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Restoration of herbivory on Caribbean coral reefs: are fishes, urchins, or crabs the solution?

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That coral reefs are in decline worldwide, particularly in the Caribbean, will come as no surprise. This decades-long decline has reached a potential tipping point as the weight of the effects of climate change have come decidedly to bear on the planet's most diverse marine ecosystem. Whether coral reefs can persist without restorative intervention is debatable, which has prompted a surge in coral reef restoration projects focusing primarily on the cultivation and transplantation of coral fragments onto degraded reefs. But that widespread approach does little to address the underlying causes of coral loss, one of which is the proliferation of macroalgae that are deleterious to corals. An emerging solution to this problem is the enhancement of herbivory on coral reefs through improved management of herbivores, artificial enhancement of herbivore settlement, or their mariculture and subsequent stocking. This review explores the nuances of the biology of well-studied Caribbean coral reef herbivores (fishes, sea urchins, and crabs) as it relates to their mariculture and investigates the promise of herbivore stocking onto coral reefs as a restoration strategy. Fish, urchin, and crab herbivores differ appreciably in life histories, which confers advantages and disadvantages with respect to their mariculture and effectiveness as grazers. Mariculture of herbivorous marine fish for reef restoration is essentially non-existent so the reestablishment of grazing fish abundance on coral reefs focuses primarily on their protection through fishery regulations, but only at a few locations in the Caribbean. Mariculture of herbivorous urchins and crabs for restoration purposes is in its infancy, but promising especially for crabs whose larval rearing is less difficult. Perhaps the biggest challenge for the mariculture of either taxon is "scaling-up" from research settings to large-scale mariculture needed for stocking. Numerous studies extol the benefits of functional redundancy and complementarity for coral reef ecosystem stability, but whether this principal applies to the restoration of grazing function is untested. We identify gaps in our knowledge of best practices for the restoration of grazing function on coral reefs and conclude with some practical guidance on the establishment of targets for macroalgal reduction, along with strategic advice on grazer stocking in a given reef habitat.

KEYWORDS

coral reef, grazer, herbivore, restoration, Caribbean

Caribbean reefs and herbivory

For 200 million years, scleractinian corals have created and maintained coral reefs - the largest, most complex biogenic structures on Earth that support >25% of the current global marine biodiversity (Kiessling, 2009; Kiessling et al., 2010). This diversity, in turn, contributes to a range of critical ecosystem services to humans including food provisioning, coastal defense, tourism, and recreational activities (Moberg and Folke, 1999). However, coral reefs have slid into a precipitous trajectory of decline during the current Anthropocene epoch (Done, 1992; Jackson, 1997). Worldwide, corals suffer from bleaching events caused by the increasing temperature of the ocean and compromised rates of calcification due to ocean acidification, both a consequence of climate change (Hughes et al., 2018; Godefroid et al., 2022). The synergistic effects of a rapidly changing climate along with local stressors such as hurricanes, eutrophication, overfishing, disease, and other disturbances have triggered the widespread loss of corals and a decline in the biological and architectural complexity of these ecosystems (Gardner et al., 2005; Alvarez-Filip et al., 2009; Harborne et al., 2017). The problems are so severe that the viability of coral reef ecosystems is now in question (Alvarez-Filip et al., 2015; Agudo-Adriani et al., 2019; McKay et al., 2022; Hoegh-Guldberg et al., 2023).

Coral reef degradation often manifests in a dramatic phase shift in benthic taxonomic dominance from corals to fleshy macroalgae (Done, 1992; Mumby, 2006a). This change, at least on Caribbean reefs, appears to represent a shift to an alternate stable state (Mumby and Steneck, 2008; Mumby et al., 2013). Macroalgae are natural components of coral reef ecosystems that serve beneficial ecological functions (Ortega et al., 2019; Fulton et al., 2020), but their overgrowth of reefs is indicative of degradation (Morand and Briand, 1996). Competition with macroalgae has a range of negative consequences for coral demographics, among them: reduced fecundity, inhibition of recruitment, suppression of growth, and reduced survival, all with deleterious cascading effects on ecosystem health (Rasher et al., 2011; Rasher and Hay, 2014; van Woesik et al., 2018; Monteil et al., 2020; Smith et al., 2022). The negative effects of macroalgae on corals result from direct interactions (e.g., shading, space pre-emption) as well as indirect mechanisms such as allelopathy (Birrell et al., 2008). Furthermore, once a reef becomes macroalgal dominated, a range of feedback mechanisms make it difficult for a reef to recover (Mumby and Steneck, 2008). For example, loss of three-dimensional structure limits grazing fish abundances, and fishes may avoid reef areas with high macroalgal density because of predation risks (Hoey and Bellwood, 2011; Dell et al., 2016; Davis, 2018). Thus on macroalgal-covered reefs, the sustainability of corals and their resilience to disturbance are compromised, particularly in the Caribbean (Mumby et al., 2007a; Roff and Mumby, 2012).

