Coral connectivity: Biophysical drivers, key knowledge gaps and emerging empirical advances

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Abstract

Coral reefs are experiencing widespread decline from climate change and anthropogenic stressors, increasing the need to understand the processes that maintain and replenish coral populations. Connectivity—the exchange of individuals between coral populations—underpins population recovery, yet major uncertainties remain in larval biology and behaviour during dispersal and settlement. This review synthesises current knowledge of the physical and biological drivers of coral connectivity across hard and soft corals. We highlight well-studied processes such as spawning timing and identify key data gaps, including buoyancy, mortality, and competency during dispersal. High variability across taxa and locations complicates the identification of general connectivity patterns, particularly for processes that are difficult to observe *in situ*. Emerging techniques—including larval colouring, time-series competency assays, acoustic enrichment, AI-based behavioural tracking and genetic barcoding—offer promising avenues to address these gaps. By summarising existing evidence and recent methodological advances, this review provides a foundation for improving empirical measurements and predictive models of coral connectivity to support conservation and restoration in dynamic oceans.

Keywords: coral, connectivity, biophysical, ocean currents, larval production, larval dispersal, larval settlement

1 Introduction

Coral reef ecosystems are some of the most diverse in the world and are important socio-economically[1,2]. Coral reefs provide essential ecosystem services as they form structure and habitats that underpin biodiversity, coastal protection to communities, nutrition and livelihoods[3–7]. In the recent decades, coral reefs have experienced mass mortality events globally, and these ecosystems, and the services they provide are in decline due to climate change and other anthropogenic pressures[8–10]. A mechanistic understanding of the processes that underpin coral population maintenance and recovery amidst increasingly frequent disturbances is urgently needed to inform the development of strategies for facilitating coral adaptation and the restoration of damaged reefs.

A key factor shaping the resilience and recovery potential of coral reefs under these pressures is connectivity, which governs the exchange of individuals between populations[11]. As sessile organisms, corals remain permanently attached to the seafloor throughout their adult life cycle, except for the gamete and larval stages. It is during these life stages that connectivity occurs. Coral reef ecosystems are typically organised as networks of shallow reef habitats that can be separated by tens to hundreds of kilometres, and their persistence following disturbance depends in part on the connections between coral populations across these habitats. Connectivity encompasses demographic, genetic and ecological processes that link populations through the movement of individuals, genes and ecological interactions. It is shaped by a complex interplay of physical, biological and ecological processes that influence the production, dispersal and settlement of coral larvae across seascapes.

Physical oceanographic processes—including large-scale ocean currents, mesoscale features like eddies and internal waves, wave- and tide-driven circulation, and wind-driven surface flows—govern the movement of gametes and/or larvae over both short and long distances[12–15]. These hydrodynamic forces create dispersal pathways that can enhance or limit connectivity within and between reefs. Biological and behavioural processes modulate how larvae interact with the physical environment. For example, the timing and duration of spawning, the buoyancy and swimming ability of larvae, and larval competency periods, shape dispersal pathways. Additionally, ecological processes, such as mortality, predation, habitat availability and behavioural responses to environmental cues, further constrain realised connectivity, meaning that dispersal does not necessarily translate into successful recruitment[16–19]. Together, the interaction between the physical and biological processes creates highly variable dispersal and connectivity patterns that can differ markedly among species, reef systems, and environmental conditions.

A high degree of connectivity is usually associated with increased resilience to disturbance due to the arrival of larvae from distant communities, which can enhance the recovery of perturbed populations[20]. However, since the connectivity of multiple marine organisms is driven by the same dispersal mechanisms[21], high connectivity can also have negative effects on coral populations due to increased exchange of diseases, invasive species or predators, e.g., crown-of-thorns starfish[22]. Despite these risks, maintaining reefs with high coral cover and high connectivity is critical because they act as major sources of healthy larvae within the network. The preservation of reefs with high coral cover and the maintenance of both the environmental and biological conditions that favour high coral cover is likely to increase coral reproduction, coral larval settlement and survivorship of coral recruits[23].

Although coral reef connectivity has been studied for several decades, our understanding remains fragmented across disciplines, spatial scales and methodological approaches. Many connectivity assessments continue to focus on large-scale circulation or average dispersal patterns, while the influence of fine-scale physical processes remains poorly quantified. Biological complexity is also often simplified, with limited consideration of how species-specific traits, behaviour, and life-history strategies interact with physical transport to shape realised connectivity. Our goal was to identify and summarise all studies documenting information on the processes underpinning coral connectivity. We separated different processes and identified studies that provided measurements or discussion of these processes for corals: physical processes (i.e., ocean currents) and biological processes (coral larvae production, biology, and behaviour from the production of gametes through to the selection of settlement location and settlement by larvae). We aimed to distinguish and summarise measurements of these processes across species and locations to reflect the diversity of reproductive strategies and connectivity patterns observed in reef-building (hard) and non-reef-building (soft) corals. We considered both hard and soft corals, aiming for a broad taxonomic scope to develop an understanding of coral connectivity across ecological contexts. We aimed to determine if there are general patterns across taxa groups and how that applies to our understanding of connectivity more widely.

2 Literature search

Coral reefs are highly diverse and speciose, with reproductive strategies and larvae biology and behaviour known to vary substantially across taxa. While scleratinian corals are the reef building corals (hard corals), and have been more widely studied, many other important corals also contribute to reef functioning, particularly in reefs at higher latitudes, such as the soft corals *Octocorallia* (e.g., *Alcyonacea* and *Gorgoniidae*, commonly referred to as soft corals). In this review, we focussed on the connectivity of both hard and soft corals with the aim of identifying studies that addressed key connectivity processes—physical processes, larvae production, larvae dispersal and larvae settlement—using modelling, laboratory experiments, or field observations.

The literature search was done on the Web of Science Core Collection on February 3, 2025. The search term used was

((Coral AND Connectivity) OR (Coral AND (Larv* OR Settl*))) NOT Fish

(where * represents a wildcard character, i.e., including all other possible word endings). We restricted the results to journal articles, excluding book chapters, reviews and conference proceedings. The search returned 2,939 papers that were published between 1990 and 2025. This search term allowed us to capture scientific literature about connectivity and larval settlement of hard and soft corals.

For the literature search, the search field “Topic” (which searches titles, abstract, author keywords and keywords plus) was used to obtain the most relevant studies. A subset of 453 papers was selected for inclusion based on relevance to coral connectivity modelling, and direct observations of coral larval production, biology and behaviour during dispersal and settlement.

3 Processes that influence coral connectivity

Coral connectivity is shaped by the combination of both physical and biological processes. Physical processes connect coral reefs through the movement of water, facilitating the transport of organic material, dissolved nutrients and carbon, and other marine organisms across ecosystems[24]. Ocean currents act as the primary driver of coral larvae dispersal. However, the realisation of connections between coral populations is contingent upon complex biological processes, such as larval production, development rates and behaviour during dispersal and settlement. These factors, coupled with larval survival and the ability to select suitable settlement sites, determine the eventual scale and efficacy of connectivity[17]. A schematic of coral larvae dispersal pathway and the processes that influence larvae production, dispersal and settlement is shown in

Fig. 1.

