Coral connectivity: How biophysical modelling choices shape connectivity inference

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Abstract

Understanding coral connectivity is essential for predicting metapopulation dynamics and guiding restoration under accelerating climate change. Connectivity facilitates the exchange of organisms among reefs and can promote recovery following disturbance. Biophysical models are widely used to predict and explore coral connectivity; however, their estimates carry substantial uncertainty arising from limitations in hydrodynamic simulations, uncertainty in larval biological processes, and interactions between these processes and natural variability. We synthesise how physical, biological, and behavioural processes are represented in biophysical models, assess key sources of natural variability and uncertainty across the literature, and provide guidance for better connectivity modelling. We show that connectivity is not a single measurable property, but a model-dependent construct emerging from interactions among hydrodynamic forcing, larval traits, and numerical implementation. These processes introduce multiple, interacting sources of uncertainty that influence the magnitude, direction, and interpretation of connectivity estimates. We identify major gaps in current understanding, including limited empirical data for larval trait parameterisation, computational constraints on representing interannual variability in ocean circulation, limited availability of fine-scale hydrodynamic models, and insufficient observational and genetic data for scale-appropriate evaluation. We also highlight untested contributors to connectivity including mesophotic reefs and eco-evolutionary dynamics, that may substantially influence connectivity. Emerging approaches–including climate projections, socio-ecological

frameworks, near-real-time modelling, remote sensing, and artificial intelligence–offer opportunities to improve the representation and prediction of connectivity. Advancing coral connectivity modelling therefore requires improved empirical biological data, careful treatment of uncertainty, scale-appropriate evaluation of model outputs against independent data, and transparent reporting of modelling assumptions.

Keywords: coral connectivity, larval dispersal, biophysical modelling, hydrodynamic modelling, particle tracking, model uncertainty

1 Introduction

Coral reef ecosystems are among the most diverse on earth and are of high socio-economic importance[1,2]. They support an abundance of marine life, provide ecosystem services and protect coastal communities from erosion and storm impacts[3-5]. However, the services they provide are increasingly threatened by climate change and other anthropogenic pressures, leading to widespread degradation of coral reef systems globally[6-8]. The persistence and recovery of coral reef systems depend, in part, on connectivity among reefs, which facilitates larval exchange and plays a fundamental role in metapopulation persistence, replenishment, and resilience, as demonstrated by theoretical and empirical studies of spatially structured populations[9,10].

Coral reef ecosystems often form patchy, shallow habitats that can be separated by large distances, making recovery and persistence after disturbance partly dependent on connectivity among reefs. Here, we define connectivity as *the exchange of marine organisms (e.g., propagules) between populations that results in successful settlement and contribution to receiving populations* (i.e., realised connectivity). While conceptually important, this definition extends beyond what most biophysical models explicitly represent, as processes such as settlement success, post-settlement mortality, growth and reproduction are rarely resolved.

Larval dispersal is influenced by oceanographic processes including currents, tides, and mesoscale features such as eddies[11-13], as well as biological traits such as spawning phenology, pelagic larval duration, mortality, and swimming behaviour[11,14-16]. Biological traits determine whether larvae survive dispersal and successfully settle. Together, these processes generate highly variable connectivity patterns that underpin reef resilience and recovery. The extent to which dispersal translates into realised connectivity and gene flow depends on successful settlement, survival, and reproduction. Accordingly, understanding both potential dispersal pathways and realised connectivity, as well as the processes linking them, is critical for effective coral reef management[11,17,18].

Direct observation of coral larval dispersal *in situ* is extremely challenging due to the small size of larvae, their complex behaviour, and the dynamic ocean conditions they experience over large spatial scales[19,20]. Consequently, several approaches have been used to infer connectivity[21], including biophysical models[22-25], genetic techniques[26-29] and recruitment-abundance relationships, which assess the relationship between adult coral cover and juvenile recruitment[30,31]. These approaches provide complementary but incomplete insights. Biophysical models couple hydrodynamic simulations with particle-tracking and biological traits to quantify potential dispersal pathways, yet may misrepresent realised connectivity due to sensitivity to hydrodynamic model choice and spatial resolution and can be computationally expensive[32,33]. Genetic approaches, including population genetics, assignment tests, and parentage analysis, can confirm realised gene flow but often poorly resolve short-term and directional dynamics without intensive sampling[28,34]. Recruitment patterns reflect demographic outcomes but do not resolve dispersal pathways and require observations across appropriate spatial and temporal scales[31]. Integrating these approaches is therefore essential for robust inference of coral connectivity.

Among these, biophysical models are the most widely used approach due to their ability to explicitly simulate the interaction between ocean circulation and larval processes[35]. Biophysical models have evolved from early Lagrangian particle-tracking approaches in the late 20th century, where larvae were treated as passive tracers advected by relatively coarse hydrodynamic fields (e.g.,[36]), to increasingly sophisticated, coupled individual-based frameworks that incorporate high-resolution ocean circulation, larval behaviour, and environmental sensitivity[37-39]. Advances in computational power have enabled finer spatial and temporal resolution, representation of vertical movements and behavioural responses, and the use of large ensembles to characterise dispersal across spatial and temporal scales[17,40]. Despite these advances, substantial uncertainty remains in coral connectivity modelling due to both limited understanding of larval biology and the difficulty of evaluating model outputs against direct observations of dispersal[35,41-43]. Modern biophysical models are increasingly mechanistic, yet their predictions remain sensitive to assumptions about biological traits and physical forcing[43]. This sensitivity contributes to substantial variation in connectivity estimates across studies, even for similar regions and species. These differences arise not only from environmental variability, but also from differences in model structure, parameterisation, and numerical implementation. As a result, connectivity should not be viewed as a single measurable ecological property, but as a model-dependent construct emerging from interacting physical, biological and numerical processes that introduce multiple and often unquantified sources of uncertainty.

The physical and biological processes underpinning coral connectivity are synthesised in detail in a companion review[44]. Here we synthesise the representation of physical, biological, and numerical processes in coral connectivity models and develop a framework for understanding how natural variability and modelling uncertainty interact and propagate through modelling systems to influence connectivity estimates. We identify key sources of modelling uncertainty, distinguishing them from intrinsic natural variability, identify untested processes that may impact connectivity and highlight knowledge gaps that require further investigation. This review complements, but does not duplicate, the comprehensive synthesis of marine larval dispersal modelling by Swearer et al.[35] by focussing specifically on coral connectivity inferred from biophysical models of larval dispersal, particularly for passive or weakly swimming larvae. While this review focusses primarily on coral reef ecosystems, relevant comparisons with other marine ecosystems are included where appropriate.

2 Literature search methods

In this review, we included peer-reviewed journal articles that used biophysical models to investigate coral connectivity and coral larval dispersal and settlement. Biophysical models were defined as models that explicitly simulate hydrodynamics in the region of interest together with larval production, biology, and behaviour during dispersal and settlement.

The literature search was conducted using the Web of Science Core Collection on 3 February 2025. The search query used was:

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

where "*****" denotes a wildcard representing all possible word endings. Searches were performed using the "Topic" field, which includes titles, abstracts, author keywords, and Keywords Plus, to capture the most relevant studies. This search returned 2,939 records published between 1990 and 2025.

Search results were restricted to journal articles, excluding books, book chapters, reviews, and conference proceedings. From the initial pool, a subset of 453 studies was selected based on relevance to coral connectivity modelling, as well as empirical studies of coral larval traits. These 453 studies were examined by Ani et al.[44] to synthesise current knowledge of the physical and biological drivers of coral connectivity across hard and soft corals. Ani et al.[44]

focussed on studies that provided field or laboratory-based insight into coral connectivity. Here, we focus on modelling studies.

Of the 453 studies, 106 were coral connectivity modelling studies. In the present review, we analyse these modelling studies to assess how biophysical models parameterise the physical and biological drivers of coral connectivity synthesised by Ani et al.[44]. The 106 modelling studies employed 33 distinct hydrodynamic models, with the remaining studies representing different applications or configurations of the same underlying models.

3 Coral connectivity modelling framework

Coral connectivity modelling involves the explicit simulation of ocean circulation within a region of interest, together with coral larval production and larval behaviour during dispersal and settlement. In these frameworks, larval behaviour is typically assumed to be weak or secondary relative to ocean circulation. The most widely used modelling framework (Figure 1) combines hydrodynamic forcing, particle-tracking and biological parameterisation to generate connectivity among reefs.

