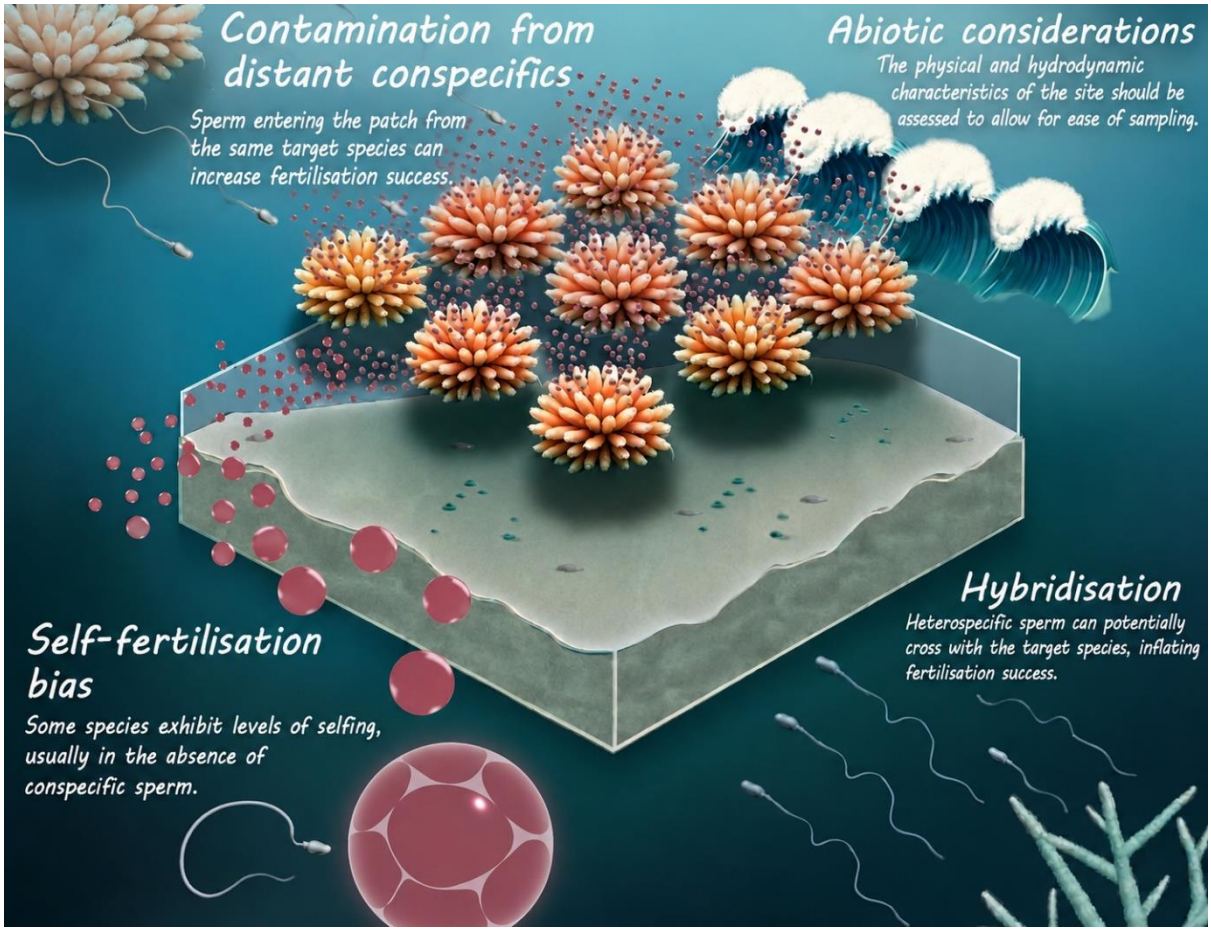


Fig. 1. Processes that can introduce bias, complicate interpretations, or generate experimental artefacts in studies of Allee effects during coral fertilisation.

Table 2. Studies reporting *in situ* fertilisation success of single species

SPECIES	SPAWNING MODE	METHOD	PATCH CHARACTERISTICS	MEANS AND (RANGES) (%)	NOTES	REFERENCE
***PSEUDOPLEXAURA POROSA* (OCTOCORAL)**	Gonochoric broadcast spawner	Plankton collection using syringes.	0.1 colonies m^{-2} (>50 cm height)	> 67 (0–85)	Fertilisation in the water column or on the colony surface. Rates fluctuated with day and location on the reef. Field experiments showed that the number of spawning colonies had a greater effect on fertilisation success than water flow conditions. Higher colony synchrony led to higher fertilisation, while sparse or asynchronous spawning reduced success.	Coma and Lasker (1997a)
***PLEXAURA KUNA* (OCTOCORAL)**	Gonochoric broadcast spawner	Plankton collection using containers.	Not reported	15 (0–68)	Fertilisation potential approach to assess ability to fertilise eggs under constant conditions.	Coma and Lasker (1997b)
***MONTIPORA DIGITATA*[1] (HARD CORAL)**	Hermaphroditic broadcast spawner	Plankton tows.	Not reported, although this species typically forms in thickets at these locations in shallow waters (Babcock personal communication).	(0–80)	Fertilisation in the water column varied widely with spawning synchrony. High fertilisation occurred during major, synchronous spawn nights; much lower success was observed during minor spawning events.	Oliver and Babcock (1992)
***ORBICELLA*[2] *ANNULARIS*, *O. FAVEOLATA*, AND**	Broadcast spawner	Plankton tows.	0–8 colonies/diver	(~0–25)	Fertilisation success was related to a linear relationship between colonies/diver (a proxy for density)	Levitan et al. (2004)

***O. FRANKSI* (HARD CORAL)**					and was synchrony dependent. On nights with many colonies spawning together, average fertilisation was ~20–30%. Corals spawning in peak synchrony had much higher success, whereas those spawning earlier or later than the main pulse experienced greatly reduced fertilisation (near zero in extreme cases).	
***GONIASTREA FAVULUS* (HARD CORAL)**	Hermaphroditic broadcast spawner (self-fertile)	Direct collection from colonies.	Intercolonial distances from 0 to ~2 m. ~1.6 m^2. Coral cover from 0 to 35%. Shallow water reef flat.	82±2	No density-dependent effects observed. Fertilisation typically occurs on or near the colony surface due to negatively buoyant eggs. Up to 50% self-fertilisation observed.	Miller and Mundy (2005)
***BRIAREUM ASBESTINUM* (OCTOCORAL)**	Gonochoric spermcaster	Direct colony collection.	Two reef sites (Panama) over 2 years (natural spawning)	(~0–20)	Manipulative and natural experiments. Extremely low embryo production despite apparently healthy populations. Fertilisation success was zero at one site, suggesting strong sperm limitation. Generally, fertilisation was lower at distances > 5 m.	Brazeau and Lasker (1992)
***PLEXAURA KUNA* (OCTOCORAL)**	Gonochoric broadcast spawner	Plankton collection using syringes.	Single reef site (San Blas, Panama); monitored over 15 months of monthly spawning events	(0–100)	Fertilisation success ranged from 0–100%, with monthly means of 0–60.4%. Variation driven by sperm limitation. Typical fertilisation around 20%.	Lasker et al. (1996)
***ACROPORA* CF. *HYACINTHUS*[3] (HARD CORAL)**	Hermaphroditic broadcast spawner	Natural experiment. Eggs contained.	Single Palauan reef; natural population study. Spacing ranged from 0 to 20 m.	0–~30, (0–~80)	Fertilisation declined sharply with distance. Colonies <0.5 m apart achieved ~30% success; at 10 m,	Mumby et al. (2024)

					success dropped below 10%, and near 0% at >15–20 m.	
***ACROPORA* CF. *TENUIS*[3], *A. DIGITIFERA*, *A.* CF. *HYACINTHUS*[3] (HARD CORAL)**	Hermaphroditic broadcast spawner	Manipulative experiments. Eggs contained.	Small lattice grids. Spacing was 1–2 m species dependent. Spawning population size ranged from 8 – 20 individuals.	(1–9; species-dependent)	High levels of control and colonies isolated from nearby population reducing interference from non-target colonies.	Ricardo et al. (2025a)
***PLATYGYRA DAEDALEA* (HARD CORAL)**	Hermaphroditic broadcast spawner	Natural experiment. Eggs contained.	Natural population on Heron Reef, GBR. Density = ~0.016 colonies m^{-2} or 0.004 colonies m^{-2} gravid colonies. Spacing = 7.7 m (gravid colonies only).	1.5	High asynchrony across months, nights and time from sunset. No outcrossing and all embryos identified were selfed.	Ricardo et al. (2025b)
***ACROPORA* CF. *HYACINTHUS*[3] (HARD CORAL)**	Hermaphroditic broadcast spawner	Manipulative experiment. Eggs contained.	Clustered radial design with a range of spacings and colony densities. 17 colonies in the central cluster at 0.7 m spacing. 1–3 m depth.	32.8 (0–95).	High levels of control and colonies isolated from nearby population reducing interference from non-target colonies.	Ricardo et al. (2026)

[1]Species assumed through deduction of possible candidate species.

[2]Previously assigned to the genus *Montastrea*.

[3]This species is undergoing taxonomic revision.

Challenges in spatially characterising populations

Population parameters used to characterise spatial distributions can be reported in many ways (Table 3), and the challenges associated with defining spatial point patterns have been well described in other reviews (Gustafson 1998, Velázquez et al. 2016). Allee effects during fertilisation raise some additional considerations.

Table 3. Conversions between spatial population parameters. Mean intercolonial distances were calculated by simulating colonies randomly (Poisson) onto a 100 × 100 m grid using 100 simulations per density.

POPULATION DENSITY (IND. M^{-2})	INDIVIDUALS PER HECTARE	AREA PER INDIVIDUAL (M^2)	MEAN INTERCOLONIAL DISTANCE (M)
0.01	100	100	5.19
0.05	500	20	2.28
0.10	1000	10	1.61
0.50	5000	2	0.71

Population density is a widely used metric to describe Allee effects across a range of ecosystems (Courchamp et al. 1999, Stephens et al. 1999) but its use in assessing Allee effects in coral fertilisation presents certain challenges. First, density is rarely reported in most monitoring programs (Edmunds & Riegl 2020), and deriving density from traditional surveys such as line-intercept transects (Dietzel et al. 2021), cannot, at present, distinguish between juveniles and adults. Additionally, the density estimate depends on the chosen survey area, and the choice of area therefore influences the final density estimate. During spatial analyses, survey boundaries (or bounding boxes) may be adjusted to more accurately reflect the spatial distribution of the data, leading to more reliable density estimates. However, in most coral monitoring programs, a fixed survey area, such as a belt transect is used, and density is calculated based on this predefined area, regardless of the underlying spatial point patterns and as such, the corresponding population density may change accordingly. Mumby et al. (2024) illustrated this point, where density measured over various spatial extents explained Allee-effect relationships less well than nearest-neighbour distance, likely because various levels of clustering occur at different spatial scales. For example, Figure 2 a-c describes three populations of equal size and density but with different spatial distributions. Here, the clustered population results in the highest modelled fertilisation success. Smaller mean spacing (or intercolonial distances) corresponds with this increase in fertilisation success. However, even spacing, even if slightly greater, outperformed the random spacing, likely because of the regularity in spacing throughout.

Population size can also influence Allee effects during fertilisation. This is illustrated when comparing fertilisation success of two populations with equal population density and spatial distributions (random) but differing population size and area (Fig. 2 d,e). The larger population results in higher modelled fertilisation success compared to the smaller population, where a greater proportion of gametes in the smaller population are lost to increased dilution at the population's boundaries (i.e., increased edge effects). In contrast, the larger population has a more extensive central region where sperm concentrations remain above the fertilisation threshold for longer, leading to higher overall fertilisation success. These simulated results are in agreement with work conducted on urchins (Levitan et al. 1992).

Coral cover is the most widely used parameter to describe coral populations during monitoring programs (Edmunds & Riegl 2020), but it is rarely collected at the species level needed to assess Allee effects and does not distinguish the number of individuals – i.e., all are pooled into an absolute cover

metric. Unlike other population metrics, coral cover inherently includes colony size, which is important because colony size directly determines total reproductive output. For this reason, any other spatial point parameter used needs to include a colony size distribution to appropriately weight individual's fertilisation contribution. Importantly, corals generally follow a size-fecundity relationship (Hall & Hughes 1996, Álvarez-Noriega et al. 2016), with smaller colonies either not spawning or having reduced output. This complicates extraction of population parameters from existing surveys, as colony size is often not included.

Mean colony spacing, also referred to as intercolonial distance or nearest-neighbour distance, is less straightforward to calculate and often requires spatial point pattern analysis. While mean spacing does not explicitly quantify clustering, it can reflect underlying spatial structure, particularly when colonies are aggregated, and thus provides a more informative measure than density alone for understanding fertilisation dynamics. As such, it is less sensitive to arbitrary boundary definitions or survey area size and offers a more ecologically meaningful measure of proximity between potential gamete sources. This makes it particularly valuable for modelling processes, such as gamete encounter rates in broadcast-spawning corals.

As other authors have argued it is unlikely that a single population parameter will sufficiently characterise all the information required (Gustafson 1998, Velázquez et al. 2016). Population density, spacing, colony size, and spatial configuration each capture different aspects of population structure. Adopting multiple parameters or using a single parameter while controlling secondary parameters within a narrow range, may be necessary to assess fertilisation outcomes reliably.

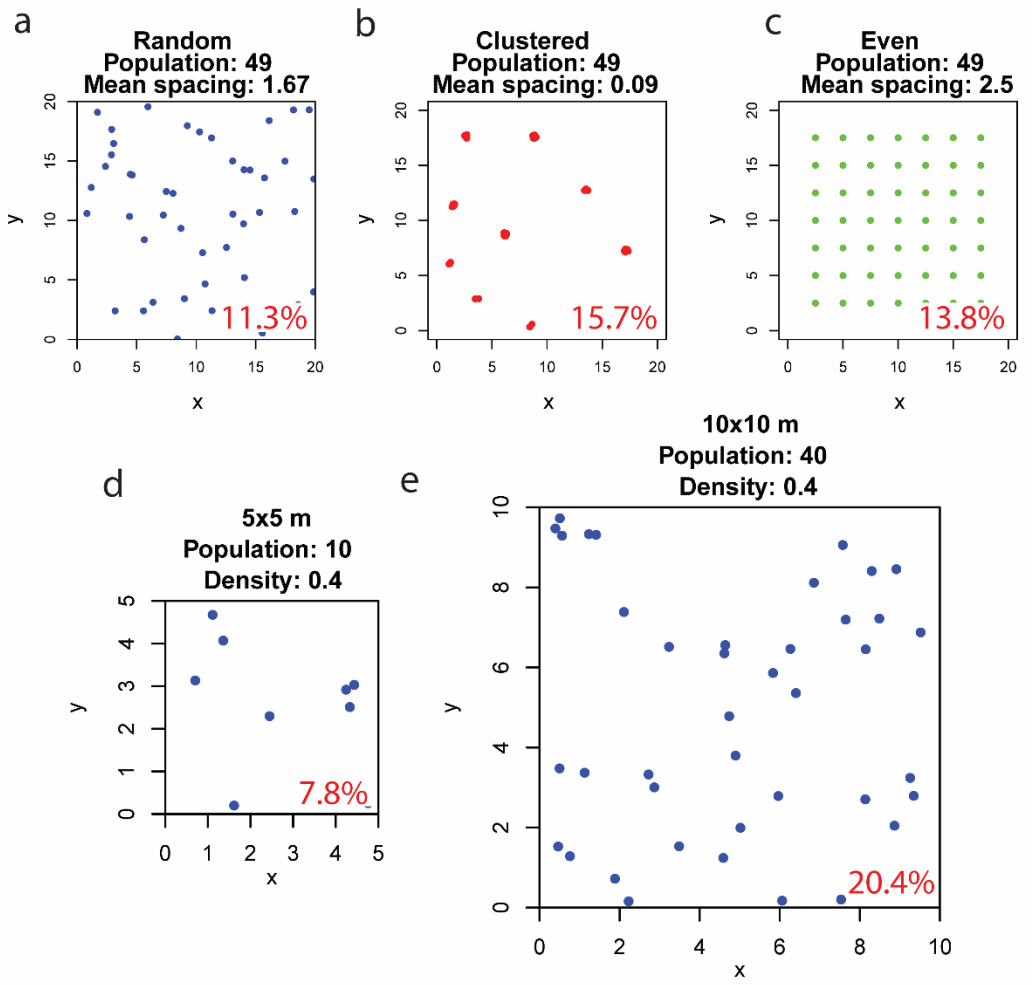


Fig. 2. (Top: a-c) Representative examples of various spatial distribution patterns using a constant population size, area, and density. Modelled mean fertilisation rates (n = 10) at a population density of 0.12 individuals m^{-2} following Ricardo et al. (2025a) correspond to random = 11.3% (95% CI: 9.4–13.2), clustered = 15.7% (95% CI: 13.3–18.1), even = 13.8% (95% CI: 11.2–16.4). (Bottom: d-e) A representative example of a constant population of 0.4 individuals m^{-2} density at two population sizes and spatial areas. Modelled mean fertilisation rates (n = 5 simulations) correspond to 7.8% (95% CI: 7.3–8.2) at a population size of 10 individuals per 25 m^2, and 20.4% (95% CI: 17.1–23.8) at a population size of 40 individuals per 100 m^2. Input model parameters: depth = 2 m; colony diameter = 25 cm; current velocity = 0.1 m s^{-1}.