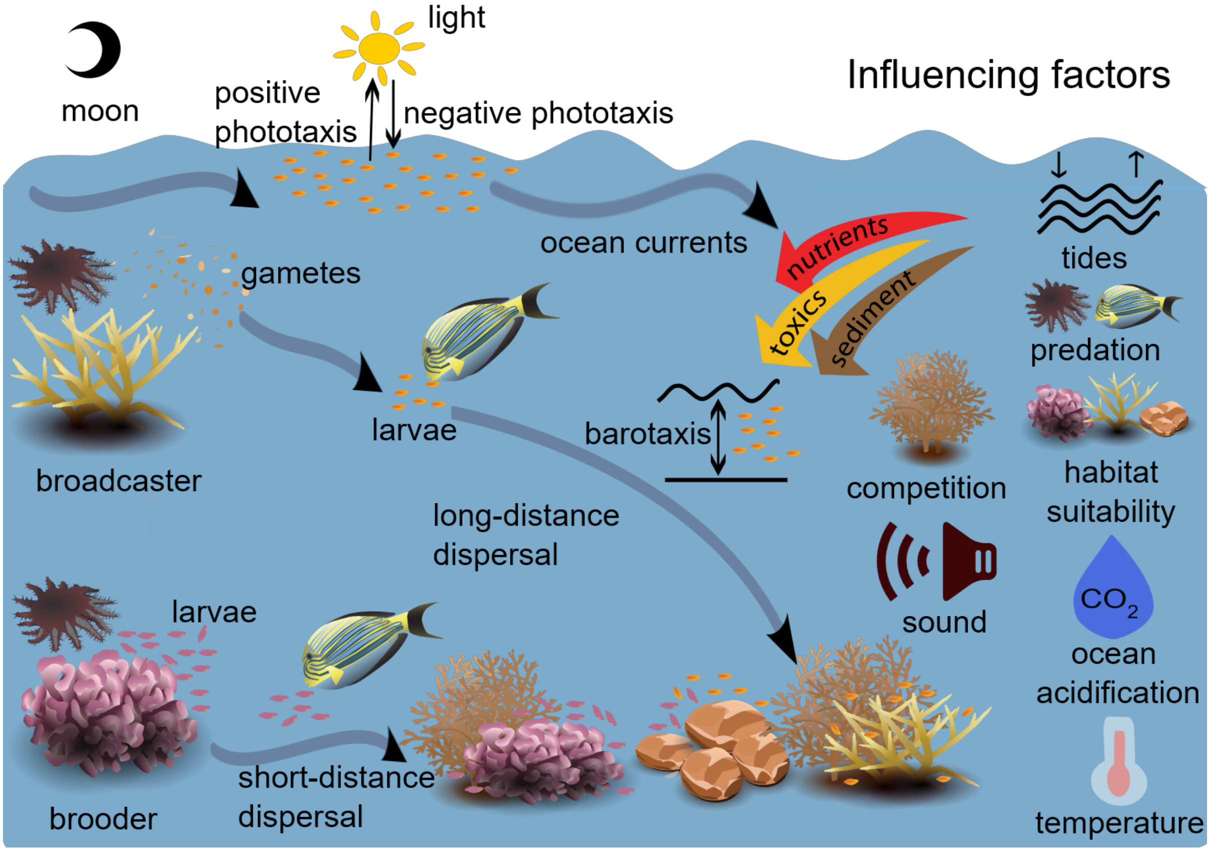

Fig. 1: Schematic showing larval dispersal pathways for broadcasting and brooding corals, and processes that influence larval production, dispersal and settlement. The processes that are represented in this figure include ocean circulation (i.e., ocean currents (3.1)), larval production (i.e., gametes and larvae release (3.2)), buoyancy (3.3.1), swimming ability (3.3.2), mortality (predation (3.3.3)), settlement (competing biota (3.4.2) and habitat suitability (3.4.1)), and behavioural responses to environmental cues (phototaxis, barotaxis, ocean acidification, sound, temperature, nutrients, toxics and sediments (3.4.3)). Icons by Saxby[25] and Woerner[26].

3.1 Physical processes

The transport and dispersal of coral larvae are fundamentally driven by the movement of seawater, so oceanographic processes play a key role in determining patterns of coral reef connectivity. Coral larvae are weak swimmers, and as such, the magnitude and direction of ocean currents at the time of release strongly influence larval dispersal[27]and coral distribution[12,14,28]. Ocean currents occur over a wide range of spatial and temporal scales, from turbulent (cm to km), to submesoscale motions (10s-100s km) lasting minutes to hours, to large-scale circulation features that extend across ocean basins and persist over seasonal to interannual timescales (Fig. 2). We identified 61 studies that modelled and/or observed how physical processes influence larval dispersal and summarised examples of how these processes operating at different spatial and temporal scales have been found to shape coral connectivity.

Large-scale ocean currents (e.g., regional or boundary currents and gyres) drive larval transport across regional to basin scales (>100 km, Fig. 2) and can carry larvae over hundreds to thousands of kilometres, creating connectivity between distant coral reef systems[14,29,30]. For example, Lopera et al.[14] demonstrated that circulation within the Seaflower Reserve, strongly influenced by the Caribbean Current and associated regional flow patterns (including the Panama–Colombia Gyre), facilitates connectivity among reef systems across the western Caribbean. Sala et al.[29] identified the Gulf Stream and eddy corridors propagating westward as key transport pathways in the Azores region, thereby facilitating the entrainment and retention of incoming particles and organisms within the Azores Archipelago. Cyclonic gyre in the Campeche Bay has been found to cause widespread dispersal of larvae with low self-recruitment on natal reefs[30].

Mesoscale features such as eddies, meanders, and fronts introduce variability into larval dispersal at smaller spatial scales (>10 km, Fig. 2). Eddies can either retain larvae near their natal reefs, thus promoting local self-recruitment and retention, or disperse them over wider areas, depending on the strength, location and duration of eddies[31–36]. For example, eddies that move across the Flower Garden Banks (submerged reefs) in the Gulf of Mexico have been shown to create short-term bursts of circulation that either retain larvae within banks or disperse larvae between banks[35]. By contrast, eddies in northern South Sea China have been shown to potentially increase the dispersal of larvae in deep waters where seasonal changes in the direction of currents could alter the direction of larvae transport[37]. Oceanic fronts in the Southern Ocean have been found to separate water masses of different properties (e.g., temperature, salinity), and act as barriers to dispersal or as pathways that enhance transport[38].

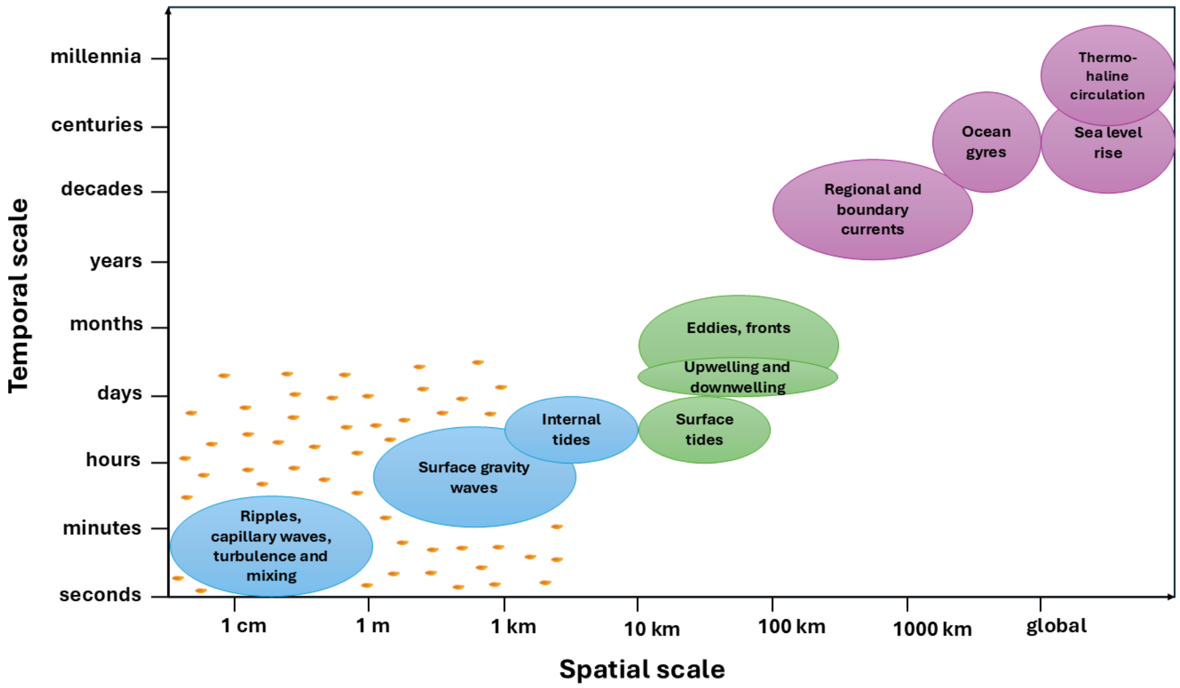

Fig. 2: Temporal and spatial scales of ocean currents. Blue symbols represent small-scale currents (<1 cm–10 km), green symbols represent mesoscale currents (10 km–<1000 km), plum symbols represent large-scale currents (>100 km) and gold symbols by Saxby[25] represent coral larvae at the spatial and temporal scales most relevant to their dispersal.

At the small-scale (<1 km), processes such as wave-, wind- and tide-driven circulation become increasingly important. Wave-induced currents, including Stokes drift and wave setup can move larvae across reef flats and toward coastal habitats, particularly in shallow reef systems[39]. By contrast, tidal flows, especially in reef passages and lagoons, can produce strong, oscillatory currents that can both retain larvae within reef systems or facilitate their export to the open ocean, depending on the timing and strength of tidal exchanges[13]. Turbulence near ocean boundaries (i.e., sea surface) can reduce the upwards swimming speed of larvae, thereby reducing the time larvae spend in surface waters during their larval stage[40], and can transport larvae to substrates even in calm conditions[41].