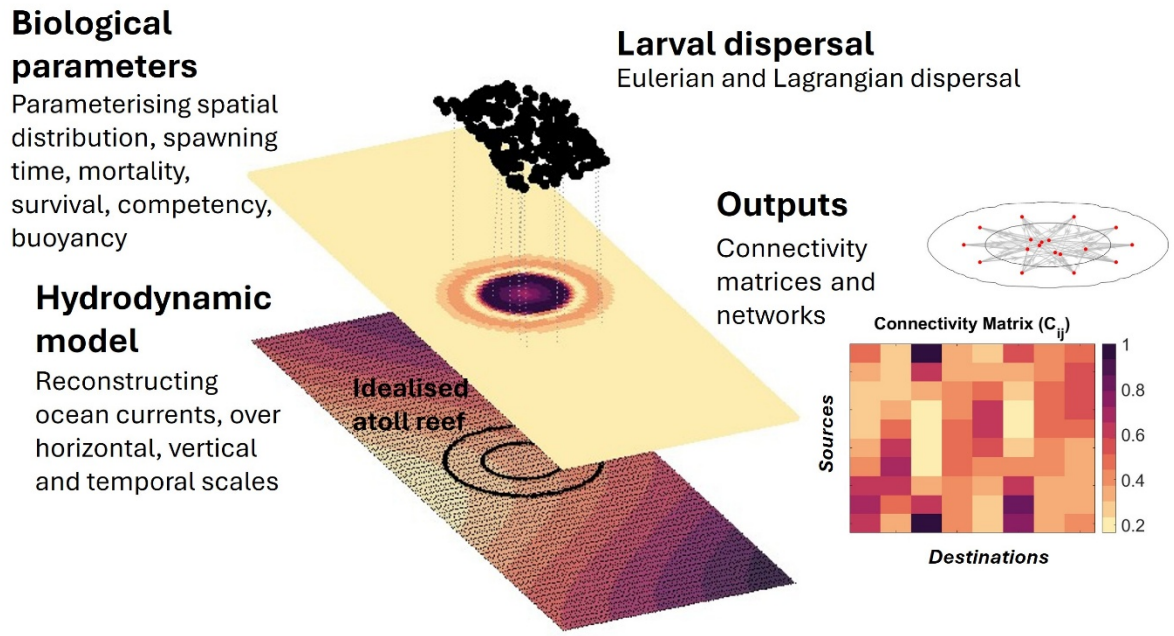

Figure 1: Schematic of the most widely used coral connectivity modelling framework.

The physical and biological drivers of coral connectivity synthesised by Ani et al.[44] provide the empirical foundation for understanding larval dispersal and settlement processes; however, their influence on inferred connectivity depends critically on how they are represented within biophysical modelling frameworks. In practice, these drivers are translated into modelling assumptions, parameter values, or simplified functions, introducing additional uncertainty that interacts with the natural variability described in empirical studies.

For example, variability in spawning phenology observed across species, cohorts, and locations[44] is rarely represented explicitly in modelling frameworks, which often assume uniform larval traits across reefs and regions. Neglecting this variability may alter simulated patterns of larval competency, survival, and settlement, with downstream implications for connectivity inference. Similarly, complex hydrodynamic processes such as vertical transport, wave-driven circulation, and reef-scale turbulence are often simplified or unresolved,

depending on model resolution and dimensionality, potentially leading to systematic differences in predicted dispersal pathways.

While identifying the relevant drivers of coral connectivity is essential, understanding how their representation (or misrepresentation) propagates through biophysical modelling frameworks to influence connectivity predictions is equally critical for advancing coral connectivity science. The following sections therefore examine how key biophysical processes are implemented across modelling approaches, highlighting where empirically-informed parameters are limited, where simplifications are introduced, and how these choices may contribute to variability and uncertainty in predicted connectivity patterns.

3.1 Hydrodynamic models

Hydrodynamic modelling is used to simulate ocean processes that transport coral larvae over various spatial and temporal scales[45]. Since the earliest computational efforts to represent ocean circulation in the 1950s[46], a wide range of global and coarser-resolution models have been made readily available and have become commonly used for connectivity studies (e.g., Operational Mercator global ocean analysis). Where time, budget, and computational resources permit, some studies develop region-specific hydrodynamic models (e.g., SHOC[47]) to better resolve local oceanographic processes that can critically influence larval dispersal pathways and reef connectivity. Importantly, these choices are closely linked to computational cost. Higher-resolution and more complex model configurations generally require greater computational resources, constraining the spatial extent, simulation duration, or ensemble size that can be practically implemented.

A diverse suite of hydrodynamic modelling frameworks is available for configuring such simulations, from open-source community models such as ROMS[48], SHOC[47], HYCOM[49], MITgcm[50,51], FVCOM[52], SLIM[53] to commercial models such as MIKE (Danish Hydraulic Institute; DHI)[54] and the commercially supported open-source Delft3D (Deltares)[55]. These models differ in their numerical formulations, grid structures (e.g., structured and unstructured), flexible temporal and spatial (horizontal and vertical) resolution, and in how they represent key physical processes such as turbulence, vertical mixing, bathymetry and boundary interactions. Differences in these modelling choices could lead to some divergence in simulated circulation fields and, consequently, in predicted larval dispersal pathways and connectivity outcomes[32,33,56]. As a result, the selection of an appropriate hydrodynamic model and configuration is guided by research objectives, dominant physical processes in the region of interest, the spatial and temporal scales being considered, and available computational resources.

A detailed evaluation of hydrodynamic models and modelling practices is beyond the scope of this review, and readers are referred to dedicated texts for comprehensive discussions (e.g.,[57,58]). Instead, the following sections focus on how key aspects of hydrodynamic model configuration–such as process representation, spatial and temporal resolution, and dimensionality–can influence coral connectivity estimates.

3.1.1 Representation of ocean processes

While coral reef systems are influenced by a suite of oceanographic processes ranging from local to regional-scale ocean currents[45], most coral reef connectivity studies incorporate only a subset of these drivers. Oceanographic processes are represented using different model configurations depending on the complexity of circulation dynamics in the region of interest. Common modelling approaches and considerations include:

- Coarser-resolution models, often implemented around offshore island systems where oceanic flow exhibits greater spatial coherence (e.g.,[35]), are less suitable when applied to more complex coastal environments or when assessing local connectivity patterns.

- Region-specific high-resolution models, implemented in complex coastal environments to resolve nearshore circulation processes such as breaking waves, tides, and upwelling that operate at fine spatial and temporal scales.
- Coupled wave-current modelling frameworks, in which wave-driven processes contributing to reef-scale circulation are represented using spectral wave models (e.g., SWAN or Simulating WAves Nearshore[59]) to capture wave transformation and radiation stresses. More comprehensive configurations may additionally include wave-current interactions or Stokes drift[60-62].
- Three-dimensional (3D) baroclinic hydrodynamic models, required to represent upwelling, stratification, gravity currents and other density-driven processes.
- Windage parameterisations, which approximate the influence of wind on floating or near-surface larvae by adding a fraction of wind velocity particle advection[60,62-64].

A further, and increasingly recognised, dimension of reef-scale hydrodynamics operates at the sub-metre scale, where the structural complexity (i.e., rugosity) of coral frameworks interacts with near-bed flow to generate small-scale turbulence, boundary-layer separation, and recirculating eddies that can enhance larval encounter rates and retention[65,66]. These processes remain unresolved in contemporary basin- to reef-scale hydrodynamic models, which typically operate at resolutions too coarse to explicitly represent coral-scale roughness and the associated turbulent structures.

Advances in high-resolution coastal ocean modelling provide opportunities to explicitly resolve physical processes that are typically parameterised in regional-scale connectivity models and may support the development of improved multiscale representations[33]. However, these approaches are computationally intensive and can constrain the spatial extent, temporal duration, or ensemble size of simulations, highlighting an inherent trade-off between resolving fine-scale processes and capturing both variability and large-scale patterns of connectivity.

3.1.2 Horizontal grid resolution: balancing process resolution and computational efficiency

The horizontal grid resolution of hydrodynamic models plays a fundamental role in coral reef connectivity studies as it determines the ability to resolve mesoscale and fine-scale oceanographic processes and local reef topography that drive larval dispersal patterns[44] and impacts processes like retention on coral reefs[24,33]. Horizontal resolution directly influences the choice of grid structure and domain configuration, with important implications for model accuracy, the representation of circulation features, and computational efficiency in connectivity simulations.

Of the 106 studies reviewed, 34 used high-resolution hydrodynamic models (horizontal grid resolutions ≤ 1 km;[24,67,68]) and 57 studies relied on coarser-resolution models to resolve ocean currents (horizontal grid resolutions ≥ 1 km;[23,69,70]). Among the high-resolution studies, 12 employed nested configurations, embedding fine-scale regional models within coarser ocean models to capture both local and large-scale circulation processes simultaneously[22,71].

High resolution models are often applied around islands, coastlines and reef systems, where complex bathymetry and topography strongly influence local circulation and larval transport[64,68,72]. However, their high computational cost often limits their application to relatively small spatial domains (100s of km^2). In contrast, coarser-resolution models are typically used in open-ocean areas, where bathymetry is simpler and circulation is dominated by large-scale currents, making them more suitable for basin- or regional-scale connectivity studies[23,69].

Nested modelling approaches provide a compromise between these two methods by allowing small-scale circulation to be resolved within targeted regions while maintaining computationally efficient coverage of surrounding oceanic domains. In addition to improving resolution where it is most needed, nesting also reduces the likelihood of artificial particle loss

at domain boundaries arising from changes in forcing conditions (e.g. wind direction) during dispersal simulations[22].

