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REVIEW ARTICLE

Employing invertebrates to restore herbivory on Caribbean coral reefs: recent developments and remaining barriers

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With coral reefs in global decline and further threatened by growing anthropogenic impacts, effective strategies for restoring these critical ecosystems are increasingly sought after. In Caribbean reefs, where disease outbreaks and fishing pressure have reduced herbivore abundances and facilitated widespread phase shifts from coral to algal dominance, herbivorous invertebrates have gained recent attention as a promising restoration tool. However, many restoration practitioners face challenges in evaluating the feasibility and anticipated outcomes of integrating invertebrate herbivores into their programs. Here we review recent developments regarding species and techniques and identify remaining barriers that require further research attention before invertebrate enhancement can be considered a scalable strategy for restoring Caribbean reefs. Bottlenecks in mariculture processes remain in the larval and juvenile rearing stages for many species that impede the scalability of invertebrate production, with significant outstanding challenges across all species in terms of stocking effectiveness and monitoring feasibility. Integrating alternative herbivorous invertebrate species can ameliorate some of these bottlenecks, and investigating the culture feasibility and grazing effectiveness of additional species holds notable research opportunities. Across research and restoration initiatives, ecological objectives and viable techniques for measuring outcomes against these objectives are needed. These findings establish research priorities for restoration and invertebrate husbandry communities alike and provide guidance for practitioners in the critical and rapidly evolving field of coral restoration.

Key words: Caribbean, coral reef restoration, grazer, herbivory, invertebrates

Implications for Practice

- Restoring herbivory on Caribbean coral reefs through enhancing invertebrate species is increasingly promoted as part of reef restoration strategies.
- Recent research and developments have illuminated the potential of several invertebrate species and made many culture techniques more feasible.
- Numerous bottlenecks still limit the scalability of this approach as a reef restoration tool.
- Substantial research is still required to improve stocking and monitoring techniques and to inform restoration strategies based on ecological effectiveness.

Introduction

Herbivory is a critical process in coral reef ecosystems, whereby the grazing of algae facilitates the health, growth, and recruitment of corals by clearing substrate and suppressing physical and chemical competition (Hoey & Bellwood 2011). Numerous fish and invertebrate species play important and often complementary roles in this process (Burkepile & Hay 2008), promoting the abundance of stony corals that underpin coral reef ecosystems and the increasingly recognized ecosystem services that they provide (Rhodes & Naser 2021).

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In Caribbean reefs in particular, recent decades have been marked by alarming declines in coral reef health and widespread shifts from coral to algal dominance (Roff & Mumby 2012; Davis et al. 2021). These phase shifts have been facilitated by regional declines in herbivore abundances, most notably the disease-induced mass mortality of the herbivorous urchin *Diadema antillarum* in 1983–1984, during which 98% of these previously abundant grazers were lost across the Caribbean (Lessios 2016). Increasing fishing pressure on many Caribbean reefs has led to declines in populations of herbivorous fish, including parrotfish, which are considered a target species on many islands due to cultural preferences and declining populations of larger predatory fish (Mumby et al. 2012). In some cases, the declines in herbivore abundances have been accompanied by increases in nutrient inputs, such as land-based fertilizers and septic run-off, which fuel algal growth and improve their competitive dominance over stony corals (Thanopoulou et al. 2022).

In response to these trends, efforts to restore Caribbean reefs have increased throughout the region. While programs propagating and replanting stony corals have become abundant, these initiatives face limitations when cultivated corals are planted in the algal-dominated conditions of many of today's reefs, often resulting in low long-term coral survival (Boström-Einarsson et al. 2020). The need for restoration approaches that restore other ecological functions on coral reefs, such as herbivory, is increasingly recognized (Ladd et al. 2018).

Herbivorous fish populations are effective in maintaining bare or cropped macroalgal communities (Arnold et al. 2010); however, their ability to do so when fleshy macroalgae are established can be limited due to the physical and chemical defenses of many algal species in their mature forms (Suchley & Alvarez-Filip 2017). Moreover, local fishing pressures, aquaculture challenges, and the lack of regulatory enforcement in most Caribbean nations make restoring herbivorous fish populations a challenging approach to reversing phase shifts back to coral dominance (see Butler et al. 2024 for a discussion of fish restoration efforts). One solution that has been gaining attention is increasing populations of herbivorous invertebrates. Invertebrate grazers such as urchins and crabs have shown to be effective non-selective grazers of turf and macroalgae, including mature species of algae considered non-palatable to herbivorous fish (Francis et al. 2019). Invertebrate grazers such as urchins and crabs are also typically less commercially sought after than herbivorous fish, though opportunistic fisheries do exist for some urchin and crab species. While still an evolving field, the use of invertebrate herbivores in coral reef restoration has demonstrated potential in recent years (Spadaro & Butler 2021; Williams 2022; Pilnick et al. 2023b). However, many restoration practitioners face challenges in evaluating the feasibility of integrating invertebrate herbivores into their programs. In this review, we highlight recent developments regarding species and techniques utilized and identify remaining barriers that require further research attention before invertebrate enhancement can be considered a scalable strategy for restoring Caribbean reefs. To provide context for our findings and discussion, we first present a brief review of invertebrate grazer species in the Caribbean and their current and prospective utility in restoration applications, followed by definitions of different invertebrate restoration pathways. We then identify recent improvements and outstanding obstacles at each stage of the restoration process and compare findings across species. We follow with an in-depth discussion of methods for establishing goals and evaluating restoration outcomes.

