Hydrodynamic Feedbacks in Coral Reefs: from Organisms to Geomorphic Development

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Abstract

Coral reefs are shaped by tightly coupled interactions among geomorphology, hydrodynamic forcing, and ecological processes. In this review, we synthesize current knowledge on how hydrodynamic processes regulate coral reef functioning across scales, from exchanges at organismal surfaces to reef-scale morphodynamics.

Hydrodynamic forcing governs mass and momentum transfer across scales through nested boundary layers, linking organismal performance, growth and ecological interactions to carbonate production, redistribution, and reef morphodynamics. Reef geomorphology modifies these flow regimes by generating spatially heterogeneous patterns of turbulence, wave dissipation, and current acceleration that regulate disturbance, substrate stability, productivity, and benthic community structure. Through carbonate accretion, bioerosion, and sediment reworking, ecological processes in turn reshape reef geomorphology.

Many reef processes respond non-linearly to hydrodynamic forcing, such that carbonate production and reef growth are maintained only within ranges of flow conditions where these processes remain mutually compatible. Rather than forming a single optimal state, these context-dependent hydrodynamic “Goldilocks” envelopes are spatially fragmented by reef geomorphology, generating mosaics of benthic states, disturbance regimes, and recovery trajectories across reefscapes. Within these dynamic environments, disturbance is not solely destructive but also contributes to reef development through the generation, transport, and stabilization of carbonate sediments and rubble. Building on these concepts, we propose hydrodynamic resilience as the capacity of reef systems to maintain or reorganize constructive flow-form feedbacks following disturbance.

By integrating hydrodynamic, ecological, and geomorphic perspectives, this review provides a framework for understanding reef spatial organization, resilience and geomorphic evolution as emergent properties of interactions across spatial and temporal scales.

Keywords

Hydrodynamics, geomorphology, coral physiology, coral demography, coral reef ecology, coral reef morphodynamics

Introduction

Oceanographic patterns interact continuously with the seabed and coastline, and these physical processes cascade into ecological outcomes, shaping the distribution, productivity, and resilience of marine communities. Coral reefs, as biogenic landforms constructed by calcifying organisms, are uniquely dependent on this interplay. Hydrodynamics influences reefs across a wide spectrum of spatial and temporal scales: from seconds-long boundary-layer processes regulating solute and gas exchange at the tissue surface, to millennial-scale forcing that governs geomorphic architecture, reef accretion and persistence through geological time. These processes do not operate in isolation: enhanced mass transfer in thinned boundary layers accelerates the growth of certain taxa, whose skeletons then contribute to the long-term reef framework accretion rate and dynamics. That same framework is continuously sculpted, eroded, and redistributed by the very hydrodynamic forces that, at the microscale, first promoted growth.

Despite this tight coupling between flow, biology, and reef structure, efforts to synthesize reef functioning have largely approached these components from parallel rather than fully integrated perspectives. Foundational syntheses have already emphasized the need to see reefs as more than ecological communities. Hopley's Encyclopedia of Modern Coral Reefs (Hopley, 2011) provided a comprehensive collection of the diverse processes shaping reef development, collating insights on ecological processes, sedimentation, reef geomorphology, and physical oceanography. Building on this integrative perspective, Kench (2011) proposed the eco-morphodynamic framework, explicitly recognizing that reef development emerges from feedbacks between ecological and geological processes operating across non-linear and often lagged timescales.

While these frameworks highlight the coupled nature of reef systems, they remain largely conceptual and do not directly quantify how these interactions translate into net reef growth or degradation. The carbonate budget concept (Perry et al., 2012, 2008; Stearn et al., 1977) addresses this by quantifying the balance between carbonate production and loss, providing a measurable link between ecological processes and geomorphic

trajectories. These budgets serve as vital indicators of reef health and long-term structural capacity, providing a bridge between ecological performance metrics and geomorphic trajectories. Budget states can vary by an order of magnitude across habitats, with narrow reef-margin zones generating most framework despite occupying a small fraction of platform area, while extensive lagoonal or rubble-dominated habitats typically exhibit neutral or negative budgets due to low coral cover and high relative bioerosion (Perry et al., 2017).

While carbonate budgets provide a quantitative snapshot of reef growth potential, they do not fully capture how these dynamics unfold over longer temporal scales or are recorded in the geological structure of reefs. Short-term ecological transitions caused by large scale disturbance may alter carbonate budgets on decadal timescales, but only some of these perturbations propagate to produce detectable geomorphic change over decades to centuries. Hubbard (2015) extends this perspective by emphasizing the importance of integrating ecological turnover with the geological record of accretion, erosion, and disturbance. His work frames reefs as dynamic systems whose present structure reflects the cumulative imprint of past ecological and physical processes.

However, even within quantitative frameworks, hydrodynamics is typically incorporated mainly as background forcing or habitat context, rather than resolved as the mechanism linking organismal performance, sediment dynamics, and geomorphic structure across spatial and temporal scales. This review aims to integrate hydrodynamic processes as the physical link connecting coral reef ecological and geomorphic feedbacks. This could be achieved by synthesizing multi-scale flow dynamics, biological performance, ecological interactions, and geomorphic processes into a single body of work. The goal is to provide a conceptual platform that can support both scientific integration and applied management. Different disciplines studying different aspects of coral reef science often describe processes in ways that remain siloed, making cross-scale synthesis difficult. Without a shared framework, reefs risk being fragmented into “ecological states,” “sedimentary deposits,” or “hydrodynamic regimes” rather than recognized as the living landforms they are. This review aims to bridge that gap by deliberately framing concepts in terminology that resonates across fields, so that a coral physiologist, a sedimentologist, and a physical oceanographer can all trace the same processes within their own disciplinary lens.

1. Fluid mechanics: boundary layer physics

Coral reefs are shaped by complex hydrodynamic processes that operate across multiple spatial and temporal scales. Large-scale flow over reefs is primarily driven by waves, tides, and mean currents, which interact with reef topography to generate circulation patterns such as cross-reef jets, backreef recirculation, and tidal pumping. These processes determine the overall residence time of water on reefs, regulate the delivery of

nutrients and oxygen to reef ecosystems, influence larval transport and recruitment (Monismith, 2007; Lowe and Falter 2015). Recent ecosystem-ecology frameworks show that coral reefs cannot be understood without considering how water movement structures the flow of energy and materials across the system. Allgeier (2024) highlights that reef productivity emerges from multiple interacting controls, including internal recycling, autotrophic production, and externally delivered subsidies, with water exchange influencing the degree to which reef habitats are connected to surrounding oceanic inputs. In this view, hydrodynamic context helps shape reef metabolism by affecting the delivery and retention of plankton, dissolved nutrients, and organic matter, alongside other environmental and biological drivers.

Energetic sustainability on reefs depends on hydrodynamic connectivity across scales. Habitat-scale circulation enhances the delivery and removal of materials that sustain community-level metabolism, while flow at organismal scales regulates solute exchange and nutrient uptake (Lowe and Falter, 2015; Monismith, 2007). At the interface between the substrate and overlying water, friction and reef roughness generate strong velocity gradients, drag, and turbulent momentum exchange. Over complex reef surfaces, roughness enhances turbulence and mixing, promoting exchange between the benthos and the overlying water column (Davis et al., 2021; Reidenbach et al., 2006).

At organismal scales, the efficiency of this exchange depends on the local flow environment surrounding coral surfaces. Increasing flow and turbulent or oscillatory renewal generally promotes transport across boundary layers, enhancing the exchange of oxygen, dissolved inorganic carbon, nutrients, and metabolic products (Reidenbach et al., 2006; Monismith, 2007). The same hydrodynamic forcing also imposes mechanical stresses on reef substrates: near-bed drag, shear, lift, and wave-induced forces govern the entrainment and transport of sediment and rubble (Pomeroy et al., 2013; Rosenberger et al., 2020). Hydrodynamic forcing therefore links biological exchange and substrate dynamics through the transfer of momentum and materials across the reef-water interface, generating both physiological opportunities and mechanical constraints.

Understanding how hydrodynamics shape boundary layer hierarchy is essential for linking physical conditions to coral physiology, productivity, and stress response (Lowe and Falter, 2015; Monismith, 2007). Boundary layers on coral reefs organize into a nested hierarchy spanning from tens of meters to micrometers, each governing distinct but interconnected transport processes (Shashar et al., 1996; Reidenbach et al., 2006). Boundary layers span a continuum from fully turbulent - chaotic, eddy-rich motion characterized by rapid mixing and high momentum transport; to laminar - smooth, orderly movement of water in parallel layers, where momentum and solute transport are dominated by viscosity and molecular diffusion. At reef and benthic scales, flow is typically turbulent and strongly influenced by waves, currents, and roughness-generated wakes and eddies. Closer to organismal surfaces, mean flow velocity declines and viscous

effects become increasingly important, while local flow structure remains strongly shaped by colony geometry. Immediately adjacent to tissues, transport across the diffusive boundary layer is dominated by molecular diffusion.

1.1. The reef-scale turbulent boundary layer

The reef-scale boundary layer (RTBL) is the 1-10 m flow region immediately above the reef substrate, where waves and currents interact with the complex coral canopy to generate intense turbulence and momentum loss (Monismith, 2007). This layer controls cross-reef exchange, flushing, and the delivery and removal of external subsidies (e.g., Allgeier, 2024). Unlike smooth seafloors, reefs create higher drag, causing rapid dissipation of wave energy and strong mixing close to the bed. Within this zone, flow is highly sensitive to the reef's geometric complexity: branching corals, mounds, and rough pavements all modify how turbulence is produced and how it decays. The RTBL therefore acts as the main interface through which offshore water masses exchange with the reef interior, setting the rate at which momentum, heat, nutrients, larvae, and suspended particles are delivered across reef environments (Monismith, 2007; Reidenbach et al., 2006).

Unidirectional tidal currents predominantly interact with larger-scale structural features such as reef passes, ridges, slope breaks, making these the principal drivers of RTBL structure during tidal forcing (Reidenbach et al., 2006). For example, lagoons are flushed preferentially through reef passes, with velocities tightly governed by channel depth and geometry (Rogers et al., 2018). When waves and tides interact, especially in macro-tidal systems, the RTBL becomes highly dynamic: breaking waves inject turbulence that propagates inward across the reef flat, enhancing mixing and reorganizing boundary layer velocity structures (Hearn, 2011).

Wave period strongly modulates reef-scale boundary layer dynamics by determining the spatial scale over which oscillatory flow interacts with reef roughness. Short period waves generate relatively small orbital excursions, making near-bed flow more sensitive to small-scale roughness elements and enhancing local turbulence and mass transfer. By contrast, long period swell produces larger orbital excursions that penetrate deeper in the water column and interact with broader geomorphic features such as ridges, spur-and-groove systems, and slope breaks, shifting hydrodynamic control toward larger spatial scales (Fig.1; Reidenbach et al., 2006; Bandet, 2009). The combined effects of wave forcing and reef morphology therefore determine how efficiently the RTBL renews oceanic water, regulates nutrient fluxes, and supports energetic coupling between offshore waters and benthic communities.

1.2. The benthic boundary layer

Above the centimeter-scale, the benthic boundary layer (BBL) is a transitional region where wakes from individual roughness elements blend into the larger, more coherent

shear flow of the RTBL. In this layer, turbulence is dominated by flow separation, eddy shedding, and recirculation zones generated by the reef's microtopography.

The thickness of the BBL varies with flow regime. Under wave-driven turbulence, the BBL becomes thinner and more vigorously mixed, increasing nutrient fluxes and solute renewal. Under calm or low-flow conditions, a thicker BBL forms with reduced shear stress and weaker mixing, limiting the transport of oxygen, nutrients, and particulate matter between the benthos and overlying water (Hearn, 2011). Under short-period waves (in contrast to long period swell; Bandet, 2009), small roughness features exert strong control on turbulence production and mass transfer, tightly regulating sediment mobilization and nutrient delivery at the bed (Reidenbach et al., 2006). In unidirectional currents, flow separation downstream of rocks or coral heads generates patchy microenvironments where nutrient availability, particle retention, and sediment deposition vary sharply over centimeter scales. Sediment scoured from the upstream side of boulders often accumulates in recirculating wakes, modifying habitat conditions for surrounding organisms (Hench & Rosman, 2013).

Benthic community composition also influences BBL structure. Three-dimensional frameworks, whether composed of living corals, dead but rugose skeletons, coralgal ridges, or carbonate boulders, increase near-bed roughness and intensify turbulence within the BBL, enhancing exchanges. Replacement of structurally complex coral framework by low-relief turf, biofilms, or flattened algal-dominated substrates can reduce geometric roughness and alter near-bed turbulence, while taller macroalgal canopies may instead generate their own drag and canopy-scale flow structure (Dubinsky and Stambler, 2011; Gowan et al., 2014; Larkum et al., 2003) (Fig. 1). These hydrodynamic shifts can reinforce degraded states via positive feedback loops linking substrate smoothing, reduced exchange efficiency, and ecological decline (Stocking et al., 2018). This sensitivity has led some to propose that boundary layer measurements could provide real-time assessments of reef health, capturing the feedback between structure, flow, and ecological function (McGillis et al., 2011).

1.3 The hydrodynamic boundary layer

The hydrodynamic boundary layer (HBL) is the millimetre- to centimetre-scale layer of decelerated flow that develops immediately above any benthic organism or roughness element. Within the HBL, flow separation, eddy formation, and recirculation zones are shaped by the three-dimensional geometry of the structure (e.g., branch spacing, plate width, algal canopy height, or surface rugosity) thereby controlling the rate of mass transfer to tissues or surfaces below. In corals, this layer directly regulates the diffusive boundary layer (DBL) and thus governs physiological processes such as photosynthesis, respiration, and calcification.

Coral colony morphology and polyp size strongly modulate boundary layer dynamics. Martins et al. (2024a) show that flat morphotypes such as table corals, with relatively low polyp density and smoother microtopography, reduce turbulence retention and hydrodynamic drag, generating thinner boundary layers and more efficient mass transfer under flow. The tabular *Acropora cytherea* maintains thinner oxygen boundary layers than *Pocillopora verrucosa* or *Porites cylindrica*, despite similar polyp sizes, highlighting the role of colony-scale morphology in shaping the HBL. By creating eddies and wakes (Fig. 1), branching corals with greater branch spacing can thin boundary layers and sustain metabolic rates under reduced flow (Bruno and Edmunds, 1998; Kaandorp et al., 2003). This architecture enhances passive exchange, with branching morphologies boosting mass transfer by ~50-70% (Reidenbach et al., 2006). This may reflect in adaptation in species such as *Pocillopora meandrina,* usually found in moderate exposure regimes, that can compensate for low-flow conditions by maintaining efficient mass transfer (Hossain and Staples, 2019). At the polyp scale, boundary layer thickness increases with polyp size: larger polyps generate thicker diffusion barriers, whereas small-polyped species sustain thinner DBLs at the same flow speed, enabling efficient mass transfer in calm water (Shashar et al., 1993). For example, *Porites lutea*, a small-polyped massive coral common in sheltered habitats, actively modifies its DBL using cilia-induced vortex flows (Fig. 1) to enhance gas exchange under stagnant conditions (Pacherres et al., 2020).

Algal DBLs are strongly influenced by both flow regime and algal structure. Photosynthesis in epilithic algal communities is often limited by mass transfer, with DBLs ranging from ~180-550 μm under moderate flow but exceeding 2 mm under stagnant conditions, reducing dissolved inorganic carbon supply (Larkum et al., 2003). Oscillatory, wave-driven flow enhances nutrient and carbon flux to algal tissues compared to equivalent unidirectional currents due to more efficient turbulent renewal at the surface (Carpenter et al., 1991). Unlike corals, which can actively thin DBLs using ciliary movements, macroalgae rely entirely on external flow, making their productivity more sensitive to low-flow conditions (Larkum et al., 2003). Although canopy height and morphological complexity are expected to influence DBL thickness (e.g., low-lying turf and CCA may experience thinner boundary layer than thick fleshy macroalgae, Fig. 1), direct comparative measurements across algal morphotypes remain limited, and most evidence derives from models or single-community measurements rather than systematic cross-taxa studies.