A simplified model for broadcast spawners

To contextualise the role of Allee effects during broadcast-spawning fertilisation, several reproductive processes first need to be considered and eventually parametrised if modelled. This review examines each stage of the spawning process, some of which are illustrated in Figure 3, and details these processes before discussing their significance in understanding Allee effects.

Most coral species, especially in the Indo-Pacific, are hermaphroditic broadcast spawners, releasing their eggs and sperm into the water column for fertilisation (Baird et al. 2009). Gametogenesis of oocytes begins approximately nine months prior to the time of spawning, whereas sperm develop only a few weeks before the event (Harrison & Wallace 1990). Often, both the egg and sperm are packed together into an egg-sperm bundle, bound by a mucous membrane (Padilla-Gamino et al. 2011). A range of environmental factors synchronise spawning to occur at predictable times of the year, with the primary factors being the change in water temperature, lunar cycle (time from full moon), and onset of darkness (Keith et al. 2016), often allowing researchers to predict spawning within a night or two of the event. Spawning in corals is often multispecific, with many species spawning on the same night, or within the same week (Fig. 4c). Yet subtle differences in reproductive timing isolate many species, often preventing hybridisation (Wolstenholme 2004, Levitan et al. 2011).

Most empirical studies and biophysical modelling of external reproduction in marine invertebrates have been conducted on organisms that release sperm from the seabed, where fertilisation is greatly influenced by benthic dispersive processes (Babcock et al. 1994, Levitan & Petersen 1995). However, the buoyancy of coral egg-sperm bundles, and the eggs themselves once the bundles break apart, confines fertilisation largely to the upper water column. Water column processes also need to be accounted for, including the ascent of egg-sperm bundles and the eventual vertical diffusion of sperm from the surface. High synchrony results in maximal gamete concentrations of colonies nearby, whereas differences in individual spawning timing can result in fertilisation of colonies at greater distances, increasing gametic mixing through dispersal, but ultimately leading to lower overall gamete concentrations and fertilisation. The specifics of these processes are detailed below and in Figure 3.

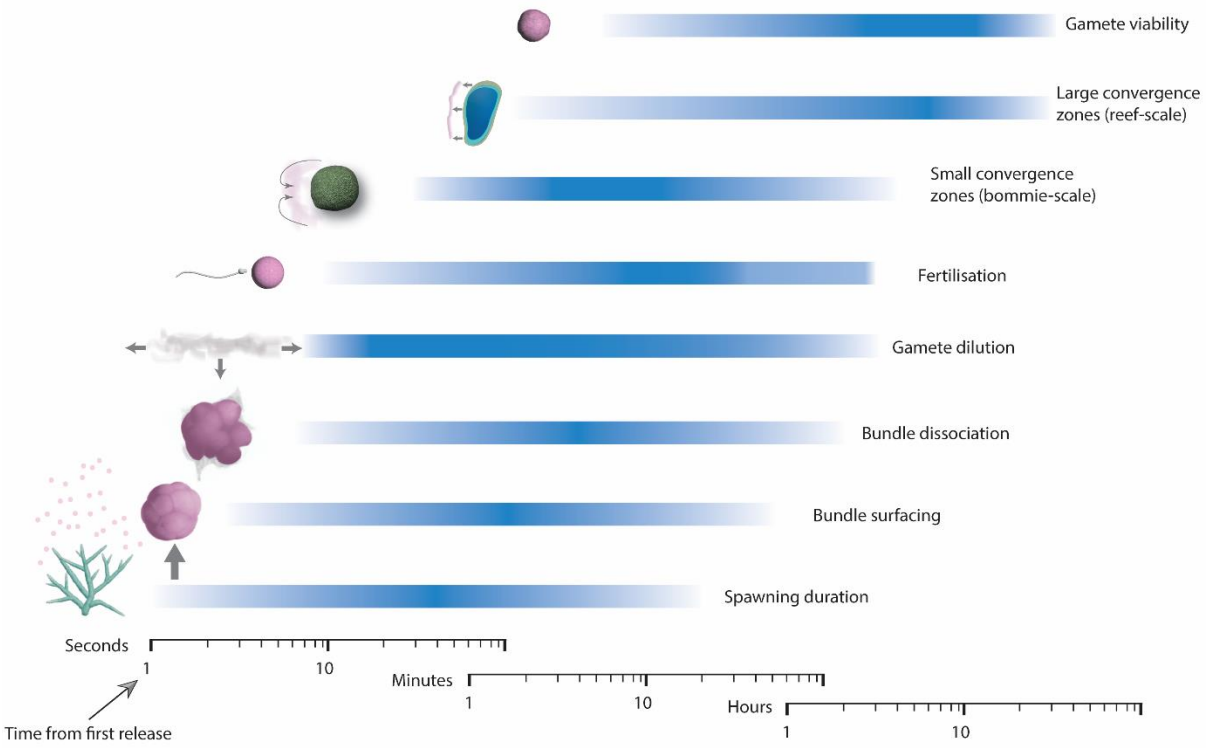


Fig. 3. The key sequential temporal processes of coral reproduction relevant during the fertilisation window. The gradient shading indicates the expected start, peak and end of the reproductive processes. For further detail and supporting literature, refer to the corresponding sections. Coral spawning is followed by bundle surfacing and dissociation, at which point fertilisation commences under sperm and egg dilution. Small scale convergent zones may begin to retain gametes, especially eggs, and at longer time frames reef-scale convergent zones result in visible slicks. Fertilisation is ceased when gametes are too dilute, and eventually lose viability.

Colony size and reproductive output

In colonial organisms, colony size and the proportion of the colony that is fertile determine the overall reproductive output of the colony. Each polyp within the colony typically releases one egg-sperm bundle, and therefore with the addition of an estimate of polyp density, the reproductive output can be determined. For many genera, polyp density generally ranges from 50 to 100 polyps cm^{-2}, but massive and submassive groups often have much lower polyp densities (Yasuda et al. 2012, Álvarez-Noriega et al. 2016, Madin et al. 2016, Henley et al. 2021).

Within a colony, infertile zones occur due to damage, immaturity, or senescence (Wallace 1985, Sakai 1998, Baria et al. 2012). The fertile zones have been estimated using histology and microscopy-based techniques to assess oocytes within different parts of the colony. For a typical non-fragmented colony, Connell (1973) described that individuals need to reach a certain size before fecundity commences, typically around 10 cm diameter for *Acropora*, after which fecundity increases progressively with colony growth. As such, a relationship between colony size, maturity and fecundity can often be derived (Hall & Hughes 1996, Álvarez-Noriega et al. 2016). The extent of the fertile zone therefore determines the reproductive colony size and, subsequently, the reproductive output of each individual.

As climate change and other stressors increasingly degrade coral populations, this may lead to a reduction in large size classes, as larger colonies will have little opportunity to reach older ages before the next disturbances occur (Riegl & Purkis 2015), possibly resulting in lower reproductive output if this loss in colony size is not offset by increased colony density (Speare et al. 2022).

Coral spawning

The release of egg–sperm bundles in many genera is not often instantaneous or tightly synchronous, but rather occurs in pulses or as a continuous plume, although there are some notable exceptions (Lotterhos et al. 2010). Total spawning time is usually complete within 2 hours (Fig. 4a), while individual spawning time is shorter. Suzuki et al. (2025) reported mean individual release times as 9 – 15 min across spawning seasons. The rate of release is reported to increase following the initial release, reaching a maximum and then gradually decreasing, indicating a right-skewed distribution (Takeuchi et al. 2022). Staggered release may be a strategy to avoid sperm swamping (Marshall & Bolton 2007), and to increase gametic mixing and dispersal. During this protracted release, the bundles are subject to water currents and turbulent forces that transport the bundles away from their point of release. Little is reported about how consequential this initial dispersal is, but assuming a typical mean current velocity of 0.1 m s^{-1} and a release over 9–15 min (Suzuki et al. 2025), egg-sperm bundles from one individual may disperse a 54 to 90 m long slick during this time. The staggering between early-released bundles and later-released bundles provides a potential mechanism for overlap and mixing of bundles between individuals.

Spawning synchrony is one of the main determinants of fertilisation success in corals, but asynchrony has been observed across spawning months and days, and within days (Oliver & Babcock 1992, Miller et al. 2016, Baird et al. 2021). One study reported complete localised outcrossing failure in a species that spawned across several hours (Ricardo et al. 2025b). Synchrony can vary across spatial scales, with individuals closest to each other more likely to spawn together, either due to microenvironmental gradients, or pheromonal cues that have mostly been hypothesised for corals but not clearly demonstrated (Levitan et al. 2011, Mumby et al. 2024). Some authors have suggested it is a bet-hedging strategy in case the main night of spawning coincides with unfavourable weather conditions (Post et al. 2001). For example, a full reproductive event was reported lost for an isolated reef on the Great Barrier Reef following heavy rain (Harrison et al. 1984).

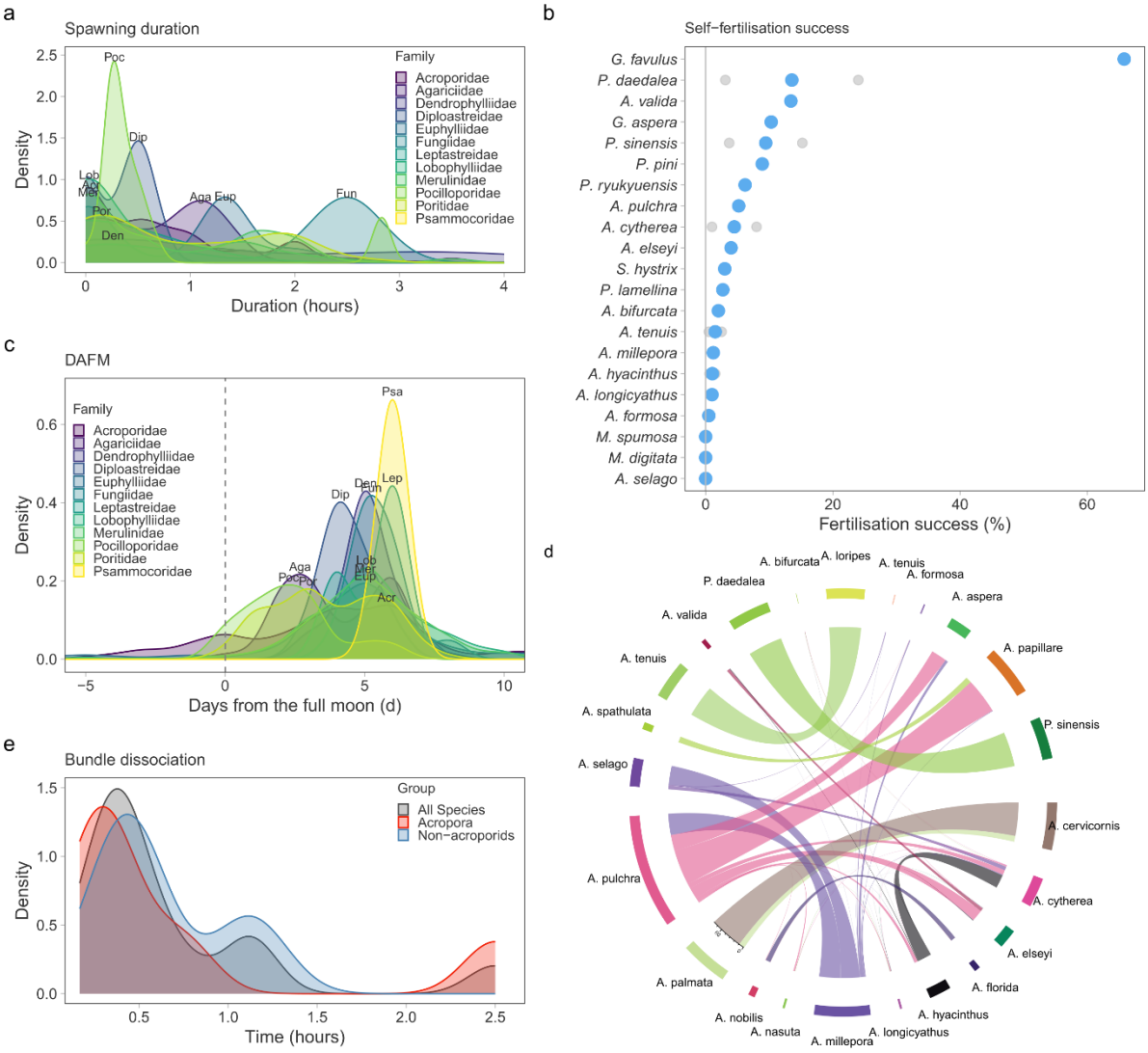


Fig. 4. Spawning and reproductive processes in hard corals. (a) Distribution of spawning duration (Coral spawning database; Baird et al. (2021)). (b) Self-fertilisation success across multiple species. Grey = individual values; blue = species mean reported in (Heyward & Babcock 1986, Miller & Babcock 1997, Willis et al. 1997, Warner et al. 2016, Ramírez-Portilla et al. 2022). (c) Number of species spawning on nights following the full moon (n = 93 species; Baird et al. (2021)). (d) Hybridisation between species reported in (Willis et al. 1997, Hatta et al. 1999, Van Oppen et al. 2002, Fogarty et al. 2012, Chan et al. 2019, Ramírez-Portilla et al. 2022). Band thickness reflects level of fertilisation success, see scale. (e) Reported bundle dissociation times in hard corals in (Kojis & Quinn 1982, Babcock 1984, Hunter 1988, Shlesinger & Loya 1991, Hayashibara et al. 1997, Wolstenholme 2004, Padilla-Gamino et al. 2011). Median values were estimated from reported ranges assuming a Gaussian distribution. Overall median dissociation time was 18 minutes.

Egg-sperm bundle ascent

Most corals have evolved packaging eggs and sperm into bundles that float to the water's surface, thereby reducing the effects of dilution by reducing the concentration to a '2D' plane (Moláček et al. 2012). Egg-sperm bundles are approximately 1 mm in diameter, with the bundle containing a sperm packet that is either neutral or slightly negatively buoyant (Padilla-Gamino et al. 2011). For *Acropora* and *Montipora*, egg-sperm bundles contain 3–15 buoyant eggs with ~10^6 sperm per bundle (Wallace 1999, Miller et al. 2018, Furukawa et al. 2020, Henley et al. 2021). Other genera have been reported to contain upwards of 50 eggs and 10^7 sperm per bundle (Madin et al. 2016, Teo et al. 2016). In static

or low flow conditions, the bundle following release rises to the water's surface at a rate of 5–10 mm s^{-1}; therefore, a bundle releasing from 10 m depth could take 20 minutes to reach the water's surface, as observed in *Orbicella* (*Montastraea) franksi* (Levitan et al. 2004). However, ascent under flow and turbulence may be elevated due to localised topographic upwelling and flow acceleration streamlines as currents intercept reef gradients, and work using a Couette device has found that turbulent forces can enhance the upward velocity of buoyant particles (Ruiz et al. 2004). For example, bundles have been observed to ascend at magnitude faster rates for some *in situ* observations compared to laboratory observations (Table 4). However, turbulent forces can easily overwhelm buoyant ascent rates leading to vertical fluctuations, making it difficult to track individual bundles and determine exact ascent rates.

Table 4. *Ex situ* and *in situ* egg-sperm bundle and egg ascent rates.

SPECIES	GAMETE TYPE	SPEED (MM S^{-1})	STUDY TYPE	NOTES	REFERENCE
MONTIPORA DIGITATA	Bundles	6.4	*Ex situ*	–	Ricardo et al. (2016)
ACROPORA MILLEPORA	Bundles	5.8	*Ex situ*	–	Ricardo et al. (2016)
ACROPORA NASUTA	Bundles	4.6	*Ex situ*	–	Ricardo et al. (2016)
ACROPORA CF. TENUIS	Bundles	4.3	*Ex situ*	–	Ricardo et al. (2016)
ORBICELLA FRANKSI	Bundles	8.3	*In situ*	Converted from 0.5 m min^{-1}	Levitan et al. (2004)
DIPLORIA STRIGOSA	Bundles	111.1	*In situ*	Converted from 9 s m^{-1}	Gittings et al. (1992)
ACROPORA CF. HYACINTHUS	Bundles	60	*In situ*	Converted from 0.06 m s^{-1}	Mumby et al. (2024)
ACROPORA CF. TENUIS	Eggs	2.7	*Ex situ*	–	Ricardo et al. (2025a)

Egg-sperm bundle dissociation

Egg-sperm bundle dissociation has almost exclusively been measured in the laboratory and reported to range from immediately following surfacing, to over an hour depending on species and prevailing weather conditions (Table 5, Fig. 4d). The dissociation occurs with the rupturing of the bundle membrane releasing the eggs and sperm. Some species, such as *Acropora millepora*, with thicker membranes can require vigorous agitation in laboratory settings to break the membrane indicating longer delay times between spawning and the earliest fertilisation (G. Ricardo personal obs.). Assessment of dissociation time *in situ* is greatly needed to better parametrise biophysical models under a range of conditions, since dispersal is dependent on gamete type and fertilisation can only occur after the bundle ruptures.

Delayed bundle dissociation also has the potential to increase gamete mixing. In scenarios when bundles dissociate rapidly, eggs will more likely fertilise with their nearest neighbours, thereby reducing the available pool of gametes downstream. Delayed dissociation may increase opportunities for spatially separated gametes to coalescence or meet in convergence zones.

Table. 5. Bundle dissociation times (decimal hours) reported for laboratory and field observations.