An alternative (or complement) to nesting is the use of unstructured or flexible meshes, which enable variable spatial resolution within a single model domain. In these configurations, small grid cells are employed around reefs and nearshore areas, while much larger cells are used offshore. This approach allows hydrodynamic models to realistically resolve both large-scale circulation and fine-scale reef-driven flows efficiently, focussing computational resources on regions of greatest ecological relevance. In total, 15 studies used unstructured or flexible-grid models[73,74], whereas 80 studies employed structured grids[25,70,75].

Where model resolution is insufficient to capture local-scale effects of reef topography on circulation and larval retention, parameterisations of the “sticky water effect” described by Andutta et al.[76]; Wolanski[77] can be implemented. This can be done by increasing water residence times in regions of high reef density to partially account for enhanced larval retention at reefs that are unresolved by the hydrodynamic grid. These approaches highlight that horizontal resolution not only affects the accuracy of simulated circulation fields but also shapes the structure and detectability of connectivity pathways.

As a result, model configuration therefore reflects a compromise between computational constraints, study extent, and the need to adequately represent key bathymetric and geomorphic controls on flow. This involves resolving features such as reef channels, passes, patch reef structures, and sharp bathymetric gradients, with finer resolution applied in structurally complex reef environments and coarser grids in relatively homogeneous domains. As such, there is no single optimal grid resolution for hydrodynamic modelling of coral reef systems, as appropriate spatial discretisation is inherently scale- and process-dependent. This is also the case for vertical resolution in hydrodynamic models described in the next subsection.

Guidance: Nested models or variable-resolution unstructured models should be used when the processes to be resolved span several spatial scales (e.g., both within-reef transport and regional-scale circulation).

3.1.3 Representation of vertical structure and processes

The vertical resolution of a hydrodynamic model (i.e., the extent to which the 3D structure of the water column is resolved) is important because vertical variations in ocean currents, temperature, and stratification can strongly influence reef hydrodynamics[78,79] and larval transport pathways[22]. Vertical structure determines how larvae experience depth-dependent flow features, including shear, stratification, and vertical motions such as upwelling and downwelling.

In our corpus, 55 studies use 2D velocity fields (surface, depth-averaged, or fixed-depth velocities) to force larval transport models[24,56,74], while 30 studies employed 3D velocity fields[22,80,81]. Among the studies using a 2D structure, 35 used surface velocities[69,82,83], 18 used depth-averaged velocities[33,56] and two studies extracted velocities at a specified depth[84].

The use of 2D velocities reduces computational cost and allows the prioritisation of high horizontal grid resolutions over resolving vertical flows. Surface velocities are appropriate if larvae are assumed to be positively buoyant during their competency period. Depth-averaged velocities are less computationally expensive and are appropriate in well-mixed waters where currents are affected mostly by barotropic processes. In deeper waters and wherever stratification is present, transport is influenced by baroclinic processes. In these settings, 3D velocity fields can better resolve the effects of vertical larval movement, as well as upwelling and downwelling processes that may significantly influence dispersal pathways. Ani et al.[22] found that the use of 3D velocity fields, compared to 2D formulations, substantially increased the number of simulated connections among reefs, highlighting the importance of depth-dependent flow and vertical transport processes in structuring connectivity patterns.

Even given a 3D baroclinic model, the number and distribution of vertical layers, the representation of the tidal free surface, and the choice between z-coordinates and sigma-coordinate structures can also be important. As a result, the choice of vertical representation can lead to systematic differences in predicted connectivity patterns, particularly in stratified or dynamically complex environments.

Guidance: Consider carefully the assumptions made regarding larval behaviour (e.g., whether larvae remain buoyant or move vertically), local hydrodynamic conditions (e.g., the presence of stratification) and the trade-off between computational speed and resolution of baroclinic processes when choosing between a 2D and 3D connectivity model.

3.1.4 Resolving temporal dynamics

The temporal resolution of a hydrodynamic model–defined by the frequency of model outputs (e.g., hourly, daily)–determines how well the timing and variability of ocean currents that transport coral larvae are resolved. Coarser temporal resolution (e.g., daily averages) can smooth or dampen high-frequency variability in ocean currents, effectively altering the magnitude and timing of transport. In contrast, finer temporal resolution allows rapid changes in currents such as tidal oscillations, episodic wind forcing, and transient circulation features (e.g., tropical cyclones) to be more explicitly represented.

In our corpus, the temporal resolution of hydrodynamic velocity outputs was not reported by most studies, limiting direct comparison of modelling approaches. Among those that did report it, 20 studies used daily instantaneous velocity outputs[85,86], five used daily mean velocities[87], and 19 used output intervals of six hours or less[88,89]. Less commonly, Treml et al.[90] used surface velocities averaged over three-day periods, while Sanvicente-Añorve et al.[91] employed mean monthly velocities to explore broad-scale dynamics.

Many key physical processes that affect dispersal, such as tides, internal waves, or short-term wind events (including tropical storms), occur on timescales ranging from hours to days and can strongly influence short-range dispersal and local retention. If the temporal resolution is too coarse (e.g., daily or longer-averaged outputs), important high-frequency current fluctuations may be missed, leading to inaccurate local-scale predictions of larval trajectories, dispersal distances, and resulting connectivity patterns[89]. Conversely, a finer temporal resolution (e.g., hourly outputs) can better resolve rapid current changes but at the cost of higher data storage requirements and computational demand. As a result, the choice of temporal resolution can systematically influence both the magnitude and spatial structure of predicted connectivity patterns. Therefore, the choice of temporal resolution represents a trade-off between accurately resolving short-term physical variability relevant to larval dispersal and maintaining computational and data storage feasibility in large-scale connectivity models.

Guidance: When simulating connectivity over longer time scales (e.g., several years) at regional spatial scales, longer timesteps with temporally averaged currents may be appropriate. When simulating short time scales or small-scale effects, it may be important to capture tidal and other sub-daily hydrodynamic processes using shorter timesteps.

3.2 Larval transport models

The structure of larval transport modelling frameworks–including the choice of transport model, timestep selection, and parameterisation of sub-grid-scale diffusivity–determines how physical forcing is translated into larval trajectories and dispersal pathways. These methodological choices influence the representation of advection, mixing, and biological processes and therefore constitute an important source of uncertainty in connectivity estimates. Consequently, uncertainty can propagate through larval transport models not only from the underlying hydrodynamic forcing but also from numerical and modelling decisions embedded within the transport framework itself.

3.2.1 Types of larval transport modelling frameworks

Lagrangian models simulate larval dispersal by tracking individual particles through hydrodynamic velocity fields, allowing trajectories and settlement events to be explicitly resolved. From these simulations, dispersal kernels and connectivity patterns can be derived. Particle tracking can be implemented either offline, where particles are advected using precomputed velocity fields (the most common approach in larval dispersal studies; e.g., Parcels, OceanTracker, Ichthyop, LTRANS), or online, where particles are integrated directly within the hydrodynamic simulation itself (e.g., MITgcm, ROMS, Delft3D, SHOC). Van Sebille et el.[92] reviewed commonly used Lagrangian modelling software and advection schemes for oceanographic applications and Griffa et al.[93] discussed Lagrangian modelling methods and considerations more broadly.

In contrast, Eulerian approaches simulate larvae as continuous concentrations of tracers that are advected and diffused by the velocity flow field. These models can reduce computational cost by directly simulating spatially explicit dispersal probabilities or likelihood (dispersal kernels) rather than tracking large numbers of individual particles, and can resolve very low larval concentrations that may be difficult to capture using classical Lagrangian approaches[94,95]. Relative to well-calibrated Eulerian models, Lagrangian approaches driven by time-averaged velocity fields may underestimate sub-grid-scale diffusion and high-frequency transport, as temporal averaging removes high-frequency variability that would otherwise contribute to particle dispersion[72,96,97].

Both Eulerian and Lagrangian frameworks allow biological processes–such as swimming, mortality, growth and settlement–to be incorporated without increasing the computational cost of the underlying hydrodynamic simulations. However, representing these processes typically increases the model complexity and computational demand, particularly as additional parameters and behavioural rules are introduced. Both modelling frameworks can support offline sensitivity analyses when biological processes are decoupled from ocean circulation, thereby reducing computational costs. However, the efficiency and practicality of such analyses depend on model implementation and study design rather than the modelling framework itself, with trade-offs in computational cost often emerging differently in Eulerian and Lagrangian approaches[43,72].

In our corpus, most studies (92) used Lagrangian particle-tracking models to simulate larvae dispersal[25,82,98], whereas 11 studies used Eulerian approaches[95,99]. Among the Lagrangian studies, 17 implemented Individual Based Models (IBMs)[100,101] and two employed Agent Based Models (ABMs)[66]. IBMs are ecological extensions of Lagrangian models that explicitly simulate individual organisms and their state-dependent biological processes such as competency acquisition/loss and mortality during dispersal. ABMs similarly represent organisms as discrete entities but place greater emphasis on autonomous decision-making, interactions among individuals, and adaptive responses to environmental conditions.