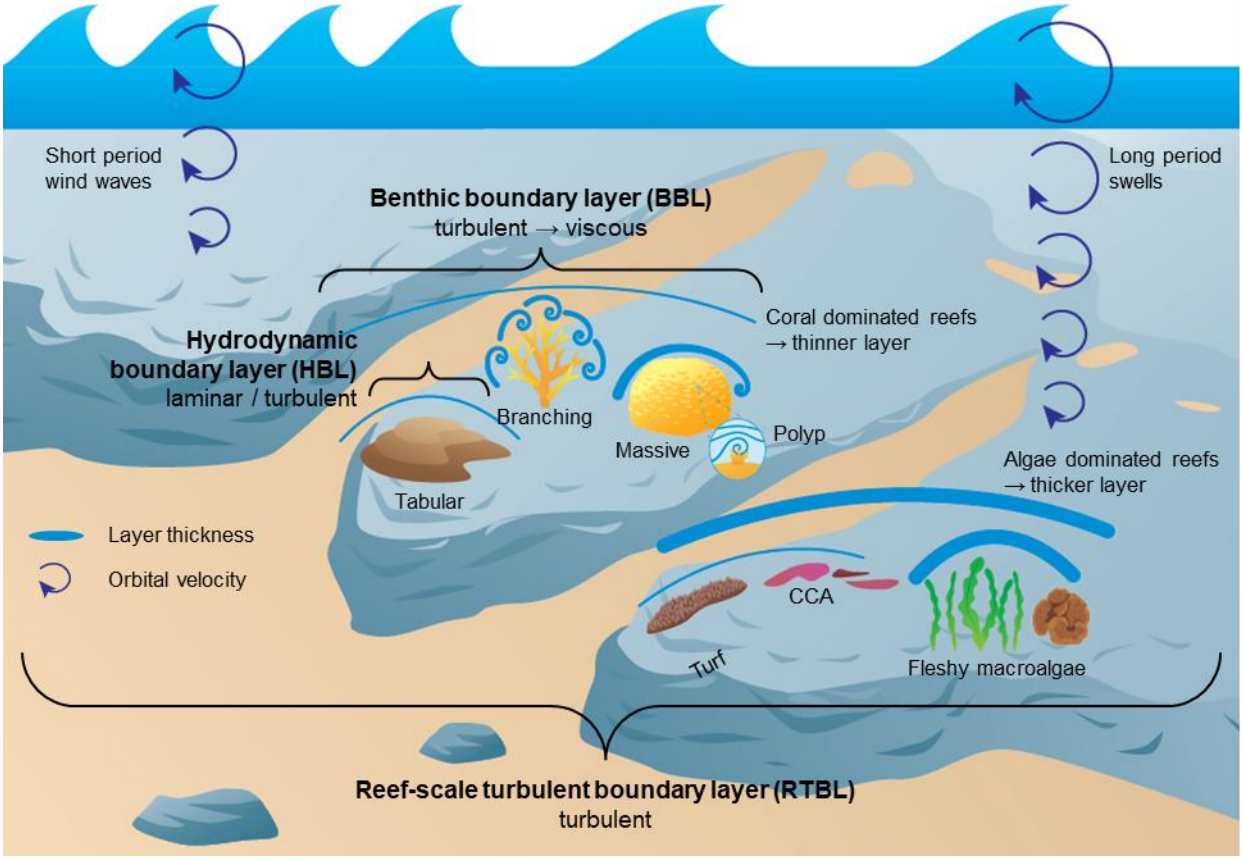


Fig. 1. Conceptual schematic of the hierarchical organization of hydrodynamic boundary layers on coral reefs. The figure illustrates boundary layer structure across nested spatial scales, from the reef-scale turbulent boundary layer (RTBL) to benthic-scale hydrodynamic boundary layers generated by biological roughness. Diffusive and concentration boundary layers are not shown. At the reef scale, boundary-layer thickness is modulated by incident hydrodynamic forcing and geomorphic roughness, with short-period waves penetrating less deeply in the water column than longer period swells. At the benthic scale, differences between coral- and algae-dominated reefs are illustrated, highlighting how organismal morphology influences hydrodynamic boundary-layer thickness. Complex coral morphologies (e.g. branching and massive forms) promote thinner boundary layers and enhanced mass transfer, whereas algal canopies and turf assemblages tend to thicken boundary layers through flow attenuation and canopy effects.

1.4 The diffusive and concentration boundary layers

The diffusive boundary layer (DBL) controls the exchange of gas and nutrients between organism tissues and surrounding seawater, and its thickness is highly sensitive to flow velocity. Faster flows thin the DBL, enhancing mass transport and physiological processes such as photosynthesis, respiration, and calcification (Lesser et al., 1994;

Patterson et al., 1991). By contrast, low-flow conditions promote thicker boundary layers, restricting gas and nutrient exchange.

The concentration boundary layers (CBL) - relative to the concentration of different solutes right above the exchange surface - are highly variable and species-specific. Flow strongly modulates CBL traits, with low flow velocity producing thicker CBLs and reduced gas exchanges. Different species also show distinct CBL profile types (diffusive, S-shaped, and complex) whose occurrence varies across flow regimes. Thinner CBLs and diffusive profiles dominated in *A. cytherea*, while S-shaped and complex profiles were more common in *Pocillopora verrucosa*, and *Porites cylindrica*, particularly under low flow conditions. Differences in CBL profiles reflect differences in coral morphology and adaptation to flow regimes, suggesting that species vary in their ability to modulate their CBL via surface cilia and skeletal shape, with consequences for respiration, photosynthesis, and resilience to stress (Martins et al., 2024a). Interestingly, ocean acidification effects on corals do not appear to be directly mediated by DBL dynamics (Martins et al., 2024b).

Beyond mass and nutrient transfer, flow velocity also shapes the thermal boundary layer (TBL), which regulates coral temperature. Thickened TBLs reduce heat dissipation and can lead to micro-scale thermal stress. Branching forms such as *Pocillopora meandrina* exhibit localized thickening of the TBL in low-flow inter-branch spaces, while plating forms like *Montipora capitata* display more uniform TBLs (Jimenez et al., 2011). Such differences help explain the patchy bleaching observed within individual colonies and the heightened bleaching susceptibility of branching morphologies under calm conditions (Finelli et al., 2007).

2. Hydrodynamics and biological processes

2.1 Physiology

Photosynthesis by endosymbiotic dinoflagellates provides most coral energetic demand but its efficiency depends in part on the thinning of DBL, which enhances the exchange of dissolved inorganic carbon, oxygen, and metabolic byproducts (Nakamura, 2010). In parallel, corals absorb dissolved inorganic nutrients such as ammonium, nitrate, and phosphate directly from seawater, a process likewise limited by mass transfer and therefore enhanced by turbulence and DBL thinning. These nutrients support essential processes such as tissue growth, symbiont maintenance, and calcification (Atkinson and Bilger, 1992). Heterotrophic feeding further supplements these sources, as tentacle extension and particle capture are optimized under intermediate flow velocities that balance particle delivery with retention efficiency (Sebens et al., 1998; Sebens and Johnson, 1991). This trophic flexibility provides a potential mechanism for resilience: under conditions where autotrophic capacity is reduced, such as during thermal stress

and bleaching, increased reliance on heterotrophic feeding can help maintain energy balance and support survival and recovery (Grottoli et al., 2006). In this context, hydrodynamic conditions influence both baseline metabolic performance and the capacity of corals to compensate for stress through shifts in energy acquisition pathways.

2.1.1 Photosynthesis and respiration

Numerous studies demonstrate that water flow enhances metabolic performance of benthic communities because thinner boundary layers improve gas exchange and reduce the buildup of metabolic byproducts. This generally promotes photosynthesis, respiration, calcification in corals, potentially enhancing resilience to thermal stress (Nakamura, 2010) but research on physiological performance highlights species-specific responses to flow regimes (Summary in Table 1, Appendix A).

Respiration and dark calcification show a stronger dependence on turbulence than photosynthesis because these processes are more strongly limited by DBL thickness and gas exchange. In *Acropora formosa*, still-water incubations produced ~25% lower respiration and ~60% lower dark calcification than stirred treatments (Dennison and Barnes, 1988), demonstrating that diffusion limitation of O_2 and CO_2 through thickened DBLs suppresses metabolic rates in low flow velocity. In situ work on *Orbicella annularis* (ex *Montastraea* annularis) showed that both respiration and photosynthesis increased with flow, but the dependency was much steeper for respiration, consistent with oxygen transport across the DBL being the dominant control on dark heterotrophic metabolism (Patterson et al., 1991). Similar patterns were observed in branching and plating species: in *Madracis mirabilis*, dark respiration increased significantly with flow across all branching morphotypes, with higher branch spacing maintaining higher respiration by preventing DBL thickening inside aggregates (Bruno and Edmunds, 1998). In *Agaricia tenuifolia*, respiration but not photosynthesis, was strongly flow-dependent, again indicating that aerobic metabolism is more constrained by diffusive transport than light-saturated photosynthesis, which can remain near maximum even in low flow (Sebens et al., 1998). Collectively, these studies show that DBL thinning disproportionately enhances respiration and dark calcification compared to photosynthesis, because heterotrophic and calcification processes require rapid removal of O_2 and protons and sustained supply of dissolved inorganic carbon, all of which are strongly limited under low-flow conditions.

Although less strongly than respiration, photosynthesis is still influenced by flow. In situ work demonstrated that increasing flow velocity enhances both maximal photosynthetic rate and respiration in *Orbicella annularis*, driven by boundary-layer thinning and improved gas exchange (Patterson et al., 1991). Finelli et al. (2007) showed that this hydrodynamic advantage is spatially structured at the colony scale: upstream-facing surfaces of *Siderastrea siderea* and *Porites porites* subjected to stronger flow velocity exhibited higher photosynthetic efficiency (4-12%). In contrast, these differences were not

recorded for plating *O. annularis* (Finelli et al., 2007, 2006). The contrasting results for *M. annularis* in Patterson et al. (1991) and Finelli et al. (2006, 2007) likely reflect differences in experimental scale and colony hydrodynamics. *M. annularis* has a smooth, domed or plating morphology that distributes flow uniformly around its surface, so that its upstream and downstream faces experience similar DBL conditions. Using direct measurements of oxygen and photosynthesis, Mass et al. (2010) showed that the immediate benefit of flow is about removing oxygen that builds up around and within coral tissues under still water. After they artificially raised oxygen levels in the surrounding water, this flow benefit disappeared entirely, confirming that oxygen removal is the key short-term mechanism. Species adapted to low-flow environments can maintain reasonable performance under calm conditions. For example, *Porites cylindrica* acclimated to low flow reached its photosynthetic maximum at lower velocities than high-flow conspecifics, demonstrating physiological plasticity, yet overall metabolic rates were still lower in stagnant water (Rex et al., 1995). Other species show a stronger dependence on flow. In *Galaxea fascicularis*, Schutter et al. (2010) found only modest increases in photosynthesis with flow, but growth and calcification increased substantially at higher velocities, even though photosynthetic carbon supply actually declined, indicating that flow-driven exchanges (e.g., removal of oxygen buildup, improved supply of dissolved inorganic carbon) support growth more than photosynthesis itself. These interpretations are supported by Osinga et al. (2017) who showed higher flow velocity substantially increased respiration capacity, nutrient uptake, and skeletal growth in *G. fascicularis* despite only moderate changes in photosynthesis.

Together, these studies demonstrate that while many corals can maintain photosynthetic function in low flow conditions, respiration, photosynthesis and calcification are frequently enhanced under higher flow velocities. Boundary layer thinning improves gas exchanges and can enhance carbonate chemistry at the site of calcification. These findings collectively show that hydrodynamics impose functional ceilings that differ by species, skeletal morphology, and acclimation history.

Benthic algae photosynthesis is also particularly responsive to flow regimes. Epilithic algae rely on water motion to maintain efficient gas and dissolved inorganic carbon exchanges (Larkum et al., 2003). While algae are more tolerant of oxygen buildup than corals, their productivity is limited under stagnant conditions. Oscillatory flow significantly enhances both primary productivity and nitrogen fixation of reef algal assemblages compared to more laminar or unidirectional conditions (Carpenter et al., 1991). Turf shows steep increases in productivity with rising flow, controlled primarily by boundary layer dynamics rather than nutrient availability (Carpenter et al., 1991; Carpenter and Williams, 2007). This agrees with findings on the epilithic algal community - turf-dominated, sediment-trapping benthic assemblage that colonizes hard reef substrates, where thinner DBLs under moderate flow enhanced oxygen efflux, nutrient delivery, and photosynthetic

rates (Larkum et al., 2003). Also fleshy macroalgae (*Gracilaria cornea*) can experience an instantaneous increase in photosynthetic rate in high flow velocity (Mass et al., 2010).

2.1.2 Nutrient uptake

Reefs are net nutrient consumers and heavily rely on hydrodynamic transport for productivity (Johannes et al., 1972). Reef crests and forereefs, where oscillatory wave motion is strongest, often show the highest uptake rates acting as efficient nutrient filters (Cuet et al., 2011; Wyatt et al., 2012).

Wind and wave motion appear to be strong drivers of nutrient uptake rates (Steven and Atkinson, 2003), as these are fundamentally mass transfer limited and strongly depend on DBL thickness (Atkinson and Bilger, 1992). The thickness of the DBL and the mass transfer efficiency is dictated by bottom friction and turbulent energy dissipation (Thomas and Atkinson, 1997), with substrate roughness increasing turbulence and creating fine-scale variability in uptake rates (Pujol et al., 2019). Reef roughness may also increase the surface area available for nutrient uptake while maintaining volume (Hearn, 2011). Uptake increases nonlinearly with turbulence, approximating a quarter-power law (Falter et al., 2004). While moderate turbulence boosts nutrient flux, the benefits decline at high turbulence (Zhang et al., 2011) and uptake rates can even decrease under extreme wave activity (Hearn, 2011).

Benthic community composition also mediates responses. Flow velocity enhances nutrient delivery to all reef benthos, but taxa differ in how effectively they capitalize on this supply. In nutrient-poor (oligotrophic), high-flow reef systems, corals typically maintain productivity via tight internal recycling (symbiont-host nutrient retention loops), and moderate external uptake (Wyatt et al., 2010). Coral uptake rates show species-specific physiological limit, with uptake plateauing at high concentration levels, independently of flow velocity. For example, nitrate concentrations around 6 µM exceed the uptake capacity of *Pseudodiploria strigosa*, and this limitation appears independent of flow velocity (Badgley et al., 2006). Although their “high” and “low” water-motion treatments did not alter these responses, Stambler et al. (1991) emphasize how shifts in nutrient availability can overwhelm the mass-transfer advantages typically conferred by flow, as ammonium concentrations of 7-15 µM may disrupt coral-algal balance by suppressing calcification and favoring symbiont proliferation in *Pocillopora damicornis*. Although boundary layer dynamics and colony morphology are known to influence mass transfer strongly, few studies measure nutrient uptake rates for individual coral species under controlled flow. Most nutrient enrichment experiments assess growth or physiology without quantifying nutrient fluxes or DBL-mediated limitations, and direct species comparisons are rare. As a result, the mechanistic link between hydrodynamics, nutrient delivery, and species-specific performance deserves further investigation (Houlbrèque and Ferrier-Pagès, 2009).

Nutrient flux experiments demonstrated that phosphate and ammonium uptake by reef algal communities increases sharply with flow, reflecting the dominant role of mass transfer limitation rather than nutrient availability per se (Atkinson & Bilger, 1992; Thomas & Atkinson, 1997). Fleshy macroalgae form flexible canopies that create slow-moving water within their fronds, thickening DBLs and restricting uptake in calm conditions. Only under oscillatory, wave-driven turbulence do they attain high uptake rates (Carpenter et al., 1991). Turf assemblages show the strongest response: their short, filamentous structure maintains thin DBLs under modest velocities, enabling rapid nutrient acquisition that continues to rise with increasing flow (Carpenter & Williams, 2007).

When reef systems receive elevated nutrient inputs, strong flows may favor algal proliferation as algae show superior nutrient capture capacity under enriched conditions compared to corals (Cuet et al., 2011; Wyatt et al., 2010). Even though higher flow thins coral DBLs and improves mass transfer, their overall capacity for dissolved nutrient uptake remains far lower than that of algae. Algal groups with high surface-area-to-volume ratios and less internal recycling exploit external nutrient fluxes more efficiently than corals, which are constrained by DBL thickness and slower uptake kinetics (Den Haan et al., 2016). Under conditions of elevated turbulence and nutrient enrichment, the competitive balance could shift toward algal proliferation, as algae more efficiently exploit increased nutrient fluxes, often outcompeting corals even in systems where corals dominate under oligotrophic, moderate-flow conditions (Den Haan et al., 2016; Wyatt et al., 2010).

Ecosystem-scale patterns align with these physiological responses. Following Typhoon Bopha in Palau, Roff et al. (2015) showed that post-disturbance chronic wave exposure almost entirely determined the spatial extent of macroalgal phase shifts. Extensive blooms of *Liagora* sp. occurred only at impacted sites experiencing high wave exposure. Exposure explained ~90% of the variance in bloom occurrence, whereas herbivory and coral decline were not significant predictors. These results are particularly notable because Indo-Pacific reefs typically show lower macroalgal responsiveness than Caribbean systems, indicating that when disturbance opens space, wave-driven productivity can override grazing and drive short-lived but intense algal expansion (Roff and Mumby, 2012).

2.1.3 Prey capture

Many Scleractinian corals supplement autotrophy with heterotrophic feeding, capturing plankton and particulate organic matter. The efficiency of this process is tightly coupled with water flow, which regulates both the delivery of suspended food and the mechanics of tentacle extension, polyp behavior, and particle retention (Summary in Table 2, Appendix A).

Prey capture peaks at intermediate velocities, with efficiency dropping at both extremes (Sebens et al., 1996; Sebens and Johnson, 1991). At very low flow velocity, encounter rates can be limited, while at high velocities, prey could be advected past the feeding structures before capture. For example, *Montastrea cavernosa* and *Porites porites* achieved peak capture rates at ~10 cm s^{-1}, with performance dropping off at higher speeds (Sebens et al., 1998). A modelling study of coral growth and prey capture in different flow regimes shows that corals are able to modify their local flow environment reducing input velocities to speeds that promote prey capture (Hennige et al., 2021).