SPECIES	STUDY TYPE	MIN (H)	MEAN (H)	MAX (H)	NOTES	REFERENCE

GONIASTREA ASPERA	Laboratory	–	0.50	–	Bundles break up after 30 min of reaching the surface	Babcock (1984)
ACROPORA FLORIDA	Laboratory	–	0	–	Immediately broke apart	Hayashibara et al. (1997)
ACROPORA HYACINTHUS	Laboratory	–	0	–	Immediately broke apart	Hayashibara et al. (1997)
ACROPORA NASUTA	Laboratory	–	0	–	Immediately broke apart	Hayashibara et al. (1997)
MONTIPORA DIGITATA	Laboratory	0.75	–	1.50	45-90 min	Hunter (1988)
MONTIPORA VERRUCOSA	Laboratory	0.75	–	1.50	45-90 min	Hunter (1988)
FAVITES ABDITA	Laboratory /Field	0.05	–	1.00	A few min to an hr after reaching the surface	Kojis and Quinn (1982)
LEPTORIA PHRYGIA	Laboratory /Field	0.05	–	1.00	A few min to an hr after reaching the surface	Kojis and Quinn (1982)
FAVIA FAVUS	Laboratory	0.17	–	0.58	10 to 20 min after spawning	Shlesinger and Loya (1991)
PLATYGYRA LAMELLINA	Laboratory	0.17	–	0.58	10 to 20 min after spawning	Shlesinger and Loya (1985)
ACROPORA DIGITIFERA	Laboratory	0.08	–	0.25	5-15 min (from table)	Wolstenholme (2004)
ACROPORA GEMMIFERA	Laboratory	0.08	–	0.50	5-30 min (from table)	Wolstenholme (2004)
ACROPORA HUMILIS	Laboratory	1.00	–	4.00	1-4 hrs (from table)	Wolstenholme (2004)
ACROPORA MONTICULOSA	Laboratory	0.50	–	1.00	30-60 min (from table)	Wolstenholme (2004)
ACROPORA SAMOENSIS	Laboratory	0.08	–	0.50	5-30 min (from table)	Wolstenholme (2004)

Gamete maturity

The egg is hypothesised to be immature until the release of the first polar body, and possibly also the second polar body release. The first polar body is a small cytoplasmic exclusion that results from uneven cell division during meiosis I, marking the transition from an immature to a mature egg phase (Schmerler & Wessel 2011). The second polar body release occurs at the time of fertilisation (Schmerler & Wessel 2011). In some marine organisms, the site of the polar body release may result in the fertilisable fraction of the egg (Freeman & Miller 1982). In corals, it is thought that polar body release occurs within 30 minutes after spawning (Babcock & Heyward 1986, Heyward & Babcock 1986, Okubo & Motokawa 2007), and that eggs may be infertile before that point. It is hypothesised that a delay in polar body release may be used as a mechanism to prevent self-fertilisation (Babcock &

Heyward 1986). However, Ricardo et al. (2025a) found that in *Acropora* cf. *tenuis*, eggs broken free of bundles prematurely and exposed to sperm within a few minutes of spawning did not result in different levels of fertilisation success than those exposed 30 minutes later.

Sperm in some species are initially immobile while in high concentrations but are quickly activated as the sperm dilute (e.g., *A.* cf. *tenuis*), whereas other species appear to have fully motile sperm at the point of bundle rupture (e.g., *A. millepora*). While contact times are variable between species, some experiments examining egg-sperm contact times have shown that the mature eggs are fertilisable within a few minutes of exposure to sperm, and often less than 30 minutes (Iguchi et al. 2009, Nozawa et al. 2015, Buccheri et al. 2023). Together, this suggests that, *in situ*, the timing of bundle dissociation may be the key factor determining when gametes become fertilisable, rather than egg immaturity in the genus *Acropora*.

Sperm swimming and egg-sperm encounters

Sperm swim irregularly and in helical patterns, and speeds have been reported from 250 µm s^{-1} (0.00025 m s^{-1}) to 350 µm s^{-1} (0.00035 m s^{-1}) (Farley 2002, Morita et al. 2006, Buccheri et al. 2026a). Given horizontal and vertical current velocities on reefs are typically in the range of 0.001 to 1 m s^{-1}, sperm swimming alone provides limited diffusion and mixing of gametes (Hata et al. 2017). However, sperm swimming velocity plays a role in egg-sperm encounter rates, and chemotaxis of the egg may allow the sperm to navigate to a conspecific egg when in proximity, potentially increasing their swimming speed (Coll et al. 1994, Morita et al. 2006). In other free-spawning invertebrates, gamete recognition proteins are species-specific and rapidly evolving as a way to optimise fertilisation success under varying spawning densities, where selection pressures differ between sperm-limited and sperm-saturated conditions (Levitan & Ferrell 2006).

Like other marine invertebrates, only a fraction of the egg is assumed to be fertilisable and combined with other factors such as sperm viability and helical swimming directions, many egg-sperm contacts are required to achieve successful fertilisation (Vogel et al. 1982). Egg-sperm encounters increase exponentially with sperm concentration. As such, the *fertilisation efficiency* (sensu Styan (1998)), which is the actual fertilising egg-sperm contacts as a proportion of all predicted egg-sperm contacts, may be less than 5% for corals (Buccheri et al. 2026a).

Fertilisation

Typically, a minimum sperm concentration of 10^3 sperm mL^{-1} is needed to initiate fertilisation and maximum fertilisation (saturation) often begins at 10^5 sperm mL^{-1} (Nozawa et al. 2015, dela Cruz & Harrison 2020, Buccheri et al. 2023, Chamberland et al. 2025). The exact moment of fertilisation is difficult to ascertain in corals, even under microscopy. Unlike in urchins, no immediate structural changes to the fertilised egg are obvious in corals following fertilisation (G. Ricardo, pers. obs.), although such changes have been documented in urchins (Vacquier et al. 1973). The most reliable method for inferring the time of fertilisation is to use the timing of first cell cleavage, based on controlled fertilisation assays conducted under the same environmental conditions (e.g. temperature). First-stage cleavage for most embryos is reached within 2h from fertilisation in many species (Okubo et al. 2013), and given that adequate fertilisation is achieved within 1 min of egg–sperm contact (Buccheri et al. 2023), fertilisation can be coarsely inferred from this time.

Polyspermy and water chemistry at elevated gamete concentrations

While the focus of this review is related to inverse-density dependence, some aspects need to be discussed in the context of negative density dependence. Some genera exhibit a reduction in apparent fertilisation success at high sperm concentrations, commonly attributed to a weak or absent

polyspermy block (Styan 1998). In this case, multiple sperm fertilise an egg resulting in chromosomal abnormalities and disruption to cell division (cleavage), subsequently causing irregular development and failure of the embryo. From an evolutionary standpoint, species with efficient blocks to polyspermy are likely those where spawning might result in saturating levels of sperm concentrations (Marshall & Bolton 2007); for example, the widespread genus *Acropora* that dominates coral cover in much of the Indo-Pacific has an efficient polyspermy block (Morita et al. 2006, Nozawa et al. 2015). Alternatively, an absence of polyspermy blocks may not have evolved in species that rarely reach saturating sperm concentrations. Interestingly, there are some conflicting results where the same genera have shown strong and absent polyspermy effects such as *Favites*, *Platygyra* and *Acropora* (Oliver & Babcock 1992, Fogarty et al. 2012, Nozawa et al. 2015, Buccheri et al. 2023). For species that exhibit strong polyspermy blocks, the level of fertilisation success can be indicative of the background sperm concentration at the time of the fertilisation, whereas for species with weak polyspermy blocks, low fertilisation may indicate both low and high sperm concentrations, making interpretations more challenging. Further, polyspermy may not always manifest in fertilisation inhibition, but rather a flattening of the fertilisation curve (Styan 1998).

Intraspecific gamete incompatibility

One-to-one cross experiments have revealed that gametes do not always achieve the same level of fertilisation success between individuals of the same species, with some crosses incompatible and some unidirectional compatibility (Willis et al. 1997, Baums et al. 2013, Miller et al. 2018). This is probably most well documented in the Caribbean where fertilisation success of some of the major framework species fail to consistently achieve >50% fertilisation success, in addition to already low and declining population densities, increasing concerns that Allee effects are already occurring under current reef degradation (Birkart & Álvarez-Filip 2025, Manzello et al. 2025). However, mixed pool crosses regularly achieve high levels of fertilisation success, indicating that fertilisation success is not random, and that mixed pool embryos may represent clustering or incomplete mixing, with some pairwise combinations of parents contributing disproportionately to embryo generation (Baums et al. 2013, Iwao et al. 2014). One explanation for some trends is that cryptic species (i.e. genetically distinct groups within morphologically defined species) may lead to absent or reduced compatibility (Sheets et al. 2018).

Selfing and parthenogenesis

In many corals, self-fertilisation is thought to be low (<3%) even in ideal laboratory conditions but still needs to be considered when considering Allee effects where *in situ* fertilisation can also be low (Fig. 4b). Selfing in corals could occur by syngamy of gametes originating from a single polyp (autogamy), or by syngamy of gametes from different polyps (geitonogamy) (Carlon 1999). Similar to hybridisation, gamete recognition mechanisms prevent self-fertilisation in many species, and is generally low (often less than 2%) in *Acropora* (Hatta et al. 1999). Self-fertilised embryos are genetically similar to the adult; and therefore, self-fertilisation can lead to inbreeding depression—another Allee effect. Little work has been conducted to determine the extent that selfed embryos are maintained in the population. Some genera exhibit high levels of self-fertilisation when exposed to high sperm concentrations for long contact times in absence of non-self conspecifics (Miller 1994, Willis et al. 1997). This results in selfed embryos being delayed in development relative to non-selfed embryos, often by a few hours. It is unknown whether selfing is an adaptive response to Allee effects, or if it is merely an unintended response to the break-down of self-recognition systems over time. Some authors have suggested that gonochorism may have evolved to reduce the probability of self-fertilisation (Guest et al. 2012). Parthenogenesis, the development of an embryo without fertilisation, has been identified in corals, particularly in brooding species (Combosch & Vollmer 2013, Levitan et al. 2025). Outside of laboratory

experiments, *in situ* selfing rates are poorly understood (Baums 2008). However, a recent study during a high asynchronous spawning of *Platygyra daedalea* indicated that all of the few embryos produced resulted from selfing (Ricardo et al. 2025b). Selfing may result in lower embryo survival than non-selfed counterparts (Baums 2008), but is largely unknown.

To assess selfing, gametes of the parent need to be held in isolation from other spawning conspecifics. The risk of contamination creating false positives can be high and is often given as an explanation for samples with elevated selfing rates (Szmant et al. 1997). However, genetic work has indicated that selfing may be inconsistent between individuals and therefore should not be automatically ruled out. Few studies have investigated sperm concentration, contact time on selfed embryos, and studies reporting need to be interpreted in the context of long contact times and elevated sperm concentrations, which are unlikely under natural conditions; therefore, it is likely self-fertilisation is actually lower than those values reported. To assess parthenogenesis, sperm need to be washed free from the eggs immediately after bundle dissociation. Genetic work may further help differentiate the two asexual modes of reproduction.

Hybrid embryos

Hybridisation complicates interpretation of Allee effects during fertilisation because of the uncertainty in the ongoing fitness of these hybrid individuals compared to individuals produced from intraspecific crosses. While the role of hybridisation in adult populations is debated, there is evidence that hybridisation is widespread in corals despite there being few unambiguous examples of hybrid species (Richards & Hobbs 2015). The lack of spatial and temporal reproductive isolation in many sympatric species of reef corals that participate in the multispecific annual coral spawning event allows for gametes of numerous species to interact, and one-to-one cross fertilisation experiments have shown low to moderate success following interspecific fertilisation (Figure 4e). For example, Willis et al. (1997) found one-third of the *Acropora*, *Montipora* and *Platygyra* tested displayed evidence of early-stage hybridisation through embryogenesis, with survivorship generally comparable to congeneric crosses. Using molecular techniques on adults, eighty-one species of coral in total have shown evidence of hybridising, including approximately 15% of Acroporidae (Hobbs et al. 2022). Similar to intraspecific crosses, they may only function unidirectionally – e.g., one species' eggs will cross-fertilise with the other species' sperm, but not vice versa (Chan et al. 2019).

For those species that do not cross-fertilise, gamete compatibility, gamete recognition and reproductive isolation barriers may be sufficient. Chemotaxis of the egg may be an important mechanism for avoiding hybridisation (Coll et al. 1994, Morita et al. 2006), and gamete recognition systems (GRSs) such as allorecognition molecules and specific loci that act cooperatively have been associated with self/non-self-recognition in marine invertebrates (Sawada et al. 2004, Harada et al. 2008) and reviewed by (Evans & Sherman 2013). However, under low sperm concentrations, hybridisation may increase (Isomura et al. 2016, Kitanobo et al. 2016). While there is evidence of F1 hybridisation occurring, this generation may not be able to produce viable gametes for further generations, although nonsterile crosses have been occasionally observed (Isomura et al. 2016, Kitanobo et al. 2022a). Hybridisation is proposed to increase under reef degradation, as the effective population size (N_e) decreases, which may counter Allee effects during fertilisation (Pinsky et al. 2023).

Gamete viability

Acropora have relatively long gamete viability periods compared with other marine organisms such as echinoderms (Styan 1998), with gamete half-life often exceeding 6 hrs (Willis et al. 1997, Omori et al. 2001, dela Cruz & Harrison 2020), although some studies report shorter durations (Table 6). The initial reduction in gamete viability is likely due to depleted dissolved oxygen in the sperm environment

(Oliver & Babcock 1992, Simpson et al. 1993, Styan & Butler 2000), and some studies have bubbled air into the bulk sperm (Willis et al. 1997, dela Cruz & Harrison 2020), thus potentially extending sperm lifespan beyond what may occur *in situ* (i.e., high sperm concentrations would dilute under turbulent conditions). However, actual measurements of water chemistry are lacking in coral (but see Buccheri et al. (2026a)). In other marine invertebrates, this has been referred to as the 'respiratory dilution effect' where there is a negative relationship between sperm concentration and gamete longevity. Nonetheless, in most natural settings, dilution likely limits the fertilisation window well before ageing effects become significant.

Eggs have also been shown to decompose, sometimes commencing within a few hours of spawning, and are especially relevant to low-flow and possibly deoxygenated water typical of dense coral slicks. Oliver and Babcock (1992) reported eggs of *Platygyra sinensis* decomposing within 3 hr of spawning in the laboratory. Omori et al. (2001) reported reasonably high fertilisation success (~65–78%) in embryos found the next morning (~10 am), although eggs were already observed to be decomposing, indicating that developing slicks of embryos suffer from survivorship bias and that the true fertilisation success is lower than the number reported.

Table 6. Effects of gamete age on fertilisation success. Note that '>' denotes that the threshold was not reached within the tested time intervals.

SPECIES	EC50 HALF-LIFE (APPROX.)	SPERM CONCENTRATION	NOTES	REFERENCE
PLATYGYRA ACUTA	6	10^6	No aeration	Chui et al. (2014)
ACROPORA MILLEPORA	8	Unknown	Aeration	Willis et al. (1997)
MONTIPORA DIGITATA	>2.5	10^5–10^6	Not described	Oliver and Babcock (1992)
FAVITES PENTAGONIA	>2	10^5	Not described	Oliver and Babcock (1992)
PLATYGYRA SINENSIS	3.5	10^5–10^6	Not described	Oliver and Babcock (1992)
ACROPORA MILLEPORA	5	10^5	Aeration	dela Cruz and Harrison (2020)
ACROPORA CF. TENUIS	5	10^5	Aeration	dela Cruz and Harrison (2020)
FAVITES COLEMANI	3	10^5	Aeration	dela Cruz and Harrison (2020)
ACROPORA CF. TENUIS	7	10^7	Not described	Omori et al. (2001)
ACROPORA MILLEPORA	2.5	10^5	Approximate 30 min gamete processing time added.	Ricardo et al. (2015)
ACROPORA PALMATA	<4-5	~10^6	Not described	Fogarty et al. (2012)
ACROPORA CERVICORNIS	>4-5	~10^6	Not described	Fogarty et al. (2012)

Gamete quality

Fertilisation kinetics models (described below) suggest that only a small fraction of potential egg-sperm contacts actually result in successful fertilisation (Vogel et al. 1982). Among the many reasons, sperm quality is a major factor. Morphological abnormalities with the sperm have been shown to be associated with sperm motility, which is a strong measure of fertilisation success (Hagedorn et al. 2017, Zuchowicz et al. 2021, Amaral et al. 2022). For *Acropora hyacinthus*, motile sperm are approximately 25% of the total sperm concentration (Zuchowicz et al. 2021), however, this value is likely to change between spawn seasons and perhaps days within the spawning cycle.

Not all eggs in marine invertebrates are capable of fertilising, even given optimal fertilisation conditions, leading to gamete wastage (Lehtonen & Dardare 2019). In *Acropora*, maximum fertilisation success in laboratory studies is routinely >75% (Nozawa et al. 2015). However, some studies have found maximum fertilisation at lower levels, even when sufficient sperm concentrations were supplied (Coma & Lasker 1997b, Miller & Babcock 1997). In many organisms, aneuploidy, defined as an abnormal number of chromosomes, can lead to early developmental failure or inviability. However, little research has investigated whether aneuploidy contributes to reduced fertilisation success or early embryonic arrest in corals (Kenyon 1997). Other factors such as mutations, epigenetic modifications and physical damage could also contribute to some inviable eggs (Gallo et al. 2022). Predictions of total embryos generated fertilisation models need to account for this incomplete fertilisation capacity.