Current and Prospective Invertebrate Grazer Species

Several species of invertebrates have been considered for restoration due to their grazing capacity, historical densities, total algal consumption, diet preferences, and foraging behaviors. Sea urchins (class Echinoidea) are often targeted because of their important roles as herbivores on Caribbean reefs (Ogden & Lobel 1978). The urchin species *Diadema antillarum* has been the primary focus of many herbivore restoration efforts to date (Table 1) due to their high historical densities and their documented ability to graze down macroalgae and facilitate coral growth and recruitment (Edmunds & Carpenter 2001; Myhre & Acevedo-Gutiérrez 2007; Idjadi et al. 2010).

Following the mass die-off of *D. antillarum* in 1983 and the more recent disease outbreak in 2022–2023 (Hylkema et al. 2023), the role of other invertebrate grazers in controlling algal growth has been investigated (see Butler et al. 2024 for a detailed comparison of grazing rates and ranges), and several have recently been introduced into active restoration programs. The urchin *Echinometra viridis*, for example, is an influential herbivore on many Caribbean reefs (Kuempel & Altieri 2017; Shulman 2020), especially where other herbivore populations have been depleted (Sangil & Guzman 2016). They have been shown to greatly reduce macroalgal cover on leeward reefs when in high densities (Shulman 2020) and have been positively correlated with coral cover in some studies (Bologna et al. 2012). While *E. viridis* exhibits far more cryptic behavior and can be less effective in controlling exposed algae than *D. antillarum* (McClanahan 1999), recent studies suggest they can have comparable grazing impacts, though they may need to be stocked at higher densities (Sangil & Guzman 2016; Shulman 2020; Butler et al. 2024). *Echinometra* spp. are known to be bioeroders (Brown-Saracino et al. 2007), which, when exceeding coral reef carbonate production, can have negative implications for reef structure and integrity (Glynn & Manzello 2015) and should be considered when developing strategies to utilize these species for the purposes of reef restoration.

Tripneustes ventricosus, an urchin that is often associated with seagrass beds as well as coral reefs, is also being increasingly considered for and incorporated into reef restoration efforts. The species can better cope with chemically defended and calcified species of macroalgae (Francis et al. 2019) and has been observed on reefs that were previously dominated by *D. antillarum*, foraging on mature macroalgae that are less preferred by other herbivores (Haley and Solandt 2001). While a slower per capita grazer than *D. antillarum*, *T. ventricosus* is a promising restoration tool as an effective consumer of algal communities of varying species and successional stages and has been shown to positively impact coral growth in ex situ experiments where *D. antillarum* had negligible impacts (Dakin et al. 2024).

Several studies have also illuminated the capacity of herbivorous crabs to control algal proliferation, especially within the

Table 1. Documented herbivorous invertebrate stocking efforts by technique across four primary candidate species.

	Diadema antillarum	*Echinometra viridis*	*Tripneustes ventricosus*	*Maguimithrax spinosissimus*
Assisted natural recovery	Hylkema et al. (2022a)			
Translocation	Nedimyer and Moe (2006) Macia et al. (2007) Burdick (2008) Dame (2008) Wynne (2008) Ripple (2017) Delgado and Sharp (2021) Chiappone et al. (2021) Olmeda-Saldaña et al. (2021) Pilnick et al. (2023b, 2023a)	Williams (2023)		Spadaro and Butler (2021)
Culture from settlers	Hylkema et al. 2022b) Williams (2016) Williams (2018) Williams (2022) de Breuyn et al. (2023) Wijers, van Herpen et al. (2024)			
Culture from gametes	Wijers, van Herpen et al. (2024)	Williams (2023)	Williams (2023)	

Mithracidae family (Coen 1988; Stachowicz & Hay 1999; Spadaro & Butler 2021). Although nearly all species within this family are reef-dwelling grazers, *Maguimithrax spinosissimus* has become a primary restoration candidate due to their large size and ability to consume macroalgae at rates exceeding that of nearly all other fish and invertebrate grazers in the region (Spadaro & Butler 2021), though studies explicitly related to the restoration of this species remain limited (Table 1). *Maguimithrax spinosissimus* grazes on species that other herbivores often avoid, such as calcified and chemically defended algae, ultimately reducing algal cover by 50–85% while significantly increasing coral recruitment and enhancing reef fish community abundance and richness (Spadaro & Butler 2021). While their ecological impacts are less documented, other mithracid species are worth considering in reef restoration efforts. For example, *Mithraculus* spp. living in *Porites divaricata* thickets off the coast of Belize reduced algal epibiont cover from 75 to 10% (Coen 1988), while *Mithraculus forceps* exhibits a similar mutualistic relationship with *Oculina arbuscula* coral hosts (Stachowicz & Hay 1999). The grazing rates of multiple *Mithraculus* spp. crabs, particularly *M. coryphe*, approach those of the larger-bodied *M. spinosissimus* when scaled for biomass and occur at much greater natural densities when appropriate habitat conditions are available (Spadaro 2019).

Many other invertebrate grazers live on coral reefs and are native to the Caribbean (Carpenter 1997). However, very little is known about their ecology, and restoration efforts have not yet been attempted. Further investigation of the herbivory dynamics of these complex ecosystems and the cultural feasibility of additional species will help identify priority candidates for consideration in restocking efforts.

Population Enhancement Techniques

Numerous approaches have been used to enhance local invertebrate herbivore abundances (Fig. 1). These different approaches vary greatly in terms of the level of resources and expertise required, as well as in scalability and efficacy.

Translocation

Translocation simply entails collecting adult invertebrates from one location and moving them to another location. The simplicity of this approach relative to other population enhancement techniques has made it by far the most utilized in existing herbivore restoration studies (Table 1). While this approach can be valuable for understanding the potential ecological impacts of increased invertebrate abundances (Chiappone et al. 2021; Olmeda-Saldaña et al. 2021; Spadaro & Butler 2021) as well as responding to highly localized disturbances such as ship groundings, employing this approach for broader restoration efforts could have detrimental effects on existing natural populations, including reductions of spawning capacity, particularly for species like *D. antillarum* where overall abundances are low compared to historical distributions. Thus this approach should be treated with caution and not considered for restoration at larger scales.