Wind-driven currents can either enhance or reduce local retention. Onshore wind-driven currents in the Upper Florida Keys transport particles across shelf areas thereby enhancing local retention of particles and reducing dispersal distances[42]. However, on the North West Shelf of Australia, wind and currents modified by cyclones can increase larval dispersal distance across shelves, thereby reducing larval retention[13,15]. For instance, depending on the timing of cyclones and their proximity to the reef, ocean currents have been shown to alter the dispersal pathway within Mermaid Reef by either decreasing or increasing larval retention[13]. Cyclone-modified currents have been found to increase the dispersal distance of larvae and connect widely separated reefs within the North West Shelf[15]. Cavalcante et al.[32] showed that wind-induced temperature variations can reduce or increase coral physiological stress and mortality. Wave action driven by annual monsoonal winds in Guam has been found to increase coral recruitment by shifting the benthic community structure from cyanobacteria to desired crustose coralline algae (CCA) for larval settlement[43].

Patterns of ocean circulation are influenced by reef size and structure, particularly in reef-dense areas[44–46], via the creation of eddies and recirculating flows caused by increased friction and reduced circulation[45]. These complex circulation patterns can enhance local retention of larvae on their natal reefs and self-recruitment due to high water retention times[45,47]. Although high flows and advection from source reefs reduce their ability to retain larvae[20]. Andutta et al.[44] showed that a “sticky water effect” is generated when prevailing currents in reef-dense areas in the Great Barrier Reef (GBR) are directed around and away from high reef density regions. The sticky water effect generated by small-scale currents in reef-dense areas of the GBR has been shown to decrease flushing, increase the residence time of water and subsequently increase self-seeding and reduce connectivity between areas of high and low reef density[44,46].

The interactions of physical processes at scales from global ocean circulation to localised dynamics together shape the patterns of coral reef connectivity that underpin the resilience, recovery, and genetic structure of coral reef populations worldwide. Indeed, both local retention and long-distance dispersal of larvae can affect the short-term recovery of coral populations following disturbances (e.g., disease and pest outbreaks, coral bleaching and tropical cyclones) as they require larval supply from remaining coral populations.

3.2 Larval production

Coral connectivity begins with the production of gametes or larvae by coral colonies at a source reef. The production of gametes or larvae depends on the mode of larval production, and the timing and duration of spawning. We identified 51 studies that observed the release of gametes and/or larvae *in situ* and in laboratories. Below, we summarise examples of how larvae production influence larvae dispersal and provide measurements of the timing and duration of coral spawning across species and locations.

3.2.1 Modes of reproduction

Corals exhibit two primary sexual systems, namely gonochorism and hermaphroditism. Gonochoric species are either male or female, each producing sperm or eggs respectively. Hermaphroditic species produce both eggs and sperm within a single colony, either sequentially or simultaneously. Alongside these sexual systems, there are also two major modes of fertilisation and larvae development: brooding and broadcasting. In brooding corals, fertilisation occurs internally, i.e., the egg and sperm meet inside a coral’s polyps, and they release developed larvae into the water. Broadcasting corals release gametes (eggs and/or sperm) into the water, such that fertilisation and larvae development occurs externally.

These different modes of reproduction result in very different time frames for dispersal and settlement across coral taxa. Broadcast spawners generally exhibit more variation in their population structure and colony density on a reef than brooders[48]. Larvae of broadcasting species generally require three to seven days to acquire competency before settlement[49–54] and exhibit upward swimming behaviour after acquiring competency when there are no settlement cues[51]. However, larvae of some broadcasting species such as *Goniastrea retiformis* and *Platygyra daedalea* on the GBR have been found to acquire competency as early as two to three days after fertilisation[54]. Larvae of broadcasting species are generally considered to travel much further distances before settling than brooding corals. For example, on the GBR, *Acropora valida*, *Acropora humilis* and *Platygyra daedalea* (broadcast spawners), have been found to disperse further than larvae of brooding corals (*Seriatopora hystrix* and *Stylophora pistillata*), which rely on self-recruitment for population maintenance and recovery[53].

In brooding corals, fertilisation and larvae production occur internally, i.e., the egg and sperm meet inside a coral's polyps. Brooding corals typically release fertilised larvae, although in some species larvae are instead clones of the parent[55,56]. Some brooding coral species (e.g. *Pocillopora damicornis*) can also assume broadcast spawning as an added reproductive strategy[57]. Larvae of brooding corals have the capacity to rapidly settle hours or days after release[49–53]. For instance, larvae of brooding corals *Acropora brueggemanni, Pocillopora damicornis* and *Heliopora coerulea* have been found to settle faster than larvae of broadcasting *Acropora tenuis*[18]. In the absence of settlement cues, larvae of brooders mainly swim downwards within the first two weeks of spawning and settle quickly[51]. In combination, these factors generally result in a high rate of local retention in brooding corals as larvae are most likely to settle immediately after release and near closely related adults or conspecifics[58,59].

The soft coral, *Rhytisma fitrum*, shows external surface brooding, which involves brooding of fertilised eggs and subsequent development of embryos for 5–7 days on the surface of female colonies before the detachment of larvae[60]. The interaction of surface brooding with high synchronous spawning and fecundity has been credited with the fertilisation success in the gorgonian *Paramuricea clavata*[61].

3.2.2 Timing and duration of spawning

Timing of spawning is important as it determines the environmental conditions that coral gametes and larvae will experience, which can be favourable or unfavourable for their fertilisation and survival. The timing of most coral spawning events around the world is highly synchronised with lunar cycles, occurs between sunset and dawn and varies across locations and species (Table 1). However, some coral species, such as *Agaricia agaricites*[62] and *Oculina varicosa*[63] spawn with no lunar periodicity, and some *Pocillopora* species spawn in the early morning[57]. Table 1 summarises the spawning times and locations of coral species reviewed in this study. This complements the comprehensive spawning database created by Baird et al.[64] that contains coral spawning times for Indo-Pacific corals.

Table 1: A summary of the location, timing and duration (when information is available) of spawning of coral species that were reviewed in this study.

Location	**Species**	**Timing and duration of release**	**References**
Caribbean	*Favia fragum*	Lunar cycles throughout the year	[62]
Indo-Pacific (Singapore)	*Acropora hyacinthus*, *Pectinia lactuca* and *Platygyra sinensis*	5 days after full moon in March or April between 8:00 p.m. and 10:00 p.m.	[65–67]
Eastern Pacific	*Pocillopora damicornis* and *P. elegans*	A few days before and after full moon	[68]

Caribbean	*Agaricia agaricites*	Summer and spring, with no lunar periodicity	[62]
Great Barrier Reef	*Acropora* sp., *Acanthastrea lordhowensis*, *Acanthastrea* sp., *Mycedium elephantotus*, *Favites* sp.	2–8 days after full moon between 7:00 p.m. and 9:25 p.m.	[65,69]
Caribbean	*Antillogorgia americana*	5–7 days and 15 days after full moon in November between 5:45 p.m. and 10:00 p.m.	[16]
Nanwan Bay, southern Taiwan	*Pocillopora damicornis, Seriatopora hystrix* and *Seriatopora caliendrum*	Lunar cycles throughout the year	[70–72]
Red Sea	*Stylophora pistillata*	1–12 nights after full moon from March to June	[73]
Florida Shelf	*Oculina varicosa*	Late summer and autumn, with no lunar periodicity	[63]
South Korea	*Dendronephthya gigantea*	Periods of full and new moon (field) No lunar periodicity and continuous release between July and September (laboratory)	[74]
Singapore	*Heliopora coerulea*	Second quarter of the lunar phase, after March and April full moon	[75]
Western Australia	*Acropora* spp. *Porites* spp. *Isopora* spp. and *Seriatopora* spp.	Lunar cycles in March and/or April and October and/or November Throughout spring to autumn on Kimberley Oceanic reefs and during summer in the Pilbara region During many months on Kimberley Oceanic reefs	[76]
Singapore and The Philippines	*Heliofungia actiniformis*	Lunar cycles from February to May	[77]

		between 10:00 p.m. and 1:00 a.m. for 16 nights (Singapore) and from March to June for 10 nights (Philippines)	
Singapore	*Pocillopora damicornis*	After a new moon for 13 days	78
Caribbean	*Diploria labyrinthiformis*	10 and 13 days after full moon during daylight hours between May and September	79
Red Sea	*Sarcophyton auritumon*	A single night annually on a full moon night in July	80
Guam	*Sinularia polydactyla*	4 and 5 nights after full moon from 6:20 p.m. to 9:35 p.m. (or longer) between March and June	81
Northwest Atlantic	*Gersemia fruticose and Duva florida*	Lunar cycles from April to early June at any time during the day (laboratory)	82
Lakshadweep, India	*Acropora muricata, Acropora cytherea, Acropora hemprichi* *Acropora nobilis*	Closer to full moon in February between 9:00 p.m. and 10:00 p.m. Closer to full moon in March from 9:30 p.m. to 10:00 p.m.	83
Mediterranean	*Eunicella singularis* *Corallium rubrum*	1 month release 2 days before full moon 1 month release 1 day after full moon	84
Northwestern Philippines	*Isopora cuneata* *Favites colemani and Favites abdita*	Spawned after sunset until midnight in March and April 7–8 days between full moon and the last quarter of May	85 86
Brazil	*Siderastrea stellata*	Spawned for 2 days during the last quarter in January and during the change from a new moon to the first quarter in April	87

The timing of spawning in brooding corals can also impact post-release performance. Larval traits such as size, symbiont density, photosynthetic potential, protein content, energetic status and settlement have been shown to vary by day of release across species[70,88–93]. Larvae released at the peak of spawning have been shown to be larger and more likely to settle compared to early-release of larvae during the spawning period, and such within-brood differences may continue into later development[70]. For example, larvae of *Favia fragum* released near sunrise crawled on substrates or attached loosely to substrates at a higher rate and had a higher settlement success than those released near sunset[90]. The peak release of larvae near sunrise can help larvae exploit light cues for rapid settlement, thereby shortening their duration in the water column and promoting local retention[94].