Additional approaches include simplified dynamic dispersal models[102] and the use of satellite-tracked surface drifters to infer transport pathways empirically[103,104]. These frameworks differ not only in how dispersal is represented, but also in how uncertainty, biological complexity, and computational trade-offs are balanced. Therefore, the most appropriate choice of modelling approach for simulating connectivity depends on the spatial scale and oceanographic context of the study area, the specific scientific or management questions being addressed, and the level of biological detail required.

Guidance: Either Lagrangian or Eulerian methods can be used, though some effects (such as variable biological traits within a population of larvae) are easier to implement in a Lagrangian framework. In the case of nested-grid domains, treatment of boundary conditions can be an important source of error in Eulerian approaches.

3.2.2 Timestep selection

The accuracy of larval dispersal simulations and model stability depend on the quality and temporal resolution of the underlying hydrodynamic forcing. However, the choice of timestep in particle tracking is not always matched to the resolution of the velocity fields, introducing additional numerical error. Indeed, timestep selection is a fundamental but often under-reported component of particle-tracking models that strongly influences numerical stability, biological realism, and the detection of larval settlement. The particle-tracking timestep controls how frequently particle positions are updated relative to the underlying hydrodynamic fields and biological processes. From a numerical perspective, the timestep must satisfy stability and accuracy constraints, commonly expressed through Courant-Friedrichs-Lewy (CFL) conditions. These require particle displacements per timestep to remain small relative to the spatial scales over which velocities vary. If the timestep is too large, particles may overshoot velocity gradients or unresolved flow features, leading to inaccurate trajectories and biased dispersal estimates[93].

Conversely, using timesteps that are much smaller than the temporal resolution of the hydrodynamic outputs can substantially increase computational cost without necessarily improving the accuracy of simulated trajectories. In addition, the timescales of biological processes–such as larval swimming behaviour, vertical migration, mortality, and settlement–must be considered when selecting timesteps. These processes often operate on timescales comparable to, or shorter than, typical particle-tracking timesteps, and failure to adequately resolve them can lead to systematic errors in larval trajectories, survival, and settlement outcomes. In practice, selecting a particle-tracking timestep involves balancing numerical stability, the temporal resolution and spatial variability of velocities, biological timescales, and computational efficiency.

The choice of timestep should depend on the spatial resolution of the hydrodynamic model and the maximum current velocity in the region of interest; specifically, the timestep should be smaller than the ratio of grid size to maximum flow speed. Smaller timesteps are required when high-frequency processes–such as tidal currents that vary over minutes to hours–are resolved, whereas larger timesteps may be adequate when simulations are forced by temporally averaged circulation fields. Timestep selection should also consider the spatial scale of reef polygons used for larval release and settlement, as large particle displacements per timestep can cause larvae to traverse small reef features without settlement being detected. Consequently, finer timesteps are required when resolving high-frequency flow variability or fine-scale reef geometries, while coarser timesteps may be sufficient for larger reef polygons and temporally averaged flow fields. Timestep selection not only affects numerical accuracy but also governs the extent to which fine-scale ecological processes and habitat interactions are resolved in connectivity simulations.

Only 25 studies in our corpus explicitly reported the timestep used to simulate particle trajectories, despite its importance for numerical stability, biological process representation, and settlement detection. Of these, 17 studies used timesteps between 1 and 10 min to simulate particle trajectories[105,106], four studies used timesteps between 30 and 45 min[107], and four studies used timesteps between 1 and 4 h[108].

Overall, timestep choice constitutes an important and frequently under-reported source of uncertainty in particle-tracking biophysical models, with the potential to systematically bias larval dispersal pathways, settlement rates, and inferred source-destination relationships, especially for small reef features and regions influenced by high-frequency flow variability.

Guidance: Select timesteps such that particle displacements remain small relative to both hydrodynamic grid spacing and reef habitat dimensions. Smaller timesteps are recommended

when resolving high-frequency flow variability or settlement on small reef features, whereas larger timesteps may be appropriate for temporally averaged flow fields and larger reef habitats.

3.2.3 Sub-grid-scale turbulence and diffusivity

Because hydrodynamic models cannot explicitly resolve all small-scale (turbulent) processes, modelling frameworks typically incorporate parameterisations of sub-grid-scale variability through horizontal and vertical diffusion schemes[92,93]. These are commonly implemented using stochastic displacement schemes, often formulated as random-walk terms that add additional displacement to particle trajectories. The magnitude of this spreading is controlled by the eddy diffusivity coefficient K, introducing perturbations that mimic unresolved turbulence[109]. In our corpus, 41 studies explicitly used diffusion coefficients to parametrise sub-grid-scale turbulence and diffusivity[67,110,111].

Diffusivity is typically parameterised based on model grid scale, empirical estimates from drifter or dye studies, or calibrated through sensitivity analyses to reproduce observed spreading rates[37,109,112,113]. A common guiding principle is that K should be consistent with the effective mixing scale of unresolved turbulence relative to the model resolution. Coarser-resolution models generally require larger diffusivities, whereas higher-resolution models can use smaller values because more turbulent processes are explicitly resolved.

While these approaches improve realism by representing unresolved mixing processes, diffusivity primarily acts to introduce variability at spatial and temporal scales that are not resolved by the hydrodynamic model. As such, it is generally interpreted as modulating particle trajectories at scales smaller than the model grid, rather than altering the large-scale advective structure of dispersal pathways. Although diffusivity parameterisations are physically intended to represent unresolved turbulent mixing, they may also implicitly capture other unresolved sources of variability influencing particle trajectories and dispersal outcomes.

Guidance: Select diffusivity coefficients based on hydrodynamic grid spacing and the expected scales of unresolved turbulent mixing, with larger values generally required for coarser-resolution models and smaller values appropriate for higher-resolution models.

3.3 Parameterising larval biology and behaviour

A realistic coral connectivity model should model the transport of virtual larvae and account for the production, biology and behaviour of virtual larvae during dispersal and settlement.

3.3.1 Larval production

Spawning is implemented in biophysical models by adjusting the timing and duration of larval release using a wide range of assumptions, reflecting both variability in coral spawning phenology and limited empirical constraints. Thirty-five modelling studies assumed the timing and duration of larval release coincide with coral spawning events observed *in situ*[67,74,114]. Of these, 22 studies assumed spawning occurred between 1 and 10 days after the full moon or quarter moon and persisted for at least three days[100,115]. Where regional spawning phenology was uncertain, alternative assumptions were made: Romero-Torres et al.[116] assumed spawning coincided with peak annual sea surface temperatures, whereas Bracco et al.[117] released larval cohorts seasonally to account for unknown spawning timing in *Callogorgia delta*.

Across studies, spawning timing was parameterised using diverse release strategies that vary in both temporal resolution and duration. Of the 35 studies, 12 studies released particles during evening hours, typically between 8:00 p.m. and midnight[33,118]. This is consistent with observed spawning phenology of several coral species synthesised by Ani et al.[44]. Seven studies released particles daily throughout the assumed spawning periods[88], five studies assumed a

single monthly release[23]. Other approaches included gradual larval release over multiple days[73], repeated releases spanning tidal cycles or fixed multi-day windows[119,120], hourly releases over extended periods[121], and weekly or seasonal releases over multi-year simulations[111,117,122]. Some studies released larvae exclusively during daylight hours[68], while others aligned larval release with tidal or lunar cycles[123] or explored a broad range of release timings to characterise dispersal outcomes under diverse environmental conditions[124].

Despite this diversity in implementation, relatively few studies explicitly assess how these assumptions influence connectivity outcomes. Releasing particles according to species-specific spawning observations enables more accurate representation of reproductive phenology, while multi-day release windows capture variability in oceanographic conditions during spawning events. Vogt-Vincent et al.[89] found that daily oceanographic variability exerted the strongest influence on connectivity patterns, highlighting the importance of high-frequency processes in coral dispersal. They further demonstrated that spawning duration was a more influential parameter than the precise timing of spawning onset, as spawning spread over multiple days reduced variability in predicted larval settlement arising from stochastic oceanographic conditions. These findings suggest that simplified or poorly constrained representations of spawning phenology may introduce substantial bias in predicted dispersal pathways and settlement patterns.

Like the parameterisation of spawning phenology, differences also exist in larval release strategy. Twelve studies released virtual larvae in proportion to reef surface area or live coral cover, thereby representing spatial variation in reproductive potential[87,125]. While biologically realistic, this approach can introduce unequal sampling precision among source reefs, therefore influencing the structure of connectivity outputs and system dynamics. In contrast, 43 studies released equal numbers of particles from each reef or site[67,126,127], ensuring consistent statistical precision but requiring reproductive output to be incorporated subsequently when deriving flow-based connectivity estimates (see Section 3.4). Uniform release strategies maintain consistent effort among sources, eliminating bias in precision and allowing reproductive output to be incorporated through post-processing. Nine studies explicitly examined the sensitivity of connectivity estimates to the number of released particles per source reef[87,128]. While several studies found little sensitivity to particle number[71,128] indicating sufficient particle sampling, others reported that increasing release numbers improved the stability and precision of connectivity estimates[115,129]. This highlights the importance of conducting a convergence assessment to ensure adequate sampling effort.