Caution is warranted when interpreting maximum fertilisation success as evidence of egg infertility under high sperm concentrations. While overt polyspermy can be identified by a sharp decline in fertilisation success at excessive sperm levels, more subtle forms of polyspermy may not reduce fertilisation outright (Styan 1998). Instead, they can cause a plateau or 'flattening' of the fertilisation curve, potentially giving the misleading impression that some eggs are infertile.

Hydrodynamics and bathymetry

As hydrodynamic processes ultimately result in various levels of dilution and possibly reconcentration of gametes, they directly affect gamete encounters and thus play a key role in shaping Allee effects during fertilisation. Yet the unpredictability of such conditions may result in varying degrees of fertilisation regardless of adult densities or their spatial distributions (Yund 2000). Most coastal hydrodynamic research has been based on lower complexity environments such as river channels, sandy beds and oceans, rather than the structurally complex habitats of coral reefs (Shchepetkin & McWilliams 2005, Benedini & Tsakiris 2013). Moreover, hydrodynamic processes at the water's surface have received far less attention than those near the seabed in coral reef environments (Monismith 2007). Wind, waves, and currents advect egg-sperm bundles away from their point of release, with currents being the dominant advective force (Fig. 5c). Turbulence, generated by the interaction of wind, waves and currents with the water column, enhances mixing and dispersion. Shear layers, formed by velocity gradients, contribute to both dispersal and dispersion, while convergence zones, driven by fronts or eddies, can accumulate buoyant particles and create concentrated spawn slicks (Oliver & Willis 1987, Gouezo et al. 2025) (Fig. 5a). Small-scale eddies and Langmuir circulation windrows create localised mixing and microaggregations (Kingsford et al. 1991, Coffroth & Lasker 1998). Additionally, water stratification may confine coral spawn within the surface layer, limiting vertical mixing. These factors apply at different spatial scales and vary considerably in space and time. As such, there is an unpredictable component to assessing Allee effects during coral fertilisation. Dominant processes that influence spawn concentration on a wave-exposed windward reef face, will likely be very different from those on the leeward side. Moreover, windward bathymetric features

shaped by wave exposure, such as spurs and grooves, may also trap gametes in ways analogous to surge channels on temperate reefs (Denny et al. 1992). Metrics and terminology used to describe hydrodynamic and turbulence parameters are provided in Table 7.

Table 7. Relevant hydrodynamic and turbulence parameters in coral reef environments.

PARAMETER	SYMBOL	TYPICAL VALUES	NOTES	MEASUREMENT/DERIVATION METHOD
CURRENT VELOCITY	$U, u, \bar{u}$	0.1–1 m/s	Mean flow speed; varies with tidal cycles and local topography.	Acoustic Doppler Velocimeter (ADV), Acoustic Doppler Current Profiler (ADCP).
SHEAR VELOCITY	u_*	0.005–0.1 m/s	Typically, 5–10% of the mean flow speed; influenced by seabed roughness.	Derived from velocity profiles or Law of the Wall equation.
DRAG COEFFICIENT	C_d	0.001–0.01	Represents frictional resistance; varies with flow conditions and reef structure.	Estimated from velocity profiles and pressure measurements.
STOKES DRIFT VELOCITY	u_s	0.01–0.1 m/s	Wind-induced surface particle transport; influences larval dispersal.	Computed using wave and wind models.
TURBULENT KINETIC ENERGY	k, TKE	10^{-4}–10^{-2} m^2/s^2	Energy per unit mass from turbulence; higher near reef structures.	Derived from ADV turbulence measurements.
TURBULENT DISSIPATION RATE	ε	10^{-6}–10^{-3} m^2/s^3	Rate of energy dissipation; higher in energetic reef zones.	Estimated from velocity fluctuations and TKE budget equations.
TURBULENCE INTENSITY	I	0.01–0.3	Ratio of velocity fluctuations to mean flow velocity; indicates turbulence levels.	Derived from ADV measurements and spectral analysis.
DIFFUSIVITY	D_x, D_y, D_z	10^{-3}–10^{-1} m^2/s	Rates of turbulent diffusion in respective directions; influence pollutant dispersion.	Derived from dye release experiments or numerical models.
LANGMUIR CIRCULATION STRENGTH	—	Variable	Influences surface mixing and convergence zones; strength depends on wind and wave conditions.	Observed using surface drifters and dye release experiments.
BOUNDARY LAYER THICKNESS	δ	0.1–1 m	Thickness of flow-affected region near the seabed; influences nutrient exchange.	Measured using velocity profiles from ADV or ADCP.

Bundle and egg diffusion

Upon reaching the water surface, egg-sperm bundles are exposed to the water surface shear, and wind- and wave-driven turbulence that may act in different ways compared to the water column current. Under low wind conditions, egg-sperm bundles are generally expected to follow the same advective direction as the ambient current, limiting gametic mixing across the reef. Stokes drift, a net forward transport of particles arising from the unclosed orbital paths of surface gravity waves, is a persistent feature of wave-driven surface environments. Combined with wind speed, these processes can form Langmuir circulation windrows, i.e., streaks that run parallel to the wind, which may aggregate gametes into lines and rows (Chang et al. 2019). The stickiness of the mucous coating of bundles also creates aggregating properties, keeping many egg-sperm bundles within closer proximity to each other than other buoyant plankton. Other water properties such as water surface tension and hydrophobic properties of the gametes may act to resist planar dispersion (Singh & Joseph 2005, Crimaldi 2012, Crimaldi & Zimmer 2014). Further, less predictable and localised turbulent forces around reef bommies (isolated reef patches) and edges may interact with egg-sperm bundles, increasing mixing, dispersal, but also locally concentrate or trap bundles.

Eggs are expected to follow many of the same processes as egg-sperm bundles. Eggs are marginally smaller at ~150 to 700 µm diameter, depending on the species (Wallace 1999, Madin et al. 2016), and lack the sticky mucus coating of the egg-sperm bundles, likely reducing some of the aggregation effects proposed for egg-sperm bundles. Eggs are only slightly less dense than seawater (Ricardo et al. 2025a), and thus small waves and surface turbulence can submerge eggs temporarily creating an upper layer suspension as opposed to a surface slick (Oliver & Willis 1987, Moláček et al. 2012).

Sperm diffusion and dilution

The diffusion and dilution of sperm is the main mechanistic factor leading to reduced fertilisation, and, when combined with low initial sperm concentrations, produces 'sperm limitation' (Levitan & Petersen 1995). Coral sperm are only a few microns wide and typically less than 50 µm in length, and at this scale exhibit characteristics of both dissolved tracers and particulates. They advect and diffuse through the water column similar to tracer dye but also likely sink due to their negative buoyancy and flocculation (Kono et al. 2020, Lin & Nozawa 2021, Ricardo et al. 2025a). *In situ* sperm concentrations have been reported to decrease rapidly following spawning (Omori et al. 2001). Within a few hours of spawning, fertilisation potential at 1 m depth has been found to be similar to the water's surface, suggesting a gradual downward flux over time following bundle dissociation (Oliver & Babcock 1992). Padilla-Gamino et al. (2011) reported that sperm packets from bundles sank, a finding reported in the laboratory under near static conditions (Kono et al. 2020). Other studies have shown that *in situ* sperm concentrations are generally suboptimal ($< 10^5$ sperm mL^{-1}) (Kitanobo et al. 2022b) and virtually no sperm can be detected in the water's surface 3 h following spawning (Oliver & Babcock 1992).

As sperm concentrations *in situ* often fall below detection limits of typical measuring equipment such as hemocytometers, fertilisation potential provides an alternative, albeit coarse, method for assessing sperm concentration in the field (Oliver & Babcock 1992). By sampling *in situ* water samples during and after spawning and using these samples to fertilise eggs spawned *ex situ*, sperm concentrations can be estimated indirectly through established laboratory-derived sperm concentration–fertilisation relationships. However, this approach is complicated in species prone to polyspermy effects, where fertilisation follows a hump-shaped curve (Oliver & Babcock 1992). In such cases, intermediate fertilisation rates may indicate either low or excessively high sperm concentrations, though these elevated concentrations can often be inferred from water cloudiness and by confirming sperm

presence microscopically. Notably, fertilisation potential experiments hold sperm concentrations constant, allowing prolonged contact times that do not occur *in situ*. Additionally, this method assumes eggs are present at the point of sample collection, which may not reflect natural dispersion of the eggs. Consequently, fertilisation potential serves as a better indicator of sperm concentration than of actual fertilisation success, as it tends to overestimate fertilisation rates occurring in the field.

Turbulent diffusion can easily overwhelm most smaller-scale diffusive processes such as random walk and Fickian diffusion and therefore is a primary driver of sperm concentration decrease in field conditions. In open lagoonal settings, where horizontal boundaries are absent, eddy size is primarily constrained by depth (Fischer et al. 1979). Further, the extreme seafloor roughness of coral reefs generates additional turbulence (Monismith 2007). As with bundles and eggs, surface turbulence can exacerbate the downwelling and dispersion of sperm.

Because sperm diffusion is driven by concentration gradients, a higher background concentration of sperm in the surrounding water shallows these gradients and slows the diffusive loss of any individual's sperm cloud. Within a species, this implies that larger or denser local aggregations of spawning adults should sustain higher sperm concentrations for longer, extending egg–sperm contact times, supported by our modelling (see Patch population size and density). Extending the same logic between species is more speculative: simultaneous release by multiple species raises the total gamete concentration and could, in principle, slow the dispersal of each species' sperm cloud, although heterospecific sperm contributes no fertilising capacity and the benefit is therefore an indirect, physical one. If such an effect operates, it may have acted as one of several non-mutually exclusive selective pressures favouring spawning synchrony, alongside predator satiation, shared environmental cues, and avoidance of within-species sperm limitation. We raise it here as a hypothesis warranting investigation rather than an established driver of mass spawning.

Vertical mixing and water depth

While coral spawn releases are often recognised by conspicuous slicks which form in low energy conditions (Oliver & Willis 1987), turbulence, especially from wind and waves but also currents, increases vertical diffusion and mixing of the spawn cloud (Wolanski et al. 1989, Jones & Monismith 2008). The buoyant ascent velocities, υ, of coral eggs and egg-sperm bundles range from 5 to 10 mm s^{-1} under static conditions (Table 3). Although egg-sperm bundles and eggs are often described as *highly buoyant*, their near-neutral buoyancy means that these gametes are frequently subject to vertical mixing processes. The critical turbulent kinetic energy (TKE) needed to overcome this buoyancy is approximated using $TKE_{crit} = \upsilon^2$, and is calculated as 6×10^{-5} m^2 s^{-2}. TKE was measured using an Acoustic Doppler Velocimeter (ADV) deployed on a reef section exposed to wave and wind forcing characteristic of many reef environments. Values ranged from 4.5×10^{-5} to 6.3×10^{-1} m^2 s^{-2} with a median of 5.2×10^{-2} m^2 s^{-2}, often exceeding this threshold by up to four orders of magnitude. These findings indicate that turbulence in these habitats is sufficient to mix buoyant gametes vertically, with potential temporary sinking followed by resurfacing during periods of reduced turbulence. Such conditions likely result in dynamic vertical oscillations, enhancing dispersal and influencing spatial distributions of gametes.

Water depth is thought to increase dilution in marine spawning invertebrates, as there is a greater volume of water for sperm to disperse vertically, and fewer barriers to maintaining the concentration gradient (Levitan 1998, Babcock et al. 2000). In shallow water, rapid mixing of the water column quickly reduces the concentration gradient, in turn reducing the vertical flux of sperm. Unlike some other marine broadcast spawners that can move and aggregate in shallow water (Levitan 1998), corals are sessile and thus have little control over increasing fertilisation. Species better adapted to shallow

habitats may therefore be less susceptible to Allee effects. Stratification from temperature and salinity differences may act to prevent sperm concentrations from mixing through the water column in some waters, although this remains untested.

Water column shear flow

Water flowing across the reef acts as a major driver of dilution which impedes fertilisation processes (Coma & Lasker 1997b). As currents move along or over the reef, the friction of the seabed roughness, and to some extent the water surface, increases shear resulting in depth-dependent flow and turbulence (Davis et al. 2021). Turbulence increases with shear stress, which arises from layers of water moving at different speeds. Stronger flow creates greater shear stress and a correspondingly thicker benthic boundary layer, meaning velocity attenuation extends further from the seabed resulting in creating depth-dependent velocities (Reidenbach et al. 2006). When current velocities are high relative to dispersion processes, gametes form a long, thin gamete plume orientated downstream (Ricardo et al. 2026). Advective processes can also move spawn into deeper water, where the absence of a nearby seabed means the vertical concentration gradient between the sperm-rich surface layer and the sperm-depleted water column below is steeper, accelerating downward diffusive flux and increasing the rate of dilution relative to shallow reef environments. Alternatively, low flow velocities in shallow reef environments may trap the sperm at high concentrations and extend gamete contact times, possibly resulting in high fertilisation success and a weakening of inverse density-dependent fertilisation relationships (Miller & Mundy 2005).

Shear stress on gametes

Shear is also created adjacent to gametes as they move as a result of turbulence. While the dilutive effects of turbulence are well recognised, the role of shear stress in fertilisation success in marine spawners remains a topic of debate, particularly in the context of benthic spawning echinoderms. Mead and Denny (1995) initially proposed that turbulence-induced shear as eggs and sperm spin and 'tumble', measured by eddy dissipation rates (ε), could reduce egg-sperm encounter rates and increase cell damage. Laboratory experiments revealed a unimodal-type effect, where low levels of shear initially lead to a small increase in fertilisation success, but higher shear levels strongly inhibited fertilisation. However, Denny et al. (2002) later revised the original ε estimates used in the experiment, revealing that fertilisation inhibition occurred only at the highest ecologically relevant turbulence levels, specifically when ε exceeded 1000 W m^{-3}. Moreover, Gaylord (2008) provided direct continuous *in situ* measurements for ε, which indicated that inhibition of fertilisation from high ε is unlikely over extended temporal periods but may arise during brief, intense turbulence events.

For coral spawning, where fertilisation instead takes place in the water surface layer, ε typically ranges through orders of magnitude from 10^{-7} to 10^{-1} W m^{-3} with median values of ~10^{-4} W m^{-3} under wind-induced surface layer shear (MacKenzie & Leggett 1993, Huang et al. 2012), but can exceed these values in breaking waves to >10^{2} W m^{-3} (George et al. 1994, Gaylord 2008). Therefore, assuming the same inhibition mechanisms as observed in urchins, risks of shear are generally transient under wave-induced environments. However, work on corals in wind flumes suggest that fragmentation and deformation of embryos shortly after fertilisation might occur as low as ~10^{-4} W m^{-3}, which under their conditions related to ~28 km h^{-1} windspeed (Buccheri et al. 2026b), and other studies showing ongoing survivorship of these embryo and larval fragments being reduced (Okubo et al. 2017). Therefore, shear stress may present as a greater risk to downstream developmental stages than those associated with fertilisation and Allee effects.

Wind and waves

Mass spawning has been proposed to have evolved to coincide with calm periods (Van Woesik 2010). However, wind conditions during spawning are routinely reported as comparable to mean conditions (Willis & Oliver 1990, Heyward & Negri 2012, Buccheri et al. 2026b). Indeed, lower fertilisation rates have been observed on windier nights compared with more calm conditions (Mumby et al. 2024). Floating gametes such as egg-sperm bundles and eggs will likely be more influenced from these water surface processes than sperm (Wolanski et al. 1989), which behave more similar to dissolved particles through diffusion (Ricardo et al. 2025a). Particle releases of stearic acid (lipid-filled particles ~2–4 mm in diameter, replicating egg–sperm bundles) showed greater coalescence than dissolved dye tracers (Fig. 5b). More importantly, under wind and wave forcing the buoyant particles and the dye followed divergent trajectories from a shared release point, each remaining internally coherent while separating from one another (Fig. 5b). Because buoyant gametes track wind-influenced surface processes while sperm disperse with the bulk water like a dissolved tracer, compatible gametes released in close proximity may be physically separated before fertilisation occurs. This represents a density-independent failure mode: fertilisation may decline under wind not only through dilution, but through the spatial decoupling of eggs from sperm, such that even adequate local colony densities cannot guarantee gamete contact.

Wind-driven currents can also be substantial. At Lizard Island on the Great Barrier Reef, wind-driven current velocities far exceed tidal-driven current velocities (Johansen 2014), with current velocities increasing substantially at 15 to 20 knots (28 – 37 km h^{-1}) (Philipps & Bellwood 2024). Others have reported that even as little as 18 km h^{-1} can be sufficient for wind-driven mixing to become the dominant process (Pattiaratchi 1994).

Wind may therefore be an underappreciated driver of variability in Allee effects, capable of depressing fertilisation on windier nights independent of population density, and of decoupling reproductive outcomes from the spatial and demographic conditions that otherwise govern them.

Reconcentration of coral slicks

Topographical and water property (temperature, salinity, density, etc) fronts are created around coral reefs and provide areas for slicks, especially eggs and embryos, to reconcentrate. However, whether these fronts have any effect on fertilisation depends on two points i) how long it takes the gametes to reach the front under the prevailing advection-diffusion conditions, and ii) whether diluted sperm can be reconcentrated. For example, a topographical front that typically forms on leeward sides of reefs may be a great distance from the spawning corals in the lagoon, and therefore unlikely to reach the front before gamete dilution occurs. This distinction matters because eggs and sperm reconcentrate by different physical routes. Buoyant gametes such as eggs and bundles accumulate at convergence fronts because they float and are swept along the surface as water downwells beneath them. Sperm, behaving as a dissolved tracer, can only be concentrated where the water itself accumulates, but hydrostatic balance prevents water building up at a front. Consequently, fronts may restore the egg pool without restoring fertilising sperm concentrations, meaning convergence zones could elevate egg density while fertilisation remains sperm-limited.