Assisted Natural Recovery

Assisted natural recovery (ANR) is the process of enhancing the settlement of invertebrate larvae in situ (Hylkema et al. 2022a). For *D. antillarum*, this has included specialized settlement substrates such as bio-balls (Hylkema et al. 2022b) that promote larval settlement by providing appropriate settlement surfaces and structures. The substrates can also increase post-settlement survival by providing shelter in the first vulnerable weeks after metamorphosis, as well as suitable feed for the settlers. This approach can only be successful in regions with high larval supply and requires information on spatial and temporal settlement patterns to maximize efficacy (Klokman & Hylkema 2024). Local ecological conditions can also influence the utility of this approach, including macroalgal abundance which has been shown to reduce successful

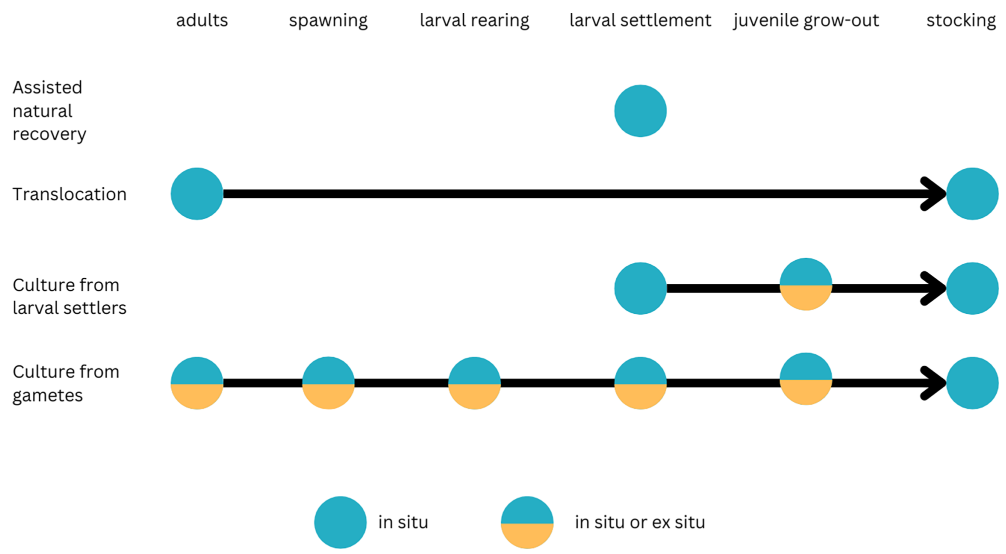

Figure 1. Current techniques for enhancing populations of herbivorous invertebrates. Circles represent the life stages of each population enhancement technique, with blue indicating stages performed in situ and blue and yellow representing processes that can be conducted either in situ or ex situ. The juvenile grow-out process includes post-settlement care.

D. antillarum recruitment by providing habitat for micropredators (Williams et al. 2011).

Culture From Settlers

Similar to ANR, specialized settlement substrates are used to promote larval settlement of invertebrates in the wild, but these settlers are then collected from the substrates, reared in land-based nurseries (Williams 2016, 2022) or in in situ structures (Brittsan et al. 2023), and stocked on the reef as young adults. Apart from *D. antillarum*, other urchins and crabs also recruit to the mid-water collectors, though typically in lower abundances. More data are needed to determine the efficiency of this approach for other species and to understand the potential influences of timing, location, and substrate on settlement species.

Culture From Gametes

In the most intensive but controlled approach, gametes are collected from the spawning of adult invertebrates and then reared through larval settlement and juvenile grow-out until they reach a sufficient size to be stocked in wild habitats. For *D. antillarum*, this approach has required extensive research and refinement and has only been completed in ex situ environments, particularly because of the sensitivity of larvae and settlers and the relatively long (approximately 40-day) duration of the larval phase (Pilnick et al. 2021, 2022). *Tripneustes ventricosus* and *E. viridis* urchins have also been successfully cultured from gametes ex situ, with less challenging larviculture processes than *D. antillarum* due to shorter larval durations (approximately 24 [Williams 2023] and 12 [Astudillo et al. 2005] days, respectively) and smaller, less fragile larval structures. *Maguimithrax spinosissimus* crabs have an even shorter larval duration, with approximately 5–6 days between hatching and the first crab (Turini et al. 2021). The culture of *M. spinosissimus* from gametes has been done successfully both in situ and ex situ, with egg-bearing females separated from other broodstock and placed in cages with fine mesh screens (in situ) or in isolated seawater tanks (ex situ) to collect larvae once hatched.

Recent Developments and Remaining Barriers in Restoration Processes

Much progress has been made in recent years to facilitate the numerous steps involved in rearing and stocking herbivorous invertebrate species. However, notable challenges and areas for further research remain. Figure 2 visualizes these barriers and knowledge gaps in the context of four primary species candidates.

