Coral Reefs
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PERSPECTIVE

The rise of long-sediment-laden algal turfs: an additional negative feedback process limiting reef resilience

Mark C. Ladd[1] · **Andrew A. Shantz**[2] · **Alastair R. Harborne**[3] · **Andrew G. Bauman**[4] · **Alain Duran**[3]

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Abstract In an era of increasing disturbances, understanding the capacity for coral reefs to recover and the drivers that underpin resilience is critical for predicting the health of future coral reefs. Traditional resilience paradigms for Western Atlantic reefs suggest that high herbivore biomass and low macroalgal cover are tenets of resilient systems. Yet, it is clear that some locations, such as Florida's reefs, and potentially other locations, are not well explained by this paradigm. Here, we suggest that the proliferation and increased dominance of long-sediment-laden algal turfs (LSATs) create an additional negative feedback process that helps explain the compromised resilience of Florida's reefs and further extends the existing Western Atlantic model. Collectively, coral mortality, reef flattening, and intense grazing appear to have created a series of negative feedback processes that reinforce a flat, sediment-laden benthos that impedes the recovery of already diminished coral populations. Importantly, feedbacks associated with LSATs could be strengthened in the presence of high herbivore biomass, thereby undermining foundational expectations of resilience based on grazing pressure alone. Here, we outline this destructive cycle and provide support for the mechanisms that drive these feedbacks. Although we focus on the ecological context of Florida's reefs, our expansion of the conceptual framework will likely apply to other reef systems in the Caribbean with similar ecological attributes. Mounting evidence suggests that LSAT dominance represents a novel ecosystem state for Western Atlantic reefs.

Keywords Coral reef · Negative feedbacks · Long-sediment-laden algal turfs · Parrotfish · Resilience · Bioerosion · Herbivory · Hysteresis

Introduction

As global coral populations continue to decline, understanding their capacity to recover and the drivers that underpin resilience is critical for predicting the health of future coral reefs (Bellwood et al. 2004; Putnam et al. 2017). To this end, decades of coral reef research have been synthesized to inform an understanding of reef resilience for the Western Atlantic (*e.g.*, Mumby et al. 2007a). Under this paradigm, processes that facilitate coral success underpin a series of positive feedbacks that support the persistence of structurally complex reefs (Mumby and Steneck 2008). Top-down control by herbivores (*e.g.*, parrotfishes and urchins) is a particularly critical process for preventing, and potentially reversing, shifts from coral to macroalgal dominance following large-scale disturbances (Bellwood et al. 2004; Hughes et al. 2007; Burkepile and Hay 2009; Kubicek and Reuter 2016). Recruitment-driven population recovery in turn hinges on larval supply, suitable recruitment substrate, and the post-settlement survival of corals (Ritson-Williams et al. 2016; Gouzeau et al. 2019; Edmunds 2023; Edmunds et al. 2024). Without top-down control, macroalgae can rapidly colonize open spaces and prevent the settlement, survivorship, and growth of new corals, thereby limiting the recovery

✉ Mark C. Ladd
mark.ladd@noaa.gov

[1] Population and Ecosystems Monitoring Division, NOAA Southeast Fisheries Science Center, Miami, FL, USA

[2] Cooperative Institute for Marine and Atmospheric Research, University of Hawai'i at Manoa, Honolulu, HI, USA

[3] Department of Biological Sciences, Institute of the Environment, Florida International University, Miami, FL 33199, USA

[4] National Coral Reef Institute, Nova Southeastern University, 8000 N Ocean Drive, Dania Beach, FL 33004, USA

of coral populations following disturbances (Hughes et al. 2007; Adam et al. 2015).

When corals die and fail to recover, the expected trajectory of change in the Western Atlantic follows a transition from coral- to macroalgal-dominated reef systems (Littler & Littler 1985; Hughes 1994; Scheffer et al. 2001; Mumby & Steneck 2008; Schmitt et al. 2019). Phase shifts from coral-dominated to macroalgae-dominated reefs are problematic because of negative processes: Macroalgae often outcompete corals for space, reduce recruitment opportunities, and alter reef dynamics by providing suboptimal habitat for associated species, including the loss of structural complexity necessary to support large grazing fish populations (Hughes et al. 2007; Mumby and Steneck 2008). Once established, degraded states can hinder efforts to restore coral dominance, even when initial stressors are mitigated (Mumby 2009; Steneck et al. 2019). These unexpected dynamics are often explained by hysteresis, a phenomenon in which the return to coral-dominated states requires significantly more effort than might be expected because of negative feedback processes (Scheffer et al. 2001; Mumby et al. 2013).

In an era of rapid global environmental change, coral reef paradigms require evolving scientific approaches, refinement, and recognition of a more nuanced understanding to capture the dynamics of contemporary coral reefs (Williams et al. 2019). For example, in the Western Atlantic, evidence shows that benthic trajectories of Florida reefs are poorly represented by the prevailing resilience model, with coral cover typically < 5% but high grazing intensity and only modest macroalgal cover (Ruzicka et al. 2013; NCRMP 2018; Shantz et al. 2020). Consequently, on contemporary Florida reefs, and possibly other locations, additional pathways that explain reef trajectories may be missing from our conceptual model of reef change. Here, we propose that additional negative feedback processes promote the proliferation and stability of long-sediment-laden algal turfs (henceforth, LSATs; Goatley et al. 2016) and help explain compromised resilience on Florida's coral reefs (Fig. 1). Mounting evidence suggests that LSAT dominance may represent a widespread novel ecosystem state for Western Atlantic reefs (Duran et al. 2024). Interestingly, in addition to terrestrial inputs from increasing coastal populations (Rogers and Ramos-Scharrón 2022), a portion of the sediment available to accumulate in LSATs is of biogenic origin, created from the bioerosion of calcium carbonate reef framework by parrotfish protected to increase grazing and promote resilience (Bruggeman et al. 1996; Molina-Hernández et al. 2022; 2024). Consequently, the ecological context of Florida's reefs provides an interesting case study on the challenges of establishing well-meaning conservation initiatives in isolation while failing to address other stressors that erode resilience, including climate change, disease, and decreased water quality.