Corals display a suite of morphological and behavioral adaptations that optimize prey capture under distinct flow regimes, and these adaptations vary markedly among species. Massive and dome-shaped species such as *Montastraea cavernosa* perform best in low-to-moderate flow, where their large polyps and elevated surfaces increase particle encounter rates by retaining water and prolonging prey residence time over the colony surface (Sebens et al., 1996,1998). In contrast, branching species such as *Porites porites* and *Madracis mirabilis* can exploit higher flow regimes, as interbranch vortices increase both encounter rates and delivery of zooplankton into capture zones (Sebens et al., 1998; Sebens and Johnson, 1991).

Even within a single species, differences in colony morphology and positioning relative to flow can dramatically alter feeding performance because each configuration creates a distinct hydrodynamic environment. In *Agaricia agaricites*, as exemplified by Helmuth and Sebens (1993), encrusting morphotypes capture particles efficiently because flow passes directly across their surface and avoids prey being swept past in high flow. By contrast, bifacial plating forms intercept the current differently: when oriented perpendicular to flow, the upstream face experiences strong, continuous delivery, while the downstream face forms a stable separation bubble where eddies slow, recirculate, and retain prey. This self-generated wake allows bifacial plates to feed effectively on both sides, but only when oriented correctly as plates aligned parallel to flow experience weaker velocity gradients and markedly lower capture rates. These examples illustrate that feeding success depends on how colony shape interacts with flow direction to modulate particle encounter, retention, and delivery at the polyp scale.

Polyp morphology also reflects hydrodynamic specialization. Some species from calmer environments, including massive corals like *Montastraea cavernosa*, possess large, widely spaced polyps capable of precise, active prey capture when water movement is slow. By contrast, corals from high-flow habitats such as *Madracis mirabilis* possess small, densely packed polyps that can capture prey rapidly and continuously under strong flow, where prolonged tentacle extension would be inefficient or impossible (Sebens and Johnson, 1991). Small polyps also maintain naturally thinner diffusive boundary layers, improving solute exchange in calm environments, even when they are not optimal for capturing larger prey (Shashar et al., 1993).

Species with intermediate strategies further highlight the diversity of hydrodynamic niches. *Porites porites*, with its moderately sized and spaced polyps and branching yet relatively robust morphology, exhibits broad flow tolerance. It feeds reasonably well across a range of velocities but does not reach the high prey capture rates of *Madracis mirabilis* in turbulent flow nor the efficiency of large-polyped massive corals in calm water (Sebens et al., 1998). This positions *P. porites* as a generalist, capable of persisting across varied hydrodynamic forcings but not physiologically optimized for either extreme.

2.2 Demography

2.2.1 Fecundity and fertilization

In the Indo-Pacific, synchronized mass spawning is the dominant reproductive mode for reef-building corals (Baird et al., 2009). During these events, gamete bundles containing eggs and sperm are released into the water column, where they rise and typically disaggregate within the upper meter. Fertilization success in this surface zone is highly dependent on hydrodynamic forcing, which regulates bundle breakup, gamete dispersion, and encounter probabilities. Levitan (1995) showed that water flow can influence fertilization success in free-spawning invertebrates by mediating a trade-off between gamete dilution, transport, and encounter rates, alongside other factors such as spawning density, synchrony, and gamete traits. Weakly turbulent conditions maintain high local sperm concentrations and promote fertilization near spawning colonies, whereas strong turbulence accelerates plume dilution and reduces fertilization success unless compensated by dense aggregations and tight spawning synchrony. Mechanistically, moderate flow turbulence may enhance fertilization by prolonging contact between gametes (Crimaldi, 2012; Denny and Shibata, 1989). This occurs when turbulence stretches gamete clouds into filaments that get repeatedly coalesced, generating short-lived but intense local concentration peaks that produce higher encounter rates than predicted from mean dilution alone (Crimaldi and Browning, 2004). After turbulence has aggregated gametes into proximity, sperm motile capacity can bridge the remaining spatial gap to the eggs (Crimaldi and Zimmer, 2014). At the same time, excessive turbulence can accelerate dilution, separating sperm and eggs due to differences in diffusivity and buoyancy and reducing fertilization efficiency (Crimaldi, 2012; Denny and Shibata, 1989).

Authors speculate that corals may mitigate excessive-turbulence related risks through reproductive timing strategies that align spawning with calm conditions such as neap tides with weaker currents or low wind speed windows (Babcock et al., 1986; Van Woesik, 2010). Still, sperm dilution remains a primary bottleneck even without excessive flow, unless high gamete densities are released simultaneously (Oliver and Babcock, 1992). Although low sperm concentrations lead to lower overall fertilization success, they may reduce polyspermy risk, reinforcing a delicate trade-off (Styan and Butler, 2000).

Experimental data by Buccheri et al. (2025, accepted) underscores the species-specific effects of turbulence on early embryo development. In wind-forced flow simulations, *Acropora millepora* and *Platygyra daedalea* embryos predominantly showed deformities associated with moderate survival, while *A. tenuis* and *A. spathulata* exhibited higher fragmentation and mortality. This implies potential adaptive differences in embryonic robustness across species, with species more commonly found in exposed environments showing higher survival. Adaptations in *A. millepora* are also suggested by the capacity of embryo to continue cleavage despite high fragmentation rates (up to 45%), yielding smaller yet viable larvae (Heyward and Negri, 2012).

2.2.2 Larval dispersal

Larval dispersal is a critical phase in coral life histories, linking reproduction, recruitment, and population connectivity. Outcomes depend on pelagic larval duration, larval behavior, and the spatiotemporal variability of ocean currents and their interaction with reef topography at multiple spatial scales (Cowen and Sponaugle, 2009).

At the regional scale, hydrodynamic forcing such as wave energy, turbulence, current velocity, internal waves, upwelling fronts, and mesoscale eddies strongly shape dispersal trajectories. These large-scale oceanographic features determine how far larvae travel and whether they are retained locally or exported downstream (Gawarkiewicz et al., 2007). Larval dispersal is governed by complex, multiscale physical processes - such as boundary layers, cross-shelf exchange, and retention zones - that severely limit our ability to directly measure dispersal kernels and require integration of physical oceanography with biological inference (Gawarkiewicz et al., 2007).

Other than hydrodynamic environments, reef geomorphology is a critical physical filter: headlands, bays, reef passages, platforms, and channel networks can create areas of enhanced retention, delayed flushing, or efficient export. The coastal boundary layer, formed by the interaction of flow and coastline geometry, slows cross-shore transport, enhancing local retention and delaying offshore dispersal. Larval behaviour can partially overcome these constraints: some species vertically migrate to position propagules in flow layers with more favourable transport, while others may spawn during circulation regimes that promote export (Largier, 2003).

Once aggregated into buoyant spawn slicks, coral embryos and early larvae are advected within complex reef-scale flow fields, where convergence zones, eddies, and turbulent and wind-induced transport interact to either retain propagules near natal reefs or export them across inter-reefal seascapes (Wolanski et al., 1989). Willis and Oliver (1990) provide rare empirical evidence from direct field tracking, showing that buoyant coral larvae aggregate along hydrodynamically generated fronts and wakes in topographically complex reef environments. Aggregations were observed along fronts associated with buoyancy differences between water masses, with boundary layer mixing at reef surfaces

and within island wakes. Secondary currents associated with these fronts accumulated the buoyant larvae into linear slicks. These fronts may be found in proximity to islands, reefs and coastal headlands. Hence, local topography may determine where larval aggregations occur as well as the fine-scale structure of these patches. Sammarco et al. (1991) proposed that seasonal prevailing currents during spawning influence spatial patterns of coral recruitment, ultimately shaping reef geomorphology through differential lateral growth and leaving hydrodynamic signatures in reef asymmetry. Higher recruitment rates correspond to the windward side of the studied reefs, a common trait of moderate exposure coral communities (Madin and Connolly, 2006; Storlazzi et al., 2002)

The interaction between broad-scale ocean circulation and reef topography therefore can produce a mosaic of connectivity regimes. Some reefs act as net sources of larvae, others as sinks, and a subset functions as critical stepping-stone connectors maintaining metapopulation persistence across broad spatial scales (Treml et al., 2008). The timing of spawning relative to prevailing circulation further influences trajectories, with extreme events such as cyclones capable of transporting larvae to distant or atypical locations. Connectivity pathways can vary under different climatic and oceanographic states, including large-scale climate oscillations (e.g., ENSO), which can reorganize regional dispersal patterns and ecological connectivity (Munday et al., 2009). Grimaldi et al. (2022) modeled larval transport on an isolated atoll and showed that oscillatory tidal flows and storm-driven currents could alternately trap larvae within reefs or export them to remote areas, depending on event timing. However, many coral larvae are retained relatively close to their natal reef, while a smaller fraction is transported over longer distances, resulting in a balance between local retention and regional connectivity (Cowen and Sponaugle, 2009).

Short-term variability in hydrodynamic forcing driven by tidal phases can also influence dispersal distances and retention. During ebb tide, falling sea level constrains the denser water mass close to the seabed, generating downward vertical velocities that increase the likelihood of larvae reaching and settling on the substrate (Chacon-Gomez et al., 2013). At the coral canopy scale, generated turbulence and recirculation slow horizontal advection and extend larval residence times near the substrate (Hamilton et al., 2025). Flow can vary dramatically over scales of ≤1 m: currents accelerate over convex coral heads but descend into depressions, enhancing retention in local microhabitats (Koehl et al., 2007).

2.2.3 Coral settlement and recruitment

Wave motion and current flow exert strong influences on the earliest life stages of corals. Larval swimming speeds vary by species (0.08-6.49 mm s^{-1}), but remain 1-4 orders of magnitude lower than typical reef currents, meaning contact time with the substrate is overwhelmingly flow-mediated (Hata et al., 2017). Unidirectional currents produce weaker

drag and lift than oscillatory wave motion, potentially facilitating more successful attachment (Reidenbach et al., 2021). High-energy environments with strong wave action may discourage settlement, likely through surface instability and enhanced bioerosion, as suggested for Micronesian reefs (Mumby et al., 2013). Rugosity elements at multiple scales create flow refugia by generating recirculation zones where water velocity slows, allowing larvae to maintain longer contact with the substrate (Hata et al., 2017). Fine-scale roughness (cm-dm) produces near-surface attachment eddies, meso-scale features (e.g., coral heads) generate flow separation zones, whereas reef-scale geomorphology influences whether larvae are retained on reef flats and lagoons or exported offshore (Carlson et al., 2024; Hata et al., 2017). Larvae settling on exposed, protruding surfaces with high width-to-height ratios experience higher dislodgement under wave forcing, as these geometries remain more fully exposed to flow and bed shear stress, whereas larvae in the lee of roughness elements benefit from localized flow attenuation and increased retention (Reidenbach et al., 2021). Field observations from the Great Barrier Reef show markedly enhanced settlement on the undersides of settlement tiles, which act as flow refugia in shallow high-velocity habitats (Drake et al., 2025).

Although not coral specific, studies on water motion effects on larval behavior (Koehl et al., 2007; Koehl and Hadfield, 2010) gave particular attention to how flow distributes chemical plumes of dissolved settlement inducers. Because waves move water back and forth rather than in one steady direction, the resulting oscillatory flow keeps chemical plumes from being swept away as quickly as they would be by an equivalent-speed unidirectional current. This oscillatory motion increases the time that larvae remain above a patch of cue-releasing substrate and therefore increases their likelihood of encountering the settlement cue. Longer residence over the plume also increases the chance that larvae detect the cue strongly enough to trigger downward swimming and settlement.

Most laboratory work has been conducted under moderate currents (≤10 cm s^{-1}) or idealized wave regimes, capturing only a subset of the energetic conditions found on reefs (Hata et al., 2017; Reidenbach et al., 2021, 2009). Field studies validate that larvae preferentially settle in recirculation zones and low-shear microhabitats, whereas oscillatory wave action increases drag and lift on exposed surfaces (Drake et al., 2025; Carlson et al., 2024). However, relatively few experiments span the full diversity of turbulence intensities, colony morphotypes, adhesive strengths, or flow intermittency typical of natural reef settings. As a result, while the underlying physical mechanisms are robust (turbulence-enhanced contact time, wave-driven dislodgement, and topographic flow refugia) their generality across the full range of reef hydrodynamic environments remains underexplored. A major gap persists in linking these fine-scale mechanistic results to the broader spatial variability in flow environment and habitat-specific flow regimes that govern settlement patterns at different scales within reef systems.

2.2.4 Coral growth

Water motion enhances metabolic performance by thinning diffusive boundary layers and improving mass transfer, but it also imposes drag, abrasion, and dislodgement forces that can limit growth or survival. Only a few studies have directly quantified these relationships experimentally. Jokiel (1978) performed multi-species experiments under controlled flow agitation and demonstrated that habitat associations reflect true physiological differences rather than mere correlative patterns. The species *Pocillopora meandrina*, typically found in exposed slopes, showed no growth under low flow, only modest growth under intermediate agitation, and overall required far higher velocities than those produced in the laboratory. The *P. damicornis* from semi-protected areas exhibited intermediate growth optima, while the lagoonal *Montipora verrucosa* grew rapidly across all flow treatments, confirming that calm conditions do not inherently limit its performance. Sebens et al. (2003) showed that *Agaricia tenuifolia* experiences reduced net growth under in-situ extremely turbulent oscillatory flow, postulating that mechanical stress and elevated respiratory demand outweighed the metabolic benefits of enhanced mass transfer. By contrast, moderate increases in artificial bidirectional flow (10–25 cm s^{-1}) significantly elevated the growth of *Galaxea fascicularis* through synergistic effects on net photosynthesis and improved removal of photosynthetically produced oxygen, especially under high irradiance (Schutter et al., 2011, 2010).

Hydrodynamics also influences colony architecture. Flow shapes skeletal morphology by promoting more compact, mechanically robust skeletons in high-energy regimes. In *Madracis mirabilis*, branch density and orientation change predictably with flow exposure, producing thicker, more closely spaced branches under strong flow to minimize drag and resist breakage (Kaandorp et al., 2003). Similarly, sustained experimental flow exposure (15-20 cm s^{-1}) in *Pocillopora verrucosa* results in increased biomass, chlorophyll, protein content, polyp density, and reproductive output compared to low-flow treatments where ~50% mortality occurred and colonies developed open, delicate morphologies (Chindapol et al., 2013). At the colony scale, hydrodynamic self-shading and localized flow reduction within branching morphologies further generate intra-colony variation in growth, with edge or upstream branches of *Agaricia*, *Porites*, and *Siderastrea* spp. experiencing enhanced mass transfer and higher growth relative to sheltered interior regions (Sebens et al., 2003).

The available evidence supports the idea that hydrodynamics regulates coral growth through mass-transfer limitation and mechanical stress, but the strength, direction, and optimal range of these effects have been rigorously quantified for only a handful of species. Across taxa, however, the general pattern is consistent: corals grow best where water motion is sufficient to enhance metabolic exchange but not so strong as to impose excessive mechanical loads. Recognizing these hydrodynamic-morphological-

physiological linkages is essential for predicting reef resilience, species distributions, and recovery potential under shifting flow regimes in a changing ocean.