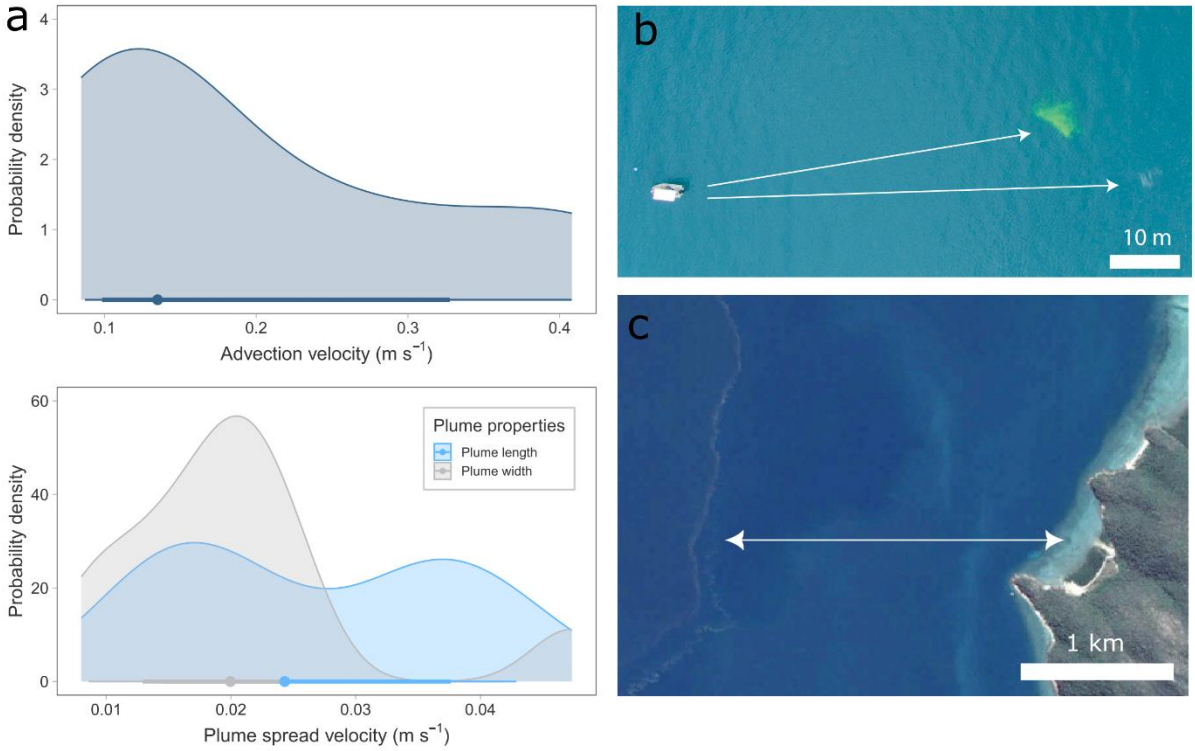


Fig. 5. Hydrodynamic influences on buoyant and dispersive particles. (a) The advection velocities from the centroid of tracer dye plumes, and visible planar spread of tracer dye plumes (n = 11 releases). (b) A frontal boundary ~2 km from Orpheus Island, Great Barrier Reef, marked by a phytoplankton line running parallel to the reef. (c) Diverging trajectories of neutrally buoyant tracer dye (simulating sperm) and buoyant particles (stearic acid, simulating coral bundles and eggs) release at the water's surface, illustrating the additional influence of wind on buoyant dispersal. Image from Google © 2025 Maxar Technologies.

Biophysical modelling

Biological component

Biophysical models are used to predict fertilisation success in externally spawning marine invertebrates by simulating gamete dispersal and encounters under hydrodynamic conditions (Levitan et al. 1991, Babcock et al. 1994, Teo & Todd 2018). For corals, colony reproductive output is commonly predicted based on species-specific colony traits, including colony size, the extent of fertile zones, polyp density (which in most species typically corresponds to the number of egg–sperm bundles, as most polyps release a single bundle), and the number of eggs and sperm per bundle, as described above.

Fertilisation kinetics models are then used to estimate fertilisation success based on principles of bimolecular kinetics. These models were originally derived from classical kinetic theory to estimate collision rates of gas particles moving in random motion against a solid surface (Rothschild & Swann 1949). In this context, sperm concentration (S_0) is treated analogously to gas particles, and collision rates are estimated using values for egg concentration (E_0), egg radius, and sperm swimming speed. A number of models have been proposed for spawning invertebrates, see Lehtonen and Dardare (2019) for review. The most frequently used approach was first proposed by Vogel et al. (1982) and later refined by Styan (1998) to allow for a polyspermy block, where the proportion of monospermic fertilisations, φ_{mono}, i.e. successful fertilisations, is:

$$\varphi_{mono} = 1 - e^{-x} - (1 - e^{-x} - xe^{-x})(1 - e^{-b})$$

with

$$x = F_e \frac{S_0}{E_0}\left(1 - e^{-\beta_0 E_0 \tau}\right) \text{ and}$$

$$b = F_e \frac{S_0}{E_0}\left(1 - e^{-\beta_0 E_0 t_b}\right)$$

where *x* is the average number of potential fertilisers per egg, and *b* is the mean number of extra fertilising sperm that will contact an egg in a time period (t_b) in the population of eggs already contacted once (Styan 1998). If $t_b = 0$ (i.e., there is an immediate polyspermy block after fertilisation), then the model is simplified to the same as Vogel's equation:

$$\varphi_{mono} = 1 - e^{-x}$$

Two parameters within these equations deserve further special consideration. First, egg concentration (E_0) is often added to models under the assumption that eggs absorb a certain fraction of non-fertilising available sperm, thereby decreasing the concentration of sperm. However, this effect has been found to be negligible in sea urchins (Levitan et al. 1991), and appears similarly irrelevant for corals at tested concentrations of 3 to 300 cells mL^{-1} at long contact times (~2.5 h) (Ricardo et al. 2025a). The absence of an E_0 effects mean that a reduced Styan model can be derived because the egg-absorption terms in the full model enter only through the factor $(1 - \exp(-\beta \cdot E_0 \cdot \tau))/E_0$, which reduces to $\beta \cdot \tau$ whenever the exponent $\beta \cdot E0 \cdot \tau$ is small. Therefore, at or below the tested upper bound of 300 eggs mL^{-1}, the equations can be written as:

$$x = F_e S_0 \beta_0 \tau \text{ and}$$

$$b = F_e S_0 \beta_0 t_b$$

Further research is needed to determine whether higher egg concentrations above the range tested in Ricardo et al. (2025a) influence fertilisation success.

Second, an important component of the kinetics models is the 'fertilisation efficiency' (*Fe* or β/β_0, *sensu* Styan (1998)), which is the ratio of the realised collision-rate constant (β) to the theoretical rate constant (β_o), predicted under bimolecular assumptions. If *Fe* = 1, then all egg-sperm collisions result in fertilised eggs, but any inefficiency during fertilisation, such as non-fertile regions of the egg, results in the proportion becoming less than 1. As β cannot be easily measured, it is estimated by optimising fertilisation kinetics models to fit empirical fertilisation data, using other known parameters as inputs. Uncertainty in *Fe* likely results in the greatest error in fertilisation biophysical models, as reported by Ricardo et al. (2025a), with predicted fertilisation rates ranging from 10% to 80% depending on the *Fe* value used. Poor fits during optimisation may also affect *Fe* estimates, or *Fe* itself may be dynamic – varying with other parameters or over time (Buccheri et al. 2026a). Improving the estimation of *Fe* remains a key priority for future fertilisation modelling efforts.

Hydrodynamic component

The hydrodynamic component of the models is fundamentally rooted in Fickian diffusion principles, with flux of gametes proportional to *D*, the diffusion coefficient, and dC/dx, the concentration gradient. For spawning invertebrates, a widely adopted model is the analytical Gaussian plume model under steady-state assumption introduced by Denny (1988) based on the seminal turbulence modelling equations of Csanady (1973). This model often assumes a continuous release of particles from a single point source and has been validated with field observations for many echinoderms and other taxa. For corals, these models are likely most applicable to brooding gonochoric species, where males release sperm upstream of brooding females, but for broadcast-spawning species with pulsed

and staggered releases of gametes, numerical advection-diffusion equations may be more appropriate and allow greater complexity to be built into the model. However, solving these equations numerically involves a trade-off: implicit schemes are more stable and less prone to numerical oscillations, while explicit schemes are faster to compute but more susceptible to instability. Crimaldi and Zimmer (2014) argue that simple fertilisation models based on mean concentrations such as those described above, fail to capture the dynamic and instantaneous nature of fluid stirring. These heuristic models treat gametes as passive scalars and neglect the fine-scale aggregation and filament formation driven by turbulent eddies (Crimaldi 2012). As a result, they miss transient high-concentration events where local sperm and egg densities are temporarily elevated, enhancing fertilisation rates prior to dilution. By relying solely on mean fields, such models may systematically underestimate fertilisation success, particularly in turbulent reef environments where instantaneous flow structures can dominate gamete encounter dynamics. However, fine-scale aggregations have not yet been incorporated into biophysical models and would be computationally resource intensive at sub-metre scales. Their influence may be approximated and incorporated through sub-grid scale parametrisations or multipliers derived from fine-scale simulations or laboratory data, although this has not been attempted.

Underlying these models is the dispersion constant *D*. A simple approximation for *D* was introduced by Elder (1959) using $D = c \cdot h \cdot u_*$, where *c* is a mixing coefficient (or coefficient of proportionality), *h* is the water depth, and u_* is the friction velocity. Fischer et al. (1979) report transverse (cross-stream) mixing coefficients of *c* between 0.1 and 0.2, but these can increase substantially under meandering flow (Jones et al. 2008). Longitudinal (downstream) mixing coefficients are thought to be approximately the same, but are difficult to measure because shear flow dominates dispersion (Fischer et al. 1979). Values of c = 0.067 for vertical mixing coefficients are commonly used for coral reefs (Wolanski et al. 1984, Teo & Todd 2018, Ricardo et al. 2025a), but have not been adequately validated in these environments for coral sperm diffusion. The mixing coefficient can depend on a multitude of factors such as depth, width (in channels), current velocity, bed steepness, and bed roughness. Further, because various eddy sizes can occur simultaneously, particles closer together will behave differently to those spread apart, reflecting the size of the eddy they are in. The size of turbulent eddies directly influences the distribution of gametes, with larger eddies promoting widespread dispersal and smaller eddies contributing to localised mixing. In lagoon environments, the vertical dimension (depth) typically limits the maximum eddy size, as turbulence is constrained by the smallest spatial scale among the downstream (x), cross-stream (y), and vertical (z) directions.

Friction velocity (u_*), also known as shear velocity, is a measure of the near-bed shear stress exerted by the current. It typically ranges from 5 to 10% of the depth-averaged current velocity ($\bar{u}$) and can be estimated using several methods. These include the logarithmic law of the wall when vertical velocity profiles are available (Von Kármán 1931, Levitan 1995), or from depth-averaged formulations based on drag coefficients when these are known (Jones et al. 2008, Lentz et al. 2017). In wave-exposed environments, shear-related velocities might be disrupted by wave-related turbulence, and estimates for u_* have been derived from turbulent energy parameters (Reidenbach et al. 2006). The effect of the friction velocity also causes depth-dependent current velocities, sometimes leading to elongation of the slick downstream in higher flow conditions, which again can be estimated from the logarithmic law of the wall (Fischer et al. 1979).

Similarly, at present biophysical fertilisation models of external spawners have largely ignored wind and wave processes, and their interaction with current velocity. These factors may work to increase and decrease fertilisation in several ways as discussed above.

Methods to assess Allee effects

Experimental design

Experimental designs aimed at assessing sperm limitation face challenges due to the ephemeral nature of spawning events, the small size of gametes, unpredictable hydrodynamics, and the typically multispecific synchronous spawning behaviour. Consequently, a range of creative approaches and methods have been developed to gather evidence, albeit none are without limitations (Table 8). Sites characterised by low genetic diversity and clear reproductive isolation between coral species are typically the most suitable for such studies.

Experimental manipulations enable control over specific variables. For example, creating artificial spawning patches can reduce contamination risk and allow deliberate manipulation of the patch's spatial characteristics. Using mesh containers to enclose eggs controls parentage, prevents contamination, and facilitates tracking. However, each layer of manipulation introduces some degree of artificiality, which should be carefully considered when interpreting results.

Table 8. Various approaches to assess Allee effects during coral fertilisation

EXPERIMENTAL APPROACHES	ROLE	EXPLANATION	PROS	CONS
PLANKTON SAMPLING	Direct measurement	Eggs and embryos are tracked with drifters and sampled by plankton nets.	Relatively simple to conduct in the field.	Challenges in interpreting individual species fertilisation.
SINGLE EGG DONOR WITHIN GAMETE CLOUD	Direct measurement	Eggs from a single colony are placed in mesh containers and floated through the gamete cloud. Gametes are sourced from colonies spawned on board or in the lab.	Known maternal genotype/species; effective at low sperm concentrations.	Possibly less representative because of incompatibility. Time constraints placed on preparing the container and waiting for onboard colonies to spawn. Container advection speeds may not exactly match spawn advection speeds.
MULTIPLE EGG DONORS WITHIN A SLICK	Direct measurement	Eggs from multiple colonies are placed in separate mesh containers and deployed directly into the gamete slick. Exposure occurs over the natural fertilisation window.	Multiple genotypes improve fertilisation estimates; field-based deployment is often faster.	Requires large dive teams; container advection may differ from natural plume transport.
FERTILISATION POTENTIAL	Proxy	Instantaneous sampling of sperm slicks followed by lab crosses with eggs.	Useful proxy for sperm concentration; informative for species with strong polyspermy blocks.	The eggs are exposed to long contact times, which likely inflates the actual fertilisation rate, and therefore caution should be used when comparing to actual *in situ* fertilisation success.
PARENTAL ASSIGNMENT	Analytical tool	Genetic identification of parents from offspring to infer mating and dispersal patterns.	Mechanistically rich; captures realised reproductive success and compatibility.	Resource-intensive and costly; requires specialised expertise; often limited by small sample sizes, missing data, and potential biases in interpretation.

Genetic approaches

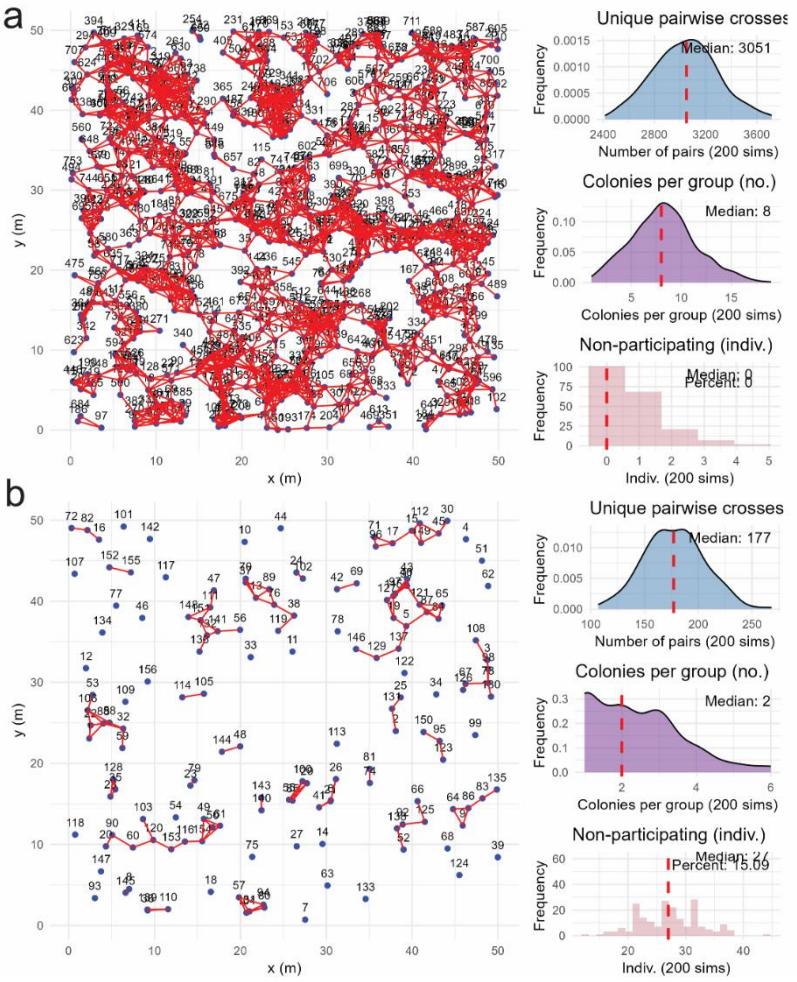
Molecular techniques are increasingly being used to identify parent-offspring relationships in marine taxa and offer a valuable tool to understand fertilisation patterns in corals. Unlike bulk fertilisation estimates (counting all the eggs and embryos in a sample), parental assignments mechanistically determine relationships with spatial factors such as pairwise parental distances, and therefore are not at risk of broad confounding influences seen in observational studies. However, data are often qualitative because observations from sequenced progeny are not often randomly selected and only represent a fraction of possible pairwise crosses. Coffroth and Lasker (1998) and Brazeau et al. (1998) used randomly amplified polymorphic DNA markers to assess contributions between parents and various modes of reproduction. Ayre and Miller (2006) used allozyme electrophoresis to make inferences for the brooder *Isopora palifera* (previously *Acropora palifera*). Stoddart et al. (1988) note that maternal phenotypes can dominate in larvae for up to 17 days, which may limit the ability to detect sexual reproduction using this method. Dubé et al. (2020) used twelve microsatellite markers in the hydrocoral *Millepora cf. platyphylla* and Warner et al. (2016) used ten microsatellite markers to investigate sperm dispersal from brooders of the *Seriatopora hystrix* complex, and found 82% of colonies reproduced within 10 m of each other. Lasker et al. (2008) used microsatellites on the brooding octocoral *Pseudopterogorgia elisabethae*. Recently Ricardo et al. (2025b) used SNP paternity assignments on a natural, asynchronous spawning patch of submassive *Platygyra* corals, finding no embryos resulted from outcrossing and only a small proportion from selfing; i.e., a clear Allee effect. Ricardo et al. (2026) then found paternity relationships of table coral *A.* cf. *hyacinthus* were largely driven by the parents' alignment with the current direction and the distances between parents using a manipulated patch of spawning colonies.