The duration of spawning varies across species and locations. Most corals around the world release larvae for at most four hours between sunset and midnight and many corals do this over multiple nights (Table 1), although some corals release larvae for more extended periods. For example, the brooding corals *Pocillopora damicornis* and *Euphyllia glabrescens* have been observed to release larvae all day with two peaks in the morning and night, whereas *Tubastraea aurea* release larvae throughout the day without consistent peaks[94].

The cold-water coral, *Lophelia pertusa*, exhibits asynchronous or extended spawning[95]. Extended spawning occurs when spawning is prolonged across multiple nights, lunar cycles, or seasons. Extended spawning effectively enhances the source strength stability[96] and could prevent coral populations from releasing larvae into conditions that are not favourable, thereby reducing the risk of losing a year's worth reproductive output during a single spawning event[63,97]. For instance, the extended spawning events exhibited by mesophotic coral populations in the Gulf of Eilat/Aqaba, northern Red Sea, have been linked to large reproductive output when shallow coral populations had depleted their reproductive material[98]. Split spawning, which occurs when the annual mass-spawning event of a coral population is divided across two or more consecutive months, instead of a single, highly synchronised spawning event, is another factor that can influence coral connectivity. Split spawning has been shown to increase coral larval supply and connectivity between reefs in the GBR, particularly in areas where connectivity is low and highly variable[99], although it had no measured effect on the reproductive output of coral colonies in Scott Reef, Western Australia[100].

Brooders generally have multiple reproductive cycles per year, have small colony sizes, produce fewer larvae than broadcasters and exhibit opportunistic life histories that allow them to colonise unstable habitats such as shallow reefs[101,102]. High recruitment rates of brooders may be associated with their release of competent larvae[101]. Conversely, broadcast spawning corals are generally larger in size, have a short annual spawning cycle and are most likely to colonise stable habitats[102]. Colony size modulates larval dispersal through its disproportionate influence on reproductive output; specifically, the colonial architecture of corals allows larger colonies to achieve significantly higher larval production than their smaller counterparts[103].

3.3 Larval dispersal

Aside from physical processes and larval production, coral larval dispersal is shaped by a suite of biological processes that determine larval movement, survival, and settlement. Together, buoyancy, swimming behaviour, survival dynamics, and the duration of competency interact to influence how far larvae travel, their behaviour in the water column, and their likelihood of successfully recruiting onto a reef. After spawning, coral larvae float in the ocean for hours to days or weeks, before sinking or actively swimming to the seafloor for settlement.

3.3.1 Buoyancy

Buoyancy variations in coral gametes and larvae determine their vertical positioning in the water column, influencing their fertilisation and transport and dispersal patterns. Larvae with a positive buoyancy tend to stay near the surface of the water or float in the upper layers. These larvae are more likely to be carried by surface currents, which are typically faster and more variable than deeper currents, potentially increasing the likelihood to be carried over large distances[32,104,105]. Larvae floating at the surface are also subject to direct wind advection (“windage”) and transport due to the influence of waves (“Stokes drift”), which together can have a substantial impact on dispersal[106]. Conversely, larvae with negative buoyancy tend to sink to deeper parts of the water column and are subject to bottom currents that are slower but more stable compared to surface currents[107]. These larvae may travel shorter distances compared to positively buoyant larvae via deeper, slower-moving water masses. Neutrally buoyant larvae neither sink nor float, rather they are suspended in the water column for longer periods, which allows their local retention or dispersal over long distances[108,109].

Larval buoyancy and active larval behaviour, like swimming, provide clear settlement distribution patterns[110]. Buoyancy can change with the age of the larvae. Immediately after spawning, larvae of most coral species will remain positively buoyant and located near the surface for a few days until they become negatively or neutrally buoyant and are able to change their vertical position in the water column[16,42,111,112]. Positively buoyant larvae remain close to the water surface until a positive settlement cue is contacted in shallow water, while negatively buoyant larvae settle on various natural substrates[62].

Brooders are most likely to travel from the ocean surface to the benthic layer within a day or two after spawning, whereas broadcasters remain buoyant for a longer period before changing their vertical position[112]. However, eggs spawned by broadcasters can be neutrally or negatively buoyant, which is typically determined by egg size (smaller eggs are more likely to be neutrally or negatively buoyant e.g., fungiids)[112] and spawning strategy[113]. For example, in *Goniastrea favulus*, the eggs and sperm ooze out of the polyps as a sticky mass and remain attached to the surface of the corals[113].

Differences in the dispersal periods of larvae among coral species have been associated with variations in their lipid content, which is used for buoyancy and as a source of energy[18]. High lipid content increases larval buoyancy and subsequently increases the dispersal distance of larvae[18]. Larvae become negatively buoyant when they use up their lipid stores[18,114] and may change their vertical position in the water column either by active swimming or passive sinking[111,112].

3.3.2 Swimming behaviour

The swimming behaviour of coral larvae also affects larval dispersal distances[18,112], but its contribution to larval dispersal in comparison to ocean currents is negligible[115]. There is limited information in the literature on larval swimming speed. Coral larvae are weak swimmers and cannot swim against horizontal currents[41], but larvae can change their vertical position in the water column in response to variations in water pressure[67,116]. For instance, larvae from *Porites astreoides* have been found to swim upwards when exposed to increasing pressure and downwards when pressure is decreasing[116]. This allows them to remain below surface waters where UV radiation and sea surface temperature are high[116].

Vertical swimming behaviour of larvae is believed to be important during microhabitat selection, which occurs in the boundary layer where currents are weak and eddies can entrain and transport larvae to substrates for settlement[115]. For example, the swimming behaviour of negatively buoyant *Agaricia humilis* larvae enables its positioning in shallow water and influences the distribution of individuals[117].

Larvae from *Favia fragum*, *Agaricia agaricites*, *Lophelia petusa*, *Pocillopora damicornis, Antillogorgia americana* and *Oculina varicosa* actively swim upwards for a short or an extended period before swimming downwards for settlement[27,62,95,118,119]. This behaviour allows larvae to move from the benthic boundary layer to the mixed layer where they are more readily dispersed by stronger surface currents, thereby promoting long-distance dispersal[40,95]. By contrast, larvae from *Acropora millepora*, *Acropora hyacinthus*, *Pectinia lactuca, Platygyra sinensis*, *Montastrea faveolate* are passively dispersed for a period before acquiring weak active swimming abilities to slowly migrate downwards[42,67,120].

3.3.3 Survivorship and competency

Accurate measurement of larval survivorship and competency in the field is extremely challenging given the small size of larvae, their rapid developmental changes, and the complexity of their interactions in rapidly changing oceanic conditions. As a result, much of our current understanding comes from controlled laboratory experiments, which provide valuable insights, but do not fully capture the variability of natural coral reef environments. A summary of measured pre-competency periods and "Pelagic Larval Duration (PLD)" of coral species reviewed in this study is provided in Table *2*.

Table 2*:* A summary of measured pre-competency periods and pelagic larvae duration (PLD) (when information is available) of coral species that were reviewed in this study. No available data is represented by dash (–). Asterisk (*) denotes that larvae were observed as still competent to settle at the final observation timepoint (usually beyond 30 days), although *Acropora hyacinthus, Dipsastraea matthaii,* and *Dipsastraea pallida* were found to settle beyond 70 days[54].