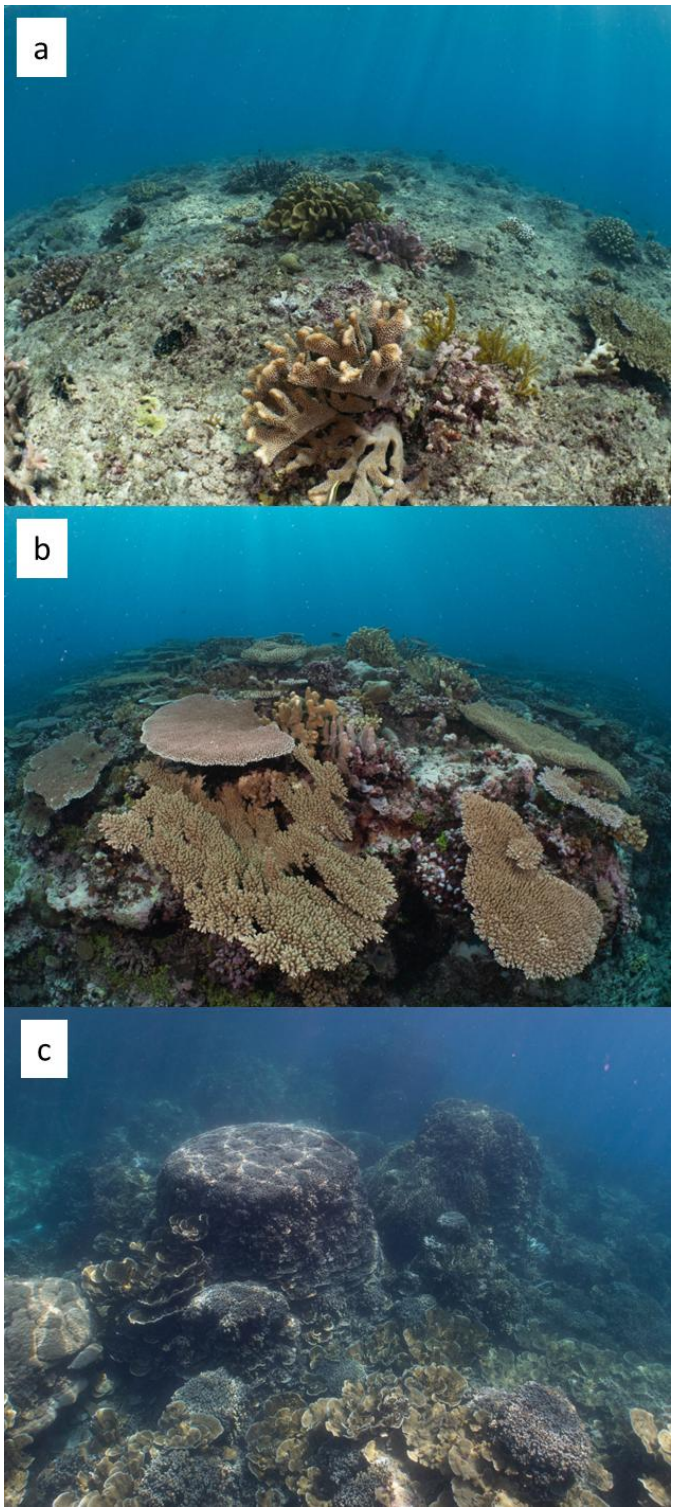
3. Hydrodynamics and ecological processes

3.1 Direct effects of flow

3.1.1 Benthic zonation

The influence of wave exposure on reef communities arises from a set of underlying hydrodynamic mechanisms that operate across scales, linking flow structure to organismal performance and ecological outcomes. As stated in previous sections, by thinning the DBL, flow velocity may promote physiological performance and nutrient uptake in both algae and coral (Dennison and Barnes, 1988; Falter et al., 2004; Larkum et al., 2003), and coral polyp prey capture with effects and velocity thresholds varying between species (Sebens and Johnson, 1991). At the same time, hydrodynamic forcing imposes mechanical constraints. Wave orbital velocities and associated bed shear stress generate drag and lift forces on coral colonies, with susceptibility to dislodgement depending on colony morphology, attachment strength, and local flow conditions (Madin et al., 2014; Storlazzi et al., 2002).

Wave exposure is therefore primary physical driver structuring benthic communities on coral reefs, with consistent shifts in community composition observed along gradients of hydrodynamic energy (Done, 1982; Williams et al., 2013). High-energy reef crests and forereefs are typically characterized by low-lying algal assemblages (e.g., turf algae and crustose coralline algae) and corals with compact, encrusting, or otherwise mechanically robust morphologies that can withstand wave-induced stress (Fig. 2a) and substrate scouring (Madin and Connolly, 2006; Storlazzi et al., 2002). For example, in Lizard Island, Great Barrier Reef, *Acropora gemmifera* and *Isopora palifera* can persist on high-energy reef flats due to drag-resistant skeletal morphotypes. Skeletal features such as verrucae in *Pocillopora meandrina*, commonly found in exposed settings, can reduce drag and enhance feeding efficiency, conferring a performance advantage under turbulent conditions (Jokiel, 1978). In contrast, more moderate-energy environments often support faster-growing and more structurally complex coral taxa, including branching and tabular forms (Fig. 2b), where physical disturbance is less frequent or intense (Madin and Connolly, 2006).



The absence of frequent hydrodynamic disturbance favors competitive exclusion, as supported by observations of low-diversity, *Porites-Montipora* spp. dominated assemblages in sheltered patch reefs and back-reef habitats (Fig. 2c) where hydrodynamic disturbance and grazing are relatively low (Aronson and Precht, 1995; Huston, 1985; Williams et al., 2013). These patterns reflect the combined effects of mechanical disturbance and recovery dynamics: intense wave forcing can remove or damage fragile colonies and periodically reset benthic communities, while lower disturbance regimes allow competitive interactions and growth to play a larger role in structuring assemblages (Connell, 1979; Huston, 1985). On the other hand, monopolization by a few species may also occur in physically harsh settings where only stress-tolerant taxa can persist, and in some calm environments, chronic stressors such as sedimentation, eutrophication, or bioerosion prevent any single species from fully occupying space, generating substantial deviations from these general patterns.

Fig. 2. Coral assemblages within different ranges of exposure: a) high exposure reef slopes with low coral density, characterized by turf, CCA cover and flow-resistant morphotypes such as *Pocillopora* spp (Uchelbeluu Reef, Palau); b) moderate exposure reef, with mixed assemblages of tabular *Acropora* spp. and pocilloporids (Uchelbeluu Reef, Palau); c) calm water, low disturbance assemblage in lagoonal reef, with high coral cover composed by large *Montipora* and *Porites* spp. (Cemetary Reef, Palau).

Reef assemblages reflect long-term co-development between hydrodynamic forcing, disturbance history, substrate properties, and species-specific traits (Connell et al., 1997), rather than simple relationship with wave climate (Davies and Marshall, 1980; Dechnik et al., 2016; Kennedy and Woodroffe, 2002). Local flow conditions are shaped by interactions between flow energy and reef geomorphology, generating fine-scale spatial variability in velocity, turbulence, and shear stress meaning that wave exposure is strongly mediated by substrate and local flow refugia rather than simple linear gradients of energy. At Palmyra Atoll, Gove et al. (2015) showed that intra-atoll gradients in wave-driven bed shear stress and bathymetric complexity generate non-linear, threshold-type responses among benthic functional groups, including shifts from CCA to turf algae at defined stress levels and morphological reorganization of corals along exposure gradients. Similarly, Wright et al. (2025) show that a minimally impacted atoll can be dominated by sand and rubble (~60% cover), with coral distribution structured primarily by slope and wind exposure. Patterns observed on remote reefs are consistent with classical disturbance theory (Connell, 1978), which predicts that community structure reflects the balance between disturbance and recovery rather than a tendency toward uniformly high coral cover. What these systems reveal, however, is that hydrodynamic forcing and geomorphology can act as primary drivers of this balance, generating substantial spatial heterogeneity even in the absence of human impacts.

Rather than producing smooth gradients in community structure along exposure or depth, flow-substrate interactions generate mosaics of benthic states that can shift abruptly over relatively small spatial scales (Connell, 1978; Gove et al., 2015). These spatially varied responses arise because the mechanisms linking flow to biological processes are themselves non-linear. For example, localized small increases in flow velocity can sharply elevate dislodgement risk once mechanical limits are exceeded (Madin and Connolly, 2006) or enhance sediment transport once critical shear thresholds are reached, leading to rapid changes in substrate availability and recruitment success (Rosenberger et al., 2020; Sartori et al., 2025; Storlazzi et al., 2002). Simulation experiments show that fore-reef geomorphologies (e.g., buttresses, outer ridges, spur and grooves) attenuate wave energy, producing alternating high- and low-energy zones over metre-scale distances (Graus and Macintyre, 1989). Aronson and Precht (1995) observed storm-transported coral debris in spur and grooves periodically breaking the competitively dominant foliose coral *Agaricia tenuifolia*, opening space for other species and increasing coral assemblage evenness and producing mosaics of species turnover. The influence of reef geomorphology on wave exposure regimes can be further modulated by seasonal storms and annual wind patterns, creating temporally heterogeneous habitats that allow assemblages at different successional stages to coexist within the same reefscape (Page-Albins et al., 2012). These dynamics can produce abrupt shifts in dominant functional groups, such as transitions from coral- to algae-dominated assemblages or from stable substrates to mobile rubble fields (Gove et al., 2015). Adjacent areas within

the same reef may occupy different points along disturbance-recovery trajectories, driven by localized hydrodynamic regimes rather than broad-scale exposure categories (Connell, 1978; Graus and Macintyre, 1989). This spatial pattern highlights the importance of resolving fine-scale flow-topography interactions when interpreting reef structure and dynamics. The modulation of wave energy by geomorphic features - such as slope breaks, terraces, spurs and grooves, and bathymetric position - determines near-bed shear stress, sediment mobility, and disturbance impact, thereby shaping recruitment, competitive dynamics, and species filtering. Advancing predictive models of reef zonation therefore requires integrating hydrodynamic thresholds with high-resolution geomorphic structure, recognizing that physical forcing does not act uniformly across space but is refracted, dissipated, and amplified by the reefscape itself.

3.1.2 Coral dislodgement

Hydrodynamic disturbances set fundamental limits on coral survival by defining the thresholds at which colonies are dislodged. These thresholds vary widely with coral skeletal morphotype, size, flow environment and underlying substrate stability. Plating and branching corals fail at lower velocities, whereas massive and encrusting forms exhibit greater stability but slower recovery potential (Cheung et al., 2025; Madin, 2005; Madin and Connolly, 2006). Scaling effects further complicate this as dislodgment risk increases disproportionately with colony size for corymbose, tabular and branching morphologies, creating a trade-off where larger colonies achieve higher fecundity yet are more prone to mechanical failure (Madin, 2005; Madin et al., 2014) . However, the overall mechanical integrity of coral colonies is determined by the variable strength of the reef substrate to which they are attached, rather than by the strength of their carbonate skeleton. Colonies attached to rubble or unconsolidated sediments are far more vulnerable to dislodgement than those anchored to bedrock, regardless of skeletal morphology (Madin and Connolly, 2006; Massel and Done, 1993). Spatial variation in wave exposure and substrate stability drive community-level patterns, with fragile morphologies restricted to sheltered zones while only robust, well-anchored forms persist in high-energy habitats (Madin and Connolly, 2006). Even massive colonies can be dislodged during cyclone waves, illustrating that all morphologies are vulnerable under sufficiently intense hydrodynamic forcing. Importantly, dislodgement risk is not determined by morphology alone: survival is also strongly influenced by substrate stability, with colonies attached to solid bedrock exhibiting consistently higher survival than those rooted in unconsolidated rubble, independent of size, shape, or storm intensity (Massel and Done, 1993).

While dislodgement often reduces colony size and can cause mortality, it can also facilitate rapid clonal expansion in branching corals. Cyclones generate large numbers of viable fragments, and when these land on stable substrates they can reattach and contribute to population recovery rather than decline (Foster et al., 2013; Highsmith,

1982). This mechanism helps explain how branching taxa persist in disturbance-prone environments despite higher mechanical vulnerability. Survival of fragments varies by species and habitat. For example, large fragments of *Acropora intermedia* and *A. millepora* showed higher reattachment and survival than small fragments of *A. hyacinthus*, with higher survival rates on the reef flat than in crest or slope habitats (Smith and Hughes, 1999). Fragments on high-energy reef crests are more frequently transported, buried, or abraded and rarely survive (Smith and Hughes, 1999). Reattachment success is highly context-dependent as fragments deposited onto rubble fields or unconsolidated sediment rarely persist (Foster et al., 2013; Massel and Done, 1993). Furthermore, fragments initially show reduced fecundity relative to intact colonies, even when survival is successful, indicating time-lagged reproductive capacity (Smith and Hughes, 1999). Coral fragmentation can act as either a demographic subsidy or a mortality pathway depending on hydrodynamic forcing and substrate stability, meaning mechanical thresholds alone cannot predict demographic outcomes.

3.1.3 Coral bleaching

When corals experience elevated temperatures and irradiance, symbiont photosynthesis can become impaired, potentially leading to the production of reactive oxygen species (ROS) and other forms of metabolic stress. While oxidative stress has long been proposed as a key mechanism underlying bleaching, more recent work highlights the role of host-symbiont metabolic imbalance and nutritional dynamics in shaping bleaching responses. Thick DBLs trap ROS, allowing them to accumulate and initiate bleaching (Nakamura, 2010; Nakamura and Van Woesik, 2001). Moderate flow (~20 cm s^{-1}) reduces bleaching risk because by thinning the DBL and accelerating the removal of harmful byproducts that accumulate under heat and light stress. Although, only certain aspects of this mechanism have been experimentally demonstrated in a small set of species. Jokiel et al. (1997) showed that *Pocillopora damicornis* maintained under higher flow (~11 cm s^{-1}) produced significantly higher concentrations of UV-absorbing mycosporine-like amino acids than colonies kept in lower flow velocities or still water, even under identical UV exposure. Fifer et al. (2021) show corals acclimated to high-flow environments exhibiting upregulated expression of heat-shock proteins, antioxidants, and immune genes prior to thermal stress, suggesting that flow can prime molecular stress-response pathways that contribute to faster or more robust recovery during bleaching. Controlled flume experiments on *Stylophora pistillata* showed that colonies kept under moderate flow (~20 cm s^{-1}) recovered zooxanthellae density and chlorophyll concentrations far faster than those in near-still water (≤3 cm s^{-1}). Nakamura and Yamasaki (2005) reared corals in moderate-high flow for >1.5 years which led to significantly higher growth and survivorship under experimental heat stress than low-flow controls. The study attributes this resilience to chronic flow-enhanced gas exchange and improved metabolic condition, showing that long-term hydrodynamic acclimation can

raise thermal tolerance rather than only providing short-term cooling. Hydrodynamic conditions may also influence bleaching resilience through their effects on heterotrophic feeding.Corals capable of increasing heterotrophic intake have been shown to maintain energy reserves and exhibit higher survival and recovery following thermal stress (Grottoli et al., 2006). Conversely, results from Lentz et al. (2024) found that very high flow velocities (~50 cm s^{-1}) reduce bleaching recovery in *Montipora capitata*, *Pocillopora meandrina*, and *P. acuta* in controlled flume experiments. The authors suggest that at these extreme velocities, frequent polyp retraction, increased tissue shear, and possible micro-abrasion may elevate energetic costs and slow recovery, but these mechanisms were not directly measured.

Controlled experiments show clear mechanistic pathways by which flow can reduce bleaching, yet translating these results to natural reefs is less straightforward, as field studies reveal more complex and sometimes contradictory outcomes depending on local thermal history, geomorphology, and hydrodynamics. During the 1998 mass bleaching in Japan, corals in high-flow areas (50-70 cm s^{-1}) largely survived, while those in adjacent low-flow zones (2-3 cm s^{-1}) suffered near-total mortality (Nakamura and Van Woesik, 2001). More recent in situ observations reported flow speeds of ~0.15 m s^{-1} delaying bleaching compared to ~0.03 m s^{-1} (Page et al., 2021). A basin-scale modelling study for the GBR (Cheung et al., 2025) reported that reefs experiencing higher flow velocities (>0.3 m s^{-1}) consistently showed reduced bleaching at a given degree heating week whereas reefs with lower velocities exhibited disproportionately high bleaching even under moderate heat stress. Conversely, McClanahan et al. (2005) found that high-flow sites bleached more severely. These contrasting results highlight that the relationship between hydrodynamic forcing and bleaching is context-dependent and likely mediated by multiple interacting factors. These may include differences in thermal history, local water residence times, light and nutrient regimes, and species composition, all of which can influence coral susceptibility and recovery. As such, flow cannot be interpreted as a universally protective or detrimental factor, but rather as one component of a broader set of environmental controls shaping bleaching outcomes.

3.2 Indirect effects of flow

3.2.1 Competition with other organisms

Competition for space is a fundamental ecological process on coral reefs, shaping community structure, successional trajectories, and ecosystem resilience. Because reef-building corals and their competitors (algae, sponges, ascidians, and other benthic organisms) rely on the same limited substratum, their interactions largely determine whether reefs maintain coral dominance or shift toward alternative states.

While flow redistributes oxygen plumes around corals and algae, zones of markedly low oxygen consistently form at coral-algal contact interfaces as it was shown for *Favia* sp.

and *Chaetomorpha* sp., providing direct evidence for hypoxic microhabitats during competitive interactions (Haas et al., 2013). Hypoxia persistence at the algal-coral interface emerges under no-flow conditions, as the DBL thickens not allowing for successful exchanges (Brown and Carpenter, 2013). In situ analysis from Wangpraseurt et al. (2012) did not identify the same extreme hypoxia conditions but DBLs were ~3 times thicker at coral-algal interfaces, restricting mass transfer and facilitating allelochemical accumulation.

Water motion can modulate primary productivity and resource acquisition for both coral and algae. In high-exposure habitats, disturbance-tolerant groups such as turf algae and CCAs are common. These low-lying forms resist dislodgement and can capitalize on enhanced nutrient and gas exchange (Steneck and Dethier, 1994) which is greater under high flow because of thinner DBLs (Carpenter and Williams, 2007). Low-lying state and thin DBLs in turfs are maintained through grazing, preventing self-shading and detritus accumulation. This grazing-dependent renewal is a defining feature of turf systems, which persist only under sustained herbivore pressure (Steneck and Dethier, 1994). Intermediate exposure can support both corals and foliose/corticated macroalgae, generating mosaics of intense space competition (Roff et al., 2015). In sheltered, low-flow habitats where breakage risk is reduced and there is high nutrient delivery, delicate, tall-canopy macroalgae may be advantaged (Steneck and Dethier, 1994). Red algae (e.g., *Amansia rhodantha*), thick turf and cyanobacteria are considered stronger competitors with corals because they generate relatively thick DBLs (~3 mm) compared with weaker competitors such as CCA or thin turf (~0.5 mm), and thicker DBLs correlate with higher rates of algal overgrowth and coral smothering. Canopy height and orientation can therefore sustain thick DBLs even in higher-flow settings, reinforcing algal advantage where grazing is insufficient to crop the canopy back (Jorissen et al., 2016; Mumby and Steneck, 2008; Steneck and Dethier, 1994). Grazing rates are in turn modulated by exposure regimes, as discussed in the following section.