Disturbances typify Florida reefs and alter ecological contexts

Coral communities in Florida have declined for at least 50 years as a consequence of disease outbreaks, thermal stress events, and chronic local stressors like sedimentation and pollution (Jackson et al. 2014). Regional disease events starting in the 1970 s marked a turning point on Florida's reef, driving catastrophic losses of Acroporids and massive corals (Dustan 1977, Porter and Meir 1992, Richardson and Voss 2005; Lirman et al. 2014), as well as the near extirpation of herbivorous sea urchins (Lessios 2016). These catastrophes were followed by a series of new disease outbreaks, cold-water mortality events (Porter et al. 1982; Roberts et al. 1982; Lirman et al. 2011), and six major coral bleaching events (Manzello 2015). By 2014, mean coral cover across Florida reefs was ~ 6.7% (NOAA National Coral Reef Monitoring Program 2018) when a novel disease, stony coral tissue loss disease (SCTLD), emerged to cause mass mortality of numerous species and decimate remaining coral populations (Precht et al. 2016; Muller et al. 2020). The onset of SCTLD coincided with recurrent bleaching events (2014 and 2015) and a new reality for Florida's reef in which temperatures in the Florida Keys have exceeded the traditional 4 °C heating week bleaching threshold every year since (NOAA Coral Reef Watch 2018). These annual thermal stress events have driven further declines of Florida's corals, punctuated by the 2023 marine heat wave, which shattered previous records for heat stress on Florida's reefs. This marine heat wave caused catastrophic losses of the already severely depleted populations of the key reef-building species *Acropora palmata* and *A. cervicornis,* two of the few species not impacted by SCTLD, resulting in a significant setback to years of coral restoration efforts (Williams et al. 2024; Manzello et al. 2025). Coinciding with the loss of live coral cover on Florida's reefs, there has been a near complete shutdown of recruitment of the remaining reef-building species (i.e., *Orbicella* and *Montastraea*). Despite the potential for high larval connectivity within the Florida Reef Tract (Frys et al. 2020) and potential larval supply from reefs in Cuba and the Yucatan Peninsula in Mexico (Holstein et al. 2014), a three-year recruitment study across the Florida Reef Tract (2015 to 2018) found no *Orbicella* or *Montastraea* recruits and a single *Acropora* recruit (Harper et al. 2023), indicating that one or more processes operating on Florida's reefs are contributing to reduced recruitment.

Contemporary Florida reefs: fundamental shifts in benthic communities and ecological processes

One of the most striking shifts in benthic composition on Florida's reefs is the proliferation of LSATs. LSATs develop