Broodstock Maintenance and Spawning

Refinements in maintaining and spawning broodstock populations have made these processes relatively reliable across herbivore species of interest (Fig. 2). Many sea urchins have distinct reproductive cycles characterized by seasonal changes in gametogenesis and spawning time (Walker et al. 2015). Adult food quality and quantity also strongly influence reproduction; high protein content diets, for example, have been shown to directly increase gonad growth rates (Russell 1998; Lawrence & Lawrence 2004). Reproductive adults can be conditioned to produce gametes and spawn year-round in ex situ systems by manipulating temperature and photoperiod regimes and providing high-quality live macroalgae and/or formulated diets. Spawning of conditioned urchins can be reliably induced with potassium chloride injections, but additional methods, including acetylcholine injections (Guete-Salazar et al. 2021), physical agitation of broodstock individuals, and temperature changes (Pilnick et al. 2021), have also been used successfully. In depauperate species like *D. antillarum*, heat shock treatments where ex situ broodstock populations are exposed to increased water

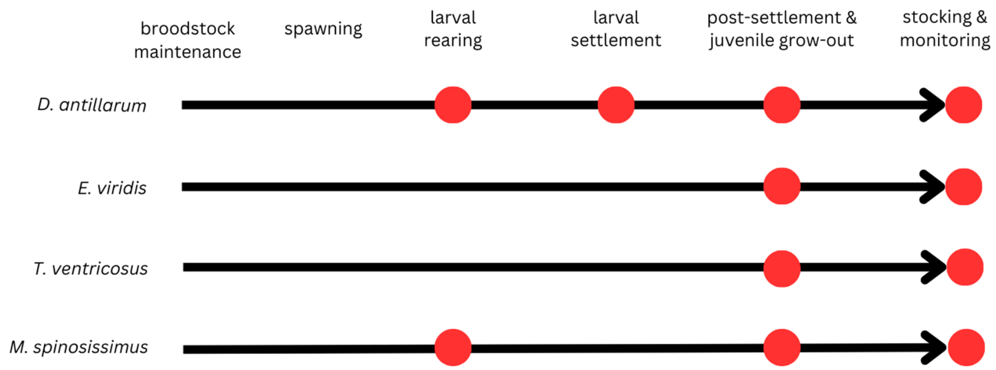

Figure 2. Current barriers (red circles) within herbivore enhancement processes across four primary candidate species. The stocking and monitoring stage remains a barrier across all species, while post-settlement and juvenile grow-out also pose many challenges and opportunities for further research.

temperatures after a period of cool temperatures to mimic seasonality may be preferred as a less invasive method with a lower risk of morbidity or infection. It is possible to spawn wild adults in a similar manner directly after collection without maintaining a broodstock population year-round in ex situ systems (Wijers et al. 2023); however, attempts are more likely to succeed during natural reproductive periods.

In *M. spinosissimus* culture, the transportation and maintenance of broodstock populations posed initial challenges, but insights into water quality sensitivities—particularly dissolved oxygen—have reduced these barriers. When housed ex situ, food is provided strategically to avoid water quality deterioration, and sufficient water circulation at night ameliorates potential water quality issues when unconsumed macroalgae switch from photosynthesis to respiration. Maintaining broodstock in cages in situ can ameliorate some water quality concerns, depending upon culture location, and improved cage designs and placement can reduce the risk of predation from octopus and other species. In some culture from gamete programs, ovigerous females are collected from wild populations, which reduces the challenges of maintaining broodstock populations but may also limit production depending on the availability of berried females and accessibility to collection sites.

Spawning any species ex situ requires consideration of implications for the genetic diversity of offspring populations as well as genetic impacts on wild populations (Lorenzen et al. 2010; Kettenring et al. 2014). Smaller-scale culture programs, such as those currently producing invertebrates for reef restoration purposes, typically group spawn, where broodstock individuals are placed in a single container before gametes are released and fertilized eggs are collected. This method is not ideal for maximizing genetic diversity, as it is unlikely that broodstock individuals will contribute equally to the captive-reared cohort. Alternative techniques will need to be integrated into future large-scale restoration efforts to enhance genetic diversity among offspring and avoid inbreeding, including maximizing the number of and genetic diversity among parents, balancing the contribution among parent pairs, and collecting and exchanging wild broodstock at regular intervals. Parentage analyses can help inform these strategies by determining the effective genetic contribution from spawning broodstock and the diversity of the captive-reared cohort. Additional research is also required to understand the genetic structure of wild populations and potential discord with the genetic structure of stocked populations. *Diadema antillarum* populations, for example, are well mixed from the Upper Keys to Dry Tortugas (Chandler et al. 2017), so the risk of introducing potentially negative traits from cohorts spawned from Florida Keys broodstock is low, but little information exists regarding genetic structures of populations in other geographic areas and for populations of other invertebrate species discussed here.

Larval Rearing

The rearing of larvae once hatched poses significant challenges for both *D. antillarum* and *M. spinosissimus* restoration (Fig. 2). Several features of *D. antillarum* larvae make them particularly challenging to rear, and while new techniques have greatly improved outcomes, it remains a hurdle in efficient *D. antillarum* culture. *Diadema antillarum* larvae are both negatively buoyant and physically fragile, with arms prone to breaking when in contact with hard surfaces and/or turbulent shear (Pilnick et al. 2021; Wijers et al. 2023). Ex situ survival rates were incredibly low until the development of techniques to suspend larvae in the water column, such as the shaker bottle method (Wijers et al. 2023) and the use of pseudo-Kreisels (Pilnick et al. 2021). Insights into optimum nutrition have increased larval survival rates of *D. antillarum* (Pilnick et al. 2022; Wijers et al. 2023), though *D. antillarum*, *E. viridis*, and *T. ventricosus* all have planktotrophic larvae that require exogenous food resources during development, and the process of culturing algal food supplies is an additional cost in the rearing process. *Diadema antillarum* are also particularly sensitive to water quality issues such as the presence of heavy metals, requiring precise and reliable filtration systems and monitoring (Bielmyer et al. 2005). The exceptionally long larval duration of *D. antillarum* means that these physical, chemical, and nutritional sensitivities must be ameliorated over an extended period of time (Pilnick et al. 2022). While ongoing research and developments have facilitated success in culture from gamete programs in recent years, the process remains relatively intensive regarding required resources and technical experience, making it less accessible to many practitioners. The shorter larval durations and less sensitive larvae of *T. ventricosus* and *E. viridis* facilitate simpler and more effective larval rearing than *D. antillarum* (Fig. 2; Cameron 1986; Creswell 2011; Guete-Salazar et al. 2021).