Sedimentation further mediates competition in flow-dependent ways. In laboratory flumes, high flow reduced sediment accumulation at *Porites sp.*-turf interfaces and minimized coral tissue damage, underscoring how hydrodynamics could also counteract sediment-mediated competition (Gowan et al., 2014). Flow can also modulate the relative success of corals versus other benthic suspension feeders. For example, sponges and tunicates can outcompete octocorals under high-flow conditions because their filtering structures more efficiently intercept fine particles in turbulent flows (Kim and Lasker, 1997). By mediating both the intensity and the outcomes of competitive interactions, hydrodynamics emerges as a central driver of reef community structure, providing the physical framework within which competitive processes unfold.

3.2.2 Grazing and top-down control of macroalgal assemblages

Herbivory is a major, though not exclusive, driver of benthic community structure on coral reefs. Grazers shape which algal assemblages develop, their functional traits, and the competitive environment corals face. Grazers also help maintain open substrate, facilitating coral recruitment, survival, and post-disturbance recovery (Mumby et al., 2006). Herbivory interacts with algal traits and the local hydrodynamic, nutrient and sediment regimes determining whether reefs tip toward coral dominance or toward persistent algal states. Different herbivore taxa (e.g., echinoderms, gastropods, fish) and guilds (e.g., scrapers, excavators, browsers) reduce algal canopy height, and epiphyte loads in distinct ways, thereby modulating the intensity of coral-algal competition (Bonaldo and Bellwood, 2009; Burkepile and Hay, 2008; Mumby and Steneck, 2008).

Hydrodynamic forcing can strongly modulate herbivory by constraining grazer performance. For example, grazing by the sea urchin *Diadema antillarum* is markedly reduced under high wave surge due to attachment limitations and dislodgement risk, whereas herbivorous fishes are less constrained due to their mobility. As a result, algal biomass can increase during periods of high wave activity when urchin grazing is suppressed, despite continued fish presence (Foster, 1987). Grazing gastropods (e.g. trochids and turbinids) are important consumers of epilithic algal communities, removing biofilms and early successional turf algae and thereby contributing to substrate maintenance and coral recruitment. These organisms rely on substrate adhesion for locomotion and are therefore likely sensitive to hydrodynamic stress. Studies from wave-swept environments indicate that increasing flow velocity and surge can limit attachment stability and reduce foraging efficiency (Denny, 1988), suggesting that grazing by gastropods may be constrained in high-energy reef settings. The interaction between hydrodynamic forcing and benthic organisms grazing remains poorly quantified on coral reefs, with most studies describing their ecological roles without explicit consideration of flow regime.

While moderate exposure fosters herbivore fish-driven resilience by sustaining both productivity and grazing, extreme exposure reduces the diversity and intensity of grazing. Wave exposure acts as an environmental filter that reshapes reef fish assemblage composition (Bejarano et al., 2017; Fulton and Bellwood, 2005), exerting indirect effects on benthic processes. Hydrodynamic forcing selects for different herbivore swimming “designs” (laterally compressed vs. fusiform body plans), altering which species feed effectively under high wave energy. Herbivore functional groups differ in swimming performance and exposure tolerance. However, as shown by Bejarano et al. (2017) at extreme exposure some level of grazing can still be preserved by response diversity - where species more tolerant to strong flow regimes will take the place of less tolerant ones. Exposed reefs often support more roving grazers (e.g., as parrotfishes and surgeon fishes), since turbulence enhances both plankton delivery and algal productivity

(Friedlander et al., 2003). However, the relationship is not strictly linear. While moderate exposure can support high herbivore biomass and activity, extreme wave exposure reduces herbivore richness, abundance, and bite rates through strong environmental filtering of species composition and behavior (Karkarey et al., 2020). Enclosure experiments indicate weaker herbivore control of algal growth in exposed reefs; however, this pattern must be interpreted cautiously, as algal productivity itself also varies along exposure gradients, making it difficult to isolate top-down grazing effects from bottom-up production dynamics.

Despite the central role of herbivory in reef dynamics, the interaction between grazing processes and hydrodynamic forcing remains poorly resolved. Most studies examine herbivore effects independent of flow regime, or describe exposure only qualitatively, without quantifying how flow velocity and turbulence influence grazing efficiency, attachment, and foraging behaviour.

3.2.3 Corallivory

Corallivory is a major ecological force on reefs, shaping coral demography, colony morphology, and community trajectories. By modulating both predator behavior and prey performance, hydrodynamics may mediate coral-predator interactions.

Currents can enhance coral growth through improved metabolic performance, while turbulent fluctuations may suppress corallivory by reducing predator bite rates (Lenihan et al., 2015). Lenihan and Edmunds (2010) simulated corallivory in varying flow and temperature regimes. *Pocillopora verrucosa* experienced strong flow-injury interactions because its apical growth zones, which corallivorous fishes preferentially bite, are simultaneously the most exposed to hydrodynamic stress. Under low-moderate flow, *P. verrucosa* shows compensatory growth after injury, but high flow combined with injury compromises growth at the tips and reduces overall performance, despite high flow being optimal for uninjured colonies. Massive *Porites* spp., in contrast, shows a more(Moran et al., 1988) uniform healing response across flow treatments due to their extensive gastrovascular network, thick tissues, and even distribution of growth across the colony surface (Edmunds and Lenihan, 2010).

Water flow also appears to mediate the presence of crown of thorns starfish (*Acanthaster planci*). This species does not occur regularly in high-energy settings, where strong waves and surge limits tube feet attachment stability, in turn limiting feeding efficiency (Moran et al., 1988). As a result, they are rarely found in abundance on exposed reef crests, despite the dominance of preferred prey such as *Acropora* spp. Outbreaks are typically concentrated on moderate- to low-energy reef slopes, back-reef zones, and lagoons, where calmer conditions facilitate movement, attachment, and aggregation (Pratchett et al., 2017). Therefore, high energy habitats are relatively insulated from crown of thorns

predation, while sheltered environments experience disproportionately high mortality during outbreaks.

Conversely, parrotfish predation and bioerosion appears to be disproportionately higher in high-flow environments. Both Hoey and Bellwood (2008) and Thomson et al. (2024) demonstrate that wave-exposed, outer-shelf reef habitats experience higher rates of bioerosion and coral predation relative to more sheltered environments. At Ningaloo Reef, Thomson et al. (2024) quantified some of the highest experimentally measured erosion rates recorded globally, with reef slope habitats exhibiting ~3.7 kg $CaCO_3$ m^{-2} yr^{-1} of direct external erosion - more than three times lagoonal rates. This pattern was tightly linked to higher parrotfish biomass, greater urchin densities, elevated water velocities, and increased structural complexity on exposed slopes. External erosion strongly correlated with maximum water velocity and parrotfish grazing intensity, indicating that hydrodynamic energy and predator abundance are mechanistically coupled. Similarly, across the Great Barrier Reef shelf gradient, Hoey and Bellwood (2008) found that although parrotfish densities decline offshore, biomass increases on outer-shelf reefs due to the presence of large excavators, particularly *Bolbometopon muricatum*. Despite its rarity, *B. muricatum* accounts for a disproportionate share of bioerosion and coral predation. However, elevated grazing intensity in these environments is unlikely to be driven directly by hydrodynamic exposure. Instead, studies from Palau show that herbivore biomass is strongly associated with shallow, highly productive reef flats that provide resource subsidies, with grazing tracking algal productivity rather than exposure per se (Roff et al., 2018). In this context, grazing is primarily driven by the availability of benthic and endolithic phototrophs, which vary with light and substrate characteristics (Steneck and Dethier, 1994), whereas corallivory remains largely species-specific, being substantial only where *B. muricatum* is present, and otherwise incidental in most parrotfishes (Bruggemann et al., 1994).

Interactions between hydrodynamic forcing and corallivory remain unevenly resolved across taxa. For parrotfishes, many studies implicitly incorporate hydrodynamic gradients through comparisons across reef zones and exposure regimes, although flow is rarely quantified mechanistically (Edmunds and Lenihan, 2010; Hoey and Bellwood, 2008; Lenihan and Edmunds, 2010; Lenihan et al., 2015; Thomson et al., 2024). In contrast, research on other major corallivores, particularly crown of thorns starfish has largely focused on outbreak dynamics, nutrient enrichment, and larval supply, with limited consideration of how flow conditions influence movement, attachment, and feeding efficiency. This represents a key gap, given that hydrodynamic forcing is likely to constrain predator performance and spatial distribution, with potential consequences for coral mortality patterns across reef environments.

4. Hydrodynamics and coral reef geomorphology

Coral reefs accrete through a combination of vertical framework growth (aggradation) and lateral expansion (progradation), as reef builders grow and wave-driven transport redistributes rubble, sediments, and framework fragments across reef platforms (Davies and Marshall, 1980; Kennedy and Woodroffe, 2002; Marshall and Davies, 1982). The relative importance of these modes varies with accommodation space - available space between the seabed and ocean surface - hydrodynamic energy, and the composition of calcifying communities (Montaggioni, 2005). Exposed reef margins typically experience high rates of coral growth and carbonate production, yet frequent storm breakage and intense physical reworking limit long-term vertical preservation in shallow settings, promoting lateral redistribution of debris into adjacent reef-flat, back-reef, and lagoonal environments (Davies and Marshall, 1980; Perry et al., 2017; Thomson et al., 2024). Carbonate systems are known to accrete most effectively within intermediate energy regimes, where carbonate production is high but sediment export does not overwhelm accumulation (Schlager, 2005). On coral reefs, this manifests as paradox of high-energy environments: strong hydrodynamic forcing can promote rapid carbonate production, efficient flushing, and early cementation, yet the same forcing also enhances framework breakage, rubble mobility, and sediment export (Gischler et al., 2019; Montaggioni, 2005).

Evidence from Holocene reef records shows a wide range of responses to post-glacial sea-level rise, including reefs that kept pace, reefs that lagged, and reefs that ultimately drowned (Neumann and Macintyre, 1985; Montaggioni, 2005). Whether reefs aggrade, prograde, or ultimately “give up” by failing to keep pace with sea level rise depends on both carbonate production and how sediments and rubble are retained, stabilized, and reorganized into persistent substrates. Reef interiors are composed of irregular layers of intact framework, rubble, and unconsolidated deposits, reflecting a history of repeated disturbance and recovery rather than smooth vertical growth (Hubbard, 2015; Montaggioni, 2005). Reef accretion is non-linear, meaning reefs develop through alternating phases of coral framework construction, physical collapse during storms or mortality events, and subsequent reworking and redistribution of rubble and sediments. These constitute the raw material for subsequent reef growth, provided they can be retained and stabilized (Hubbard, 2015; Rasser and Riegl, 2002). Over longer temporal scales, however, these episodic pulses of accretion, erosion, and reworking are often smoothed within chronostratigraphic records, producing the appearance of relatively steady reef growth (Kennedy and Woodroffe, 2002; Schlager, 2005). This averaging effect can obscure the short-term processes through which oceanographic forcing, sediment flux, disturbance, and ecological dynamics interact to drive reef development and geomorphic change.

4.1 Sediment origin and transport

Sediments on coral reefs derive from both terrigenous inputs and reef-generated carbonate production, with their relative importance varying strongly among settings (Rogers, 1990; Woolfe and Larcombe, 1998). Terrigenous sediments originate from river discharge, coastal erosion, land clearing, and resuspension of nearshore deposits, and are most influential on nearshore and continental shelf reefs where chronic delivery can alter light regimes, smother benthic organisms, and modify settlement conditions (Rogers, 1990; Woolfe and Larcombe, 1998). In contrast, most sediments on reefs are biogenic carbonates produced within the reef system itself. Reef-generated sediments arise through skeletal production by calcareous organisms, bioerosion of coral framework, and physical breakdown during wave and storm events. Carbonate sediments on reefs are generated through multiple biological pathways. Among the dominant sediment producers via bioerosion are parrotfishes, which generate large volumes of sand-sized particles through grazing and egestion (Perry et al., 2015, 2012). Other important sediment sources include primary carbonate producers such as calcareous green algae (e.g., *Halimeda* spp.), whose post-mortem disintegration supplies substantial fine sediment fractions to lagoons and back-reef environments (Drew, 1983), and larger benthic foraminifera, whose tests may dominate reef-flat, beach, and island sands in some systems (Hallock, 1981). The relative contribution of these sources varies with community composition, location within a reef system, and hydrodynamic forcing, but together they constitute the principal reef-generated sediment reservoirs that are redistributed, stabilized, or exported through hydrodynamic processes, linking ecological production to the development of reef sedimentary features, such as aprons and islands. Despite the central role of reef-derived carbonate sediments in many reef environments, experimental and field studies of sediment stress on corals have disproportionately focused on terrigenous/siliciclastic loads associated with runoff and dredging, and relatively few studies explicitly compare carbonate versus siliciclastic sediments under controlled deposition and resuspension regimes (e.g., Ricardo et al., 2017, 2015).

Sediment transport on coral reefs is highly variable across spatial and temporal scales. Wave energy and tidal cycle participate in daily sediment movement, strongly structured by reef geomorphology (Sartori et al. 2025). Field studies on fringing reef-lagoon systems show that wave breaking at the reef crest generates wave-driven currents that intermittently mobilize carbonate sediments stored on reef flats, flushing them landward into lagoons and shoreline sinks during energetic wave events (Pomeroy et al., 2013). Under moderate wave conditions, sediments accumulate temporarily on reef flats as thin veneers and mobile deposits, creating a supply-limited system in which subsequent transport depends on antecedent sediment availability (Rosenberg et al. 2020). Highly exposed outer reef flats are frequently cleared of loose sediment during strong wave events, whereas inner reef flats experience more sporadic sediment movement and

temporary accumulation. Lagoons, by contrast, retain sediment for much longer periods due to reduced hydrodynamic energy (Rosenberger et al., 2020). This results in highly directional sediment transport pathways, with net lagoon ward fluxes from the reef flat into back-reef aprons and depressions where declining energy promotes deposition, grain-size sorting, and temporary storage (Harris et al., 2014; Vila-Concejo et al., 2013). Meaningful sediment transport and geomorphic change are often restricted to higher-energy events (Harris et al., 2015). Storms and cyclones therefore exert a disproportionate influence on reef sediment dynamics and reef sedimentary environments evolve through episodic, geomorphologically mediated transport events rather than continuous, uniform redistribution. However, post-disturbance reworking under moderate wave climates determines whether sediments remain mobile, are exported off-platform, or become retained within reef interiors (Harris et al., 2014; Rosenberger et al., 2020).

Reef geomorphology feeds back on sediment transport by structuring flow pathways and residence times. Back-reef aprons, reef depressions, spur and groove systems, and tidal channels act as selective conduits or traps, creating spatially heterogeneous zones of erosion, bypass, and accumulation (Harris et al., 2015, 2014; Sartori et al., 2025). For example, grooves and channels can focus flow and facilitate sediment motion during strong tide or wave pulses (Sartori et al., 2025), while aprons and lagoons promote sediment retention under calmer conditions (Harris et al., 2014). These feedbacks mean that sediment suspension, transport, accumulation and stabilization on reefs is a function of how geomorphology transforms and dissipates hydrodynamic energy.

Gravity-driven sediment transport processes may also contribute to the export of carbonate material from reefs. Once unconsolidated sediments accumulate beyond local stability thresholds, they can collapse and move downslope under gravity, even under relatively weak ambient flow conditions (Baas et al., 2025). These processes are likely influenced by sediment grain size, cohesion, slope angle, and substrate stability, although their role in reef sediment dynamics remains poorly resolved.

Importantly, the composition and grain-size distribution of reef sediments are themselves strongly influenced by biological processes. Bioeroders, particularly excavating parrotfishes, generate substantial volumes of fine carbonate sediment through grazing and framework erosion (Perry et al., 2022). While this production of fine material may temporarily enhance turbidity and sediment stress on corals, it also increases the availability of mobile carbonate sediment that can be redistributed by hydrodynamic and gravitational processes. This links ecological breakdown processes directly to geomorphic sediment redistribution and suggests that biologically mediated sediment fining may play an underappreciated role in the development and evolution of sediment chutes and escarpments (see Section 4.3 Reef Geomorphology).