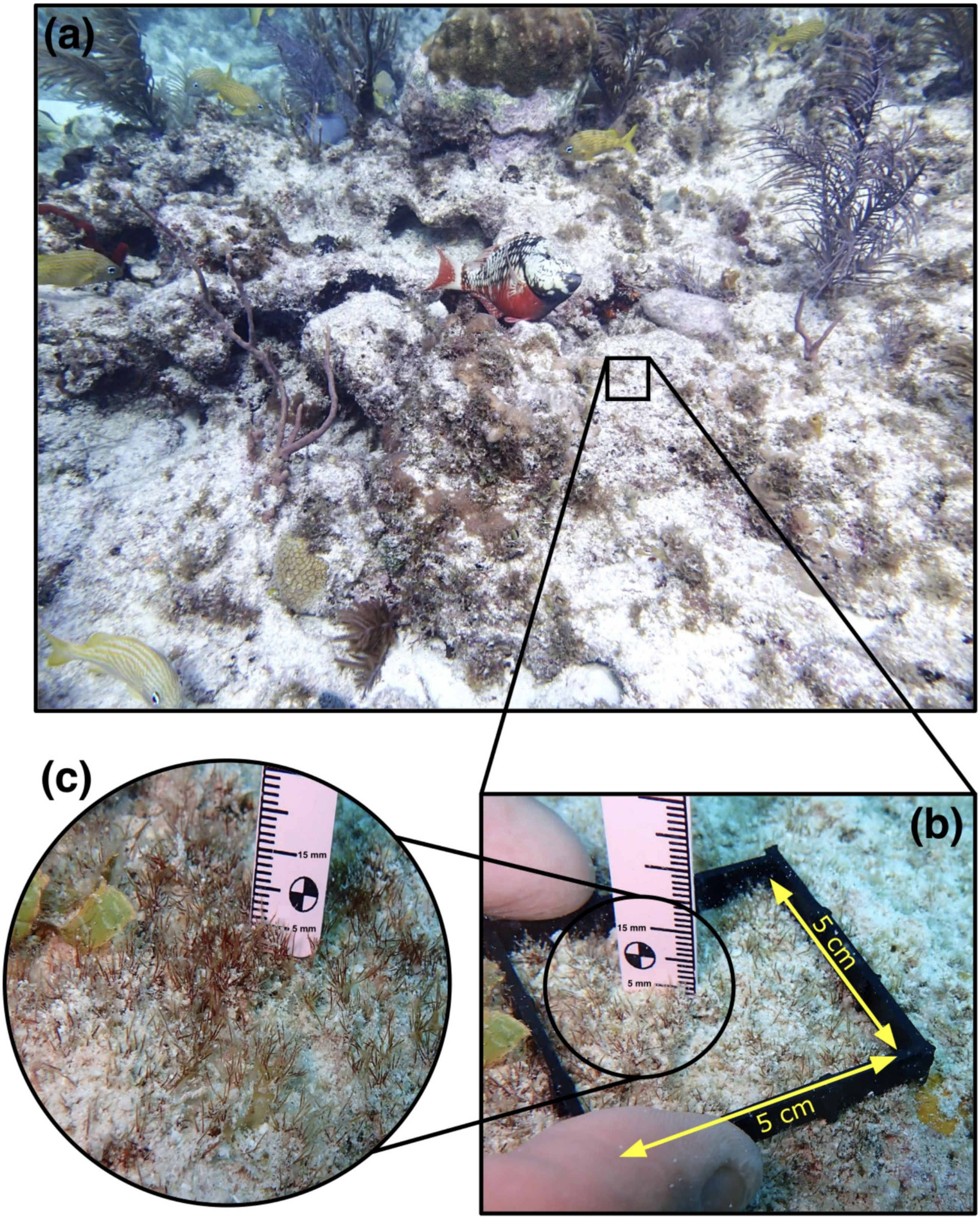

Fig. 1 **a** A coral depauperate LSAT-dominated reef in Florida, **b** close-up photograph of intact LSAT, and **c** the same area with the sediments removed from the turf algae near the ruler

when there is an increase in the accumulation and retention of sediments within the short, productive algal turfs that are commonly targeted by herbivores (Goatley et al. 2016; Speare et al. 2019; Duran et al. 2024). Data from the National Oceanic and Atmospheric Administration's National Coral Reef Monitoring Program (NOAA NCRMP) show that sediment-laden algal turfs now cover > 30% of the benthos across Florida's reefs (NCRMP 2018), and other data show up to 60% cover of LSATs at some reefs (Speare et al. 2019; Duran et al. 2024). Changes in south Florida's benthic community composition mirror global patterns suggesting that low-lying algal turfs are increasing in abundance and poised to dominate future reef systems (Tebbett et al. 2023). The increasing abundance of LSATs coincides with declines in reef accretion, and the vast majority of reefs in southeast Florida are now in a state of net erosion, with some locations losing as much as ~ 8.5 kg of calcium carbonate m^{-2} $year^{-1}$ (Toth et al. 2018; Morris et al. 2022).

Declines in reef accretion on Florida's reefs will likely further weaken positive feedback processes that promote recovery and expose a nuanced challenge for Florida's reefs–grazing by parrotfishes. Thirty years of legal protection have allowed south Florida reefs to house some of the largest and most abundant parrotfish populations in the Western Atlantic (Shantz et al. 2020; Zuercher et al. 2023). Grazing and removal of algae ('realized function' sensu Bellwood et al. 2019) are key ecosystem functions important for controlling macroalgal growth. However, intense grazing by parrotfishes can also negatively affect coral recruit survival via incidental mortality (Edmunds 2023), serving as a potential mechanism limiting coral recovery. Additionally, without reef accretion grazing by parrotfishes can increase net bioerosion and the loss of structural complexity (Molina-Hernádez and Álvarez-Filip 2024). The loss of complexity promotes the establishment of low-lying algal turfs that when containing high sediment loads can impair coral growth, reduce recruitment, and thus hinder reef recovery (Speare et al. 2019). Due to the lack of vertical relief and an increasing supply of sediments from terrestrial (Fabricius 2005; Erftemeijer et al. 2012) and biological (Bruggeman et al. 1994; Perry et al. 2020) sources, algal turfs eventually become saturated with sediment and are avoided by parrotfish, which in turn are hypothesized to redirect grazing to increasingly scarce rugose areas and further accelerate reef flattening (Tebbett et al. 2020a, b). Collectively, coral mortality, reef flattening, and intense grazing appear to have created a series of negative feedback processes that reinforce a flat, sediment-laden benthos that impedes the recovery of already diminished coral populations. Below, we outline this destructive cycle and provide support for the mechanisms that drive these feedbacks. Here we focus on the ecological context of Florida reefs; however, our conceptual framework, which extends the existing resilience paradigm in the Western Atlantic, will likely apply to other reef systems in the Caribbean with similar ecological attributes. Although sediment-related processes on Indo-Pacific reefs are important (Tebbett and Bellwood 2019; 2021), resilience processes are markedly different (Roff & Mumby 2012) and therefore the application to these reefs is unclear.