Rearing the larval stages of *M. spinosissimus* also poses numerous challenges for restoration programs. Low survival rates among larvae are thought to be attributed to both predation (including cannibalism) as well as physical loss through screens and cage openings (Creswell et al. 1986). Ex situ culture can ameliorate some of these challenges, particularly regarding loss of larvae, but requires stringent practices to maintain stable and consistent chemical and physical water quality parameters, as noted above. Luckily, *M. spinosissimus'* larval stage is only a few days long, and the lecithotrophic larvae do not require external food sources, reducing the time and intensive care necessary during this sensitive phase (Turini et al. 2021). To reduce predation of larvae across urchin and crab species, algae introduced to tanks or cages as food for larvae must be carefully inspected and cleaned to prevent other predatory organisms from entering. Alternatively, algae may be cultured, which adds complexity and scope to the system as the mass of algae required to feed cultured crabs at scale is substantial.

Larval Settlement

Larval settlement has been a limiting factor in *D. antillarum* restoration outcomes in many ANR, culture from settler, and culture from gamete programs, though recent insights are shedding light on this process (Fig. 2). In ANR and culture from settler programs where settlement is occurring in situ, advancements have increased settlement efficiency. A comparison of settlement substrates revealed that *D. antillarum* settles on a variety of substrates, but settlement is highest on bio-balls and doormat materials (Hylkema et al. 2022b). If employed in the settlement season, which varies slightly throughout the Caribbean but seems to be April through September in Curacao (Vermeij et al. 2010), Puerto Rico (Williams et al. 2009), St. Eustatius (Hylkema et al. 2022b), and Saba (Klokman & Hylkema 2024), collection can be relatively efficient if settlement hotspots are identified (Williams et al. 2011; Hylkema et al. 2022b; Klokman & Hylkema 2024). In any in situ settler collection program, natural larval supply is inherently variable and highly sensitive to changes in wild populations, such as the 2022 *D. antillarum* mortality event.

In ex situ culture from gamete programs, provision of the microalgae *Rhodomonas lens* leading up to settlement supports the development of physiological traits indicating metamorphic competency (Pilnick et al. 2023a). Cues from two calcareous algae, *Halimeda* spp. and crustose coralline algae (CCA), induced the highest settlement rates among other cues provided ex situ, while ceramic tiles or Petri dishes overgrown with biofilm provided an effective combination of physical and chemical cues (Pilnick et al. 2023a; Wijers, van Herpen et al. 2024). Programs working with *E. viridis* and *T. ventricosus* have had fewer challenges settling larvae than with *D. antillarum*, with substrates fouled with biofilm and CCA proving successful in facilitating settlement (Williams 2023). Preliminary evidence suggests *Ulva* spp. and *Thalassia testudinum* may act as settlement cues for *T. ventricosus*, while peyssonnelids such as *Ramicrusta* spp. may deter settlement (Williams 2023).

Post-Settlement and Juvenile Grow-Out

The grow-out of post-settlement and juvenile organisms to sizes sufficient for restocking is a notable constraint in the scalability of restoration programs across species, particularly in the sensitive period immediately following larval settlement to the benthos (Fig. 2). Low survival rates in these stages are challenging for *M. spinosissimus* restoration and likely result from post-settlement predation, cannibalism, and/or nutritional deficits relative to diets sufficient to support proper molting. Further, gut chemistry shifts with ontogeny in *M. spinosissimus*, complicating the provision of effective diet composition in the species (Chávez-Rodríguez et al. 2020). Similar to the larval stages, mortalities in *D. antillarum* post-settlement juveniles are attributed to water quality sensitivities, predation, and suboptimal nutrition (Vaughan 2010; Williams 2020; Pilnick et al. 2022).

Across all species, space and practical limitations of life support systems can limit the scale of ex situ culture programs. Insufficient space can stunt (or limit) growth, facilitate disease and parasite infections, and lead to physical damage and physiological differences among individuals, such as low urchin spine density (Sharp et al. 2018) or increased cannibalism among crustaceans (Romano & Zeng 2017). The large amount of waste produced by high concentrations of invertebrates also poses a substantial water quality challenge in ex situ systems. One solution currently being investigated is the integration of multiple trophic levels in the culture system. Integrated Multi-Trophic Aquaculture (IMTA) systems that marry aquaculture with hydroponics (e.g., "aquaponics") are now common approaches, with the increasing inclusion of algae in these production systems (Ridler et al. 2007; Knowler et al. 2020). With the production of grazers for restoration, the IMTA model presents an interesting opportunity to capitalize on the nitrogenous waste of the culture target to produce turf and macroalgae, which can, in turn, be used to feed the herbivorous or omnivorous grazer species.

A major determinant of scale and system capacities is the size that herbivores are reared to before release. While larger individuals typically experience lower predation rates once released, they require increasing financial, labor, and space investment for grow-out. Finding the ideal size for stocking involves estimating size-dependent mortality curves for each species in each location and, potentially, habitat type to both minimize the investment in culture and maximize post-release survival and retention (Spadaro 2019; Spadaro & Butler 2021). For *M. spinosissimus*, these parameters were estimated in the Florida Keys using 24-h tethering assays on forereef and patch reef habitats (Spadaro 2019; Spadaro & Butler 2021). In both habitat types, a strong inflection point in the mortality curve by animal size was observed at approximately 30 mm carapace width (CW), where mortality rates decreased from approximately 80 to 20%, offering a clear target for juvenile grow-out operations.