4.2 Rubble generation and stabilization

Storms, bioerosion, and coral mortality generate large volumes of rubble which may persist as unstable substrate for years to decades, potentially reducing coral survival unless retained and stabilized (Hubbard, 2015; Kenyon et al., 2023a; Rasser and Riegl, 2002). Whether rubble is stabilized or repeatedly re-mobilized depends primarily on hydrodynamic forcing, fragment morphology, and the duration of low-energy stability windows (Kenyon et al., 2023a). Branching coral rubble is highly mobile and easily reworked, while larger, massive fragments are more readily retained and provide longer-lived substrates once immobilized (Kenyon et al., 2023b). Cross-reef transport, storage, and stabilization of rubble are governed by the interaction between disturbance frequency and hydrodynamic thresholds. Natural rubble binding is a critical but slow process requiring months to years of relative hydrodynamic stability, during which rubble remains immobile long enough for biological binders and early cementation to develop. Holocene evidence for natural rubble binding identified crustose coralline algae, sponges, microbial crusts, and cementation as key binding agents (Kenyon et al., 2023a; Wulff, 1984). However, whether this successional pathway can proceed depends on whether rubble remains immobile for sufficiently long stability windows. Experimental measurements of bind strength across reef environments show that recently bound rubble typically fails at relatively low velocities (~1 m s^{-1} after ~4 months), but binding strength increases rapidly with time and binder succession (~2-3 m s^{-1} after 12-18 months) under stable conditions (Kenyon et al., 2025). High-energy reef crests and exposed slopes frequently exceed these thresholds, repeatedly re-mobilizing rubble and preventing consolidation, whereas sheltered fore-reef, back-reef, and reef-flats can experience sufficiently long calm periods to allow binding and diagenetic cementation to proceed (Rasser and Riegl, 2002). Flow regimes also shape who binds rubble: weak, flexible binders (e.g., turf algae, macroalgae, sponges) dominate under low stability and confer limited resistance to breakage, while stronger, calcifying binders dominate where rubble remains stable long enough, dramatically increasing resistance to subsequent wave forcing (Kenyon et al., 2025). Rubble stabilization and binding processes control whether disturbance-generated material is exported, temporarily stored, or reorganized into enduring substrates, thereby setting the conditions for subsequent geomorphic development and reef growth.

At the coarser end of the substrate spectrum, boulder ridges represent a distinct mode of reef stabilization created by rare, extreme wave events. During powerful storms or cyclones, very large coral blocks and limestone boulders, sometimes meters in size, are removed from the reef crest or upper fore-reef and deposited elsewhere (Terry et al., 2013). Because of their large mass, these boulders are moved only during exceptional events and then remain effectively immobile under normal wave conditions. As they accumulate, they form ridges or clusters that dissipate incoming wave energy and trap finer rubble and sediments landward of the ridge or in the wake of boulders (Collin et al.,

2013; Terry et al., 2013). These create sheltered zones where biological binding and coral recruitment can occur. In this way, extreme disturbances can paradoxically produce persistent geomorphic features that enhance long-term substrate stability.

4.3 Reef Geomorphology

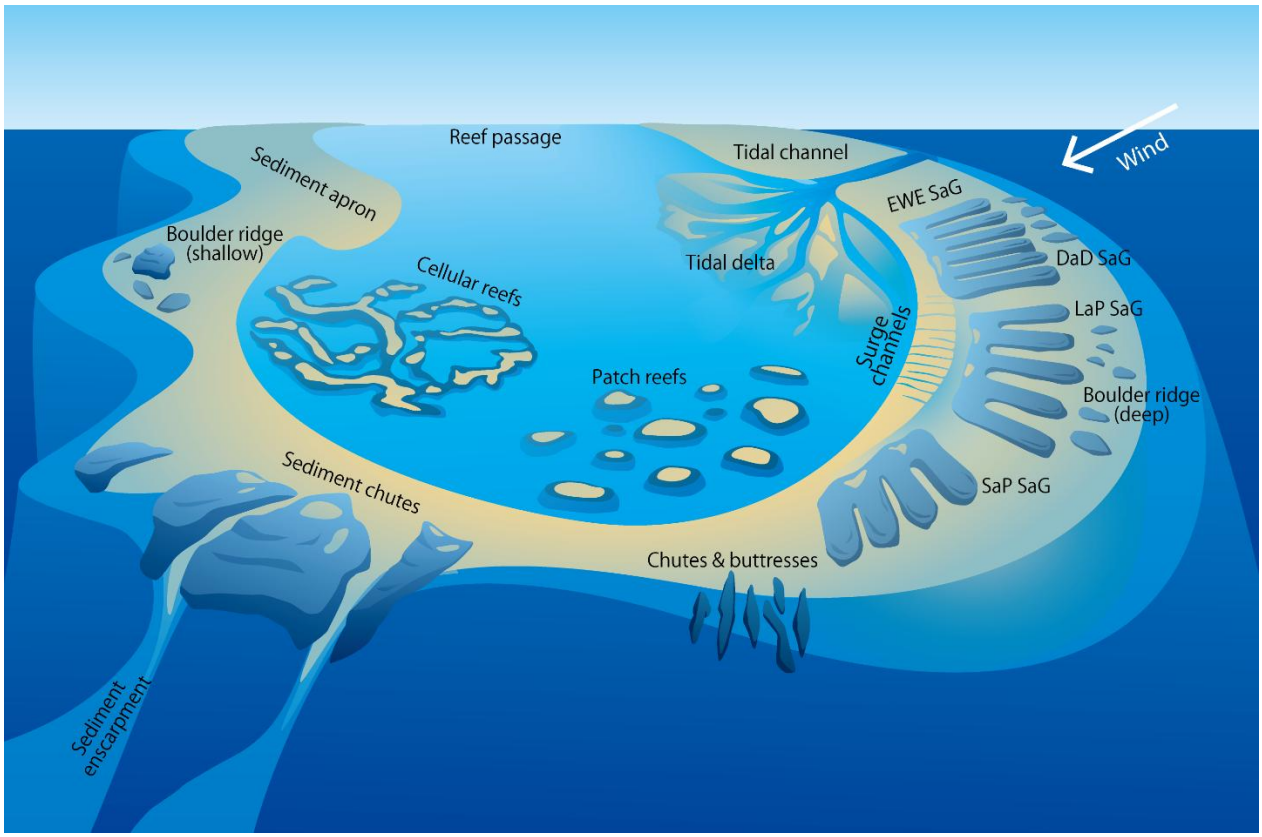


Fig. 3. Schematic representation of cited reef geomorphologies including spur and groove (SaG), following Duce et al. (2016) morphometric classification i) deep and disconnected (DaD), ii) exposed to wave energy (EWE), iii) long and protected (LaP), and iiii) short and protected (SaP).

While antecedent topography can strongly influence initial reef architecture and growth trajectories, numerous studies demonstrate that many characteristic reef geomorphologies and zonation patterns emerge through self-organization driven by feedbacks between hydrodynamics, sediment transport, and biological construction rather than being simple expressions of inherited substrate relief (Blanchon, 2011; Hall, 1999; Mistr and Bercovici, 2003; Schlager and Purkis, 2015; Stoddart, 1969; Xi et al., 2025).

At a global scale, oceanic and barrier reef geomorphologies align with hydrodynamic forcing exhibiting a characteristic zonation (Blanchon, 2011; Lutzenkirchen et al., 2023). At the seaward edge, the reef crest forms the principal breakwater, dissipating wave

energy. Landward of the crest, the reef flat is typically broad and shallow, supporting sediment deposits shaped by tidal exchange and episodic wave overwash. The reef slope extends seaward from the crest, with leeward slopes characterized by drop offs, or windward slopes commonly dominated by spur and groove systems that channel sediment and wave energy. Lower, deeper slopes give way to terraces, sand aprons and detritus talus (Fig. 3). Behind the crest and flat, the back-reef and lagoonal environments are often dominated by long-term sediment infilling, where patch reefs and cellular reefs can accrete and reef islands can be formed (Fig. 3, 7; Blanchon, 2011; Schlager and Purkis, 2015; Xi et al., 2025). Wave exposure acts as a primary organizing force across coral reef systems, strongly influencing carbonate production, framework preservation, sediment redistribution, and geomorphic development. In high-energy environments, reefs commonly develop shallow reef flats and low, discontinuous crests that dissipate wave energy while promoting frequent framework breakage and lateral sediment export (Hopley, 2011; Kennedy and Woodroffe, 2002). Carbonate material generated through breakage and bioerosion may then be transported landward or redistributed across the reef platform, contributing to beach formation, reef-flat accretion, or sediment infilling depending on geomorphic setting. In contrast, more sheltered environments experience reduced mechanical stress, allowing greater framework preservation, more irregular reef margins, and more localized carbonate accumulation, with accretion occurring primarily in place rather than through large-scale sediment redistribution (Montaggioni, 2005).

Wave-exposed morphologies

On exposed reef flats, Blanchon (2011) describes surge channels as narrow, often straight to sinuous incisions that cut across the flat platform of on high-energy coral-algal flats and algal rims, aligned with prevailing wave direction (Fig. 3). Breaking waves generate strong cross-reef currents that are funneled through weak points in the coral-algal framework, progressively deepening and stabilizing channels over time. Tides can dominate reef-scale circulation when the tidal range is large relative to reef flat elevations, or in comparatively low-energy wave climates, driving oscillatory flows across reef flats and through channels that are comparable to or larger than wave-induced currents (Fan et al., 2024; Grimaldi et al., 2022). Under these conditions, tidal water-level gradients modulate wave setup and cross-reef flows, and the reef flat can act as a barrier and completely dissipating wave energy at low tide, as well as concentrating flow through topographic lows (Hearn, 1999; Pomeroy et al., 2013). This interaction of tides and geomorphology can produce surge-like flows through channels and troughs even in the absence of extreme wave forcing, suggesting that both wave and tidal forcing should be considered in interpretations of surge channel formation and maintenance. Ecologically, surge channels enhance flushing of the back-reef and lagoon, acting as conduits for water, sediment, and nutrients, while also serving as natural escape pathways for excess energy. Their margins are commonly armored by encrusting coralline algae and low-lying

coral growth forms that can withstand high shear stress, while the channelized area remain largely free of framework due to continual scouring.



Fig. 4. Spur and groove geomorphology at Elusive Reef, Southern Great Barrier Reef (picture courtesy of Johnny Gaskell).

One common and well-known example of wave-exposed reef morphology on reef fronts are spur and groove (SaG) systems. These ridges (spurs) separated by narrow channels (grooves) oriented parallel to the dominant wind direction, develop under moderate to high wave exposure, where erosion and ecological accretion interact to shape the reef front (Fig. 3, 6). Hydrodynamic studies show that SaGs generate distinct circulation patterns, with onshore flow over spurs and offshore jets through grooves, producing counter-rotating cells that efficiently flush sediments and debris from reef slopes (Da Silva et al., 2020; Rogers et al., 2013; Sartori et al., 2025). Morphometric surveys confirm that erosion vs growth dynamics and groove length and orientation scale with wave exposure; with shorter coral growth-dominated forms dominating low exposure regimes, and erosion-dominated elongated morphologies in high exposure habitats (Fig. 6; Duce et al., 2016). Other than promoting coral growth in moderate exposure, spur tops show high cover of short productive algal turfs and CCA, compared to grooves or adjacent reef flat areas, which are dominated by low-productivity sediment laden turfs (Duran et al., 2024) which may inhibit coral settlement (Birrell et al., 2005).

The outer reef front exhibits a variety of morphologies that reflect both direct wave forcing and intrinsic pattern formation. Reefs often develop buttresses and chutes (Fig. 6): steep, alternating ridges and channels that act as conduits for downslope sediment transport while dissipating incident wave energy (Blanchon, 2011). While these features are commonly linked to hydrodynamic forcing, whether from chronic exposure or episodic storm disturbance, their organization is not always directly imposed by wave climate (see “Self-organizing morphologies” section below).

Tidal current dominated morphologies

Reef systems with substantial tidal forcing develop passages shaped by reversing currents, including tidal channels that connect open ocean, reef flats, and lagoonal waters (Fig. 3, 5). Colin (2009) documents how tidal exchange structures reef passes and channels in Palau, highlighting the importance of tidal currents in driving circulation on fringing and patch reefs within lagoons. Tidal channels can be deep (>100 m), stemming from antecedent geological structures such as riverbeds (e.g., West Pass, Palau) or relatively shallow (10-15m) and choked, likely formed as lagoon drainages over time (e.g., Ulong Channel, Palau). Deep channels carry cooler, nutrient-rich, highly oxygenated oceanic waters into the lagoon, resulting in nutrient enhancement and water cooling. Tidal channels are characterized by varied current patterns, stemming from underlying topography, tidal range and weather, as strong winds may shift normal current regimes (Colin, 2009). These geomorphologies may host widely different benthic communities, affected by their flow regimes, depth and sedimentary dynamics (Fig. 5).

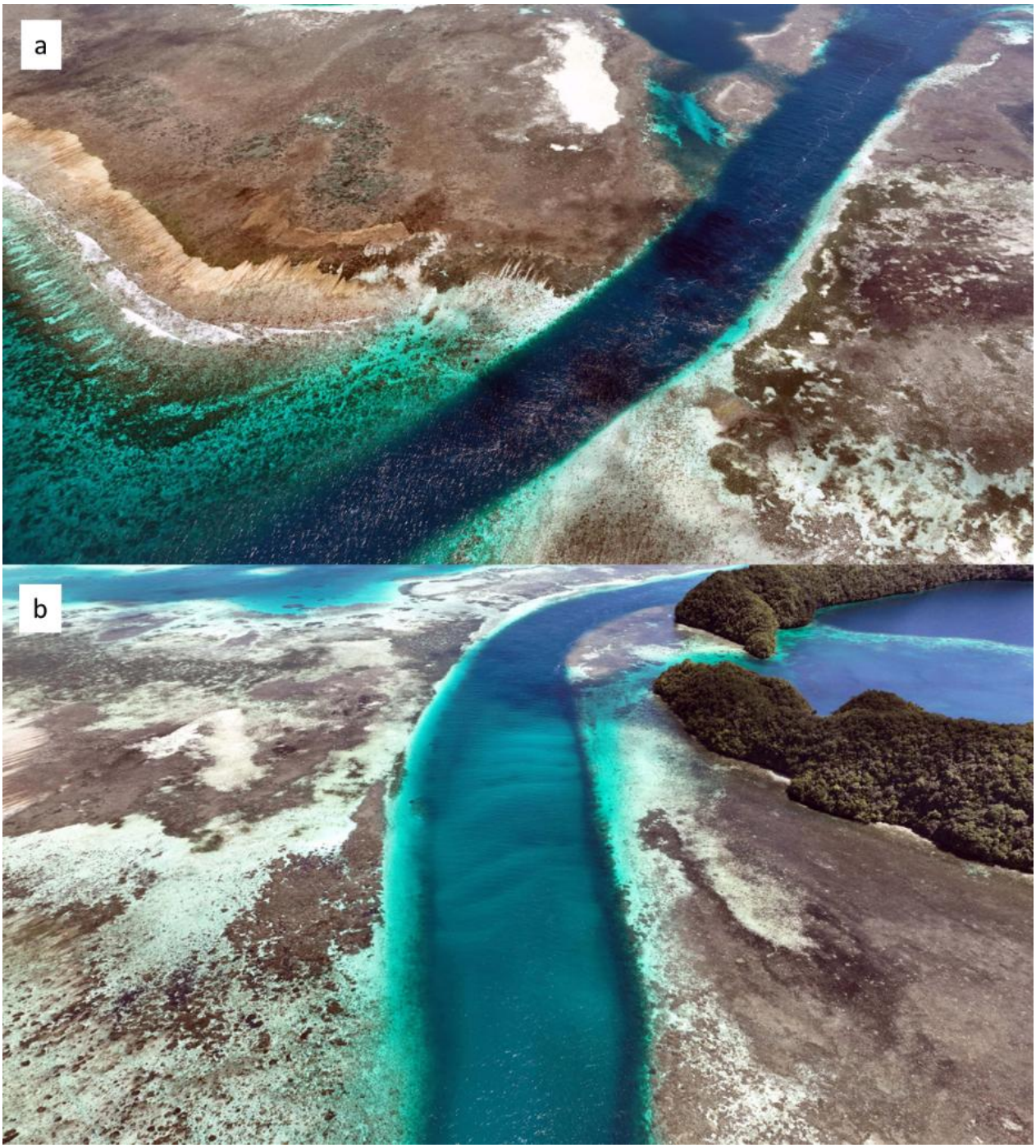
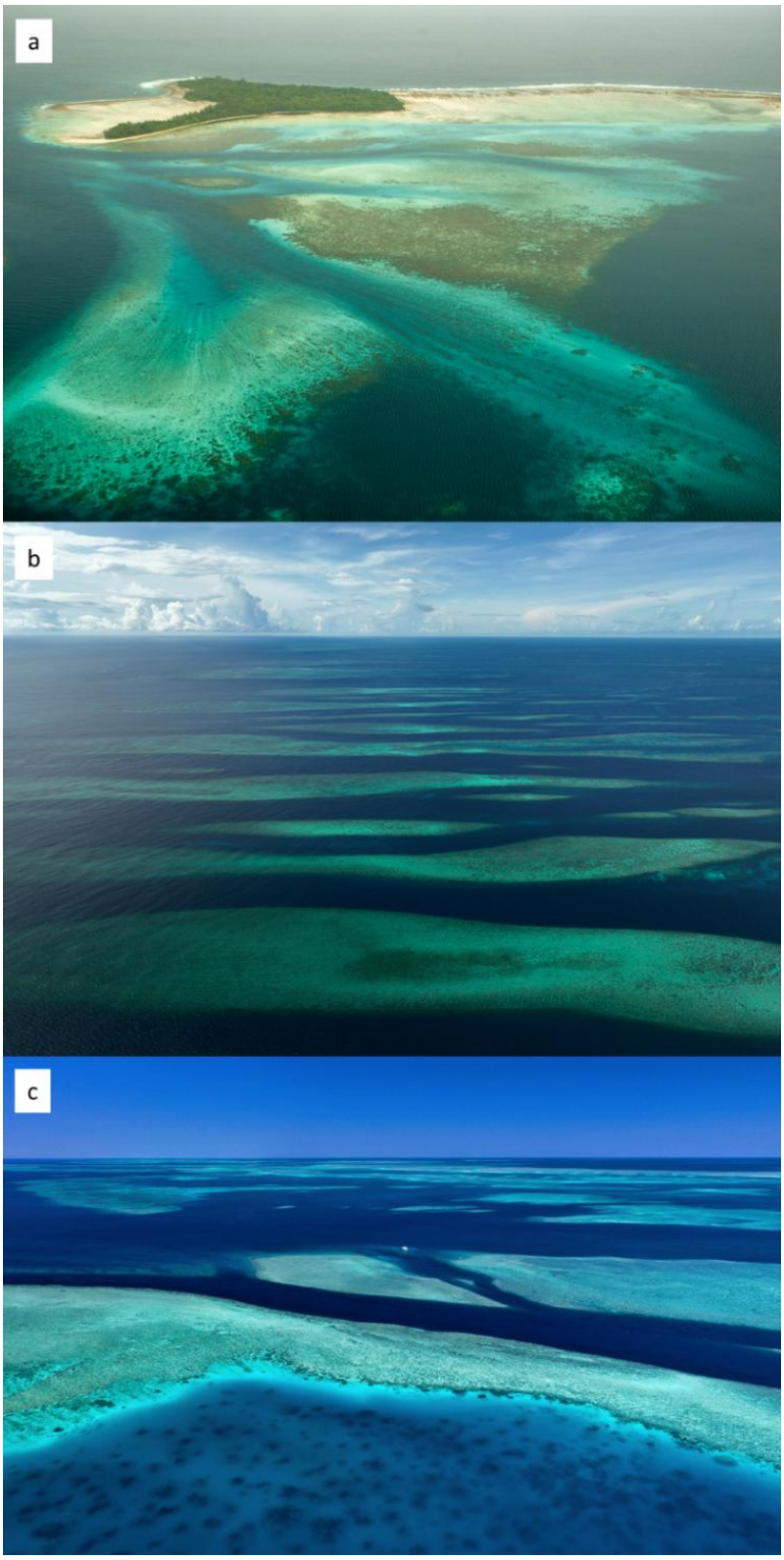