The importance of herbivory as a critical driver of macroalgal assemblages and, in turn, of coral assemblages was perhaps first recognized in the early 1960s (Randall, 1961). By the 1970s, sea urchins and several groups of reef fishes (e.g., parrotfishes, Scaridae; surgeonfishes, Acanthuridae) were identified as the major controllers of coral reef macroalgae (Figure 1; Sammarco et al., 1974; Ogden, 1976; Ogden and Lobel, 1978). Research in the 1980s explored coral-algae-herbivore relationships, demonstrating the positive indirect effects of herbivory on corals (Sammarco, 1980; Hay, 1981; Steneck and Watling, 1982; Steneck, 1983), exemplified by the sudden Caribbean-wide die-off of a prominent urchin grazer (*Diadema antillarum*) in 1983–84 that demonstrated the functional importance of herbivores on coral reefs (Lessios, 2016). The mass mortality of *D. antillarum* sparked an explosion of research on reef herbivory as evident in the threefold increase in publications following that event (Lessios, 2005). Still, there was scientific debate regarding the primacy of herbivory versus eutrophy in driving macroalgae abundance on coral reefs (Hughes, 1994; Lapointe, 1997; Hughes et al., 1999; Lapointe, 1999). Moreover, the importance of herbivory for the resilience of Pacific coral reefs is less clear than in the Caribbean (Roff and Mumby, 2012).

Although the importance of grazing as a key driver of reef resilience seems unequivocal (Mumby et al., 2007a), abundant herbivores may not guarantee high coral cover or low macroalgal cover. For example, in the absence of urchins even relatively unexploited parrotfish populations do not provide sufficient grazing pressure if nutrient levels are elevated or hurricane disturbances are frequent (Mumby et al., 2006a). Similarly, when coral cover becomes very low, even unexploited parrotfish populations may not provide sufficient grazing pressure to shift reefs toward coral-dominated states without additional grazing and improved coral recruitment (Mumby et al., 2007a).

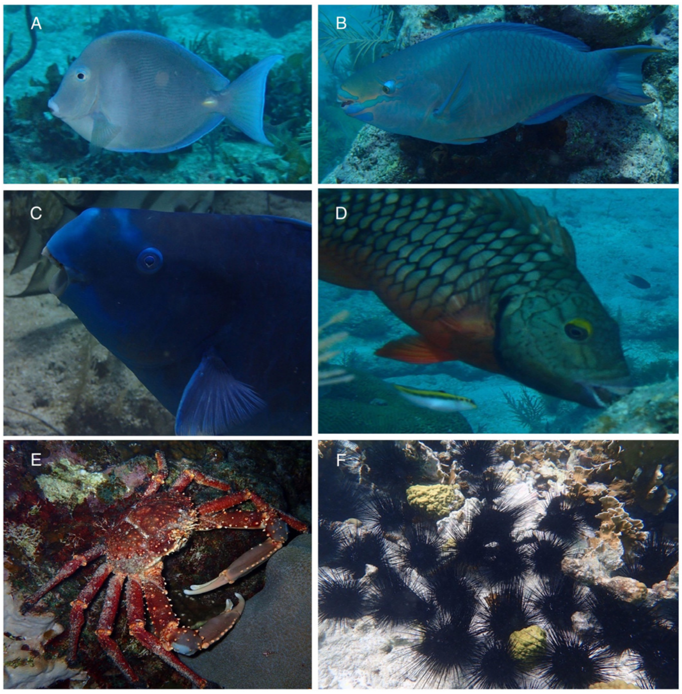

FIGURE 1
Photos of common Caribbean reef herbivores. **(A)** Blue Tang, *Acanthurus coeruleus;* Acanthuridae (photo credit: Alain Duran). **(B)** Queen Parrotfish, *Scarus vetula*; Scaridae (photo credit: Alain Duran). **(C)** Blue Parrotfish, *Scarus coeruleus*; Scaridae (photo credit: Alain Duran). **(D)** Stoplight Parrotfish (initial phase), *Sparisoma viride*; Scaridae (photo credit: Alain Duran). **(E)** Caribbean King Crab, *Maguimithrax spinosissimus*; Mithracidae (photo credit: AJ Spadaro). **(F)** Long-spined Sea Urchin, *Diadema antillarum*; Diadematidae (photo credit: Alwin Hylkema).