Species	**Mode of reproduction**	**Pre-competency period (≈ days after spawning)**	**PLD (≈ days after spawning)**	**References**
Platygyra daedalea	Broadcaster	3	–	54,121
Goniastrea favulus	Broadcaster	2	–	121
Antillogorgia americana	Broadcaster	4	58	16
Platygyra sinensis	Broadcaster	2	–	67
Pectinia lactuca	Broadcaster	2	–	67
Plexaura kuna	Broadcaster	4	–	122
Acropora brueggemanni	Brooder	1	–	18
Pocillopora damicornis	Brooder	< 1	100	18,123
Acropora tenuis	Broadcaster	3–4	–	18,54
Orbicella faveolata	Broadcaster	3–5 or 4–7 (with or without settlement cue)	–	124,125

Acropora spp.	Broadcaster	7–8 or day 10–11 (with or without settlement cue)	–	124
Heliopora coerulea	Brooder	< 1	30	123
Acropora hyacinthus and *Acropora spicifera*	Broadcasters	3	–	126
Corallium rubrum	Broadcaster	–	16–42	127
Goniocorella dumosa	Brooder	1	8	128
Acropora latistella, Favia pallida, Pectinia paeonia, Goniastrea aspera, and Montastraea magnistellata	Broadcasters	–	195–244	111
Pseudodiploria strigosa	Broadcaster	3	8	129
Orbicella franksi	Broadcaster	22	120	129
Dendronephthya gigantea	Brooder	< 2	–	74
Favites chinensis	Broadcaster	1–2	56–63	52
Goniastrea aspera	Broadcaster	2–3	63–70	52
Heliofungia actiniformi	Broadcaster	1	–	77
Cyphastrea serailia	Broadcaster	–	26	130
Acanthastrea lordhowensis	Broadcaster	–	78	130
Goniastrea australensis	Broadcaster	–	56	130
Gersemia fruticosa	Brooder	3	70	82
Acropora cytherea	Broadcaster	12	22	83
Acropora muricata	Broadcaster	12	20	83
Litophyton arboreum and Nephthea sp.	Brooders	–	57	131
Xenia umbellata	Brooder	–	76	131
Parerythropodium fulvum fulvum	Brooder	–	64	131
Dendronephthya hemprichi	Broadcaster	–	74	131
Heteroxenia fuscescens	Brooder	–	49	132

Acropora glauca, Acropora longicyathus, Acropora millepora, Lobophylia hemprichi, Porites cylindrica, Porites lobata, Mycedium elephantotus and Dipsatraea pallida	Broadcasters	4	*	[54]
Montipora aequituberculata, Diploastrea helipora,Galaxea fascicularis, and Oulophyllia crispa	Broadcasters	3	*	[54]
Goniastrea retiformis	Broadcaster	2	*	[54]
Acropora loripes and Acropora intermedia	Broadcaster	5	*	[54]
Acropora austera	Broadcaster	6	*	[54]

Larval survivorship influences larval dispersal and subsequent recruitment patterns. The development time of larvae before acquiring competency for settlement and the PLD have been shown to vary substantially across coral species (Table *2*). Larvae from most broadcast-spawning corals become competent for settlement three to seven days post-release[16,54,122,124,126], while larvae of brooders generally acquire competency within one day after release[18,74,123,128].

Larval dispersal distances and recruitment intensity increase with PLD and late start of competency[129,133], while larval survivorship decreases with PLD[127,129,134]. Connectivity models have indicated that shortened longevity of larvae due to climate change reduces connectivity between islands and alters larval traits that promote connectivity[135]. The daily survival rate of *Acropora muricata* and *Acropora valida* larvae has been observed to decrease from 100% to 50% at the end of the first week post-spawning and fall to 10% between the second and the third week[134]. Similarly, between 16 and 42 days after release, the survivorship of larvae from *Corallium rubrum* decreased from 95% of the initial total to 5%[127]. More than half of larvae generated from *Seriatopora hystrix* occurring in the mesophotic zone settled within 24 hours after they were released, which can cause a reduction in the vertical movement of larvae to shallow reefs and their long-distance dispersal[136].

There is a general trade-off between the number of coral larvae produced and the size and energy resources allocated to each larvae[137]. The recruitment success of lecithotrophic (i.e., non-feeding) coral larvae is largely influenced by the size of larvae[88]. Larvae from lecithotrophic corals may extend their longevity and dispersal potential by several weeks by entering a low-metabolism state immediately after acquiring competency[138]. Small larvae have less energetic reserves and consequently shorter competency periods[54], lower larval survival and lower recruit sizes leading to reduced post-settlement survivorship[139]. By contrast, large larval size allows for longer competency periods and subsequently enables long-distance dispersal[54,140–142]. In addition, low metabolic rates are believed to increase larval dispersal potential, thus enhancing coral population connectivity[143]. Symbiotic larvae from *Acropora tenuis* have higher survivorship than its aposymbiotic larvae due to a lower lipid consumption rate in symbiotic larvae[144]. Symbiotic larvae possess algal symbionts which provide energy via photosynthesis, whereas aposymbiotic larvae lack symbiotic algae and rely solely on their own energy until they acquire symbionts from the environment.

Background (not considering e.g., predation) larval mortality rates have been shown to vary throughout the larval stage, with high initial mortality rates, followed by low and constant mortality rates, and increased mortality towards the end of the PLD[111]. Larval mortality rates depend on several factors, including, sediment accumulation[145], predation[62,146], water temperature[93,147,148], salinity[149] and chemicals from other coral species (i.e., heterospecifics)[119]. Higher early mortality of larvae suggests a higher rate of local retention relative to the rate of long-distance dispersal because even if the potential of long-distance dispersal events exists, most larvae will die before being transported very far. Therefore, high mortality rates reduce the extent of connectivity between coral populations thereby decreasing the recovery potential of populations following disturbances that affect most reefs within a local area.

3.4 Larval settlement

As with larvae survival and competency, larvae settlement is difficult to study. It has most commonly been done using settlement tiles composed of artificial substrate in the field and laboratory. Coral larval settlement is dependent on a range of abiotic and biotic factors, including habitat suitability, competition for space from other coral species and marine organisms, and environmental factors.

3.4.1 Habitat suitability

Successful larval settlement requires the selection of suitable habitats by larvae and is dependent on a variety of biotic and abiotic factors[149,150]. Coral larvae are more likely to settle in grooves, crevices, undersurfaces and vertical surfaces than in upward-facing or exposed microhabitats[151–156]. Larvae from the azooxanthellate *Tubastraea coccinea* settle on crevices or vertical surfaces, where competition with fast-growing zooxanthellate coral species that use light as a source of energy is reduced[153,154]. Wide-grooved tiles deployed in the field have been found to protect coral recruits from grazing while reducing the accumulation of sediments and enabling higher water flow and light intensity[157].

Coral abundance rapidly declines with depth: both growth and fecundity are higher in shallow water corals than in deep water corals[27,60,98]. Reef aspect is also important. Relative to reef flat habitats, macroalgal cover was found to be 95% lower in reef slope habitats, while the available substrate for settlement and rate of coral larval settlement doubled[158]. Some macrophytes can reduce larval settlement and survival even in the presence of preferred substrate[159]. For example, larvae from *Orbicella faveolata* have been observed to avoid habitats with sponges, sediment and red filamentous algae and settle on habitats with green filamentous algae[160]. The red-brown encrusting alga, Peysonneliaceae *Ramicrusta* sp. has been found to increase the mortality of *Porites astreoides* and *Favia fragum* and is identified as a lethal threat to Caribbean coral recruits[161].

Crustose coralline algae (CCA) have been reported to facilitate the settlement of coral larvae[62,115,122,162–165]. However, this is not the case for all coral species: *Montipora aequituberculata*, *Mycedium elephantotus*, and *Porites cylindrica* larvae did not settle when exposed to extracts of the CCA *Porolithon onkodes*[166]. Among 15 CCA taxa studied in a laboratory experiment, Lithophyllaceae species have been identified as the most effective inducer of larval settlement of coral species from the GBR, with *Titanoderma* cf. *tessellatum* being responsible for inducing over 50% of settlement in 14 of the 15 studied coral species[165]. *Orbicella faveolata* larvae require cues from *Lythophyllum cogestum* and *Titanoderma protypum* to settle, and have been found not to settle in the absence of CCA[125]. CCA communities that occur in regions of high sediment accumulation have been found not to induce coral larval settlement[167], while living fragments of CCA species have been shown to induce higher larval settlement and metamorphosis than dead fragments[166,168]. Successful coral larval settlement is influenced by the complex interactions between CCAs, the bacterial communities on the surface biofilm of CCAs, and larval behaviour[169–171]. Larval settlement of some Caribbean corals has been induced by Tetrabromopyrrole, a compound produced by the bacterium *Pseudoalteromonas* sp. from the surface biofilm of a CCA[172,173]. The red pigment cycloprodigiosin isolated from *Pseudoalteromonas rubra* has been shown to induce larval settlement of *Leptastrea purpurea*[174] and that of four brooding and five broadcasting coral species at rates of 40% to 93%[175].