Overall, variability in spawning phenology and larval release strategy represent major and frequently under-explored sources of uncertainty in connectivity modelling, with daily-scale differences in spawning timing having the potential to outweigh seasonal or annual assumptions in shaping dispersal and settlement outcomes.

Guidance: Parameterise spawning over realistic multi-day windows using observed spawning phenology of focal coral species. Release equal numbers of particles from each source site to ensure consistent sampling precision, with variation in reproductive output incorporated subsequently through flow-based connectivity metrics. Conduct a convergence assessment to ensure that sufficient particles are released from each site to achieve stable connectivity estimates.

3.3.2 Larval survivorship and mortality during dispersal

Thirty-eight studies represented larval mortality during dispersal using fixed daily mortality rates and/or time-dependent survival functions. Of these, 24 studies used constant daily mortality rates[33,130], while 14 studies used time-dependent functions such as Weibull and generalised Weibull distributions to represent larval mortality[67,81].

Depending on the species considered, both constant and time-dependent mortality formulations have been applied, sometimes within the same modelling framework[131]. Several studies have incorporated age-dependent mortality, for example, by increasing mortality rates over time to reflect declining larval viability[132]. In other cases, mortality is implemented numerically by randomly removing particles at each timestep or day[22,24], with particles representing either individual larvae[22,71] or cohorts of larvae[24]. These choices have important implications for numerical precision and the interpretation of connectivity estimates, as cohort-based approaches reduce stochastic noise but can obscure variability among individuals. Treating each particle as an individual larva increases stochasticity, which may be desirable if the goal is to capture uncertainty.

Additional approaches include delaying the onset of mortality to retain larvae during early dispersal[67,114] and exploring alternative functional forms[73]. Sensitivity analyses indicate that the most appropriate functional representation may vary among species[102], highlighting substantial uncertainty in how larval survival is parameterised.

The numerical implementation of mortality therefore interacts with its biological formulation. Importantly, the uncertainty associated with connectivity estimates is primarily governed by the number of particles used in the simulation, with low particle numbers leading to increased sampling error regardless of how mortality is implemented. Time-dependent mortality functions allow mortality to be redistributed across ontogeny, increasing the relative influence of larvae that survive to later developmental stages, where behaviour and physical transport can more strongly shape connectivity.

Overall, the representation of larval mortality during dispersal constitutes an important yet poorly understood source of uncertainty in coral biophysical models, with both biological parameterisation and numerical treatment influencing the precision and structure of inferred connectivity.

Guidance: Larval mortality limits connectivity distance and it is important to include it when modelling connectivity over larger spatial scales. When using particle-tracking approaches, remember that each particle usually represents a cohort of larvae, within which there will be a distribution of survival outcomes over time: probabilistic representations are appropriate.

3.3.3 Acquisition and loss of settlement competency

Forty studies modelled larval dispersal from broadcast-spawning corals using fixed maximum larval competency periods (or pelagic larval durations, PLDs) derived from observational or experimental data to represent settlement potential[22,83,126]. Here, “fixed” refers to prescribing a single maximum competency duration for all particles, such that larvae are assumed to be capable of settlement up to this cutoff age, without representing variability in the onset or probability of competency through time. Six studies modelled larval dispersal of both broadcast -spawning and brooding corals[133], while two studies focussed exclusively on brooding corals using fixed values of maximum competency duration[134]. Additionally, 31 studies did not specify coral species that were modelled but nonetheless used fixed maximum competency or PLD values[80,99,135].

Across the corpus, 34 studies used fixed values to characterise larval acquisition of competency[80,82,83]. In contrast, seven studies assumed larvae acquired and lost competency at constant rates following a minimum pre-competency period, based on experimental observations[61]. A further 10 studies modelled competency using time-dependent functions, including log-normal distributions, gamma cumulative distribution functions, exponential functions, age-dependent sigmoid functions, Weibull and generalised Weibull distributions[74,81].

Competency functions represent the proportion of a larval cohort available for settlement as a function of time since release[73,102,136], whereas competency acquisition and loss rates describe the daily transition into or out of competency[125,137]. In coral biophysical models, Figueiredo et al. [73,136] show that time-dependent competency functions enable a small subset of long-lived

larvae to disproportionately influence connectivity, in contrast to simplified fixed competency windows. The use of acquisition and loss rates allows both local retention and long-distance dispersal to emerge dynamically. In contrast, fixed competency windows do not represent the temporal dynamics of larval development and may therefore bias estimates of both short- and long-distance dispersal.

The choice of competency function therefore directly shapes the tail of the dispersal distribution. Applying probability distributions to represent competency allows a small number of long-lived larvae to persist long enough to establish biologically meaningful connectivity between distant reefs, even when most larvae have comparatively short competency windows. As shown by Figueiredo et al.[73], functional representations of competency loss are particularly influential in shaping connectivity outcomes, although the most appropriate function remains species-specific[102].

Uncertainty in how larval competency is parameterised–particularly the widespread use of fixed competency windows instead of time-dependent functions–may bias both short- and long-distance connectivity estimates by failing to capture the small fraction of long-lived larvae that drive biologically meaningful connections between reefs. Additionally, uncertainty from unknown and/or variable competency dynamics within and across coral species is a major challenge[44].

Guidance: Where empirical data are available, use time-dependent competency functions to represent the acquisition and loss of larval competency, as they more realistically capture competency dynamics and influence connectivity outcomes. The choice of competency function and its parameterisation should be species-specific. In the absence of empirical data, a long or unbounded competency window may be useful to explore the maximum potential connectivity and a sensitivity analysis should be conducted to understand the effect of this uncertainty.

3.3.4 Larval buoyancy and swimming behaviour

Buoyancy and vertical movements of larvae are implicitly incorporated in 2D models through assumptions about larval vertical position, such as the use of surface, depth-averaged, or fixed-depth velocity fields, whereas they are explicitly represented in 3D models. Eleven studies assumed larvae were neutrally buoyant[105,123], five studies assumed positive buoyancy[119] and one study assumed negative buoyancy[124]. Radford et al.[68] assumed larvae were initially neutrally buoyant for four hours post-release, becoming positively buoyant between 4 and 16 hours after release. This transition allows for differences in spawning timing and early aggregation followed by near-surface accumulation prior to competency. These assumptions are consistent with observations of larval buoyancy synthesised by Ani et al.[44].

Twenty-five studies treated larvae as passive particles without vertical migration, ontogenetic changes or active swimming behaviour[82,83,100], whereas six studies incorporated active swimming behaviour after release[43,87,138]. These approaches range from simple assumptions of depth-independent movement to more complex representations of ontogenetic or depth-dependent behaviour. For example, some studies assume depth-dependent swimming capabilities[126], while others represent ontogenetic shifts in behaviour, such as larvae transitioning from passive transport to active vertical positioning prior to settlement[129]. More complex behavioural formulations include staged dispersal models in which larvae are initially transported passively, followed by an active settlement phase in which they seek suitable substrate at target depths during daylight hours[43]. These assumptions are consistent with observed larval swimming behaviour synthesised by Ani et al.[44].

Assumptions about larval buoyancy and vertical swimming behaviour represent a key and often underexplored source of uncertainty in biophysical models. These processes determine the depth horizons that larvae occupy and, consequently, their exposure to vertically structured

currents. Because ocean current direction and magnitude can vary substantially with depth, differences in vertical position can lead to divergent dispersal trajectories and connectivity patterns[139]. Furthermore, variability in buoyancy and swimming behaviour can occur both among individuals and through ontogeny, meaning that simplified or uniform representations may not capture the full range of dispersal pathways, introducing uncertainty into predictions of transport and settlement, and ultimately into inferred connectivity patterns.

Guidance: If larval buoyancy or vertical migration behaviours are known, consider including these in a 3D connectivity modelling framework. If not, but currents are vertically structured, consider addressing this as part of an uncertainty analysis.

3.3.5 Settlement assumptions and habitat detection criteria

Twenty-one studies assumed that larvae settled on the first or any suitable reef habitat that they travel over during the competency period[22,73,74,131,137]. This settlement condition captures the ability of competent larvae to detect the presence of suitable habitats for settlement through physical and chemical cues. However, settling on only the first suitable reef habitat likely creates reef "shadows" of no settlement (in the lee of the first habitat) and underestimates maximum dispersal distances. Of the 21 studies, 10 studies assumed competent larvae settled over a reef at fixed settling rates[61,90,100,138], which can be proportional to the reef cover in the habitat[61]. This formulation governs the probability of settlement at destination reefs and allows larvae to pass over reef habitats without settling due to biotic and/or abiotic factors.

Seventeen studies tracked particle trajectories over the full pelagic larval duration and inferred connectivity from particle distributions across the simulation period[71,140]. In these approaches, settlement is not always explicitly resolved in time and space along the trajectory, but instead connectivity is estimated based on the locations reached by particles during or at the end of the dispersal period. While this allows identification of potential destination reefs and the spatial extent of dispersal, it does not explicitly account for when settlement may occur along the pathway.