Box 1. Gametic mixing under various adult densities

High-density populations promote greater gametic mixing and enhance the genetic diversity of progeny by enabling larger and more overlapping breeding units. In contrast, as populations degrade and intercolonial distances increase, breeding units become smaller and more fragmented, leading to greater isolation. To illustrate this, the positions of virtual gravid adult colonies were simulated on a 50 × 50 m grid using a random (Poisson) distribution via the R package *spatstat* (Baddeley & Turner 2005). Two population sizes (1000 and 100 colonies per grid) were modelled, corresponding to densities of 0.4 and 0.04 colonies m^{-2}, respectively, using a hard 3 m proximity threshold based on median intercolonial distances reported by Ricardo et al. (2026), across 200 simulations.

At the high population density, simulations produced a median of 3051 unique pairwise crosses, compared to just 177 at low density. Breeding groups of the high-density population comprised a median of 8 colonies, whereas low-density groups contained only 2. Notably, while no colonies were reproductively isolated in the high-density scenario, 15% of colonies in the low-density patch were entirely isolated, unable to cross with any other individual.

Gametic mixing is connected to the concepts of Minimum Viable Population (MVP) size and genetic Allee effects (Luque et al. 2016). MVP benchmarks, conventionally were derived as 50 individuals to avoid inbreeding depression and 500 to retain long-term adaptive potential (Franklin 1980, Franklin & Frankham 1998), although some argue these values to be gross underestimates (Reed & Bryant 2000). While corals and other marine broadcast spawners are generally capable of greater genetic connectivity through open populations during the pelagic larval stage, gametic mixing during spawning sets an upper bound on the genetic diversity of locally produced offspring. For restoration, it has been suggested that 4 to 6 outplanted genets placed in proximity may be sufficient to achieve fertilisation and address genetic compatibility issues (Baums et al. 2019), while 10 to 35 individuals may retain substantial genetic diversity (Shearer et al. 2009). However, a critical concern is that outplanting corals reared *ex situ* may reduce the effective population size and genetic diversity in the wild—a phenomenon known as the Ryman–Laikre effect (Ryman & Laikre 1991). Restoration that successfully overcomes fertilisation Allee effects using outplants could therefore erode genetic diversity if outplants are derived from few parent colonies and dominate subsequent reproduction.



Restoration and marine ornamental harvesting considerations

The need for restoration activities to consider possible Allee effects during coral fertilisation has been hypothesised for some time (Baums 2008). Coral restoration is expensive, and corals grow slowly, so methods for outplanting must be strategic. Restoration approaches often need to take into account numerous additional considerations other than Allee effects during fertilisation solely, some of which include: i) the size of the patch is sufficient for other ecological benefits (Ladd et al. 2018), ii) connectivity: the patch is placed where larvae can be dispersed to sink reefs (Doropoulos & Babcock 2018), and iii) genetic diversity: patches placed to allow gene exchange between subpopulations (Ladd et al. 2016, Ladd et al. 2018, Baums et al. 2019). While this review focuses specifically on fertilisation dynamics, it acknowledges the importance of these additional restoration considerations.

Positive interactions, such as mutualism and facilitation, are another important component of restoration design. In areas of low resources such as bare substrate, positive interactions between species are particularly important (Silliman & He 2018). Clumped planting designs have been found to be more successful for a number of coastal marine and terrestrial species (Silliman et al. 2015, McCallum et al. 2019). Conversely, the growth rate of patches is related to the edge to area ratio, so the benefits of larger clumps could be offset by creating numerous clumps. Likewise, high density patches have also been suggested for corals (Unsworth et al. 2023).

Patch population size and density

Modelled predictions of how population size and density influence fertilisation success and subsequent embryo production are shown in Figure 6. Fertilisation success is more strongly influenced by population density than by population size, as indicated by the predominantly vertical contour lines representing fertilisation success intervals (Fig. 6a). However, embryo production depends on both factors: a larger population with moderate fertilisation success can produce similar embryo numbers to a smaller population with higher fertilisation success (Fig. 6b).

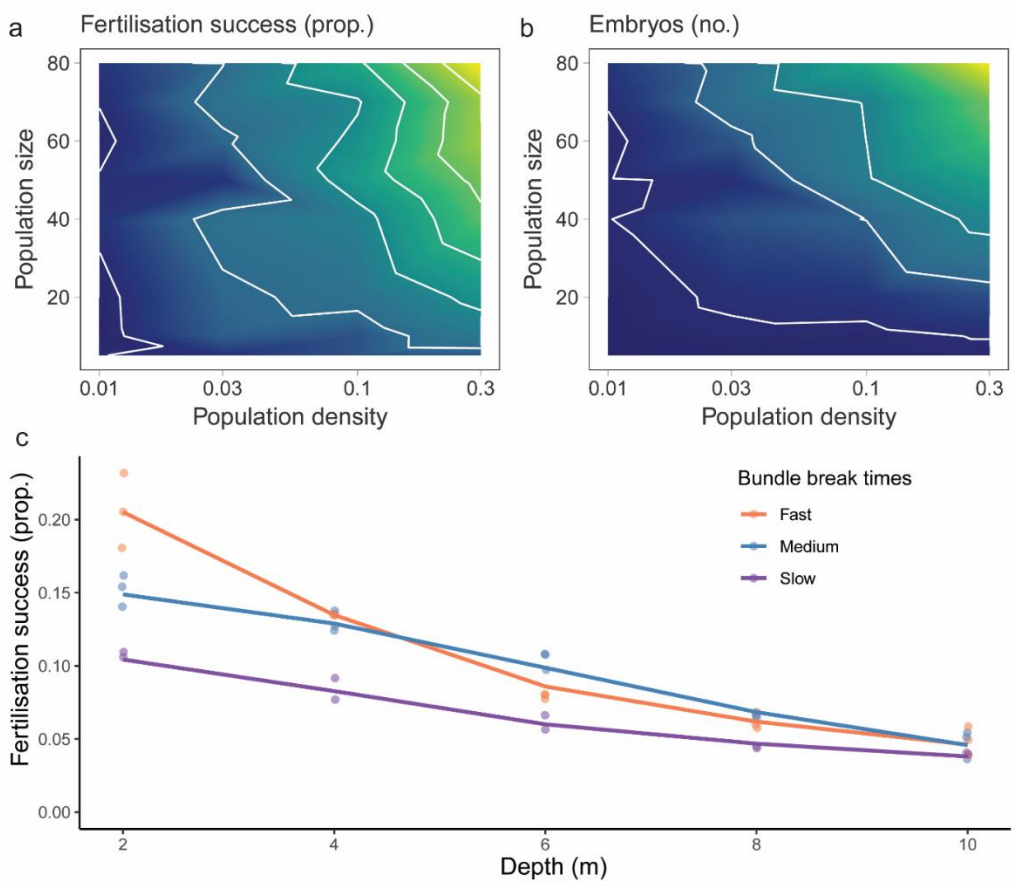


Fig. 6. Modelled effects of population size and density on (a) fertilisation success and (b) embryo production. Contour lines represent 1%, 5%, 10%, 15%, 20%, 25% fertilisation success in (a), and 10^5, 5×10^5, 10^6 embryos in (b). Model parameters: depth = 2 m, colony diameter = 25 cm, current velocity = 0.1 m s^{-1}, with colonies randomly distributed in space. (c) The modelled effect of water depth on fertilisation successes at fast (200 s), medium (1050 s) and slow (1800 s) bundle dissociation times. Model parameters: colony diameter = 25 cm, current velocity = 0.1 m s^{-1}, population density = 0.8 colonies m^{-2}, with colonies randomly distributed in space.

The subtle increase in fertilisation success at larger population sizes is likely driven by a broader sperm cloud footprint and reduced edge effects, which together help maintain higher sperm concentrations over space and time. Modelling suggests that while peak concentrations may be similar across patch sizes, larger aggregations sustain sperm levels above fertilisation thresholds (typically ~10^3 sperm mL^{-1}) across a greater area and for longer durations, extending the effective fertilisation window and enhancing success.

Modelling also shows that water depth and synchronisation of fertilisation can greatly affect fertilisation success (Fig. 6c), as discussed earlier. Shallow water tends to retain higher sperm concentrations for longer, as the seabed constrains vertical mixing and limits the downward loss of sperm from the surface layer (See section Vertical mixing and water depth). Species that synchronise gamete release in shallow water (and where it is retained) therefore achieve the highest fertilisation success.

While component Allee effects on fertilisation are evident in both panels for a spatial distribution resembling a natural population, the results also offer guidance for restoration efforts. Specifically, colonies should be outplanted at both high densities, and with sufficiently large population sizes i.e. >20 individuals. Further increases in fertilisation success are predicted when using a clustered

outplanting design, as described earlier. One approach to further exploit clustering is proposed by Suzuki et al. (2020) who designed a cradle system that concentrates egg-sperm bundles from spawning colonies, thereby restricting their dispersal and enhancing fertilisation success. Regardless of the system used, if the objective of restoration is to cover a larger spatial area, and to ensure sufficient larval production, many clusters will be required.

Allee effects during outplants of heat tolerant lineages

An extension of adult outplanting involves adding heat-tolerant corals into degraded systems with the intent that their beneficial genes will spread through the population (Quigley 2024). This intervention depends on several critical assumptions and sequential ecological and genetic conditions. First, outplanted corals must achieve sufficient fertilisation success with the natural population, overcoming Allee effects associated with small population size or low density. Next, heat tolerance must have substantial heritability, with minimal trade-offs to ensure progeny inherit and express these beneficial traits (Humanes et al. 2024, Quigley 2024). However, because the number of progeny from outplanted corals will initially be small relative to the existing natural population, strong selection pressure favouring heat-tolerant traits is required to counteract genetic drift, which would otherwise tend to eliminate these beneficial genes by chance. Finally, these offspring must survive recruitment processes, where typically high mortality rates mean that a large number of recruits is necessary to establish a lasting genetic impact (Yund 2000, Chong-Seng et al. 2014).

Allee effects during marine ornamental collections

Current harvest management frameworks for coral, including quota-based systems operating in Australia's aquarium fisheries, Indonesia's CITES-linked species quotas, and Fiji's regulated live coral trade, typically track abundance or mass without accounting for the spatial structure or size distribution of the remaining population (Hoeksema 2026). From an Allee effects perspective, this may be insufficient to prevent localised reproductive failure. As described in this review, large colonies in close spatial proximity generate disproportionately high gamete concentrations, have the largest fertile zones, and produce the highest modelled fertilisation success. Selectively removing these individuals does not only reduce population size; it may alter the size and spatial configurations that theory and experimental evidence suggest buffer populations against sperm limitation. This mirrors, in reverse, the principles underlying restoration outplanting design, where clustered, size-structured configurations are deliberately created to exceed fertilisation thresholds. Spawning potential ratio (SPR) frameworks, widely used in finfish fisheries to assess reproductive output relative to an unfished baseline (Goodyear 1989, Hordyk et al. 2015, Prince et al. 2015), offer a possible conceptual model for incorporating these dynamics into harvest management, but would require some adaptation for corals. A coral-specific SPR may need to weight reproductive output not by biomass alone, but by colony size distribution and spatial configuration, reflecting the nonlinear relationship between colony density, spacing, and fertilisation success described by the kinetics models earlier in this review. Developing such a framework represents a research priority, though it first requires empirical validation of the link between harvested size distributions, realised fertilisation success, and downstream recruitment in wild populations.

Remaining questions and future directions

Debate over Allee effects

While primarily referencing non-sedentary species capable of aggregation, Yund (2000) argues that Allee effects are uncommon among free-spawning invertebrates. They also suggest that experimental studies might overestimate Allee effects, as eggs are often collected before their viability ends, potentially truncating their fertilisation potential. Yund (2000) suggests that sampling natural

populations is largely free from bias, because these allow for reproductive strategies that promote fertilisation success, and that may be removed in manipulative studies. However, as outlined above, natural population sampling of Allee effects during fertilisation in corals is not without limitations. It can be influenced by survivorship and sampling biases, as well as complications such as hybrid dysfunction, including reduced fitness or sterility, all of which can obscure or underestimate the strength of Allee effects. Crimaldi and Zimmer (2014) further argue that fine-scale aggregations enhance fertilisation above modelled predictions because of instantaneous mixing processes. Whether this fine-scale concentration meaningfully boosts fertilisation in coral reef environments, as opposed to the echinoderm systems where it has mostly been demonstrated, remains untested. Denny (1988) initially predicted very low fertilisation success on wave-swept shores given the rapid dilution expected under such energetic conditions. Subsequent work identified surge channels as a mechanism capable of trapping spawn and sustaining fertilisation at far higher levels than the surrounding habitat (Denny et al. 1992), demonstrating that structural complexity can locally offset otherwise prohibitive dilution. Questions persist as to why local populations continue to be maintained if Allee effects are widespread, particularly among rare or non-model species that typically occur at low densities. A consistent result across studies is that fertilisation spans almost the full possible range, from near zero to 90–100%, both within and between spawning events. This variability suggests that persistence may depend less on average fertilisation success than on the occurrence of localised, episodic conditions under which fertilisation is high: convergence zones, structurally trapped water, or brief windows of calm. Where the egg pool is large, even infrequent high-fertilisation events may generate sufficient larvae to sustain a population, consistent with the argument that broadcast spawners have evolved fertilisation efficiencies adequate for persistence rather than maximised for individual events (Levitan 1995). Identifying and predicting these fertilisation pockets, spatially and temporally, therefore remains a crucial area for future research, and a potentially fruitful direction for restoration.

Future directions

Despite decades of research on external spawning in marine invertebrates, many aspects of coral fertilisation under natural reef conditions remain unresolved. *In situ* gamete concentrations and characteristics – central to understanding fertilisation dynamics – are among the least studied yet most ecologically relevant components of coral reproduction. Differences in the spatial and temporal bio-physical environment make this fieldwork inherently challenging, and it is unlikely that any single methodological approach will adequately capture the full complexity of these processes while eliminating all biases. Table 9 outlines key research questions and areas of uncertainty that limit our ability to interpret Allee effects and predict fertilisation outcomes in the field. Gaps in our understanding of gamete behaviour, hydrodynamic influences, and sampling biases highlight the need for targeted, interdisciplinary research. Multiple lines of evidence will be essential to advance fertilisation modelling under changing environmental conditions, and there remains many novel patterns and mechanisms to be explored.

Table 9. Key research questions and areas of uncertainty in understanding Allee effects during coral fertilisation.

THEME	RESEARCH FOCUS / QUESTION	RELEVANCE TO ALLEE EFFECTS / BIOPHYSICAL UNDERSTANDING
BUNDLE DISSOCIATION	How does dissociation time influence dispersal and mixing?	Determines how gametes spread or stay concentrated, affecting encounter rates critical at low densities.
EGG DISSOCIATION	How does egg dissociation vary under different water quality and	Can bias *in situ* sampling, and mask Allee effects.

	chemistry conditions? Are egg and embryo decomposition rates comparable?	
FERTILISATION RATES	How do rates differ in choice experiments (e.g. old vs young coral, self vs non-self, intra- vs interspecific)?	Highlights mate choice and compatibility factors that influence fertilisation efficiency and population viability.
CONTAINER DYNAMICS	How does gamete trapping in containers reflect hydrodynamic and atmospheric conditions?	Methodological biases can misrepresent actual fertilisation conditions; accurate tracking is essential for understanding true biophysical context.
WINDAGE & DROGUE DIVERGENCE	Do drogue and drifter trajectories represent the spawn cloud well?	If sampling diverges from spawn trajectory, Allee thresholds may be over- or underestimated.
SPERM RECONCENTRATION	Can sperm be reconcentrated *in situ* by local hydrodynamic processes? Can tracer dyes assist?	Understanding sperm dilution and reconcentration is key to identifying fertilisation failure points.
SPAWNING OUTSIDE PEAK SEASON	Can off-season spawning be utilised to allow prototyping during convenient times such as daytime?	Offers experimental opportunities to explore *in situ* fertilisation under more favourable conditions and periods.
CONVERGENCE ZONES	How do local and reef-scale convergence zones influence gamete mixing and fertilisation? Can these areas be predicted?	These zones may locally elevate fertilisation potential, mitigating Allee effects at otherwise low densities.
***IN SITU* SLICK CHARACTERISATION**	What are the spatio-temporal characteristics of spawn clouds and how do they influence fertilisation success?	Core to understanding spatial-temporal overlap of gametes; central to Allee effect thresholds.
METHODOLOGICAL INTEGRATION	Can heuristic biophysical fertilisation models be combined with advanced computational fluid dynamics software?	Integrating methods enhances reliability and helps detect subtle or cryptic Allee effects.