Processes on contemporary coral reefs give rise to negative feedbacks

Coral mortality redistributes grazing pressure and promotes bioerosion

When corals die, their skeletons are often rapidly colonized by algal turfs (Diaz-Pulido and McCook 2002; Leggat et al. 2019) and endolithic communities (Tribollet et al. 2006). Turf communities are often highly productive and palatable to herbivores (Carpenter 1985; Aedy and Goertemiller 1987; reviewed in Tebbett and Bellwood 2021) while the endolithic communities that develop in the upper layer of the dead coral skeleton can be rich in protein, lipids, and limiting nutrients (Clements et al. 2017). Parrotfishes that target epilithic algal turfs and endolithic communities are broadly classified as scrapers and excavators (Bellwood and Choat 1990; Clements et al. 2017; Adam et al. 2018), feeding behaviors that remove calcium carbonate material and contribute to bioerosion (Fyrdl and Stearn 1978; Bruggemen et al. 1994; Molina-Hernández et al. 2022). Five of the nine most common parrotfish species in Florida (*Sparisoma viride, Scarus guacamia, Sc. coelestinus, Sc. vetula,* and *Sc. taeniopterus*) feed primarily through scraping and excavating the benthos (Adam et al. 2018). Estimated bioerosion rates for *Sc. vetula* and *Sc. viride,* the parrotfish species with the highest potential to contribute to bioerosion, range from ~ 85 to 250 kg ind^{-1} $year^{-1}$, respectively, for individuals 41–50 cm in total length (Molina-Hernández and Álvarez-Filip 2024). Similarly, recent work in the Mexican Caribbean revealed that the loss of structural complexity from recently dead corals was positively associated with the presence of parrotfish grazing scars (Molina-Hernández et al. 2022). Thus, the robust parrotfish populations present on Florida's reefs have the potential to remove a substantial amount of calcium carbonate and complex structure from the reef (Morris et al. 2022).

Sediment retention decreases resource quality and availability, further concentrating grazing intensity on existing structure

As the calcium carbonate structure of coral skeletons is removed, reefs may lose vertical complexity (Alvarez-Filip et al. 2009; Bozec et al. 2015; Molina-Hernández et al.

2022). Steeper slopes, such as the near-vertical angles on the sides of dead coral colonies, retain less sediment, whereas sediment retention increases with decreasing vertical complexity (Tebbett and Bellwood 2019). Furthermore, these flatter surfaces facilitate the development of turf communities that easily trap sediments (Duran et al. 2018). Ultimately, these losses in complexity help transform more heterogeneous benthic communities comprising areas with short productive algal turfs and LSATs toward a flat, homogenous, LSAT-dominated reef state.

In turn, sediment retention within algal turf communities on increasingly flat reefs can likely impact grazing via numerous mechanisms. Increased sediment loads can reduce primary productivity (Clausing et al. 2014; Tebbett and Bellwood 2020), with one study from the Great Barrier Reef finding that sediment addition can decrease the potential yield of algal turf biomass by 2000% (Tebbett et al. 2018). Beyond severely reducing resource availability, sediment retention within algal turfs and the formation of LSATs decreases resource quality (Tebbett et al. 2020a, b) and may suppress the recruitment and growth of macroalgae predicted to increase under classic resilience paradigms (Umar et al. 1998). Foraging theory dictates that diminished resource quality requires parrotfish to graze more to acquire the same level of nutrition, effectively increasing parrotfish grazing pressure without a corresponding increase in the biomass or abundance of the population (MacArthur and Pianka 1966). Lastly, sediment loading in algal turfs reduces resource accessibility (i.e., burial by sediments), redistributing and potentially concentrating grazing pressure to other areas of the reef (Clausing et al. 2014; Tebbett et al. 2020a, b). Ultimately, sediment retention serves to reduce rates of herbivory and promotes the formation of LSATs (Fig. 2; green arrows) (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Clausing et al. 2014).