A subset of studies implemented settlement conditions based on vertical position and proximity to habitat. For example, some studies assumed larvae settled when competent individuals were located at the same depth level as the habitat[81,87,118]. This settlement condition enables the high-resolution modelling of vertical connectivity. Others incorporated explicit spatial thresholds, such as requiring larvae to be within a fixed distance of reef substrate or within shallow water depths (e.g., < 30 m deep and within 0.5 m of the reef substrate)[81,134]. Similar proximity-based approaches assume settlement occurs when larvae are transported within a minimum distance of reef habitats[25,86], reflecting the sensory capabilities of larvae during settlement. Additional formulations incorporate behavioural and hydrodynamic constraints on settlement. For example, settlement may occur when larvae encounter a surface at velocities below their swimming capacity[66]. These approaches allow settlement to emerge from the interaction between physical transport and larval behaviour, rather than being triggered solely by spatial coincidence.

Further settlement assumptions include defining connectivity between reef sites when larval density at a receiving reef exceeds a fixed threshold[141], and allowing settlement of competent larvae when they occupy grid cells meeting specific environmental and spatial criteria, such as winter water temperatures above 18 °C and proximity to land cells[80].

Because settlement is evaluated at discrete timesteps and depends on how larvae interact with reef patches in space, settlement outcomes are influenced by the particle-tracking timestep choice and the spatial resolution of reef habitats, further compounding uncertainty in connectivity estimates. Overall, assumptions about when, where, and how larvae settle constitute an often under-recognised source of uncertainty in coral biophysical models, as different settlement rules can bias dispersal distances, modify rare long-distance connectivity, and/or alter local retention depending on how larval habitat encounter and competency are represented.

Guidance: Where empirical data are available, settlement assumptions and habitat detection criteria should be based on known settlement ecology of the focal coral species and implemented at spatial and temporal resolutions appropriate to the habitat data and larval transport framework. Because the location of suitable habitat is often itself uncertain and transport pathways are also uncertain, consider an approach that allows settlement if competent larvae pass within some specified near distance of suitable habitat in the model rather than strictly requiring larvae to pass directly over defined habitats.

3.4 Connectivity outputs/measures

By combining hydrodynamic models with larval transport and biological sub-models, connectivity studies generate a range of outputs that characterise the extent, direction, and strength of potential ecological linkages among reefs. Commonly reported outputs include spatial larval dispersal patterns (e.g., networks), dispersal kernels or probability maps, Lagrangian probability density functions (LPDFs), connectivity matrices, estimates of self-recruitment and local retention, and a wide range of network-based connectivity metrics.

Spatial larval dispersal patterns describe the distribution of larvae originating from a given source reef, whereas dispersal kernels or maps summarise where larvae are likely to be transported, how far they travel, and in which directions[69]. LPDFs provide probabilistic estimates of larval transport from an origin by integrating large numbers of particle trajectories into continuous dispersal surfaces. In some Eulerian frameworks, these distributions are modelled directly, rather than derived from discrete particle trajectories.

Connectivity model outputs are commonly summarised using matrices, but different matrix formulations represent distinct ecological quantities. The probability matrix (P) describes the likelihood of larval transport from a source to a destination given larval release, mortality, behaviour, and settlement, with rows summing to ≤ 1 (where a large proportion of larvae are lost at sea and/or die without reaching a destination). The flow matrix (F) can be calculated by multiplying the probability matrix (P) by a vector representing the (relative) reproductive output from each source patch. The migration matrix (M) describes the likelihood that each settler at a destination originated from a particular source (i.e., M is the column-normalised form of F). These alternative representations of “connectivity” necessarily yield different connectivity dynamics because they represent distinct aspects of the system and provide complementary perspectives on metapopulation dynamics (e.g., a source-focussed P matrix vs a destination-focussed M matrix). When not clearly defined, their use can lead to ambiguity in the interpretation of connectivity patterns at best, and erroneous conservation priorities and decisions at worst.

Self-recruitment and local retention are frequently reported (often mis-reported) but represent distinct and non-equivalent aspects of metapopulation dynamics. Self-recruitment (SR; the diagonal elements of the migration matrix) refers to the proportion of settlers arriving at a reef that originated from that same reef, and is often interpreted as an indicator of demographic isolation. Local retention (LR; the diagonal elements of the non-row-normalised probability matrix) represents the proportion of larvae released from a reef that subsequently remain and settle on that source reef or within a defined spatial neighbourhood of their origin, and is important for local population persistence[10]. These metrics capture different ecological processes and are often only weakly correlated. A reef may retain a large proportion of locally produced larvae but still contribute relatively little to its own recruitment if external larval supply dominates (high LR, low SR). Conversely, a reef may contribute only a small proportion of locally retained larvae but still exhibit high self-recruitment if it receives minimal input from other sources (low LR, high SR). Consequently, neither metric alone provides a complete measure of demographic dependence or independence.

Connectivity matrices are often analysed using network representations, in which reefs are treated as nodes connected by directed, weighted edges representing larval exchange[141-143]. The connectivity definition used in the model and the underlying matrix formulation (e.g., probability, flow or migration matrices) determine the network dynamics and its interpretation.

Network metrics such as degree, betweenness centrality, and closeness centrality are often used to identify reefs that play disproportionate roles in facilitating connectivity, acting as stepping-stones or maintaining network cohesion. Out-degree and in-degree quantify the number of outgoing and incoming connections, providing proxies for the relative importance of reefs as sources and settlement destinations. Betweenness centrality identifies reefs that facilitate connectivity by serving as common “stepping-stones” among many sites. Clustering and community detection approaches are used to identify groups of reefs that are more strongly connected to each other than to the rest of the network, revealing potential management units or connectivity provinces[144].

As mentioned earlier, the interpretation of these metrics depends strongly on how connectivity is defined and on the underlying matrix used to construct the network. For example, networks derived from probability matrices emphasise “forward” dispersal pathways, whereas those based on flow or migration matrices incorporate variations in reef reproductive output, leading to different representations of connectivity structure. Additionally, network metrics are sensitive to the edge weight (noting that P and M are “strength-based” whereas some network algorithms require distance-based values), thresholding and normalisation, which may influence the identification of key reefs and dispersal pathways. Consequently, network-based analyses should be interpreted with care and explicitly linked to the underlying definition of connectivity, matrix formulation used, and the network algorithm employed. When applied appropriately, they provide a powerful framework for summarising complex dispersal patterns and identifying reefs that contribute disproportionately to metapopulation connectivity.

Across the studies reviewed, seven studies used LPDFs to quantify the dispersal of larvae[130,135], whereas the majority relied on connectivity matrices to summarise larval exchange among reefs. While these outputs provide complementary perspectives on dispersal and connectivity, their interpretation depends strongly on modelling assumptions, spatial scale, and whether connectivity is framed in terms of larval sources, settlement destinations, or network structure. These differences highlight that connectivity is not a single measurable quantity, but a model-dependent construct whose interpretation depends on how dispersal is defined, quantified, and analysed.

Overall, the choice of connectivity outputs and measures is an important source of uncertainty because different connectivity outputs and measures represent distinct connectivity processes and if mis-reported, can lead to erroneous interpretations.

Guidance: Select connectivity outputs according to the ecological or management question being addressed and explicitly report the underlying matrix formulation and connectivity definition used, as different connectivity measures represent distinct ecological processes and may lead to different interpretations of connectivity patterns.

3.5 Evaluation of biophysical model outputs

Modelled connectivity can be evaluated using observations of physical transport or realised connectivity, depending on the spatial and temporal scales of interest. Physical connectivity–or the underlying particle dispersal–can be assessed using tracer (dye) studies[72,145] or ocean drifters[135], which provide direct observations of water movement. These approaches are most appropriate for quantifying short-term dispersal processes and evaluating dispersal simulations of fine-scale connectivity models.

Genetic data are commonly used to assess long-term realised connectivity, which integrates dispersal through successful reproduction over many spawning events and generations. In our corpus, 16 studies explicitly evaluated connectivity model outputs using genetic data[27,72], observed larval concentrations[146] or drifter trajectories[134,135,147]. While genetic data provide valuable insights into patterns of realised multi-generational connectivity, such comparisons must be interpreted with caution as gene flow and genetic structure reflects the cumulative effects of dispersal, survival, mutation, and reproduction over evolutionary timescales, rather than demographic connectivity arising from individual spawning events or over several years.

As such, genetic data are more appropriate for evaluating long-term connectivity patterns, rather than short-term dispersal predictions. In particular, Evans et al.[148] found that fine-scale biophysical connectivity patterns were not concordant with regional-scale genetic structure, reflecting differences in spatial resolution and integration timescales.

Despite the timescale mis-match, pattern-level concordance between biophysical dispersal predictions and genetic connectivity estimates has been reported in 11 studies[27,99]. In these cases, models appear to reproduce broad connectivity features such as dispersal pathways, directional asymmetries, or barriers to exchange. While integrating dispersal simulations over multiple decades can partially reduce this mismatch, as demonstrated by Kool, et al.[149], scaling up single-year simulations alone is insufficient to reconcile ecological and evolutionary connectivity. Direct comparisons with observational data can also reveal discrepancies: for example, Oliver et al.[146] reported limited correspondence between simulated and observed larval concentrations around a coral reef.