Fig. 5. Tidal channels with differential erosion/sedimentation dynamics: a) Lighthouse Channel, Palau, eroding and transporting sediment away from the reef crest and b) Ngel Channel, Palau, accumulating sediment towards the reef crest (Sartori et al. 2025, pictures courtesy of Professor Robert Dunbar).



Tidal deltas are accumulations of sand and rubble that form at tidal channel mouths where strong reversing currents rework and deposit carbonate sediment (Fig. 3, 6a).

They act as dynamic sediment reservoirs, appearing and migrating lagoonward or seaward in response to tidal asymmetry and storm events (FitzGerald, 1996; Reeder and Rankey, 2009). Flood- and ebb-tidal deltas morphology, described by elongated shoals or delta lobes, is strongly controlled by current velocity and the interaction of tidal jets with underlying topography. These current-shaped features are integral to reef sediment budgets, modulating the transfer of sediments from exposed reef crests and outer reef flats toward lagoons and back-reef environments. Tidal deltas and sand shoals illustrate how current regimes can sculpt large-scale carbonate landforms that in turn influence circulation, sediment pathways, and habitat distribution across reef systems (FitzGerald, 1996; Reeder and Rankey, 2009; Sartori et al., 2025).

Fig. 6. Tidal deltas and deltaic reefs: a) Ngerchong ebb tidal delta, Palau; b) deltaic reef systems, far northern Great Barrier Reef; c) Cockatoo Reef, southern Great Barrier Reef (pictures b, c courtesy of Johnny Gaskell).

In contrast to tidal channels and deltas in many oceanic barrier reefs, Hopley (2011) describes extensive channelized reef tracts in the northern and central GBR, where flooded paleovalleys and tidal inlets guide circulation and sediment transport across the shelf (Fig. 6b). These settings can form deltaic reef systems, in which reef growth is closely coupled with sediment dispersal pathways, and carbonate accumulation is concentrated in sand aprons, shoals, and deltaic deposits. In some cases, reef flats and crests are fragmented or poorly developed, whereas other systems, such as the Swains reefs of the southern GBR, retain extensive reef framework development while still exhibiting strong channelization and deltaic geomorphic organization (Fig. 6c). Together, these examples illustrate how current-driven sediment transport and channelized circulation can generate a continuum of reef architectures that differ from classical wave-dominated ribbon and barrier reefs, while remaining strongly structured by hydrodynamic forcing.

Reef passes are broad, relatively shallow openings through reef barriers or outer reef tracts that allow both tidal exchange and direct wave transmission into lagoonal and back-reef environments (Fig. 3). Unlike narrow tidal channels, reef passes commonly span several hundred meters to kilometers in width and reach depths typically <30-40 m, forming low-relief corridors across otherwise continuous reef crests or outer reef slopes (Breckwoldt et al., 2022; Colin, 2009). In Palau, Colin (2009) describes reef passes as dominant conduits for lagoon-ocean exchange, where strong reversing tidal currents interact with incident swell to generate complex, energetic flow fields that enhance flushing, drive localized upwelling, and redistribute plankton, larvae, and sediments across reef interiors. Their position and geometry reflect feedbacks between hydrodynamic forcing, antecedent topography, and reef accretion and subsidence patterns. A global typology of reef passages identifies distinct classes based on distance from shore and enclosure of lagoonal waters, showing that wide lagoon-connected and open-water passages are common in barrier-reef and submerged-reef systems, where they function as major arteries of energy and material exchange (Breckwoldt et al., 2022). On the Great Barrier Reef, submerged reef passes and broad reef openings occur along outer shelf reef tracts, where they align with shelf-scale circulation and sediment pathways, facilitating cross-reef transport while allowing wave energy to penetrate deep into lagoonal basins (Beaman et al., 2008; Hopley, 2011).

Gravity dominated morphologies

Gravity-driven sediment redistribution is an important feature of reef developmenta as some carbonate material detached from the framework is transferred downslope or lagoonward, and may contribute to reef accretion, lagoon filling, and reef progradation (Kennedy and Woodroffe, 2002). Carbonate sediments that are not stabilized or retained within the reef structure may ultimately be exported beyond the reef system through

carbonate shedding processes, linking local geomorphic reworking to broader platform-scale sediment budgets (Schlager et al., 1994)

Two main gravity-driven features of reef slopes are sediment chutes and escarpments (Fig. 3). Sediment chutes are narrow, steep-sided gullies that act as preferential pathways for downslope transport of loose carbonate material, often occurring on steep reef walls. They are episodically flushed by waves or storms, repeatedly reactivating as unconsolidated sands and rubble accumulate and are remobilized, producing parallel gully-like irregular patterns across reef slopes (Hall, 1999). Escarpments represent more persistent, step-like breaks in slope profile that form where unconsolidated or semi-lithified sediments collapse. Both features reflect the fundamental role of reef steepness and substrate instability: where living corals overgrow uncemented deposits, small-scale landslides and sediment cascades can occur. Episodic disturbances such as cyclones and hurricanes can amplify these processes, rapidly destabilizing unconsolidated layers and driving mass-wasting events that transport boulders and coral blocks downslope (Hall, 1999; Stoddart, 1969).

In addition to chutes and escarpments, reefs commonly host sediment accumulations that record the downslope reworking of unconsolidated reefal material. At the base of reef slopes and terrace scarps, talus or rubble aprons form through repeated episodes of sediment and framework collapse, including storm-driven failure, gravitational slumping, and downslope transport of detached carbonate material (Fig. 3; Blanchon, 2011; Harris et al., 2014). Their composition reflects repeated episodes of mass sediment/rubble movement: storm waves, cyclones, or gravitational slumping detaching material from the upper slope, which is then redeposited. These deposits commonly consist of coarse rubble, boulders, and reworked sediment redeposited as talus fans or debris accumulations along slope breaks and deeper reef margins.

In contrast, shallow lagoonal and back-reef sand aprons (or lagoonal sand sheets) are typically shaped by wave- and current-driven sediment redistribution and contribute to the gradual infilling of protected reef interiors. Over time, these aprons may be stabilized by reef framework growth or microbial/coralline cementation, or many remain unconsolidated acting as sediment reservoirs that can be remobilized during high-energy events. Together, these features illustrate how both gravitational collapse and hydrodynamic transport contribute to reef sediment redistribution across different geomorphic settings.

Self-organization in absence of external forcing

Minor irregularities in reef topography can trigger feedbacks between flow and geomorphology, whereby hydrodynamic channeling concentrates energy into specific corridors, gradually sculpting chutes alternated by buttresses (Mistr and Bercovici, 2003). This perspective helps explain why terrace-scarp systems not exposed to wave forcing

often display rhythmic spacing and coherent large-scale organization (e.g., chutes and buttresses described by Blanchon, 2011) as these are products of internal eco-geomorphic dynamics that regulate the balance between coral growth, erosion, and sediment redistribution. Similar self-organized spatial patterning occurs in simpler morphodynamic systems, including beach cusp formation driven by feedbacks between flow, sediment transport, and evolving topography (Coco et al., 2000), suggesting that some reef geomorphologies may emerge from more general hydrodynamic and sedimentary instabilities rather than exclusively reef-specific ecological processes.

Patch reefs provide another striking example of this, often forming quasi-regular arrays across lagoonal and back-reef settings (Fig. 3, 7a). Their distribution reflects feedbacks between coral growth, sediment dynamics, and local circulation. As individual patches accrete, they modify surrounding flow fields and trap sediments, creating exclusion zones that inhibit the nucleation of new reefs nearby while leaving space at greater distances for other patches to establish (Olzewski, 2016; Xi et al., 2025).

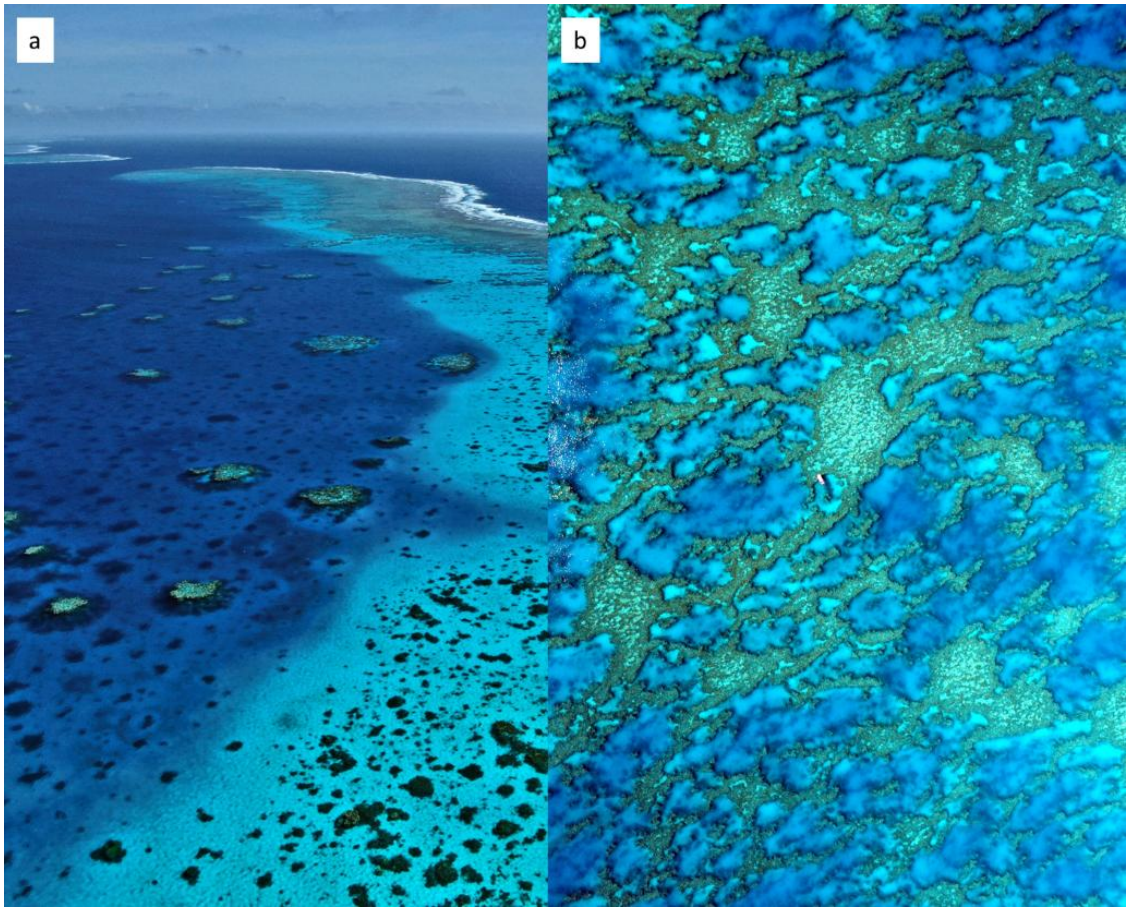


Fig. 7. Lagoonal reefs: a) patch reefs in Ribbon Reefs, northern Great Barrier Reef and b) cellular reefs in Fitzroy Reef, Capricorn Group (pictures courtesy of Johnny Gaskell).

Branching lagoonal corals play a critical role in this process by acting as biological flow modifiers. As these colonies grow, their branching or reticulate morphologies increase hydraulic roughness and baffle near-bed currents, reducing flow velocity and shear stress within and immediately downstream of the coral canopy. This hydrodynamic attenuation promotes the deposition of fine carbonate sediments (silt- to mud-sized fractions) that would otherwise remain in suspension. The accumulation of fine sediment within coral thickets stabilizes the substrate and enhances early cementation, while the surrounding water column becomes clearer due to the removal of suspended particles. Clearer water improves light penetration, reinforcing coral growth within established patches. Numerical modeling demonstrated that lagoonal patch reefs can emerge as spontaneous patterns under coupled ecological-hydrodynamic feedbacks, and over time may form interconnected ridges generating cellular reefs (Fig. 7b; Xi et al 2025), without the need for antecedent substrate controls (Schlager and Purkis, 2015), reinforcing earlier theoretical work on pattern formation in reef morphologies (Mistr and Bercovici, 2003).

Discussion

Coral reefs are the largest biological constructions on Earth, and their persistence is inseparable from the hydrodynamic environment in which they develop. Flow governs processes as disparate as organismal physiology, ecological interactions, sediment transport, and the long-term architecture of reef structures. In this sense, complexity, both ecological and structural, is an emergent property of recursive feedbacks between water motion and living reef builders, operating across scales from polyps to reef tracts.

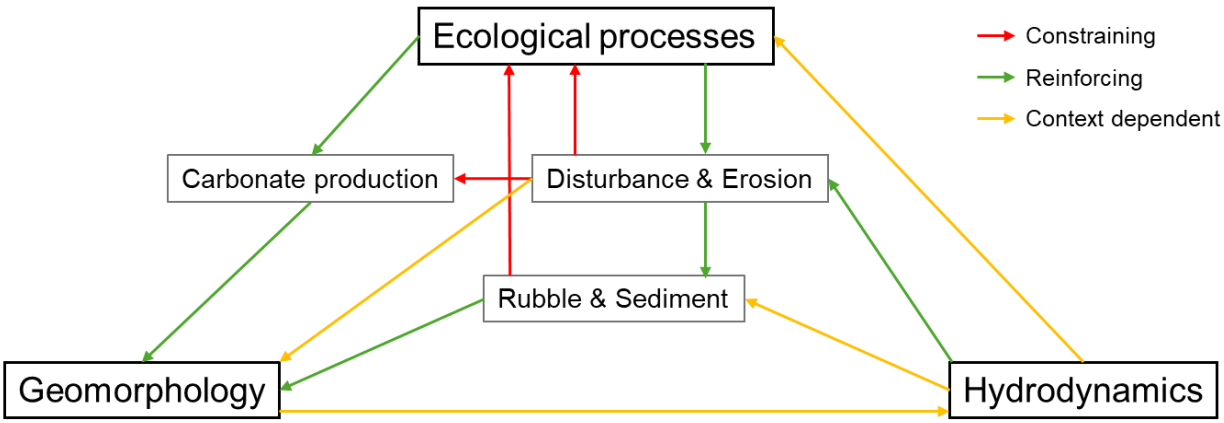


Fig. 8. Ecological processes regulate carbonate production and disturbance, generating lose material that may be used to build reef framework. Geomorphology and hydrodynamics are reciprocally coupled, shaping spatial patterns of flow energy and substrate stability. Feedbacks are classified as constraining (red), reinforcing (green), or context-dependent (yellow), reflecting that many interactions vary in direction and magnitude depending on environmental conditions.