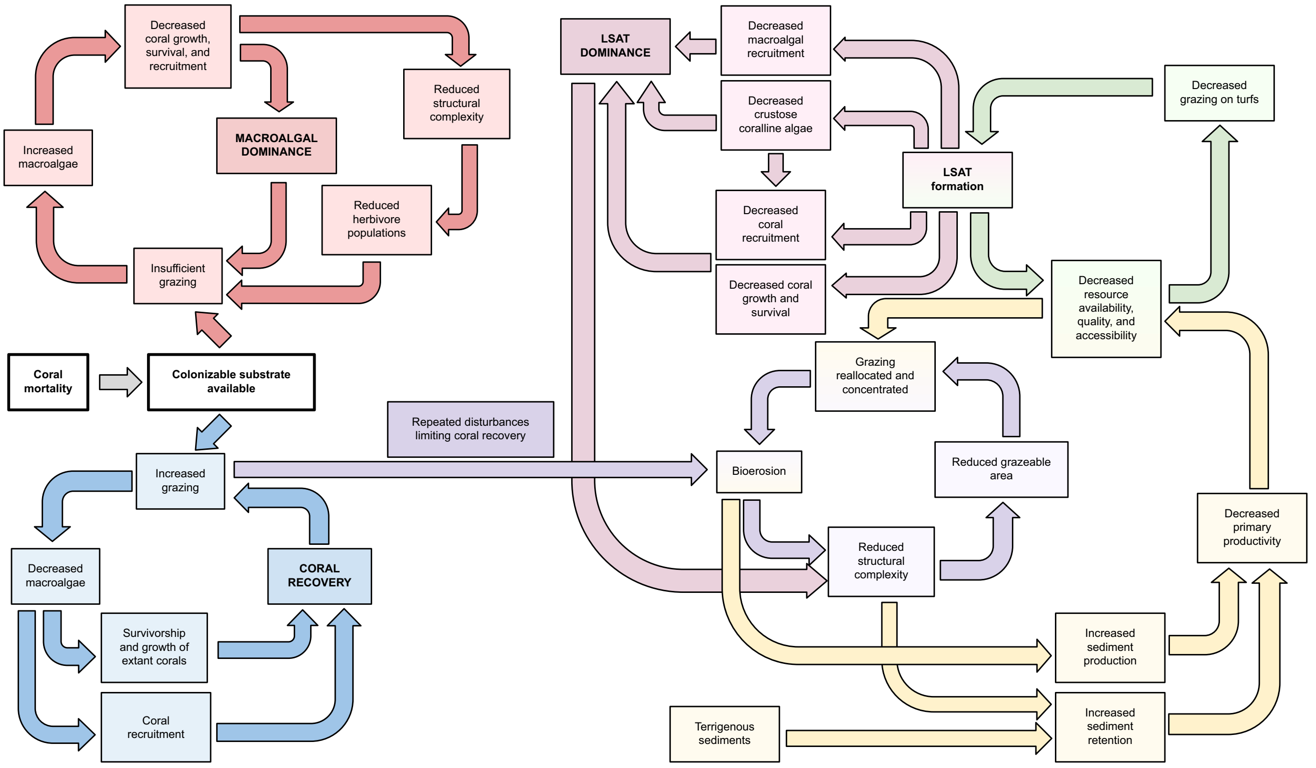

Fig. 2 Conceptual diagram illustrating top-down pathways of coral reef benthic community trajectories under different ecological conditions. Following a coral mortality event, substrate is liberated and available for colonization by benthic organisms (white boxes, gray arrow). Blue arrows and boxes represent a simplified traditional resilience pathway in which sufficient herbivory prevents macroalgal colonization and facilitates coral recruitment and recovery. Red arrows and boxes depict recovery failure whereby insufficient herbivory allows a transition to macroalgal dominance and inhibition of coral recovery. Here, we propose a third, distinct recovery failure pathway operating on reefs in Florida: Despite high parrotfish biomass, coral populations remain extremely low due to persistent disturbances and disease. Under this pathway, high grazing intensity and limited coral recovery initiates a series of reinforcing feedbacks underpinned by bioerosion and reef flattening (purple), sediment generation and retention (yellow), diminished resources for herbivores (green), promoting the formation of long-sediment-laden algal turfs (LSATs; pink). Each set of colored arrows represents a discrete feedback mechanism hypothesized to reinforce LSAT dominance and suppress coral recovery. Collectively, these feedbacks define a novel ecosystem state that is not captured by traditional reef resilience paradigms

Moreover, a reduction in herbivory on areas where LSATs develop would intensify grazing pressure and spatially concentrate them to a smaller area of the reef where LSATs are not present (i.e., areas with more structural complexity), creating an accelerating negative feedback (Williams et al. 2001; Vergés et al. 2011). In turn, the removal of structurally complex reef framework and the loss of vertical relief reduce the total surface area available for grazing and eliminate high-relief areas that support more productive and accessible algal communities (Tebbett and Bellwood 2019). Simultaneously, grazing by scraping and excavating parrotfishes can both rework existing sediments and generate new sediments via the ingestion of reef framework (Bruggeman et al. 1994). For example, applying recently developed sediment budgets to parrotfish surveys conducted in the upper Florida Keys by Shantz and Ladd (2024) suggests parrotfish may have generated between 250 and 1250 g of sediment per m^{-2} year^{-1} for at least the past decade (Perry et al. 2023; Fig. 3). Much of these biogenic sediments can be deposited back onto the reef (Bruggeman et al. 1994; Tebbett et al. 2017; Perry et al. 2020; Molina-Hernández et al. 2022), where they may be retained in algal turfs and further reinforce the sediment-driven feedback (Fig. 2; yellow arrows).

A novel ecosystem state: LSATs proliferate, accelerate coral decline, and inhibit recovery

Sediments can directly impact corals at all life history stages (Rogers 1990; Fabricius 2005; Risk 2014). Sediments can reduce coral growth rates and cause the partial or complete mortality of colonies through various mechanisms (reviewed in Fabricius 2005; Erftemeijer et al. 2012; Tuttle