Integrating genetic data with modelled connectivity using statistical and spatial analytical approaches (e.g. regression-based or spatial ecological frameworks) can offer insights into how dispersal processes contribute to observed patterns of gene flow and population structure. Future connectivity studies will benefit from adopting a weight-of-evidence approach, in which model outputs are evaluated against multiple independent datasets at comparable spatial and temporal scales, thereby improving confidence in predicted coral connectivity. This reflects a key pathway through which uncertainty in connectivity models can be evaluated and constrained using independent lines of evidence.

Guidance: Adopt a weight-of-evidence approach by evaluating connectivity model outputs against multiple independent datasets (when available) at spatial and temporal scales appropriate to the connectivity patterns being assessed.

4 Natural variability and sources of modelling uncertainty

We distinguish between natural variability, which is intrinsic to coral larval dispersal systems, and modelling uncertainty, which arises from how this variability and other poorly constrained processes are represented in coral biophysical models. Natural variability reflects real fluctuations in oceanographic and biological processes occurring across a range of spatial and temporal scales, whereas modelling uncertainty reflects limitations in data, model structure, parameterisation of biological traits, and numerical implementation. Together, these factors influence connectivity predictions and their interpretation.

Natural variability in coral connectivity arises from fluctuations in oceanographic and biological processes operating across multiple spatial and temporal scales. Temporal and spatial variability in ocean currents, spawning phenology, reproductive output, larval behaviour, competency, mortality, and settlement responses can all influence realised dispersal and connectivity patterns[44]. Several studies explicitly incorporated some of this variability by simulating larval dispersal across multiple spawning seasons or years. Seventeen studies conducted decadal or multi-decadal biophysical model simulations[150,151], 43 studies conducted multi-year simulations spanning less than a decade[87,152,153], and 16 studies simulated spawning in a single year[88,154]. Simulating dispersal across multiple years, particularly over decades, better captures interannual variability in ocean circulation, demographic processes, gene flow, and episodic dispersal events than single-year simulations, which may fail to resolve rare connectivity pathways.

In contrast, modelling uncertainty arises from methodological choices regarding the representation of physical and biological processes that drive coral connectivity. As discussed throughout this review, uncertainty can arise from hydrodynamic model configuration and resolution, the representation of oceanographic processes, particle release strategies,

numerical sampling, parameterisation of larval traits and settlement dynamics, particle-tracking timesteps, specification and location of suitable settlement habitat, and the selection of connectivity outputs and metrics. Differences in these assumptions can alter dispersal pathways, settlement probabilities, and inferred source-destination relationships, even when simulations are forced by similar oceanographic conditions.

These sources of variability and uncertainty are not independent. Rather, they interact and accumulate as models progress from hydrodynamic simulations to larval transport, biological parameterisation, settlement processes, and ultimately connectivity estimation. Consequently, uncertainty in coral connectivity modelling emerges not from any single assumption, but from the combined effects of hydrodynamic forcing, numerical implementation, sampling strategies, biological parameterisation, and natural environmental variability. Understanding how these sources of variability and uncertainty propagate through the modelling workflow is essential for interpreting connectivity predictions, assessing model robustness, and identifying priorities for future model development. The major sources of variability and modelling uncertainty and their propagation through connectivity modelling frameworks are summarised conceptually in Figure 2.

Guidance: Connectivity simulations should include multiple years or decades where possible to capture natural variability in oceanographic and biological processes. Uncertainty analyses should consider both biological and physical sources of uncertainty.

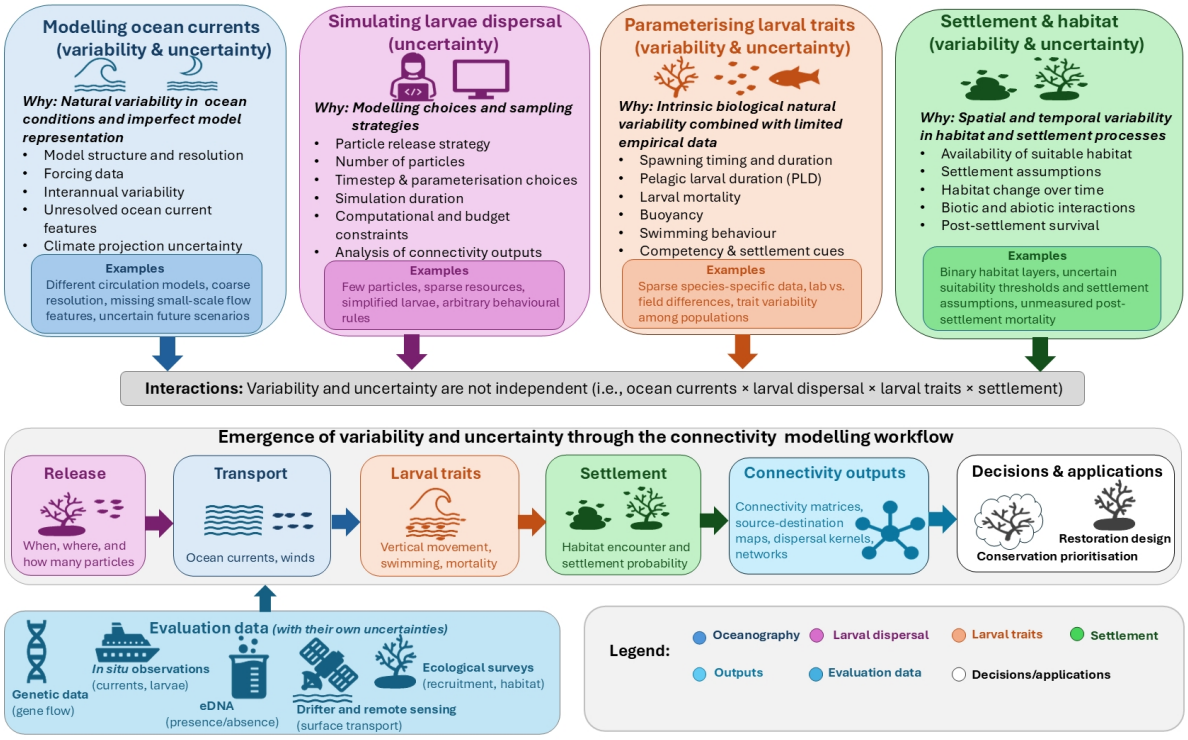

Figure 2: Conceptual framework illustrating the major sources of variability and uncertainty in coral connectivity modelling, and how they interact and propagate through the modelling workflow. Connectivity estimates are shaped by interacting oceanographic, modelling, biological and settlement processes, each characterised by intrinsic variability (e.g., variability in ocean currents, plasticity in spawning phenology, larval behaviour, competency and settlement) and additional uncertainty arising from limited data and model representation. These sources of variability and uncertainty propagate through successive stages of the modelling workflow–from larval release and transport to settlement, connectivity outputs, and interpretation–and can be amplified by aggregation and analytical choices. Consequently, identical or similar dispersal simulations may yield contrasting connectivity estimates and management outcomes.

5 Key limitations and opportunities for improving coral biophysical models

Substantial advances in recent years have improved the realism and reliability of connectivity predictions, enhancing their value for coral reef conservation and management. However, important physical and biological processes that strongly influence larval dispersal and settlement remain incompletely understood or are simplified in current modelling approaches (Figure 2). Addressing these limitations requires improved empirical knowledge, more realistic model representations, and careful consideration of how uncertainty propagates through biophysical model frameworks. The following sections highlight key gaps in understanding coral connectivity, identify untested hypotheses and outline opportunities for advancing coral connectivity modelling.

5.1 What are the gaps in understanding of coral connectivity?

Despite substantial advances in coral connectivity modelling, several key knowledge gaps remain that limit the accuracy, realism, and application of model predictions. These gaps span biological understanding, model representation, computational constraints and evaluation, and collectively influence the robustness of inferred connectivity patterns.

First, there remains insufficient empirical data, particularly from *in situ* observations and controlled experiments, to adequately parameterise key larval traits including survival and mortality, swimming behaviour and buoyancy during dispersal and settlement[44]. For example, experimental studies have found that larvae released early in the spawning window may remain competent for shorter periods than those released later (presumably due to differences in energetic reserves)[155] and that larval survival can be reduced under ultraviolet (UV) exposure[156,157]. However, no connectivity study has explicitly modelled the effects of release timing on larval competency nor incorporated mortality as a function of UV exposure, so the potential impact on connectivity is unknown.

Given the difficulty of quantifying larval traits in the ocean, current understanding of larval buoyancy, swimming behaviour, competency acquisition and loss, and survival is largely derived from laboratory experiments conducted under conditions that differ from those experienced *in situ*. For instance, a recent laboratory-based study found conditioned reef rubble and crustose coralline algae to be among the most effective cues for the settlement of 25 broadcast-spawning coral species on the Great Barrier Reef, while also providing empirical estimates of species-specific competency dynamics[158]. However, there remains limited understanding of how environmental variability influences larval behaviour, competency, and settlement decisions in the field, and how these responses ultimately affect dispersal trajectories, habitat selection, and successful recruitment. Improving knowledge of how future environmental conditions affect larval traits and dispersal processes is therefore critical for coral reef restoration and management, particularly as climate change is expected to alter ocean circulation through warming and changing atmospheric forcing, with direct implications for larval transport and connectivity patterns[17]. This gap directly translates into uncertainty in model parameterisation, as many larval traits are simplified or assumed rather than empirically constrained.