Conclusions

As coral reefs degrade globally, future reefscapes will increasingly consist of small, spatially fragmented patches, including restored populations, heightening vulnerability to Allee effects and sperm limitation. Broadcast-spawning corals depend on high local gamete concentrations for successful fertilisation, yet population fragmentation, low adult densities, and dilutive properties of hydrodynamics can drive fertilisation below critical thresholds. This review highlights how spatial configuration, colony size, flow regimes, and synchrony influence gamete encounters and reproductive success. Despite their importance, Allee effects during fertilisation remain largely underexplored in corals due to the logistical and opportunistic constraints of measuring *in situ* fertilisation during multispecies spawning events, leading to a bias toward more easily studied, reproductively isolated species. These insights are crucial for restoration: effective outplanting must consider not only population size but also spatial design, colony maturity and size, and local flow conditions to enhance fertilisation and preserve genetic diversity. Recognising and addressing Allee

effects is essential for improving coral reproductive outcomes, reef resilience, and the success of conservation and restoration strategies under accelerating environmental change.

Data availability statement

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

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References

Álvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Cumbo VR, Connolly SR (2016) Fecundity and the demographic strategies of coral morphologies. Ecology 97:3485-3493

Amaral A, Pastrana Y, Pereira C, Valente W, Godoy L (2022) Morphological assessment of free-spawned sperm in scleractinian coral: a relationship between cell morphology and motility. Mar Biol 169:136

Ayre DJ, Miller K (2006) Random mating in the brooding coral Acropora palifera. Mar Ecol Prog Ser 307:155-160

Babcock R, Franke E, Barr N (2000) Does spawning depth affect fertilization rates? Experimental data from the sea star Coscinasterias muricata. Marine and freshwater research 51:55-61

Babcock R, Mundy C, Whitehead D (1994) Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. The Biological Bulletin 186:17-28

Babcock RC (1984) Reproduction and distribution of two species of Goniastrea (Scleractinia) from the Great Barrier Reef Province. Coral Reefs 2:187-195

Babcock RC, Heyward AJ (1986) Larval development of certain gamete-spawning scleractinian corals. Coral Reefs 5:111-116

Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. Journal of statistical software 12:1-42

Baird AH, Guest JR, Edwards AJ, Bauman AG, Bouwmeester J, Mera H, Abrego D, Alvarez-Noriega M, Babcock RC, Barbosa MB (2021) An Indo-Pacific coral spawning database. Scientific data 8:1-9

Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annu Rev Ecol, Evol Syst 40:551-571

Baria MVB, de la Cruz DW, Villanueva RD, Guest JR (2012) Spawning of three-year-old *Acropora millepora* corals reared from larvae in northwestern Philippines. Bull Mar Sci 88:61-62

Baums I, Devlin-Durante M, Polato N, Xu D, Giri S, Altman N, Ruiz D, Parkinson J, Boulay J (2013) Genotypic variation influences reproductive success and thermal stress tolerance in the reef building coral, Acropora palmata. Coral Reefs 32:703-717

Baums IB (2008) A restoration genetics guide for coral reef conservation. Mol Ecol 17:2796-2811

Baums IB, Baker AC, Davies SW, Grottoli AG, Kenkel CD, Kitchen SA, Kuffner IB, LaJeunesse TC, Matz MV, Miller MW (2019) Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. Ecol Appl 29:e01978

Benedini M, Tsakiris G (2013) Water quality modelling for rivers and streams, Vol. Springer Science & Business Media

Birkart LV, Álvarez-Filip L (2025) 2023 global heatwave causes mass mortality of a keystone coral on shallow Western Atlantic reefs. iScience 28

Brazeau DA, Gleason DF, Morgan ME (1998) Self-fertilization in brooding hermaphroditic Caribbean corals: evidence from molecular markers. J Exp Mar Biol Ecol 231:225-238

Brazeau DA, Lasker HR (1992) Reproductive success in the Caribbean octocoral Briareum asbestinum. Mar Biol 114:157-163

Buccheri E, Doropoulos C, Babcock RC, Mumby PJ, Ricardo GF (2026a) Optimising fertilisation kinetics models for broadcast spawning corals in the genus Acropora. Scientific Reports

Buccheri E, Ricardo GF, Babcock RC, Mumby PJ, Doropoulos C (2023) Fertilisation kinetics among common Indo-Pacific broadcast spawning corals with distinct and shared functional traits. Coral Reefs 42:1351-1363

Buccheri E, Wuppukondur A, Ricardo G, Mumby P, Doropoulos C (2026b) Impacts of wind-driven hydrodynamics on the early stages of coral development. Mar Ecol Prog Ser 788:1-18

Caley M, Carr M, Hixon M, Hughes T, Jones G, Menge B (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27:477-500

Carlon DB (1999) The evolution of mating systems in tropical reef corals. Trends Ecol Evol 14:491-495

Chamberland VF, Bennett M-J, Speck TD, Latijnhouwers KR, Miller MW (2025) Optimizing in vitro fertilization in four Caribbean coral species. PeerJ 13:e18918

Chan WY, Peplow LM, van Oppen MJ (2019) Interspecific gamete compatibility and hybrid larval fitness in reef-building corals: implications for coral reef restoration. Scientific reports 9:1-13

Chang H, Huntley HS, Kirwan Jr A, Carlson DF, Mensa JA, Mehta S, Novelli G, Özgökmen TM, Fox-Kemper B, Pearson B (2019) Small-scale dispersion in the presence of Langmuir circulation. J Phys Oceanogr 49:3069-3085

Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33:449-461

Chui APY, Wong MC, Liu SH, Lee GW, Chan SW, Lau PL, Leung SM, Ang Jr P (2014) Gametogenesis, embryogenesis, and fertilization ecology of Platygyra acuta in marginal nonreefal coral communities in Hong Kong. Journal of Marine Sciences 2014:953587

Coffroth MA, Lasker HR (1998) Larval paternity and male reproductive success of a broadcast-spawning gorgonian, Plexaura kuna. Mar Biol 131:329-337

Coll JC, Bowden BF, Meehan GV, Konig GM, Carroll AR, Tapiolas DM, Aliño PM, Heaton A, De Nys R, Leone PA, Maida M, Aceret TL, Willis RH, Babcock RC, Willis BL, Florian Z, Clayton MN, Miller RL (1994) Chemical aspects of mass spawning in corals. I. Sperm-attractant molecules in the eggs of the scleractinian coral *Montipora digitata*. Mar Biol 118:177-182

Coma R, Lasker HR (1997a) Effects of spatial distribution and reproductive biology on in situ fertilization rates of a broadcast-spawning invertebrate. The Biological Bulletin 193:20-29

Coma R, Lasker HR (1997b) Small-scale heterogeneity of fertilization success in a broadcast spawning octocoral. J Exp Mar Biol Ecol 214:107-120

Combosch DJ, Vollmer SV (2013) Mixed asexual and sexual reproduction in the Indo-Pacific reef coral *Pocillopora damicornis*. Ecology and evolution 3:3379-3387

Connell JH (1973) Population ecology of reef-building corals. Biology and geology of coral reefs 2:205-245

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends Ecol Evol 14:405-410
Crimaldi JP (2012) The role of structured stirring and mixing on gamete dispersal and aggregation in broadcast spawning. The Journal of Experimental Biology 215:1031-1039
Crimaldi JP, Zimmer RK (2014) The physics of broadcast spawning in benthic invertebrates. Annual Review of Marine Science 6:141-165
Csanady GT (1973) Turbulent diffusion in the environment, Vol 3. Springer Science & Business Media
Davis KA, Pawlak G, Monismith SG (2021) Turbulence and coral reefs. Annual review of marine science 13:343-373
dela Cruz DW, Harrison PL (2020) Optimising conditions for in vitro fertilization success of *Acropora tenuis*, *A. millepora* and *Favites colemani* corals in northwestern Philippines. J Exp Mar Biol Ecol 524:151286
Denny M (1988) Biology and the mechanics of the wave-swept environment, Vol. Princeton University Press
Denny M, Dairiki J, Distefano S (1992) Biological consequences of topography on wave-swept rocky shores: I. Enhancement of external fertilization. The Biological Bulletin 183:220-232
Denny MW, Nelson EK, Mead KS (2002) Revised estimates of the effects of turbulence on fertilization in the purple sea urchin, Strongylocentrotus purpuratus. The Biological Bulletin 203:275-277
Dietzel A, Bode M, Connolly SR, Hughes TP (2021) The population sizes and global extinction risk of reef-building coral species at biogeographic scales. Nature Ecology & Evolution 5:663-669
Doropoulos C, Babcock RC (2018) Harnessing connectivity to facilitate coral restoration. Front Ecol Environ 16:558-559
Dubé CE, Boissin E, Mercière A, Planes S (2020) Parentage analyses identify local dispersal events and sibling aggregations in a natural population of Millepora hydrocorals, a free-spawning marine invertebrate. Mol Ecol 29:1508-1522
Edmunds PJ, Riegl B (2020) Urgent need for coral demography in a world where corals are disappearing. Mar Ecol Prog Ser 635:233-242
Elder J (1959) The dispersion of marked fluid in turbulent shear flow. Journal of fluid mechanics 5:544-560
Evans JP, Sherman CD (2013) Sexual selection and the evolution of egg-sperm interactions in broadcast-spawning invertebrates. The Biological Bulletin 224:166-183
Farley GS (2002) Helical nature of sperm swimming affects the fit of fertilization-kinetics models to empirical data. The Biological Bulletin 203:51-57
Fischer HB, List JE, Koh CR, Imberger J, Brooks NH (1979) Mixing in inland and coastal waters, Vol. Elsevier
Fogarty ND, Vollmer SV, Levitan DR (2012) Weak prezygotic isolating mechanisms in threatened Caribbean Acropora corals. PLoS One 7:e30486
Franklin I (1980) Evolutionary change in small population. Conservation biology, an evolutionary-ecological perspective
Franklin I, Frankham R (1998) How large must populations be to retain evolutionary potential? Animal Conservation forum 1:69-70
Freeman G, Miller RL (1982) Hydrozoan eggs can only be fertilized at the site of polar body formation. Dev Biol 94:142-152
Furukawa M, Ohki S, Kitanobo S, Fukami H, Morita M (2020) Differences in spawning time drive cryptic speciation in the coral Acropora divaricata. Mar Biol 167:1-10
Gallo A, Esposito MC, Boni R, Tosti E (2022) Oocyte quality assessment in marine invertebrates: a novel approach by fluorescence spectroscopy. Biological Research 55
Gascoigne J, Lipcius RN (2004) Allee effects in marine systems. Mar Ecol Prog Ser 269:49-59
Gaylord B (2008) Hydrodynamic context for considering turbulence impacts on external fertilization. The Biological Bulletin 214:315-318

George R, Flick RE, Guza R (1994) Observations of turbulence in the surf zone. Journal of Geophysical Research: Oceans 99:801-810
Gittings SR, Boland GS, Deslarzes KJ, Combs CL, Holland BS, Bright TJ (1992) Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, northwest Gulf of Mexico. Bull Mar Sci 51:420-428
Goodyear CP (1989) Spawning stock biomass per recruit: the biological basis for a fisheries management tool. ICCAT working document SCRS/89/82 10
Gouezo M, Langlais C, Beardsley J, Roff G, Harrison PL, Thomson DP, Doropoulos C (2025) Going with the flow: Leveraging reef-scale hydrodynamics for upscaling larval-based restoration. Ecol Appl 35:e70020
Guest J, Baird A, Goh B, Chou L (2012) Sexual systems in scleractinian corals: an unusual pattern in the reef-building species Diploastrea heliopora. Coral Reefs 31:705-713
Gustafson EJ (1998) Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1:143-156
Hagedorn M, Carter VL, Henley EM, Van Oppen MJ, Hobbs R, Spindler RE (2017) Producing coral offspring with cryopreserved sperm: a tool for coral reef restoration. Scientific reports 7:14432
Hall V, Hughes T (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950-963
Harada Y, Takagaki Y, Sunagawa M, Saito T, Yamada L, Taniguchi H, Shoguchi E, Sawada H (2008) Mechanism of self-sterility in a hermaphroditic chordate. Science 320:548-550
Harrison P, Wallace C (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky, Z. (ed) Coral reef ecosystems Ecosystems of the world, Book 25. Elsevier, Amsterdam, 133-207
Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. Science 223:1186-1189
Hata T, Madin JS, Cumbo VR, Denny M, Figueiredo J, Harii S, Thomas CJ, Baird AH (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. Scientific reports 7:1-9
Hatta M, Fukami H, Wang W, Omori M, Shimoike K, Hayashibara T, Ina Y, Sugiyama T (1999) Reproductive and genetic evidence for a reticulate evolutionary history of mass-spawning corals. Mol Biol Evol 16:1607-1613
Hayashibara T, Ohike S, Kakinuma Y (1997) Embryonic and larval development and planula metamorphosis of four gamete-spawning Acropora (Anthozoa, Scleractinia). Proc 8th Int Coral Reef Sym 2:1231-1236
Henley EM, Quinn M, Bouwmeester J, Daly J, Zuchowicz N, Lager C, Bailey DW, Hagedorn M (2021) Reproductive plasticity of Hawaiian Montipora corals following thermal stress. Scientific reports 11:12525
Heyward A, Babcock R (1986) Self-and cross-fertilization in scleractinian corals. Mar Biol 90:191-195
Heyward AJ, Negri AP (2012) Turbulence, cleavage, and the naked embryo: a case for coral clones. Science 335:1064
Hobbs J-PA, Richards ZT, Popovic I, Lei C, Staeudle TM, Montanari SR, DiBattista JD (2022) Hybridisation and the evolution of coral reef biodiversity. Coral Reefs 41:535-549
Hoeksema BW (2026) An unseen threat to coral reef biodiversity: the international trade of live corals for the aquarium industry as reflected by CITES records (1990–2021). Ocean Coast Manage 276:108111
Hordyk A, Ono K, Sainsbury K, Loneragan N, Prince J (2015) Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. ICES J Mar Sci 72:204-216
Huang ZC, Lenain L, Melville WK, Middleton JH, Reineman B, Statom N, McCabe RM (2012) Dissipation of wave energy and turbulence in a shallow coral reef lagoon. Journal of Geophysical Research: Oceans 117

Humanes A, Lachs L, Beauchamp E, Bukurou L, Buzzoni D, Bythell J, Craggs JR, de la Torre Cerro R, Edwards AJ, Golbuu Y (2024) Selective breeding enhances coral heat tolerance to marine heatwaves. Nature Communications 15:8703

Hunter C (1988) Environmental cues controlling spawning in two Hawaiian corals, Montipora verrucosa and M. dilatata. Proc 6th int coral Reef Symp 2:727-732

Iguchi A, Morita M, Nakajima Y, Nishikawa A, Miller D (2009) In vitro fertilization efficiency in coral Acropora digitifera. Zygote 17:225-227

Isomura N, Iwao K, Morita M, Fukami H (2016) Spawning and fertility of F1 hybrids of the coral genus Acropora in the Indo-Pacific. Coral Reefs 35:851-855

Iwao K, Wada N, Ohdera A, Omori M (2014) How many donor colonies should be cross-fertilized for nursery farming of sexually propagated corals? Natural Resources 5:521-526

Johansen JL (2014) Quantifying water flow within aquatic ecosystems using load cell sensors: a profile of currents experienced by coral reef organisms around Lizard Island, Great Barrier Reef, Australia. PLoS One 9:e83240

Jones NL, Lowe RJ, Pawlak G, Fong DA, Monismith SG (2008) Plume dispersion on a fringing coral reef system. Limnol Oceanogr 53:2273-2286

Jones NL, Monismith SG (2008) The influence of whitecapping waves on the vertical structure of turbulence in a shallow estuarine embayment. J Phys Oceanogr 38:1563-1580

Keith SA, Maynard JA, Edwards AJ, Guest JR, Bauman AG, Van Hooidonk R, Heron SF, Berumen ML, Bouwmeester J, Piromvaragorn S (2016) Coral mass spawning predicted by rapid seasonal rise in ocean temperature. Proceedings of the Royal Society B: Biological Sciences 283:20160011

Kenyon JC (1997) Models of reticulate evolution in the coral genus Acropora based on chromosome numbers: parallels with plants. Evolution 51:756-767

Kingsford M, Wolanski E, Choat J (1991) Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef. Mar Biol 109:167-180

Kitanobo S, Isomura N, Fukami H, Iwao K, Morita M (2016) The reef-building coral Acropora conditionally hybridize under sperm limitation. Biol Lett 12:20160511

Kitanobo S, Iwao K, Fukami H, Isomura N, Morita M (2022a) First evidence for backcrossing of F1 hybrids in Acropora corals under sperm competition. Scientific Reports 12:1-8

Kitanobo S, Toshino S, Morita M (2022b) Genetic variation in released gametes produces genetic diversity in the offspring of the broadcast spawning coral Acropora tenuis. Scientific Reports 12:5026

Kojis BL, Quinn NJ (1982) Reproductive ecology of two faviid corals (Coelenterata: Scleractinia). Mar Ecol Prog Ser 8:251-255

Kono T, Nakamura R, Omori M (2020) Experimental measurements of the sinking speed of sperm of an acroporid coral, Acropora tenuis, in static seawater. J Oceanogr 76:109-120

Kramer AM, Dennis B, Liebhold AM, Drake JM (2009) The evidence for Allee effects. Popul Ecol 51:341-354