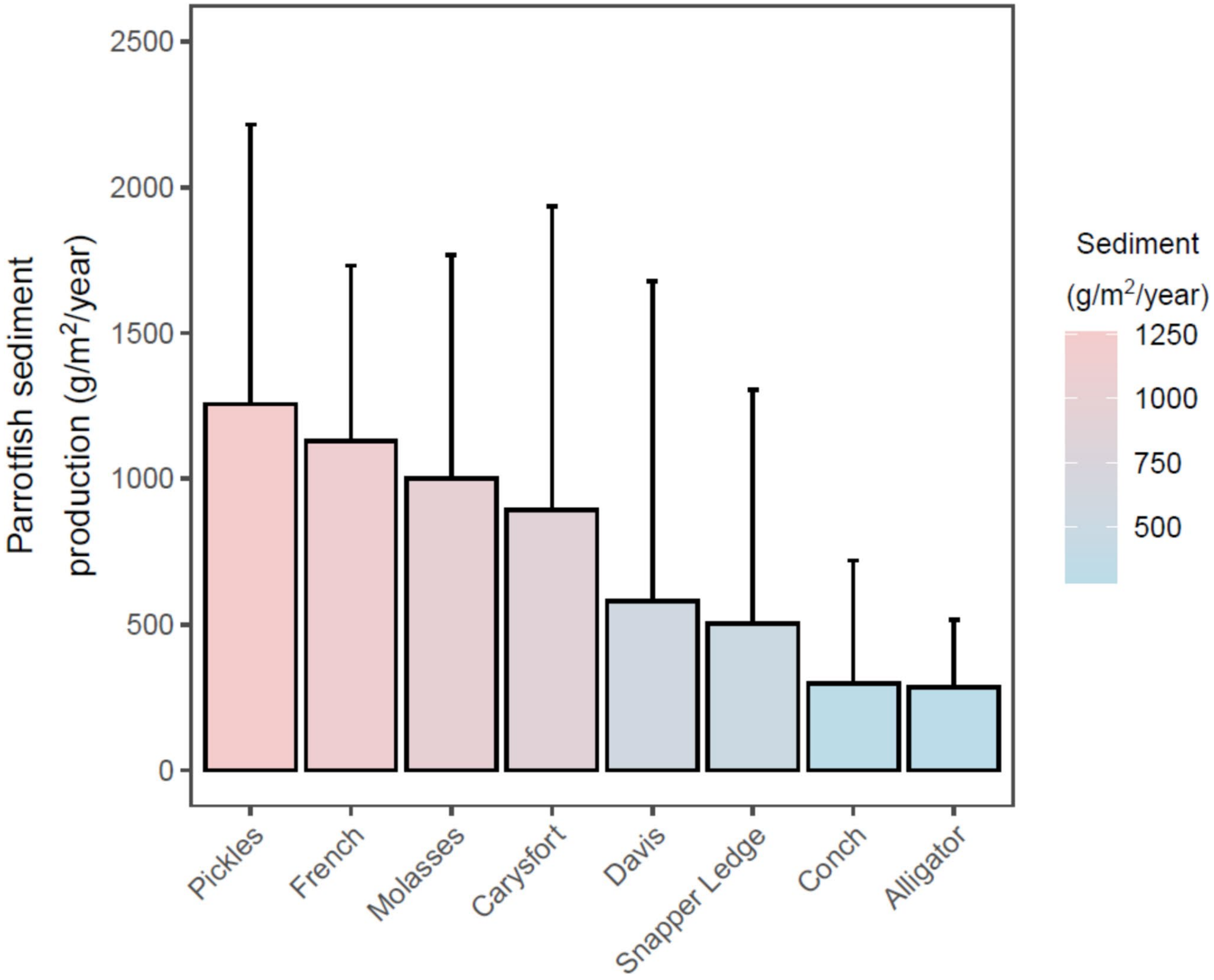

Fig. 3 Mean estimated sediment production (g m^{-2} year^{-1}) by parrotfishes at eight reef sites in the Florida Keys, USA. Error bars are ± SD. Estimates were generated using the sediment budget tool from Perry et al. (2023) and data from parrotfish surveys conducted in the Upper Florida Keys and reported in Shantz and Ladd (2024)

and Donahue 2022). Additionally, sediments can serve as a reservoir and vector for coral disease (Studivan et al. 2022). Beyond impacting coral populations, sediments trapped in algal turfs can inhibit coral recruitment (Birrell et al. 2005; Wakwella et al. 2020), a fundamental process for reef recovery. On reefs in the Florida Keys, multiple studies have found that juvenile coral abundance is negatively related to LSAT cover and that sediment-laden algal turfs can drastically reduce the settlement of major framework-building species in the Caribbean like *Acropora palmata* and *Orbicella faveolata* (Speare et al. 2019; Duran et al. 2024). Indeed, Speare et al. (2019) found that sediments in algal turfs reduced the settlement of *O. faveolata* larvae by 99% compared to turf algae alone. Additionally, the one study that has assessed the impacts of sedimentation on coral recruits in the Caribbean found that just 60 mg cm^{-2} of sedimentation reduced the survival probability of 5-month-old *Porites astreoides* to 0%, providing a substantial barrier to the recovery of coral populations (Founrey and Figueiredo 2017). In addition to directly reducing settlement, the establishment of LSATs can further reduce the potential for coral recruitment by decreasing the abundance of crustose coralline algae, an important group of benthic taxa that can promote coral recruitment (Duran et al. 2018). Cumulatively, increased sediment retention and abundance of LSATs are likely to drive further declines in coral populations and inhibit their recovery via additional coral mortality and diminished coral recruitment, further strengthening the negative feedback processes that help to lock Florida's reefs in a degraded state of continued decline (Fig. 2; pink arrows). However, this dominance by LSATs and the consequences for ecosystem functions differ from the traditional degraded state of high macroalgal cover.

The challenges of protecting parrotfishes on contemporary coral reefs

If protecting parrotfishes increases the bioerosion of valuable natural capital (three-dimensional reef structure) while simultaneously generating sediment that contributes to the cover of LSAT, the question arises of whether the ban on parrotfish fishing should be reconsidered. In isolation, there is general agreement that protecting parrotfish is a beneficial management action: There is evidence that parrotfish populations can increase when fishing pressure is removed, which increases grazing intensity, decreases macroalgal cover, and increases coral recruitment and cover in the absence of disturbances or other stressors that limit recovery (Mumby et al. 2006, Mumby et al. 2007b, Mumby and Harborne 2010; but see Bruno et al. 2019). Furthermore, experiments in Florida have shown that exclusion of parrotfishes quickly leads to high coral mortality and reefs being overgrown with macroalgae (Shantz et al. 2020) while research in areas where coral recruitment remains high has shown parrotfish are critical components of coral recovery following disturbances (Adam et al. 2014; Donovan et al. 2023). Thus, in places like Florida the problem is not necessarily too many parrotfish, but likely the decoupling of parrotfish grazing and natural coral recovery processes. If we remain optimistic about the future of reefs in the region and believe that overarching threats such as climate change and water quality will be addressed, then an intact parrotfish population will be needed to allow coral to recover.