Preference for settlement substrate is associated with the habitats in which adult coral species exist[150,176]. For instance, reef-flat coral species, *Goniastrea aspera* and *Goniastrea retiformis*, have been observed to settle mostly on tiles in shallow water, while larvae from deepwater corals, *Fungia horrida* and *Fungia repanda*, settle on tiles in deep water[150]. CCA originating from similar light conditions as the coral species have been found to induce higher levels of settlement than those from different light conditions[165]. By contrast, the presence of conspecific (i.e., member of the same species) adults has been shown to reduce larval settlement[177,178]. For example, extracts from *Platygyra daedalea* and *Fungia fungites* have been reported to show toxic effects on larvae of conspecifics[179]. Aposymbiotic larvae of *Montastraea faveolata* have been shown to preferentially settle in habitats containing zooxanthellae, and early symbiont uptake has been linked to higher coral recruitment success[180]. However, for some coral species, e.g.*, Tubastraea coccinea* and *Tubastraea tagusensis,* no preferred substrate has been identified and instead they have been observed to settle on a range of different substrates[181].

3.4.2 Competing and co-existing biota

The effects of macroalgae on the recruitment of larvae and the survival of coral recruits vary greatly between different algal and coral species[182]. For example, the brown macroalga, *Lobophora*, has been found to inhibit coral larval settlement, coral recruitment and survival of recruits of *Stylophora pistillata* and *Acropora* species[183–186], and induce the recruitment of *Acropora millepora* larvae[187]. Macroalgae can promote microbial concentrations or weaken coral resistance to infections, causing larval mortality and subsequently reducing coral recruitment success[188]. *Stypopodium zonale*, a brown alga, has been shown to reduce the settlement of *Porites astreoides* larvae[189], while *Ramicrusta* sp., a red-brown encrusting alga, has been shown to cause coral mortality and significantly reduce the amount of suitable substrate available for larval settlement[190].

Turf algae predominantly occupy bare substrates in algae-dominated areas, limiting the space for CCA and coral recruits[191]. The competitive advantage of turfs over other important benthic organisms, including corals, has been shown to reduce the accumulation of inorganic carbon, which can compromise the stability and structural complexity of reefs[191]. Turf algae inhibit coral larval settlement through the release of negative chemical settlement cues which prevent larvae from settling[192] and inhibit coral recruitment[193]. An increase in the height and density of turf algae can increase the diffusive boundary layer, thereby enhancing the accumulation of harmful metabolites and pathogens on reef surfaces, which can promote the growth of turf algae over corals[194]. However, the absence of turf algae and macroalgae may weaken the essential functional role of benthic pioneer populations in supplementing the initial nutrient and energy demands of coral communities in their recovery phase[195].

In the presence of Mediterranean CCA species, *Lithophyllum stictaeforme* and *Lithophyllum incrustans,* larvae of the gorgonian *Eunicella singularis* have a shorter PLD, which can lead to lower mortality rates, although shorter PLDs can reduce the extent of population connectivity[164]. Spatial competition through pre-emption and the overgrowth of CCA is a key factor driving coral dynamics and can overshadow the effects of larval settlement processes[196]. The competition of coral species *Balanophyllia elegans* and *Astrangia lajollaensis* with the corallimorpharian *Corynactis californica* for space has been found to reduce their abundance[197]. In the absence of fish predation, spatial competition of corals with macroalgae and other heterotrophic vertebrates have been reported to increase coral mortality, especially in crevices and holes[152].

Some coral species expand or prevent fast-growing neighbouring species from encroaching on the space they occupy through the release of toxic or aversive chemicals (allelopathy). For instance, chemical extracts from *Tubastraea faulkneri* have been shown to have lethal effects on *Platygyra daedalea* and *Oxypora lacera* larvae, and non-toxic effects on larvae from conspecifics[198]. The non-toxicity of *T. faulkneri* to conspecifics could allow larvae to settle near conspecifics without competing with other coral species for space. Chemical extracts from four hermatypic coral species, *Goniopora favulus*, *Platygyra daedalea*, *Fungia fungites* and *Oxypora lacera*, have been shown to either have lethal effects on *Pocillopora damicornis* recruits or reduce their growth rate[179]. Heterospecific extracts can deter *Pocillopora damicornis* larvae from possible settlement substrates[119]. *Acropora hyacinthus* can kill neighbouring coral species by overgrowing them and can prevent future competition by reducing the recruitment of other coral species[199].

3.4.3 Environmental factors

Environmental conditions often outweigh dispersal in determining coral recruitment. Temperature and light affect larval physiology, while sediments, pollutants, ocean acidification, and nutrient enrichment degrade settlement cues and substrates. Acoustic signals further influence larval orientation. Together, these factors determine realised reef connectivity.

3.4.3.1 Temperature

Natural differences in seawater temperature across seasons, years, and locations influence coral larval production, survival and settlement in species-specific ways. For instance, laboratory experiments of temperature increases from 29 °C to 30.8 °C were found to increase the survivorship of *Pocillopora damicornis* larvae from Luhuitou Reef, China[200]. Relative to ambient temperatures (23 °C and 27 °C), larval settlement of scleractinian corals, *Acropora solitaryensis* and *Favites chinensis* has been observed to increase, and post-settlement recruit survival has been shown to reduce, under long-term exposure to high temperatures at 29 °C and 34 °C, respectively[201]. Exposing adult *Leptastrea purpurea* in Guam to high temperature (30 °C) was found to trigger a maternal effect, which caused the release of heat-tolerant larvae with increased survival rate[202]. Thermal sensitivity also varies with symbiotic state, as seen in *Fungia scutaria* larvae from Kāne`ohe Bay where newly symbiotic larvae survived less than aposymbiotic larvae under temperature increases between 27 °C and 31 °C[203].

Regional temperature regimes shape population patterns, such as higher colony and recruit densities of *Tubastraea coccinea* in warmer waters (> 20 °C) in the South Atlantic Ocean[204]. Temperature increases between 1.5 °C and 4 °C above ambient temperature were not found to impact the settlement and mortality of *Flabellum impensum* larvae in the Western Antarctic Peninsula but increased larval developmental rate[205]. However, elevated temperatures (24 °C and 26 °C) relative to ambient 20 °C in the Mediterranean have been observed to reduce the survivorship of non-symbiotic *Corallium rubrum* larvae and have no effect on the survival of symbiotic *Eunicella singularis* larvae[84]. In the Caribbean, the size and symbiont density of *Porites astreoides* larvae have been found to peak between 26.4 °C and 27.7 °C and decline at both cooler and warmer extremes[206]. Additionally, temperature has been found to regulate reproductive timing, including lunar synchrony in brooding coral species[72] and the occurrence of split spawning[207].

Ocean warming associated with climate change is expected to alter coral connectivity in several ways by influencing both physical and biological processes. Ocean warming can:

- Alter the timing of coral reproduction and potentially shift it outside the optimal reproductive period[60,72,208]. Heated colonies of *Pocillopora acuta* from Nanwan Bay, Taiwan, have been observed to reproduce earlier and to produce smaller and fewer larvae[209].
- Reduce fertilisation success. Warmer temperatures have been found to reduce fertilisation success of *Lobactis scutaria*. The interacting effect of warm temperature with high photosynthetic active radiation had negative effects on egg and sperm physiology[208].
- Induce oxidative stress, accelerate larval competency acquisition[147,148,210,211], increase larval mortality[93,148] and reduce larval motility and settlement[124,212,213].
- Lead to earlier acquisition of competency, which can shorten larval dispersal distances[214].
- Increase the rate of larval development and developmental abnormalities[214].

Heat stress and bleaching also diminish reproductive output in adults due to reduced coral abundance (e.g., in *Acropora*[215,216]) and reduced gamete quality (e.g., in *Fungia scutaria* and *Montipora capitata*[217]). Overall, long-term warming threatens to reduce larval supply, limit fertilisation, alter dispersal patterns, and shift reproductive timing, with consequences for population persistence.

3.4.3.2 Light

Shifts in the orientation of coral recruits with depth is attributed to larval response to light at the time of settlement[151]. Light is essential for successful recolonisation of mesophotic corals to shallow reefs[218] and coloured light may be used by larvae as an indicator of settlement surface orientation, although responses are variable among coral species[219]. *Porites astreoides* larvae have been reported to have higher survival in mesophotic light conditions, suggesting increased larval longevity and extension of dispersal periods in low light conditions[220]. The step-down photophobic response exhibited by *Acropora tenuis* larvae, which involves the reduction of larval swimming speed in changing light conditions, may help these larvae to find suitable habitat for settlement[221].

Light can help larvae regulate their vertical positions in the water column during dispersal, e.g., larvae from *Pocillopora verrucosa* have been shown to aggregate near a light source[222]. This positive photo-movement may increase the extent of dispersal and promote the wide spatial distribution of *P. verrucosa* in the Indo-Pacific[222]. However, *Paramuricea clavata* larvae have been found to have a negative phototactic response, which enabled them to settle in dark habitats such as crevices and holes and might help to prevent competition with organisms that thrive in high light conditions[61].