Ladd MC, Miller MW, Hunt JH, Sharp WC, Burkepile DE (2018) Harnessing ecological processes to facilitate coral restoration. Front Ecol Environ 16:239-247

Ladd MC, Shantz AA, Nedimyer K, Burkepile DE (2016) Density dependence drives habitat production and survivorship of Acropora cervicornis used for restoration on a Caribbean coral reef. Frontiers in Marine Science 3:261

Langley C, Harrison PL, Doropoulos C (2024) Optimizing initial stocking densities of wild coral spawn slicks for mass production of larvae and settled corals for restoration. Restor Ecol:e14239

Lasker HR, Brazeau DA, Calderon J, Coffroth MA, Coma R, Kim K (1996) In situ rates of fertilization among broadcast spawning gorgonian corals. The Biological Bulletin 190:45-55

Lasker HR, Gutiérrez-Rodríguez C, Bala K, Hannes A, Bilewitch JP (2008) Male reproductive success during spawning events of the octocoral Pseudopterogorgia elisabethae. Mar Ecol Prog Ser 367:153-161

Lehtonen J, Dardare L (2019) Mathematical models of fertilization—an eco-evolutionary perspective. The Quarterly Review of Biology 94:177-208

Lentz S, Davis K, Churchill J, DeCarlo T (2017) Coral reef drag coefficients–water depth dependence. J Phys Oceanogr 47:1061-1075

Levitan DR (1995) The ecology of fertilization in free-spawning invertebrates. In: Ecology of marine invertebrate larvae. CRC Press123-156

Levitan DR (1998) 6 - Sperm Limitation, Gamete Competition, and Sexual Selection in External Fertilizers. In: Møller TRBP (ed) Sperm Competition and Sexual Selection. Academic Press, San Diego, 175-217

Levitan DR, Ferrell DL (2006) Selection on gamete recognition proteins depends on sex, density, and genotype frequency. Science 312:267-269

Levitan DR, Fogarty ND, Jara J, Lotterhos KE, Knowlton N (2011) Genetic, spatial, and temporal components of precise spawning synchrony in reef building corals of the Montastraea annularis species complex. Evolution: International Journal of Organic Evolution 65:1254-1270

Levitan DR, Fukami H, Jara J, Kline D, McGovern TM, McGhee KE, Swanson CA, Knowlton N (2004) Mechanisms of reproductive isolation among sympatric broadcast spawning corals of the *Montastraea annularis* species complex. Evolution 58:308-323

Levitan DR, Olsen KC, Best RM, Edmunds PJ (2025) Brooding and parthenogenesis enhance the success of the coral Porites astreoides relative to Orbicella annularis. Ecology 106:e70102

Levitan DR, Petersen C (1995) Sperm limitation in the sea. Trends Ecol Evol 10:228-231

Levitan DR, Sewell MA, Chia F-S (1992) How distribution and abundance influence fertilization success in the sea urchin *Strongylocentotus franciscanus*. Ecology 73:248-254

Levitan DR, Sewell MA, Chia FS (1991) Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: interaction of gamete dilution, age, and contact time. The Biological Bulletin 181:371-378

Lin C-H, Nozawa Y (2021) The release of “sperm bundles” by Acropora corals. BULLETIN OF MARINE SCIENCE 97 (1), 105-106

Lotterhos KE, Levitan DR, Traits G (2010) Gamete release and spawning behavior in broadcast spawning marine invertebrates. The evolution of primary sexual characters in animals 99:120

Luque GM, Vayssade C, Facon B, Guillemaud T, Courchamp F, Fauvergue X (2016) The genetic Allee effect: a unified framework for the genetics and demography of small populations. Ecosphere 7:e01413

MacKenzie B, Leggett W (1993) Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparisons. Mar Ecol Prog Ser 94:207-216

Madin JS, Anderson KD, Andreasen MH, Bridge TC, Cairns SD, Connolly SR, Darling ES, Diaz M, Falster DS, Franklin EC (2016) The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Scientific Data 3:160017

Manzello DP, Cunning R, Karp RF, Baker AC, Bartels E, Bonhag R, Borreil A, Bourque A, Brown KT, Bruckner AW (2025) Heat-driven functional extinction of Caribbean Acropora corals from Florida’s Coral Reef. Science 390:361-366

Marshall DJ, Bolton TF (2007) Sperm release strategies in marine broadcast spawners: the costs of releasing sperm quickly. J Exp Biol 210:3720-3727

McCallum KP, Breed MF, Paton DC, Lowe AJ (2019) Clumped planting arrangements improve seed production in a revegetated eucalypt woodland. Restor Ecol 27:638-646

Mead KS, Denny MW (1995) The effects of hydrodynamic shear stress on fertilization and early development of the purple sea urchin Strongylocentrotus purpuratus. The Biological Bulletin 188:46-56

Miller K, Babcock R (1997) Conflicting morphological and reproductive species boundaries in the coral genus Platygyra. The Biological Bulletin 192:98-110

Miller K, Mundy C (2005) In situ fertilisation success in the scleractinian coral Goniastrea favulus. Coral Reefs 24:313-317

Miller KJ (1994) The Platygyra species complex: implications for coral taxonomy and evolution.
Miller M, Baums I, Pausch R, Bright A, Cameron C, Williams D, Moffitt Z, Woodley C (2018) Clonal structure and variable fertilization success in Florida Keys broadcast-spawning corals. Coral Reefs 37:239-249
Miller M, Williams D, Fisch J (2016) Genet-specific spawning patterns in Acropora palmata. Coral Reefs 35:1393-1398
Moláček J, Denny M, Bush JW (2012) The fine art of surfacing: its efficacy in broadcast spawning. J Theor Biol 294:40-47
Monismith SG (2007) Hydrodynamics of coral reefs. Annu Rev Fluid Mech 39:37-55
Morita M, Nishikawa A, Nakajima A, Iguchi A, Sakai K, Takemura A, Okuno M (2006) Eggs regulate sperm flagellar motility initiation, chemotaxis and inhibition in the coral *Acropora digitifera*, *A. gemmifera* and *A. tenuis*. J Exp Biol 209:4574-4579
Mumby PJ, Sartori G, Buccheri E, Alessi C, Allan H, Doropoulos C, Rengiil G, Ricardo G (2024) Allee effects limit coral fertilization success. P Natl Acad Sci USA 121
Nozawa Y, Isomura N, Fukami H (2015) Influence of sperm dilution and gamete contact time on the fertilization rate of scleractinian corals. Coral Reefs:1-8
Okubo N, Mezaki T, Nozawa Y, Nakano Y, Lien Y-T, Fukami H, Hayward DC, Ball EE (2013) Comparative embryology of eleven species of stony corals (Scleractinia). PLOS One 8:e84115
Okubo N, Motokawa T (2007) Embryogenesis in the reef-building coral *Acropora* spp. Zoolog Sci 24:1169-1177
Okubo N, Toshino S, Nakano Y, Yamamoto HH (2017) Coral individuality–confluence of change physical splitting and developmental ability of embryos. Scientific reports 7:16006
Oliver J, Willis B (1987) Coral-spawn slicks in the Great Barrier Reef: preliminary observations. Mar Biol 94:521-529
Oliver JK, Babcock RC (1992) Aspects of the fertilization ecology of broadcast spawning corals: sperm dilution effects and in situ measurements of fertilization. Biol Bull 183:409-417
Omori M, Fukami H, Kobinata H, Hatta M (2001) Significant drop of fertilization of *Acropora* corals in 1999: An after-effect of heavy coral bleaching? Limnol Oceanogr 46:704-706
Padilla-Gamino J, Weatherby T, Waller R, Gates R (2011) Formation and structural organization of the egg–sperm bundle of the scleractinian coral *Montipora capitata*. Coral Reefs 30:371-380
Pattiaratchi C (1994) Physical oceanograhic aspects of the dispersal of coral spawn slicks: a review. The Bio-Physics of Marine Larval Dispersal 45:89-105
Philipps CJ, Bellwood DR (2024) The hydrodynamics of Lizard Island lagoon, Great Barrier Reef. Coral Reefs 43:881-897
Pinsky ML, Clark RD, Bos JT (2023) Coral reef population genomics in an age of global change. Annu Rev Genet 57:87-115
Post E, Levin SA, Iwasa Y, Stenseth NC (2001) Reproductive asynchrony increases with environmental disturbance. Evolution 55:830-834
Prince J, Victor S, Kloulchad V, Hordyk A (2015) Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. Fisheries Research 171:42-58
Quigley K (2024) Breeding and selecting corals resilient to global warming. Annual Review of Animal Biosciences 12:209-332
Ramírez-Portilla C, Baird AH, Cowman PF, Quattrini AM, Harii S, Sinniger F, Flot J-F (2022) Solving the coral species delimitation conundrum. Syst Biol 71:461-475
Reed DH, Bryant EH (2000) Experimental tests of minimum viable population size. Animal Conservation Forum 3:7-14
Reidenbach MA, Monismith SG, Koseff JR, Yahel G, Genin A (2006) Boundary layer turbulence and flow structure over a fringing coral reef. Limnol Oceanogr 51:1956-1968
Ricardo G, Doropoulos C, Babcock RC, Buccheri E, Khalil A, Mumby PJ (2025a) Critical thresholds of adult patch density and spacing during coral fertilization. Nature Ecology & Evolution:1-11

Ricardo GF, Doropoulos C, Babcock RC, Adam AAS, Buccheri E, Robledo N, Uribe Palomino J, Mumby PJ (2025b) Spawning asynchrony and mixed reproductive strategies in a common mass spawning coral. Ecology and Evolution 15:e71654
Ricardo GF, Doropoulos C, Humanes A, Lachs L, Martinez HM, Sartori G, Chang TKT, Chui APY, Wong ELC, Stevens JR (2026) Proximity and current alignment drives fertilisation success in a broadcast-spawning coral. Communications Biology
Ricardo GF, Jones RJ, Clode PL, Humanes A, Negri AP (2015) Suspended sediments limit coral sperm availability. Scientific Reports 5:18084
Ricardo GF, Negri AP, Jones RJ, Stocker R (2016) That sinking feeling: Suspended sediments can prevent the ascent of coral egg bundles. Scientific Reports 6:21567
Richards ZT, Hobbs J-PA (2015) Hybridisation on coral reefs and the conservation of evolutionary novelty. Current Zoology 61:132-145
Riegl B, Purkis S (2015) Coral population dynamics across consecutive mass mortality events. Global Change Biol 21:3995-4005
Rodriguez-Martinez H (2003) Laboratory semen assessment and prediction of fertility: still utopia? Reproduction in domestic animals 38:312-318
Rothschild L, Swann M (1949) The Fertilization Reaction in the Sea-Urchin Egg: A Propagated Response to Sperm Attachment. J Exp Biol 26:164-176
Ruiz J, Macías D, Peters F (2004) Turbulence increases the average settling velocity of phytoplankton cells. Proceedings of the National Academy of Sciences 101:17720-17724
Ryman N, Laikre L (1991) Effects of supportive breeding on the genetically effective population size. Conserv Biol 5:325-329
Sakai K (1998) Delayed maturation in the colonial coral Goniastrea aspera (Scleractinia): whole-colony mortality, colony growth and polyp egg production. Popul Ecol 40:287-292
Sawada H, Tanaka E, Ban S, Yamasaki C, Fujino J, Ooura K, Abe Y, Matsumoto K-i, Yokosawa H (2004) Self/nonself recognition in ascidian fertilization: vitelline coat protein HrVC70 is a candidate allorecognition molecule. Proceedings of the National Academy of Sciences 101:15615-15620
Schmerler S, Wessel GM (2011) Polar bodies—more a lack of understanding than a lack of respect. Mol Reprod Dev 78:3-8
Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model Online 9:347-404
Shearer T, Porto I, Zubillaga A (2009) Restoration of coral populations in light of genetic diversity estimates. Coral Reefs 28:727-733
Sheets EA, Warner PA, Palumbi SR (2018) Accurate population genetic measurements require cryptic species identification in corals. Coral Reefs 37:549-563
Shlesinger Y, Loya Y (1985) Coral community reproductive patterns: red sea versus the great barrier reef. Science 228:1333-1335
Shlesinger Y, Loya Y (1991) Larval development and survivorship in the corals Favia favus and Platygyra lamellina. In: Coelenterate Biology: Recent Research on Cnidaria and Ctenophora. Springer101-108
Silliman BR, He Q (2018) Physical stress, consumer control, and new theory in ecology. Trends Ecol Evol 33:492-503
Silliman BR, Schrack E, He Q, Cope R, Santoni A, van der Heide T, Jacobi R, Jacobi M, van de Koppel J (2015) Facilitation shifts paradigms and can amplify coastal restoration efforts. Proceedings of the National Academy of Sciences 112:14295-14300
Simpson C, Cary J, Masini R (1993) Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. Coral Reefs 12:185-191
Singh P, Joseph D (2005) Fluid dynamics of floating particles. Journal of Fluid Mechanics 530:31-80

Speare KE, Adam TC, Winslow EM, Lenihan HS, Burkepile DE (2022) Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef. Global Change Biol 28:1342-1358
Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? Oikos:185-190
Stoddart J, Babcock R, Heyward A (1988) Self-fertilization and maternal enzymes in the planulae of the coral Goniastrea favulus. Mar Biol 99:489-494
Styan CA (1998) Polyspermy, egg size, and the fertilization kinetics of free-spawning marine invertebrates. The American Naturalist 152:290-297
Styan CA, Butler AJ (2000) Fitting fertilisation kinetics models for free-spawning marine invertebrates. Mar Biol 137:943-951
Suzuki G, Okada W, Yasutake Y, Yamamoto H, Tanita I, Yamashita H, Hayashibara T, Komatsu T, Kanyama T, Inoue M (2020) Enhancing coral larval supply and seedling production using a special bundle collection system “coral larval cradle” for large-scale coral restoration. Restor Ecol 28:1172-1182
Suzuki G, Tashiro S, Suhara Y, Shigemura T, Fujiie W, Yoshida T, Kanyama T (2025) Duration of bundle release by Acropora aff. tenuis corals in the field. PREPRINT (Version 1) available at Research Square
Szmant A, Weil E, Miller M, Colon D (1997) Hybridization within the species complex of the scleractinan coral Montastraea annularis. Mar Biol 129:561-572
Takeuchi I, Gushi M, Das RR, Yamashiro H (2022) Spawning record of hermatypic coral Acropora digitifera documented by the action camera at one-minute interval. Plankton and Benthos Research 17:178-184
Teo A, Guest JR, Neo ML, Vicentuan K, Todd PA (2016) Quantification of coral sperm collected during a synchronous spawning event. PeerJ 4:e2180
Teo A, Todd PA (2018) Simulating the effects of colony density and intercolonial distance on fertilisation success in broadcast spawning scleractinian corals. Coral Reefs 37:891-900
Unsworth JD, Hesley D, D’Alessandro M, Carrick JV, Kaufman M, Rivas N, Lirman D (2023) Dense clusters improve efficiency and foster colony development in restored Acropora cervicornis. Coral Reefs 42:337-341
Vacquier V, Tegner MJ, Epel D (1973) Protease released from sea urchin eggs at fertilization alters the vitelline layer and aids in preventing polyspermy. Exp Cell Res 80:111-119
Van Oppen MJ, Willis BL, Van Rheede T, Miller DJ (2002) Spawning times, reproductive compatibilities and genetic structuring in the Acropora aspera group: evidence for natural hybridization and semi-permeable species boundaries in corals. Mol Ecol 11:1363-1376
Van Woesik R (2010) Calm before the spawn: global coral spawning patterns are explained by regional wind fields. Proceedings of the Royal Society B: Biological Sciences 277:715-722
Velázquez E, Martínez I, Getzin S, Moloney KA, Wiegand T (2016) An evaluation of the state of spatial point pattern analysis in ecology. Ecography 39:1042-1055
Vogel H, Czihak G, Chang P, Wolf W (1982) Fertilization kinetics of sea urchin eggs. Math Biosci 58:189-216
Von Kármán T (1931) Mechanical similitude and turbulence, Vol. National Advisory Committee for Aeronautics
Wallace C (1999) Staghorn corals of the world: a revision of the genus Acropora, Vol. CSIRO publishing
Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus Acropora. Mar Biol 88:217-233
Warner PA, Willis BL, Van Oppen MJ (2016) Sperm dispersal distances estimated by parentage analysis in a brooding scleractinian coral. Mol Ecol 25:1398-1415
Willis BL, Babcock RC, Harrison PL, Wallace CC (1997) Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. Coral Reefs 16:S53-S65

Willis BL, Oliver JK (1990) Direct tracking of coral larvae: implications for dispersal studies of planktonic larvae in topographically complex environments. Ophelia 32:145-162

Wolanski E, Burrage D, King B (1989) Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier Reef, following mass coral spawning. Cont Shelf Res 9:479-496

Wolanski E, Imberger J, Heron ML (1984) Island wakes in shallow coastal waters. Journal of Geophysical Research: Oceans 89:10553-10569

Wolstenholme JK (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). Mar Biol 144:567-582

Yasuda N, Nakano Y, Yamashiro H, Hidaka M (2012) Skeletal structure and progression of growth anomalies in Porites australiensis in Okinawa, Japan. Dis Aquat Org 97:237-247

Yund PO (2000) How severe is sperm limitation in natural populations of marine free-spawners? Trends Ecol Evol 15:10-13

Zuchowicz N, Daly J, Bouwmeester J, Lager C, Henley EM, Nuñez Lendo CI, Hagedorn M (2021) Assessing coral sperm motility. Scientific reports 11:1-13