While tethering assays have limitations (Baker & Waltham 2020), similar low-cost and direct measurements of predation risk by size should be conducted in each restoration location with each species to confirm that the target stocking size is appropriate and that resources and time are not wasted growing juveniles beyond the necessary size nor by stocking juveniles at an inappropriately small size.

An additional concern during the grow-out stage is developing "natural" or "wild" behaviors in cultured individuals, such as sheltering, diurnal activity patterns, and other antipredator responses (Sharp et al. 2018). While early iterations of *D. antillarum* culture ex situ tended to produce 'naive' individuals with different diurnal activity patterns and sheltering behaviors, recent modifications in hatchery protocols, including natural photoperiod exposure and shelter provisioning, have produced urchins with no significant behavioral differences from wild urchins (Sharp et al. 2023). In *M. spinosissimus*, *T. ventricosus*, and *E. viridis* culture, further research is required to evaluate potential behavioral differences between wild and hatchery-reared individuals and to potentially develop conditioning practices to mitigate these differences.

Stocking

One of the biggest barriers to effective restoration across invertebrate species is stocking individuals in wild habitats (Fig. 2). Many stocking efforts have resulted in low retention of introduced invertebrates, with several initiatives resulting in no detectable changes in invertebrate populations after as little as a few weeks and no ecological impacts sustained over time (Burdick 2008; Wynne 2008; de Breuyn et al. 2023; Butler et al. 2024). Part of this challenge stems from the fact that these invertebrates, particularly *D. antillarum* and *M. spinosissimus*, can be highly mobile. Individuals may disperse from or may not survive at stocking sites due to a lack of appropriate shelter (Dame 2008; Delgado & Sharp 2021; Pilnick et al. 2023b) or preferred foods (Williams 2020), high predator densities (Nedimyer & Moe 2006; de Breuyn et al. 2023; Steneck & Torres 2023; Wijers, Klokman et al. 2024), predation susceptibility due to size or naivete (Sharp et al. 2018), deterrence by aggressive competitors such as damselfish (Williams 2020), excessive wave activity (Tuya et al. 2007), or conspecific densities that are too high (e.g., resource competition and territoriality) or too low (e.g., disrupting antipredator behaviors) (Fig. 3). Using corrals or cages may enhance localized retention and facilitate the detection of ecological impacts, though these can impose additional operational and regulatory challenges and escapes do occur (Williams 2020). In a pair of *M. spinosissimus* translocation experiments, isolated patch reefs surrounded by open sand and hard bottom were successful in retaining a sufficient density of individuals to demonstrate ecological impacts of these enhanced herbivore populations over 1 year with cascading effects of the manipulation apparent through 2 years (Spadaro & Butler 2021). Another successful translocation experiment showed 22.5% retention of *D. antillarum* after 9 months, with significant impacts on macroalgal abundances observed at nearly 3 months (Pilnick et al. 2023b). These successes may have been influenced by habitat architectural complexity, the density and distribution of restocked individuals (placed in clusters), or the fact that individuals were translocated as adults already habituated to local environments. In contrast, other efforts to stock invertebrates cultured ex situ have struggled to retain individuals and, thereby, to detect ecological changes (Butler et al. 2024). The degree of philopatry and the ecological and physical factors that influence these patterns should be of primary importance when selecting restoration species and locations.

Determining whether restocked individuals emigrated, died, or are simply inconspicuous is another notable challenge for some of these relatively cryptic species, particularly when habitats have high levels of complexity. Tagging and telemetry present challenges regardless of the species in question. *Diadema antillarum*, for example, has demonstrated limited tag retention and/or low survival rates with streamer, t-bar, and pit tags all proving unreliable for long-term tracking of urchins (Rodríguez Barreras & Sabat 2015), though recent pilot studies using pit tags in large individuals suggest more promising results. *Maguimithrax. spinosissimus* and other crustaceans present a challenge in ecdysis, as any external tag is lost when the animal molts. Visible implant elastomer tags have been used to successfully track individual crabs through time (Spadaro 2019; Spadaro & Butler 2021), but the tagging process is expensive and labor-intensive. For urchins, this approach is not feasible as they have too little tissue on the outside of the test to insert the elastomer tags. Active telemetry is of great interest to better understand daily movements and home ranges of crustacean grazer species, but the hallmarks of appropriate habitat for many of these grazers (e.g., high rugosity or architectural complexity) tend to make using acoustic telemetry challenging or reduce the accuracy and precision of signal detection and tracking, while high associated costs are prohibitive to many programs. Effective tagging methods continue to challenge our understanding of invertebrate reef grazer movement and behavior and should be a priority for research and development moving forward.

Establishing Goals and Evaluating Outcomes

As discussed above, monitoring the effectiveness of herbivore restocking programs in increasing herbivore populations poses its own set of logistical challenges. However, a critical task in using herbivore stocking for restoration purposes at scale is to define ecological goals and subsequently measure success. We provide a framework for the various stages of this process in Figure 4.

Identifying and quantifying restoration targets in the context of dynamic and varying ecosystems is extremely challenging. In the case of *D. antillarum*, for example, restoration targets might be based on restoring population abundances to those common on Caribbean reefs prior to the 1983 mass mortality event, but the vast majority of Caribbean reef ecosystems have since undergone massive changes in herbivorous fish populations, reef rugosity, and macroalgal communities. Arguably, herbivory beyond that provided by pre-mortality *D. antillarum* populations would be required to restore overall reef function,