Some coral species' larvae may use spectral cues to select micro-habitats for settlement. For instance, *Porites astreoides* and *Acropora palmata* larvae settled more frequently on red and orange substrates than on other colours, which may be a strategy to help promote settlement on CCA-dominated habitats for subsequent increased recruit survival[223]. Ultraviolet radiation (UVR) has been shown to negatively affect survival, metamorphosis and settlement of *Pocillopora damicornis* larvae [224,225] but did not significantly increase larval mortality[224]. UVR has been found to exacerbate the negative effects of oil pollution by reducing *Acropora tenuis* larval settlement success[226]. *Porites astreoides* larvae have been found to exhibit the capacity to detect and avoid habitats with high UVR levels, which may contribute to their recruitment success[227]. UV-A caused a decline in the metamorphosis and settlement of *Seriatopora caliendrum* larvae, thereby extending their PLD[228] and subsequently increasing their dispersal distance.

3.4.3.3 Sediments

Sediments negatively affect coral larval settlement by preventing larvae from attaching to substrates[229], through smothering and overshadowing of settlement cues[230], reduction of light intensity[230], and the sediment-driven modification of benthic populations which can reduce the abundance of positive settlement cues[231]. High sedimentation has been shown to inhibit the recruitment of larvae on upper surfaces[232,233], inhibit embryo development[234], prevent active swimming of larvae causing mortality—especially in older larvae[235], reduce fertilisation success[66,234,236] and reduce larval survivorship and settlement[236]. Turf algae in sediment-laden substrates have been found to decrease juvenile coral abundance[237].

Sediments have been found to reduce available settlement space for larval attachment and metamorphosis, as well as the facilitative interaction between coral larvae and CCA[238,239]. Sediments contaminated with copper and zinc have been shown to prevent the settlement and metamorphosis of *Acropora micophthalma* larvae[240]. High sedimentation can reduce coral recruitment by reducing the growth and survival of newly settled recruits[241], preventing grazers from sediment-laden turf algae and subsequently decreasing available substrate for larval settlement. However, *Montipora capitata* can live in conditions of different sediment regimes without compromising its reproduction capability[242].

3.4.3.4 Ocean acidification

Ocean acidification is the reduction of ocean pH due to the dissolution of carbon dioxide (CO_2) in seawater. The effect of ocean acidification on larval dispersal and settlement is variable and much is still unknown. Ocean acidification has been found to delay the metabolism and metamorphosis of larvae[243–245] and to reduce the fertilisation[246] and settlement of larvae[243,247–249]. Lower pH was shown to reduce the growth of coral recruits by decreasing skeletal volume, septa number and calcified area for attachment on substrates[244,249]. However, three studies found no effect of acidic conditions on the early life-history of *Acropora tenuis*, *A. millepora, A. palmata* and *A. hyacinthus* corals[250,250,251].

Ocean acidification can impede larval survival and coral reef recovery through the disruption of larval settlement behaviour. Acidification has the potential to modify the benthic community composition by reducing both CCA (which, like corals, rely on calcification). This would limit the substrate for settlement and alter chemical cues from CCA and their microbial communities[243,247,252,253]. Furthermore, reduced pH can delay the establishment of symbiosis in corals and decrease the growth of coral polyps[254], and can increase the negative impacts of algal presence on corals[255].

The interaction of ocean acidification and temperature increases have been shown to disrupt spectral cues by triggering the loss of pigments and symbiotic microbes that give CCA their normal pink, purple, or red coloration, thereby inhibiting the ability of larvae to identify suitable habitats for settlement[256]. This can cause subsequent reduction of larval survival, dispersal and settlement, and decreased growth of coral recruits[244]. Extreme conditions of low pH, hypoxia and high temperatures have been observed to cause an 80% decline in CCA cover and can cause turf algae to outcompete desired CCA with implications for larval settlement[257]. There are outliers which show positive effects: for example, elevated temperatures and ocean acidification have been found to enhance the survivorship of *Pocillopora damicornis* larvae on Luhuitou Reef, China[200].

3.4.3.5 Other abiotic factors

In eutrophic (high nutrient) conditions, corals have been found to experience reduced fertilisation success[258–260], egg size and quality[259], and larval settlement rates[50,260]. Eutrophication has been shown to increase coral mortality[259], delay embryonic development[260] and promote the colonisation of bare space by turf-dominated pioneer populations[261]. High nutrient concentrations have been reported to promote macroalgal and turf algal growth, thereby reducing the penetration of light to coral colonies which causes them to outcompete corals for space and prevent coral larval settlement[262]. Eutrophication has been shown to stop the release of *Pocillopora damicornis* larvae and decrease *Montipora capitata* egg size[263]. High nutrient concentrations from coastal runoff events can exacerbate warming effects on coral fertilisation success if they occur during coral spawning events[258].

Acoustic enrichment, using healthy coral reef artificial soundscapes consisting of fish and crustacean sounds, has been found to induce coral larval settlement and facilitate coral recruitment[264–268]. By contrast, anthropogenic noise such as boat noise has been shown to alter larval settlement behaviour by inhibiting the preferential settlement of larvae on CCA[269].

Variations in salinity and nutrient concentrations had no effect on the settlement of *Favia gravida* larvae (considered to be a stress-tolerant coral specie)[270]. Hypoxia has been shown to reduce the growth and swimming capability of *Galaxea fascicularis* and *Porites astreoides* larvae, thus decreasing larval settlement[271]. Copper pollution has been found to decrease fertilisation success and larval motility, impair larval settlement and increase larval mortality[272–274].

4 Gaps in understanding coral connectivity

While advances have been made in understanding coral connectivity, direct observations of coral larval behaviour during dispersal and settlement are limited and unevenly distributed across species and locations. There is very limited *in situ* tracking of coral larvae in the water column (e.g., larval colouring[275]) due to their microscopic size, and complex behavioural traits in rapidly changing oceans. As a result, most studies use population genetics[276–279], genetic parentage[280,281] or connectivity model simulations[13,120,148,282] to estimate connectivity patterns, leaving critical gaps in predicting coral larval dispersal pathways and settlement patterns. Population genetic methods infer effective connectivity from patterns of genetic structure accumulated over many generations but struggle to capture larval dispersal distances and are slow to detect recent changes in connectivity patterns. Genetic parentage methods capture short-distance dispersal and single-generation connectivity by directly matching parents to offspring but struggle to track long-distance dispersal and long-term evolutionary connectivity. Although connectivity models predict short- and long-distance dispersal patterns, it is difficult to evaluate the accuracy of model predictions without sufficient *in situ* observations of coral connectivity.

Species-specific biases exist in direct observations of coral connectivity (Table *2* and Fig. 3). Most connectivity studies focus on broadcast-spawning corals with conspicuous spawning behaviours and typical larval traits, neglecting brooding corals and species with atypical larval traits such as benthic crawling and rapid settlement (Table *2*). Additionally, our understanding of coral connectivity is highly constrained by geographical bias because the behaviour and dispersal of coral larvae in deep seas, cold regions and the African continent are underexplored (Fig. 3). Empirical coral connectivity research is disproportionately concentrated in the GBR and the Caribbean, representing 112 of the 349 total empirical studies. Soft corals are also neglected (Fig. 3) but are important as they dominate deeper reef zones (i.e., mesophotic reefs), which may serve as refugia or larval sources for corals in degraded shallow reefs[60,208,283]. Understanding their connectivity could reshape conservation priorities. Species-specific and geographic biases in coral connectivity research result in incomplete understanding of coral connectivity across coral populations.

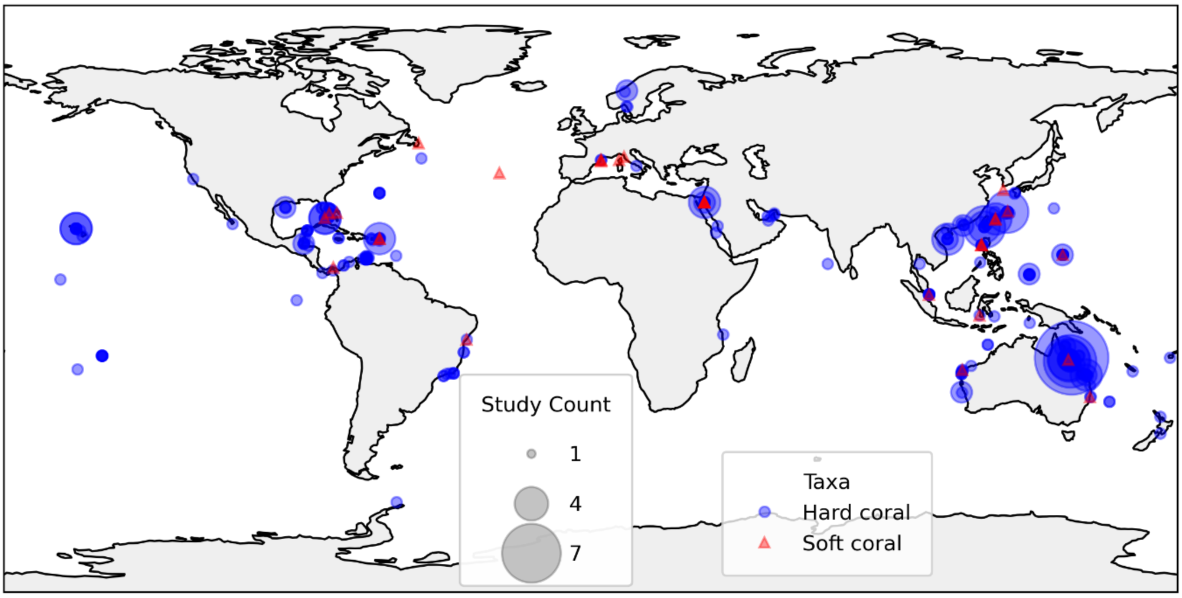

Fig. 3: Map showing the location of the empirical literature included in this review and whether these studies pertained to hard (scleractinian) corals or soft corals (indicated by colour/symbol). The size of markers indicates the number of studies (study count) at a given location. Overlapping markers from neighbouring locations result in lower transparency in the area of overlap.