In this light, removing protections from parrotfishes makes little sense. Ultimately, protecting parrotfishes is one of the most successful coral reef public awareness programs in the region. The increased knowledge of reef resilience, incorporating recognition of the importance of parrotfishes in the absence of a significant recovery of *Diadema* (Mumby 2006), has been clearly messaged to coastal communities. In addition to Florida, fishing bans have been established in over half the countries polled in a regional review, including Barbuda, Belize, Bermuda, and Honduras (Harms-Tuohy 2021). There has been no systematic effort to quantify the benefits of this policy across locations, but regional analyses are promising (Shantz et al. 2020). Indeed, large-scale analyses are challenging because of the difficulties of identifying complex trophic cascades (Mumby et al. 2022), especially across broad biophysical gradients (*e.g.*, gradients of nutrient enrichment and sediment load; Suchley et al. 2016). However, the policy is supported by theory and localized case studies (Mumby et al. 2006; Suchley and Alvarez-Filip 2017; Steneck et al. 2018; Shantz et al. 2020). Changing an effective policy sends potentially damaging messages to the public, generates confusion, and may weaken trust between coral reef managers and local resource users.

Rather than protecting parrotfishes being a policy that should be modified, it represents an interesting case study of how well-meaning conservation initiatives can have unintended consequences if instigated in isolation. A holistic approach to conserving reefs requires all global and local stressors including, climate change, water quality, disease, and overfishing of all species to be addressed (Hughes et al. 2003). In contrast, protecting parrotfishes alone maintains or increases bioerosion. Yet, coral recovery is limited by factors such as bleaching events, disease, sediment load, low coral larval supply, and high recruitment mortality (Hughes et al. 2003; Bellwood et al. 2004; Manzello et al. 2015; Edmunds 2023; Duran et al. 2024). Thus, while protecting parrotfishes can lead to the unintended consequence of reducing three-dimensional structure on reefs where corals fail to recover, this represents a failure of our efforts to address other stressors rather than an inherent problem with protecting parrotfishes. There is a growing literature on the unintended consequences of conservation, which can be categorized as flow effects (enhancing or dampening a preexisting linkage), deletion effects (removal of a preexisting linkage), or addition effects (adding new elements to a system; Larrosa et al. 2016). For example, the flow effect of protecting parrotfishes and enhancing bioerosion of three-dimensional reef structure on Florida's reefs is analogous to the protection of green turtles (*Chelonia mydas*) in the absence of natural shark predation pressure, which has led to overgrazing of seagrass that affects fish populations and carbon sequestration (reviewed by Jones et al. 2022). These unexpected ecological dynamics underscore the urgent need for fundamental research to quantify and better understand the ecological links and feedbacks that promote and stabilize LSAT-dominated ecosystem states on coral reefs (Fig. 4).

Between a rock and a hard place

While we support the protection of parrotfish in Florida and elsewhere, we must also be realistic and recognize that solving all the problems currently facing reefs appears intractable as we enter the Anthropocene (Hughes et al. 2017). Pushing to solve these problems remains critical, and begs the question whether there are other approaches to minimize the negative effects of parrotfish bioerosion. One effort that is well underway in Florida and elsewhere is coral restoration (reviewed by Boström-Einarsson et al. 2020). When successful, outplanting corals can shift carbonate budgets from negative to positive by allowing reef accretion to outpace bioerosion (Lange et al. 2024). Increasing coral cover also reduces the area available for LSAT growth and potentially generates microhabitats suitable for natural coral settlement. However, the success of coral restoration is inevitably limited while the stressors causing coral mortality remain (Hughes et al. 2023). A potentially useful complementary approach to coral restoration may be structural restoration of the complex habitat that is being lost (Yanovski & Abelson 2019). Indeed, a suite of studies has established strong links between structural complexity and coral recruitment across different spatial scales (mm to m; Edmunds et al. 2014; Carlson et al. 2024). Moreover, corals demonstrate increased success when elevated from the seafloor (Lenihan et al. 2011) and are not in contact with sediments (Clements et al. 2024), suggesting that incorporating structural restoration may be particularly important for locations like Florida where LSATs dominate. Beyond restoration, we encourage efforts to rebuild predator populations

LONG SEDIMENT-LADEN ALGAL TURFS: KNOWLEDGE GAPS & RESEARCH PRIORITIES

FORMATION & STABILITY

Knowledge Gap: Understanding mechanisms that underpin LSAT formation and stability

Research Priorities:

Drivers of sediment accumulation and retention:
- Substrate slope and surface characteristics
- Turf characteristics (composition, height, and density)
- Sediment source/grain size, water flow, resuspension rates, turbation rates

Successional dynamics of LSATs:
- Changes in turf composition as LSAT develops and stabilizes

Sedimentary processes and their relative contribution to LSAT:
- Sediment source: terrestrial vs. reef sediment
- Sediment origin: reworked vs. newly generated sediment
- Role of parrotfish in turf-sediment dynamics

PREVALENCE & DISTRIBUTION

Knowledge Gap: Identify thresholds and tipping points of LSAT prevalence across spatiotemporal, biological, and abiotic gradients

Research Priorities:

Spatial and seasonal patterns of LSAT:
- Reef zones and habitat type
- Structural relief, distance from sediment sources
- Seasonal changes in LSAT composition and abundance