Second, computational constraints impose important trade-offs in the representation of oceanographic variability, hydrodynamic complexity, and numerical sampling. Many connectivity studies simulate only a limited number of spawning events, years, or particles, restricting their ability to capture interannual variability in ocean circulation and adequately characterise rare dispersal events. Appropriate representation of potential coral connectivity generally requires simulations spanning multiple years, and ideally multiple decades, to capture variability associated with climate conditions, episodic events, and non-stationary circulation patterns[82,89]. Where continuous multi-decadal simulations are computationally prohibitive, simulating ensembles of spawning events distributed across representative years

can provide a practical alternative for sampling the range of observed circulation variability.Additionally, computational limitations often require trade-offs between horizontal resolution, vertical dimensionality, simulation duration, and study extent. Consequently, studies frequently choose between fine-scale 2D models that better resolve reef-scale circulation and coarser-resolution 3D models that explicitly represent vertical shear, stratification, baroclinic flow, and depth-dependent transport. Although hydrodynamic dimensionality can influence inferred connectivity patterns[22], the relative importance of resolving fine-scale horizontal versus vertical processes remains poorly understood. As a result, model configuration is typically guided by assumptions about dominant dispersal processes and the scientific or management objectives of the study. Resolving these trade-offs remains a key methodological challenge for improving the realism and robustness of connectivity predictions. Surrogate modelling approaches using deep learning might help to reduce these constraints.

Third, most coral connectivity models estimate potential connectivity, which captures larval dispersal and settlement but does not account for post-settlement survival or recruitment to reproductive adulthood. This distinction is critical for management, as effective connectivity (successful settlement and early survival) and reproductive or genetic connectivity (survival to reproduction) ultimately determine population persistence[42]. However, the influence of post-settlement survivorship on connectivity outcomes depends on its spatial variability. If survivorship is relatively uniform across reefs, incorporating it will have limited effect on relative connectivity patterns, whereas spatial differences in survivorship among destinations can substantially alter connectivity outcomes and persistence estimates. This creates a disconnect between model outputs and management-relevant measures of population persistence and resilience. At present, spatially-explicit and long-term data on post-settlement survivorship remain extremely limited. While local studies have quantified early survival and recruitment at individual reefs or over short time periods, comparable survivorship data integrated across reef networks and maintained over interannual to decadal timescales are largely unavailable. As a result, most biophysical models cannot reliably incorporate survivorship. If such data were available, management decisions could move beyond identifying dispersal pathways to prioritising reefs that both receive larvae and consistently support successful recruitment and population persistence. In the absence of spatially explicit survivorship information, biophysical models remain most appropriate for informing potential dispersal pathways rather than demographic outcomes, and their outputs should be interpreted accordingly in conservation and restoration planning.

Finally, there remains limited observational and genetic data suitable for evaluating coral connectivity model outputs, particularly at spatial and temporal scales comparable to those represented by biophysical simulations. While direct validation of dispersal processes is rarely feasible, different data types provide complementary, indirect constraints on modelled connectivity. Short-term physical observations, such as drifter trajectories or dyed larvae, are most appropriate for evaluating local dispersal pathways and individual spawning events, whereas genetic data integrate dispersal and successful reproduction over many generations and therefore reflect long-term, cumulative connectivity rather than event-scale transport. The use of observational and genetic data for evaluating biophysical models depends strongly on the scale and purpose of the model. Emerging approaches, such as environmental DNA (eDNA), offer potential for contributing to spatially-explicit observations of larval and adult distributions[159,160], but currently provide indirect evidence of dispersal rather than direct measures of connectivity. In principle, CRISPR-Cas9-mediated insertion of heritable DNA barcodes into coral genomes, recoverable via eDNA metabarcoding, could facilitate multigenerational in situ lineage tracking[161]. Rather than serving as direct validation, these data sources should be viewed as complementary lines of evidence that can constrain uncertainty, test the plausibility of predicted dispersal pathways, and improve confidence in connectivity estimates when interpreted within their respective temporal and ecological contexts (Figure 2).

Taken together, these gaps highlight that advancing coral connectivity science requires coordinated improvements in empirical data, modelling approaches, and evaluation frameworks, as well as closer integration between biological, physical, and computational perspectives.

5.2 What do we think might be important, but haven't yet tested?

Some processes are likely to strongly influence coral connectivity but remain largely unexplored in biophysical models due to limited empirical data and logistical constraints. Connectivity studies mostly focus on shallow reef habitats that are well mapped due to their visibility in satellites and aerial images and accessibility to divers, whereas mesophotic and deep reefs are often excluded. However, these deeper systems may act as both larval sources and settlement destinations[162-164], and may function as refugia under climate-related disturbances such as marine heatwaves and tropical cyclones. Their omission from connectivity analyses may therefore lead to incomplete or biased representations of reef network connectivity.

Biophysical models generally simulate potential dispersal without accounting for variation in post-settlement fitness or local adaptation. Corals can exhibit adaptive responses via changes in gene expression[165], and interactions among larval traits, hydrodynamic transport, and local environmental conditions may shape realised gene flow[19]. Dispersal of larvae from environmentally mismatched source reefs may not translate into successful recruitment, whereas larvae from more tolerant or warmer-source populations may enhance resilience under changing conditions[166]. Incorporating such processes would require coupling biophysical models with demographic or eco-evolutionary frameworks and is therefore best viewed as a direction for future work rather than a limitation of current biophysical models.

These factors indicate that uncertainty in connectivity predictions may not only arise from known modelling limitations, but also from processes that are conceptually recognised yet remain untested. These hypotheses highlight that key mesophotic reefs and eco-evolutionary processes remain underrepresented in coral connectivity modelling, representing key frontier areas for advancing both conceptual understanding and the predictive capability of coral connectivity models.

5.3 Emerging directions in coral connectivity modelling

Recent connectivity studies have begun to explore the use of artificial intelligence (AI) as a complementary tool in coral connectivity modelling, especially where conventional approaches are limited by data availability, scale, or complexity. AI-based image analysis and computer-vision techniques have been used to characterise ontogenetic changes in coral larval behaviour during early development[167], providing high-resolution biological data that could inform parameterisation of larval traits in biophysical models. Deep-learning approaches combined with remote sensing have also been applied to quantify reef structure and habitat connectivity[168], with potential to improve spatial representation of settlement environments. More broadly, AI offers opportunities to integrate large, heterogeneous datasets and identify non-linear relationships among physical, biological, and environmental drivers of connectivity. However, these methods remain data-dependent and non-mechanistic, and are therefore best viewed as augmenting–rather than replacing–process-based biophysical models.

Another emerging direction is the use of biophysical models in near-real-time to support larval-based restoration efforts. For example, Gouezo et al.[64] combined near-real-time, fine-scale hydrodynamic simulations with particle-tracking models to predict convergence zones of coral spawn slicks in the upper water column at Lizard Island on the northern Great Barrier Reef, enabling the identification of optimal locations for enhanced larval settlement.

Connectivity studies are also increasingly integrating climate-model projections to evaluate how larval dispersal and connectivity may shift under future ocean conditions, including

warming, altered current patterns, and increased frequency of marine heatwaves[73]. Such scenario-based approaches help identify potential climate refugia and prioritise reef areas likely to maintain connectivity under changing environmental conditions.

Finally, emerging frameworks are beginning to couple ecological biophysical models with human dimensions such as fishing pressure, governance structures, and management practices[169]. Connectivity studies may also benefit from indigenous and local ecological knowledge, which can provide valuable historical context, spatial insight, and place-based understanding of reef systems[170,171]. These integrative approaches broaden the relevance and applicability of connectivity modelling for real-world decision-making.

6 Conclusions

Coral reef ecosystems face unprecedented pressure from climate change, and the management decisions informed by connectivity models–including reserve design, restoration planning, and the prioritisation of source reefs–carry significant conservation consequences. Best-practice coral connectivity modelling is not defined by any single methodological choice, but by the appropriate alignment of hydrodynamic, biological, and numerical components with the ecological processes and spatial and temporal scales of interest. Differences in model configuration, parameterisation, evaluation, and reporting can propagate through biophysical model frameworks to produce divergent connectivity predictions, even under similar hydrodynamic forcing. Consequently, the reliability of management decisions depends not on model sophistication alone, but on the transparent reporting of modelling assumptions, evaluation of model outputs against independent data at appropriate spatial and temporal scales, and explicit consideration of uncertainty.

Progress on these fronts requires coordinated effort across empirical biology, physical oceanography and modelling, as well as closer integration with the conservation and restoration practitioners who ultimately use connectivity predictions. Meeting that challenge will determine how effectively biophysical models can support the long-term persistence of coral reef ecosystems under ongoing environmental change.

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8 Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used Microsoft Copilot to assist with language editing and improving the clarity of the manuscript text. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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