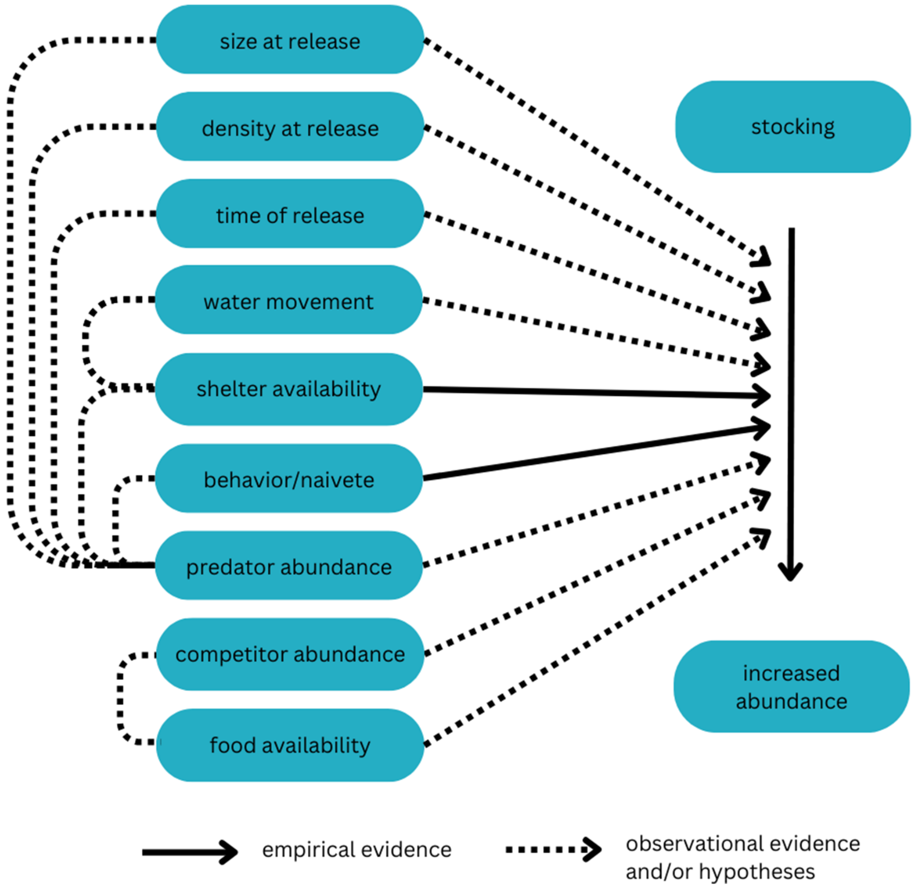

Figure 3. Factors demonstrated through empirical evidence (solid lines) or observed and/or hypothesized (dashed lines) to impact the retention of stocked invertebrates at restoration sites. Potential interactions among factors are indicated on the left-hand side. For example, the relevance of invertebrate size and predator abundance to retention are likely interdependent.

both in terms of grazing pressure and also inferably herbivore diversity. Most discussions of the effect of grazing manipulations focus on algal cover as the main effect. While this is certainly a relevant outcome, defining restoration targets may focus instead on shifting to an early successional community assemblage. In an algal community dominated by algal turfs, appropriate herbivore populations can graze productive early successional algae at rates that match algal production, maximizing energy transfer and minimizing biomass in the algal community to support high diversity in higher trophic levels (Carpenter 1986). Modeling approaches offer potential insights into setting these restoration targets, where grazing rates by species and ontogenic stage are coupled with site-specific algal community dynamics and bathymetry to estimate the number and combination of herbivores required to consume approximately 100% of daily algal productivity. Species diversity across functional niches can not only increase the grazing impact of restored herbivore communities but can also increase the resilience of these restored communities to future threats, such as disease outbreaks, in tandem with efforts to maximize the intraspecific genetic diversity of stocked individuals.

Once target herbivore abundances are established, determining stocking densities requires the consideration of numerous additional dynamics, as introduced previously. First, the attrition of stocked invertebrates due to both mortality and emigration is a major barrier to effective restoration and can be influenced by numerous factors, including predator–prey dynamics, food and shelter availability, hydrology, and the size and behavior of stocked individuals themselves (Fig. 3). Appropriate and effective tagging to measure movement and home range with respect to local conditions would inform stocking density and frequency of subsequent stocking events to maintain density and abundance. Understanding intraspecific population dynamics such as reproduction, competition, senescence, and diseases is also required to establish self-sustaining populations that maintain ecological function and will inform not only total stocking numbers but components such as sex ratios and ontogenetic stages. It is also important to consider that stocking will need to be adaptively managed as algal communities change. For example, initial stocking densities may need to be very high to impact established macroalgal-dominated communities, with lower densities needed as benthic communities shift toward lower successional stages. Similarly, late-successional algal communities may require a different