Biological drivers:
- Existing benthic community composition (e.g., coral vs. macroalgal vs. turf-dominated)
- Herbivore abundance, biomass, and composition

Abiotic drivers:
- Depth, wave energy, nutrients
- Sediment size and sediment characteristics

IMPACTS TO ECOSYSTEM FUNCTIONS

Knowledge Gap: Impacts of LSAT on ecosystem functions and ecological processes

Research Priorities:

Direct effects:
- Growth and survival of corals and other benthic organisms
- Interactions with substrates that promote coral settlement (e.g., crustose coralline algae)
- Primary productivity, nutrient cycling and storage, energy transport higher trophic levels
- Fish behavior and distribution

Indirect effects:
- Abiotic conditions (e.g., hypoxia or anoxia, accumulation of contaminants)
- Microbial dynamics (e.g., potential to serve as a reservoir for disease agents, retain/promote bloom-forming organisms, alter nutrient cycling and primary productivity)

REVERSAL & RESTORATION

Knowledge Gap: Strategies to break feedbacks that promote LSAT establishment and reinforce LSAT dominance

Research Priorities:

Herbivore restocking:
- Ability of diverse herbivore assemblages (e.g., urchins, crabs) to reduce turf cover without reinforcing sediment dynamics

Structural enhancement:
- Reduce sediment retention, increase coral recruitment, combat effects of bioerosion

Bioturbators and detritivore enhancement:
- Prevent/reduce formation and stability of LSATs; make turf algae more accessible to herbivores

Fig. 4 Knowledge gaps and research priorities that should be addressed to better understand the mechanisms underpinning the formation, stabilization, prevalence, and impacts of LSAT-dominated states on coral reefs while protecting parrotfishes. Abundant predators, such as large groupers, can reduce the abundance of smaller parrotfish through consumptive effects (Mumby et al. 2006). Due to few long-term datasets, it is very difficult to compare current parrotfish biomasses and behaviors to historical norms, but it is reasonable to assume that historically top-down controls were significantly greater. Finally, we encourage further research investigating the functional differences among parrotfishes (*e.g*., Adam et al. 2018) as this translates to a better understanding of how ecological processes vary in space (Randazzo-Eisemann et al. 2024), but also potentially through time as benthic characteristics change.

Conclusions

Florida's coral reefs exemplify the complex, compounding challenges confronting coral reef ecosystems in the Anthropocene. Here, we propose that LSATs form a series of self-reinforcing negative feedback processes that suppress coral recruitment, accelerate the loss of structural complexity by redistributing grazing pressure, and contribute to the persistence of degraded reef states that do not have high macroalgal cover. Notably, these feedbacks can emerge even under conditions typically associated with resilience—such as high herbivore biomass and low macroalgal cover—exposing critical gaps in prevailing reef resilience paradigms for the Western Atlantic (Mumby & Steneck 2008; Hughes et al. 2010).

Furthermore, large areas of reef covered in LSAT, rather than macroalgae, may represent a poorly recognized ecosystem state for reefs in the region, analogous to concerns that cyanobacterial mats may dominate some reefs (de Bakker et al 2017). In contrast to macroalgal dominance where scenarios, such as the recovery of *Diadema*, could significantly reduce macroalgae and kick-start natural recovery processes, it is not clear what biological process could change LSATs back to high productivity turf areas. While our model is grounded in Florida's ecological and disturbance history, the underlying drivers—chronic coral mortality, reef flattening, sediment retention, and bioerosive grazing—are increasingly prevalent throughout the Caribbean and beyond. Similar benthic transitions have been documented across multiple reef systems (Tebbett et al. 2023), suggesting that LSAT dominance may represent a more widespread ecosystem state on degraded reefs, particularly where herbivory remains high but recovery potential is constrained by overlapping stressors.

The ecological consequences of LSAT dominance are significant. These reefs exhibit reduced structural complexity and are unlikely to sustain the biodiversity, fishery productivity, or shoreline protection typically associated with coral-dominated systems (Alvarez-Filip et al. 2009; Graham & Nash 2013). While LSATs may support turf-associated species and provide minimal sediment stabilization, these limited functions are unlikely to compensate for the loss of foundational reef ecosystem services. Furthermore, managing LSAT-dominated reefs requires embracing the inherent complexity of conservation in an era of layered local and global stressors. Rather than reversing successful policies such as parrotfish protection, a more integrative management strategy is needed—one that simultaneously addresses sedimentation, water quality, climate change, reef restoration, and grazer functional diversity (Burkepile and Hay 2008). As reef degradation intensifies, LSAT-dominated states may become increasingly common, necessitating a shift in focus from recovery alone to also preventing the entrenchment of these low-functioning states.

To predict and manage the emergence of LSAT dominance, a targeted research agenda is urgently needed to tease apart the feedbacks and ecological dynamics highlighted in this review. To build this knowledge base, we suggest four main themes of LSAT-focused research: (1) formation and stability, (2) prevalence and persistence, (3) impacts to ecosystem functions, and (4) reversal and restoration (Fig. 4). Ultimately, the rise of LSATs challenges us to refine reef resilience theory and reframe management goals—not only around enabling coral recovery, but also around disrupting feedbacks that stabilize degraded states and limit the ecological and functional recovery of coral reef ecosystems.

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Author contributions ML and AD conceived the idea of the paper. All authors contributed to manuscript writing.

Data availability No datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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