Observing and quantifying post-settlement success in coral reef environments is difficult, yet critical for coral connectivity as many larvae may settle but fail to recruit due to competition, predation, or unsuitable habitat conditions. Failure to capture these post-settlement factors can impede our understanding of coral connectivity as they critically shape population connectivity. Furthermore, observations are often restricted to single spawning events or narrow seasonal windows, limiting our understanding of interannual variability, multi-peak spawning, and the influence of episodic environmental conditions (e.g., elevated temperatures and storms) on larval dispersal and settlement.

Finally, there is limited application of new approaches such as larval dyes[275], underwater imaging systems[51], and acoustic enrichment techniques[264–268] for enhanced observations due to logistical challenges associated with deep reef access and nocturnal sampling. Overall, these gaps constrain our ability to assess real-time dispersal dynamics, evaluate model and genetic predictions of connectivity patterns, and inform coral conservation and restoration strategies.

5 Opportunities for advancing coral connectivity science

Recent developments such as larval colouring[275], time-series laboratory studies of larval competency[54], acoustic enrichment[264–268], AI-driven behavioural tracking[51], genome-wide sequencing[284] and multigenerational tracking via genome editing[285] provide powerful tools to enhance our understanding of coral connectivity.

The use of time-series laboratory studies to provide insights into the temporal dynamics of larval settlement potential is promising. For example, in one study 24-hour assays were repeated across different coral species to predict larval competency windows and understand larval behaviour during settlement[54]. This study involved exposing larvae from 25 Indo-Pacific broadcast-spawning coral species to five common settlement cues. This type of time-series experiment can enhance the measurement of larval competency periods for the parameterisation of connectivity models. Additionally, it can inform restoration planning to improve the prediction of optimal windows for larval release and settlement and time interventions to match peak larval competency to enhance settlement success. Identifying peak competency windows can help restoration experts to better synchronise larval release with favourable environmental conditions, improving larval settlement and coral recruitment success.

Researchers are also beginning to use AI techniques such as computer vision to study coral larval behaviour and how reefs are connected. Limer et al.[51] used an automated robotic observation system and computer vision algorithms *ex situ* to identify ontogenetic coral larval behaviour during the period of early development. AI-driven behavioural tracking enables fine-scale monitoring of larval dispersal and responses to environmental conditions. This technique can refine our understanding of larval behaviour during dispersal, larval microhabitat selection, and the influence of settlement cues on dispersal outcomes. AI tools show promise in automating *in situ* large-scale analysis of larval behaviour across species and environmental conditions, accelerating discovery and improving connectivity model predictions.

Some recent connectivity studies have used larval colouring to track larval dispersal and settlement over small spatial scales in the field[275]. This technique allows colouring of large numbers of larvae using dye before release to facilitate tracking of their dispersal and settlement. It is time- and cost-efficient, scalable and can provide data for the validation of connectivity model and genetic predictions. Larval colouring allows tracking of individual coral larvae across spatial and temporal scales, enabling researchers to directly observe dispersal pathways, retention zones, and settlement hotspots. This approach can also be used to validate connectivity models and capture fine-scale connectivity patterns that are otherwise difficult to detect.

Another recent development is acoustic enrichment using healthy coral reef soundscapes consisting of fish and crustacean sounds to induce coral larval settlement[264,265]. Acoustic enrichment has demonstrated promise in attracting coral larvae to degraded reef areas by mimicking the soundscape of healthy coral reefs. This technique could be used to enhance larval retention and settlement in restoration zones, especially where natural settlement cues have been lost due to habitat degradation by climate change and anthropogenic pressures. This approach also offers emerging value for connectivity research by providing a controlled means to manipulate acoustic cues and observe how larvae respond to reef-generated signals during dispersal and settlement. By experimentally altering the soundscape, the role of acoustic cues in larval dispersal and microhabitat selection can be more precisely evaluated, thereby advancing our understanding of the behavioural mechanisms that influence patterns of coral connectivity across reef populations.

Coral connectivity studies are increasingly recognising the role of physical cues during larval settlement as larvae also respond to the physical features of settlement surfaces. Studies have found that larvae may prefer to settle on complex surfaces, which provide protection from predation and sedimentation thereby increasing coral recruitment[286]. Understanding the preferences of larvae for settlement surfaces can promote the creation of customised settlement surfaces for increased settlement success and diverse coral populations.

Another rapidly advancing field with strong potential to illuminate connectivity is genetics. Meziere et al.[284] used genome-wide sequencing to estimate generational dispersal distances and long-term gene flow between populations of two dominant *Pocilloporidae* species on the GBR with contrasting reproductive modes. Such dispersal estimates can provide valuable context for predicting population recovery following disturbances and identifying demographic links among reefs. Emerging genetic engineering techniques may further transform coral connectivity research. For example, the use of CRISPR-Cas9 to insert heritable DNA barcodes into coral genomes, detectable via environmental DNA metabarcoding, could allow multigenerational, *in situ* tracking of coral lineages[285]. This scalable method offers a promising avenue for directly observing dispersal pathways and monitoring the success of restored coral populations.

While this review did not examine hydrodynamic, particle-tracking, or biologically coupled modelling frameworks, the synthesis presented here highlights a clear opportunity for advancement. Incorporating the biological processes summarised in this review into connectivity models—and examining how these processes are represented—would substantially improve model realism and predictive skill. Systematic integration of empirical biological data with model development offers a valuable pathway for refining connectivity predictions, particularly under accelerating environmental change.

These techniques can be strategically applied to fill critical knowledge gaps and improve the reliability of connectivity model predictions and reef restoration outcomes. Collectively, these developments offer a pathway toward more adaptive, data-driven coral conservation and management. By integrating these approaches into field studies and restoration programs, researchers can improve the reliability of connectivity estimates, optimise larval supply strategies, and enhance the resilience of coral populations in rapidly changing oceans.

6 Conclusions

Coral connectivity is spatially and temporally dynamic, underpinned by complex physical and biological processes. Connectivity is essential for the resistance, recovery, and persistence of coral ecosystems. This review sheds light on the complex interplay of physical and biological processes that influence coral larval dispersal and settlement and identifies recent developments and gaps in observing coral connectivity.

We identified 453 studies with information on physical and biological processes underpinning connectivity and summarised what we know on these processes, providing measurements of them in the case of spawning timing and duration and competency. While there are many studies in the literature covering processes that shape connectivity, high variability across geographies and taxa mean that identifying general patterns and trends is difficult, with cases of contrasting results both for the same taxa in different regions, or different taxa in the same location. While significant progress has been made in observing connectivity in hard corals (Hexacorallia), soft corals (Octocorallia) remain underrepresented in the literature despite their ecological importance, particularly in mesophotic and deep reef habitats. Reefs in many parts of the world are either unexplored or underexplored, creating a critical gap in understanding and advancing coral connectivity science.

The biological differences within and between hard and soft coral taxa, namely reproductive mode, larval buoyancy, and dispersal potential offer valuable opportunities for comparative research. Hard corals, often broadcast spawners with longer competency periods (or PLD), contribute to long-distance connectivity, whereas soft corals, typically brooders, promote local retention and rapid settlement. Including both coral taxa in connectivity studies can enhance restoration strategies tailored to diverse coral populations.

New approaches such as larval colouring, time-series studies of larval competency, acoustic enrichment, AI-driven behavioural tracking and genetic barcoding are reshaping how we observe and measure coral connectivity. These approaches can enable improved connectivity model predictions, smarter restoration planning, enhanced larval retention and settlement success and scalable impacts, while providing opportunities for advancing coral connectivity science. Integrating these innovations with comparative studies across coral taxa and locations will advance a more inclusive, adaptive, and data-driven approach to coral conservation and restoration.

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