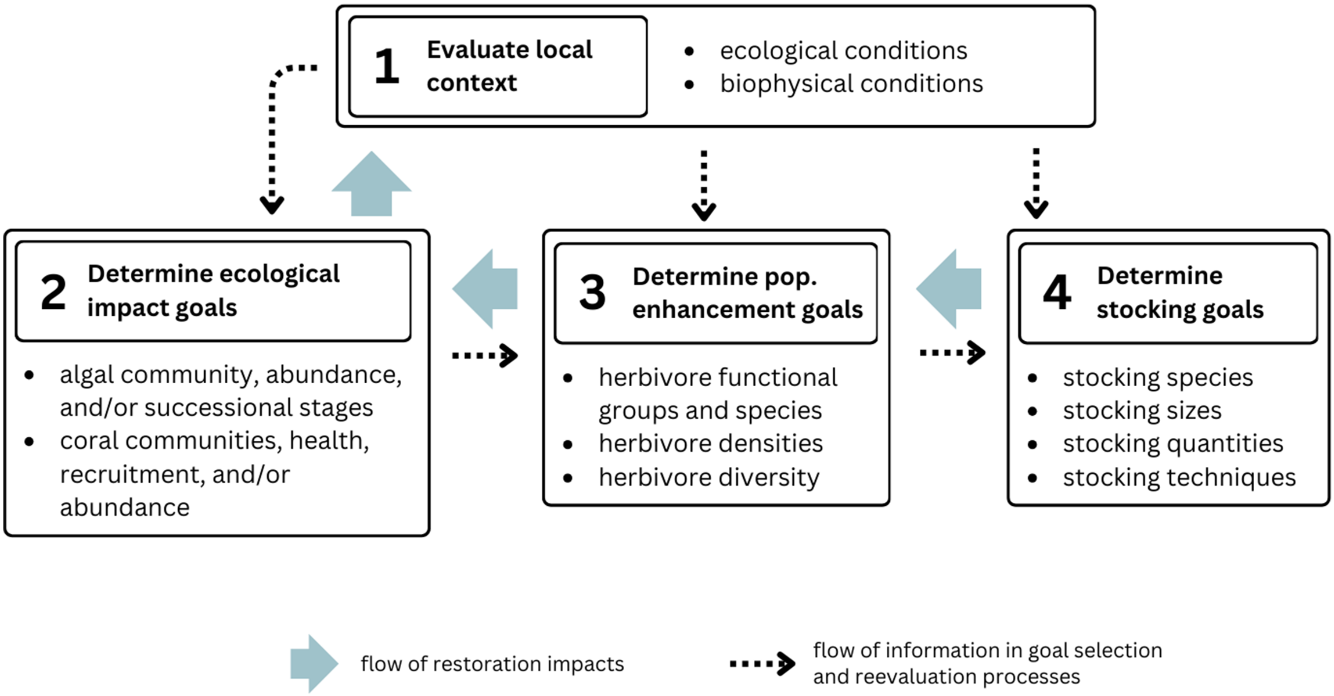

Figure 4. An ordered process for establishing stocking, population enhancement, and ecological impact goals, including the flow of information informing these decisions (dashed arrows) and the flow of impacts within the restoration process (solid arrows).

herbivore assemblage than early-successional algal communities, and, thus, the relative abundance of grazer species may adjust (or need to be adjusted) as the effect of herbivore restoration proceeds through time and/or space.

Determining whether stocking is effective in meeting targeted ecological outcomes requires monitoring not only stocking treatment but also ecological effects. Advancing our communal understanding of this field calls for monitoring that is as consistent and comparable across practitioners as possible. One tool that facilitates this is Structure from Motion (SfM) and photogrammetric monitoring technology and methods, dramatically increasing the potential precision of monitoring data over the past two decades (Bayley & Mogg 2020; Couch et al. 2021). While photo and visual quadrat sampling has afforded researchers the ability to track changes in the distribution and composition of the benthic algal community in response to disturbances and restoration interventions, SfM provides a mode of not only increasing the precision, accuracy, and spatial scale of data that can be collected within a short period of time, but also offers the capability to monitor changes at high spatiotemporal resolution in time series. As technology and methods continue to advance and develop, the richness of data available from the imagery grows as well. The ability to share imagery across monitoring programs and use consistent processing and analysis methods is an invaluable asset in enhancing data comparability.

Stocking any reared organisms in wild habitats incurs the risk of unintended negative consequences. In the case of herbivorous invertebrates, these potential impacts include excessive grazing pressure that causes net bioerosion on reefs and/or damages newly settled coral recruits (Sammarco 1980; Perry et al. 2013, 2014). In certain conditions, the disadvantage of bioerosion could start to outweigh the positive effects of coral recruit facilitations, especially on reefs where recruitment remains low due to low numbers of spawning corals. Changing the abundance and functional diversity of herbivores also runs the risk of driving shifts in algal communities that are not necessarily facilitative of coral-dominated ecosystems, such as species that are resistant to grazing or potentially aggressive coral competitors such as peyssonnelid algal crusts. Increasing densities of any species also increases the potential for disease outbreaks, which are particularly detrimental to invertebrates such as *D. antillarum*. Stocking may also increase the abundance of predators that target larval and post-settlement individuals, essentially preventing these populations from persisting locally. Close monitoring of the ecological consequences of pilot stocking treatments with different densities and species distributions is imperative in understanding the potential negative impacts that these programs may generate.

Conclusion

Whether meaningful ecological change can be driven by invertebrate herbivore restoration will depend primarily on the retention of stocked invertebrates and the scalability of rearing programs. As illuminated here, stocking and monitoring are major barriers across species, with significant knowledge gaps around factors that limit retention and how it can be improved. The most successful rearing programs can only be so valuable if reared individuals do not survive in the wild, and production output will need to be that much higher if the majority of stocked individuals do not persist on reefs. Monitoring of both stocked individuals and their potential ecological impacts has been extremely limited and almost exclusively restricted to translocation studies, which do not account for further potential issues with transitioning ex situ-reared individuals to wild environments. While the number of species being investigated for the purposes of herbivory enhancement has increased somewhat in recent years, significant knowledge gaps remain around the ecological implications of stocking different species or different species assemblages.

Once the species and abundance of stocked individuals needed to attain ecological goals are better understood, scalable and cost-effective rearing programs will be required to meet these targets in ecologically meaningful contexts. While barriers in production processes for several herbivore species have been increasingly overcome in recent years, numerous opportunities for improvement remain, notably in the larval rearing and post-settlement stage of *D. antillarum* and *M. spinosissimus*. A major bottleneck for the scalability of herbivore restoration across species is the juvenile grow-out stage, which, depending on the target size of individuals produced, is still extremely resource intensive. Data to inform optimum size at release as well as integrated production systems that can minimize or repurpose waste products will be imperative in scaling this production stage. A better understanding of the rearing processes and feasibility of an increasing diversity of herbivorous invertebrate species will increase the resilience of restoration efforts to ongoing threats and changing environmental conditions.

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