Reef dynamics emerge from tightly coupled feedbacks among ecological processes, sediment dynamics, geomorphology, and hydrodynamic forcing (Fig. 8). Ecological processes simultaneously drive carbonate production, contributing to framework construction, and disturbance-mediated erosion, generating mobile substrate in the form of sediment and rubble. Hydrodynamic forcing redistributes this material, influencing both substrate stability and its incorporation into reef geomorphology. In turn, geomorphic structure modifies local flow regimes, modulating the intensity of hydrodynamic forcing experienced by benthic organisms and substrates. These interactions create a recursive system in which ecological and physical processes co-regulate one another. The evidence synthesized in this review highlights the need to study reef organisms not as passive occupants of a physical setting, but as engineers that actively reshape their environment through growth, erosion, and structural modification. Although ecological and geological processes operate over different temporal scales, they are deeply intertwined, and understanding reef functioning or resilience requires considering them as components of a unified, co-evolving system.

The hydrodynamic Goldilocks window

Many reef processes exhibit non-linear responses to hydrodynamic forcing, with optimal performance under intermediate flow conditions (Table 1). However, these optima are process-specific and do not align perfectly across functions, indicating that reef performance emerges from overlapping, and sometimes conflicting, hydrodynamic constraints rather than a single universal optimum (Fig. 9). At high flow energy, metabolic exchange and feeding may become impaired, fertilization rates can decline through enhanced gamete dilution, and excessive shear stress may dislodge organisms (Cheung et al., 2025; Crimaldi, 2012; Crimaldi and Zimmer, 2014; Sebens et al., 1998; Zhang et al., 2011). Although some lagoonal settings maintain high coral cover, and exposed crests can support high productivity through CCA, turf assemblages, and fast-turnover corals, neither extreme necessarily maximizes long-term framework accumulation or resilience to disturbance (Nakamura and Van Woesik, 2001; Pratchett et al., 2017). Moderate exposure tends to favor fast-growing taxa while interaction with reef geomorphology shape flow refugia, enhancing species richness and diversity (Graus and Macintyre, 1989; Huston, 1985; Page-Albins et al., 2012; Williams et al., 2013). At low flow energy, sediments may accumulate and framework development can be limited, whereas excessive turbulence can prevent rubble binding and substrate stabilization, delay recovery, and enhance export of carbonate material (Gowan et al., 2014; Hearn, 2011; Kennedy and Woodroffe, 2002; Kenyon et al., 2023a; Sebens et al., 1998; Zhang et al., 2011).

These observations support the existence of a hydrodynamic Goldilocks window (e.g., Hennige et al., 2021), not as a fixed or spatially uniform domain, but as a functional envelope within which multiple processes partially align to support coral growth, turnover,

and net reef accretion (Table 1, Fig. 9). Importantly, the optima of individual processes do not coincide perfectly. As a result, reef performance does not follow simple linear gradients of hydrodynamic energy, but instead emerges from the overlap of multiple, misaligned process responses. At broad scales, these dynamics contribute to classical patterns of reef zonation along hydrodynamic gradients. However, at ecologically relevant scales, interactions between flow and substrate disrupt these gradients, producing spatial mosaics of benthic states. Reef geomorphology modulates local flow velocity and turbulence, generating sharp transitions in environmental conditions over short distances. The hydrodynamic Goldilocks window should therefore be understood as a shifting and spatially fragmented envelope, emerging where process-specific optima overlap within a given geomorphic and hydrodynamic context. Reef states therefore emerge from the balance among processes operating within these locally constrained physical environments.

Importantly, these envelopes likely differ among reef systems depending on their evolutionary history, geomorphic configuration, and prevailing hydrodynamic regime. Reef assemblages and morphologies developing under chronically high-energy environments may therefore persist under forcing conditions that would exceed the stability thresholds of reefs formed in more sheltered settings. Rather than reflecting a single optimal hydrodynamic state, reef persistence emerges from the maintenance of feedbacks operating within locally adapted ranges of flow, disturbance, sediment transport, and substrate stability.

Table 1. Summary of processes discussed in this review in low, moderate and high flow energy.

Process	Low flow	Moderate flow	High flow
Physics			
Boundary layer	Thick → diffusion-limited	Thinner → efficient exchange	Very thin → high exchange but unstable
Physiology			
Photosynthesis	Moderate, no effect in species adapted to low flow	Enhanced	Slight increase to plateau
Respiration	Strongly limited	Enhanced	High
Nutrient uptake	Limited	Enhanced	Coral: increase to plateau / saturation Algae: increase, especially under nutrient enrichment
Prey capture	Low encounter rates. Large polyped species advantaged	Optimal (balance delivery-retention)	Reduced (prey advected)

Reproduction & demography			
Fertilization	High local retention, decreased mixing	Optimal (mixing + ecounter rates)	Reduced (dilution, damaged embryos)
Settlement	Unidirectional currents produce less drag and lift than oscillatory motion	Enhanced with substrate complexity (attachment eddies)	Reduced (drag + lift)
Coral growth	Depend on species adaptation but generally mass transfer limited	Optimal for species adapted to wave exposure, higher exposure produce harder skeletons	Depends on species adapatation but can cause mechanical stress
Ecological processes			
Coral dislodgement	None	Can happen to table/branching morphotypes	Higher probability for other morphotypes
Bleaching susceptibility	High (thermal and ROS buildup)	Reduced (mixing, cooling, protein production)	Variable (mechanical stress vs cooling)
Competition with benthic organisms	Increase algal competitive advantage creating anoxic zones at coral-algal interfaces	Aid removal of sediment and anoxic zones at coral-algal interfaces, benefitting corals	May benefit organisms with higher filter-feeding capacity (sponges, tunicates)
Fish grazing	Moderate	High (productivity-driven)	Reduced efficiency (turbulence)
Invertebrate grazing	High	Moderate	Reduced (attachment limits)
Corallivory (Parrotfish)	Low-moderate	Moderate	Variable (species-driven, not flow-driven)
Corallivory (COTS)	High (sheltered habitats)	Low (attachment constraints)	Very low (attachment constraints)
Geological processes			
Sediment movement	Deposition and accumulation dominate; fine sediments settle and persist	Intermittent transport and resuspension; balanced import/export depending on wave events	Continuous resuspension and export
Rubble stabilization	High; sediment infilling and diagenetic processes are promoted	Moderate; rubble can stabilize in low energy window and exposure promotes growth of binding organisms (e.g. CCA)	Low; frequent remobilization prevents consolidation and biological binding
Morphodynamics	Weak geomorphic reworking dominated by gravity and sediment infilling	Growth, erosion, transport, deposition sustain geomorphic complexity and feature persistence	Erosional dominance; strong export with formation of scours

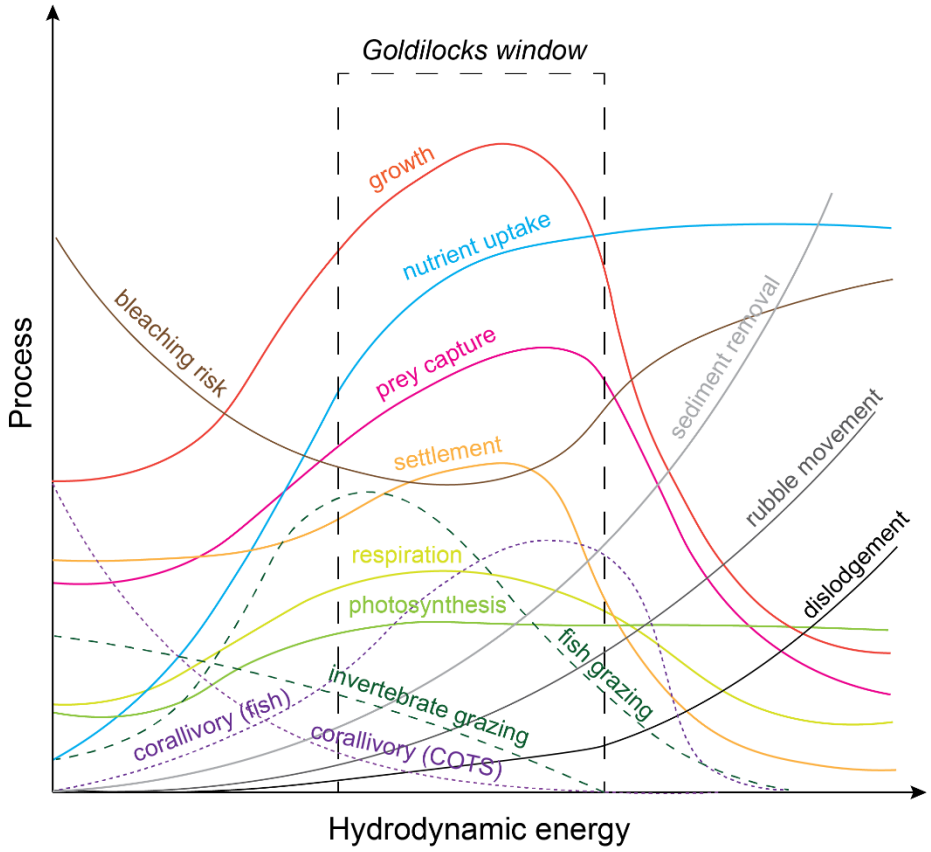


Fig. 9. Representation of the Goldilocks window of reef physiological, ecological and geomorphic processes in relation to hydrodynamic energy. Direction and shape of relationships are hypothesized from the present synthesis.

Hydrodynamic resilience of coral reefs

Ecosystem resilience has long been recognized as a multidimensional property of ecological systems (Folke et al., 2004; Holling, 1973). In coral reefs, resilience is commonly understood as the capacity to absorb disturbance while maintaining its core functions, structure, and feedbacks, including the ability to recover following perturbation without shifting into an alternative stable state (Mumby et al., 2014, 2007). Previous work has emphasized the role of grazing-mediated feedbacks in regulating these dynamics, particularly in controlling the balance between coral and macroalgal dominance (Mumby et al., 2007). However, the effectiveness of these feedbacks depends on the physical environment in which they operate, including the hydrodynamic conditions that regulate biological and ecological processes, substrate dynamics, and disturbance. Other work emphasizes geomorphic or accretionary resilience, reflected in carbonate budgets and the ability of reefs to maintain vertical growth trajectories despite disturbance (Perry et al., 2008). These perspectives capture complementary dimensions of resilience, but their

integration requires consideration of the physical processes that link them. Hydrodynamic forcing, through its control on energy dissipation, substrate stability, and benthic productivity provides a key mechanism through which ecological and geomorphic processes interact to shape reef resilience.

Disturbance is integral to this coupled system. Coral reefs persist through repeated cycles of growth, mortality, physical breakdown, redistribution, and reassembly, rather than through continuous and uninterrupted framework construction (Copper, 1992; Connell et al., 1997). Storms can directly fragment framework and generate rubble and sediment, whereas bleaching, crown-of-thorns starfish outbreaks, and other mortality events create dead framework that may subsequently be weakened by bioerosion, broken by hydrodynamic forcing, and incorporated into mobile carbonate deposits (Copper, 1992; Perry et al., 2012). Reef substrates inherit properties from past biological assemblages, disturbance history, and subsequent cementation and lithification (Olzewski, 2016; Perry et al., 2018, 2008; Perry and Alvarez-Filip, 2019). Disturbance therefore modifies the physical substrate from which future reef development proceeds. This substrate legacy influences later settlement, growth, sediment transport, and framework stability through its effects on roughness, permeability, and resistance to remobilization.

Whether disturbance contributes to reef renewal or to degradation depends on the persistence of feedbacks that regulate the balance between material production, redistribution, and stabilization**.** Feedbacks among biological growth, sediment transport, substrate stabilization, and hydrodynamic forcing can generate self-organized spatial patterns and carbonate accumulation, as demonstrated by eco-sedimentary systems in shallow marine environments (Olszewski, 2016; Purkis et al., 2016). These feedbacks operate within stability domains - ranges of environmental conditions under which positive interactions between reef geomorphology, reef-builder growth, flow energy, and framework stabilization reinforce one another (Fig. 8). Within these bounds, disturbance is not purely destructive but contributes to reef persistence by generating loose carbonate material (e.g., rubble and sand) and creating space for recruitment, thereby sustaining sedimentary and ecological feedbacks that support reef accretion and framework renewal. However, when disturbance exceeds critical thresholds, these feedbacks break down and may lead to net erosion, and shifts toward alternative configurations with distinct hydrodynamic characteristics. For example, the flattening of spur and groove structure on exposed slopes may decrease wave energy dissipation capacity, enhancing erosion and shear stress on reef crests, potentially decreasing coral settlement and promoting dislodgement.

We therefore propose hydrodynamic resilience as the capacity of a reef system to maintain or reorganize the flow-form interactions that support ecological functioning and geomorphic development following disturbance. Hydrodynamic resilience does not imply resistance to morphological change. Rather, it describes whether the coupled system can

remain within, or return to, a range of hydrodynamic and geomorphic conditions in which biological production, material transport, and substrate stabilization continue to support reef persistence. A reef may therefore reorganize taxonomically while retaining these functional interactions, or conversely recover biological cover while losing structural characteristics that previously supported effective wave dissipation, sediment retention, or substrate stability (Fig. 8).

This range of viable conditions can be conceptualized as a functional hydrodynamic envelope within which feedbacks remain predominantly constructive rather than degradational (Fig. 8). This envelope should be interpreted as spatially dynamic and habitat-contingent because reef form structures local flow fields, geomorphic units perform different functional roles within the reef system, and their constituent species vary widely in their dependence on and tolerance of hydrodynamic forcing. For example, on exposed spur and groove slopes, resilience could depend on maintaining wave dissipation capacity and efficient sediment shedding without exceeding mechanical limits of framework builders. In lagoons, resilience may be more linked to balanced residence times that allow sediment stabilization and patch reef nucleation while preventing prolonged water stagnation. In current-swept channels, resilience may depend on sustained oceanic exchange that delivers cooler water, food, larvae, and nutrients, maintaining connectivity across habitats. Hydrodynamic failure thus does not reflect deviation from a single optimal energy level, but a shift away from the flow regime that sustains the functional role of a given geomorphic setting. In this sense, the concept parallels morphodynamic frameworks in which landform configuration emerges and reorganizes through feedbacks among hydrodynamic forcing, sediment transport, and evolving geomorphology (Coco et al., 2000). Recognizing these interconnected dimensions expands existing resilience frameworks by providing a more mechanistic and contextualized basis for understanding how reefs reorganize, persist, or fail through cycles of disturbance and reassembly.

Conclusion

Maintaining reef functioning has long been a central goal of coral reef ecology and management, with extensive work emphasizing the importance of preserving key processes and feedbacks (e.g., Lam et al., 2017; Mumby et al., 2007). Resilience-based approaches have advanced reef assessment by shifting attention from ecological state alone toward the processes that sustain or restore reef function (Lam et al., 2017). However, the expression and interpretation of these processes are inherently context-dependent because reef geomorphology and hydrodynamic forcing structure the physical environments in which ecological interactions occur, shaping patterns of productivity, disturbance, substrate stability, and recovery.

Evaluating reef state or resilience without accounting for this physical context may therefore lead to misleading comparisons among habitats. Future research should explicitly incorporate hydrodynamic and geomorphic setting as central axes of reef assessment. Flow thresholds influence physiological performance, ecological interactions, organism dislodgement, sediment transport, and rubble stabilization, while geomorphology determines how these thresholds are expressed across reefscapes by modifying local wave energy, currents, turbulence, and substrate conditions. Recognizing reefs as coupled flow-form-life systems shaped by multi-scale feedbacks across space and time provides a more mechanistic basis for interpreting ecological patterns within the physical setting that produces them. Low coral cover, for example, may represent degradation in one geomorphic setting but the expected outcome of persistent hydrodynamic disturbance or sediment transport in another. Likewise, sediment-scoured features such as grooves or chutes may support relatively little coral cover while performing important geomorphic functions through sediment evacuation and redistribution.

This framework also has implications for monitoring and management. Processes governing reef resilience, including disturbance, carbonate production, substrate stabilization, and geomorphic development, arise from interactions among biological, physical, and sedimentary components, and therefore differ in the extent to which they can be directly managed. Local herbivory and land-based inputs of sediment and nutrients may be influenced through management, whereas hydrodynamic forcing, large-scale disturbance regimes, and geomorphic evolution are often only indirectly controllable or operate beyond practical intervention scales. Management should therefore account for the physical processes that constrain ecological outcomes rather than assuming that similar ecological states are attainable across all reef settings.

Interventions aimed at maintaining particular benthic configurations or suppressing disturbance may be effective where they reinforce existing physical and ecological feedbacks, but may have limited effects where underlying hydrodynamic and geomorphic processes continually reorganize the system. More broadly, the most consequential management actions may be those that reduce anthropogenic pressures that disrupt constructive feedbacks - including extractive practices, land-based runoff, and greenhouse gas emissions - while maintaining the environmental conditions under which reef growth, substrate stabilization, and recovery can occur. Management solutions should therefore work with the dynamic nature of coral reefs, rather than attempting to directly control dynamics that are fundamentally structured by ecological turnover, hydrodynamic forcing, and geomorphic legacy.

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