Finally, although models of Caribbean resilience are relatively well parameterized and tested for mid-depth forereefs, they may not necessarily apply to other habitats, such as shallow lagoonal patch reefs or sub-tropical reefs.

Responding to the growing threats to coral reefs, coral restoration programs have sprung up around the world with the intention of rebuilding the spawning stocks of reef-building corals by out-planting colonies grown in *in situ* nurseries or land-based "*ex situ*" facilities (Boström-Einarsson et al., 2020). The strategy of transplanting new corals onto degraded reefs has met with varying degrees of success (Boström-Einarsson et al., 2020), especially where macroalgae are abundant and retard the reestablishment of both transplanted and naturally recruiting corals.

In short, absent the proper benthic habitat conditions, the transplantation of corals to 'jump-start' reef recovery is doomed to failure (Arnold and Steneck, 2011). In response to this challenge, restoration science turned to two complementary objectives to increase reef herbivory: (1) regulate and better manage the fishing of piscine herbivores, and (2) restock invertebrate herbivores where their abundance has diminished. The latter alternative naturally centered on the re-establishment of *D. antillarum*, whose density in most locales never recovered to pre die-off levels (Lessios, 2016). In recent years, the potential importance of herbivory by a suite of other reef invertebrates has emerged, including urchins other than *D. antillarum* and a guild of herbivorous crabs in the Mithracidae family (Coen, 1988a, 1988b; Stachowicz and Hay, 1999a; Butler and Mojica, 2012; Francis et al., 2019; Spadaro and Butler, 2021; Zeinert et al., 2021). These findings have naturally led to consideration of invertebrate herbivores as agents of reef recovery through stock enhancement.

In contrast, the restocking of herbivorous fishes on reefs has few champions. Fish stock enhancement relying on aquaculture of young fishes, largely funded by recreational fishing fees, has a long history in freshwater, estuarine, and coastal marine systems (Lorenzen et al., 2010). But fishing of herbivorous reef fishes is generally not a recreational fishing activity. Instead, herbivorous fishes are landed by subsistence fishers, mostly in developing countries, or constitute bycatch in commercial trap fisheries (Shantz et al., 2020). So, the recreational fishery stock enhancement model is not easily transferred to coral reef systems.

The conditions required for the mariculture of reef fishes from eggs to the stocking of juveniles or adults are also considerably more complex and expensive than for most freshwater or coastal fishes that are stocked for recreational angling. This disparity due primarily to the longer pelagic larval duration and the open sea environment required for the successful larval development of most reef fishes. As an alternative, a few studies have investigated the potential use of postlarval fishes captured from the nearshore plankton as a means of assisting the restoration of fish assemblages, though not herbivorous fishes in particular (Heenan et al., 2009; Abelson et al., 2016; Cortés-Useche et al., 2021). This approach is based on the fact that fishes experience high mortality during the settlement and postsettlement phases of their life cycle, so their capture and *ex situ* rearing to a safer stocking size avoids that demographic bottleneck and the difficult task of rearing them from captive broodstocks. This methodology is still in its infancy but may become more feasible with advances in mariculture.

Instead, replenishing herbivorous reef fishes has focused on reducing their mortality from fishing through traditional fishery regulations or by establishing marine protected areas (Mumby et al., 2006a; O'Farrell et al., 2015), A controversial suggestion for solving the Caribbean's problem with macroalgal overgrowth is the intentional introduction of Indo-Pacific herbivores (e.g., Pacific rabbitfish) into the Caribbean (Bellwood and Goatley, 2017), but support for this approach is lacking because the introduction of non-indigenous species often poses significant ecological harm to marine ecosystems (Benkwitt, 2015; Alidoost Salimi et al., 2021).

Given our current state of knowledge, along with a glimmer of hope that political interest in the problem and adequate funding exist to advance this area of research, we offer a review and comparison of the biological and logistical advantages and disadvantages of the restoration of herbivores on coral reefs. We focus on the western Atlantic because many reefs in this region are targeted for restoration, much of the work on reef invertebrate aquaculture has occurred here, and the important role of herbivores on Caribbean coral reef ecosystems has been more clearly defined.

Coral reef herbivores: fishes, urchins, and … crabs?

Fishes

The pathogen-driven reduction in populations of *D. antillarum* on Caribbean reefs in the 1980s fundamentally changed herbivory patterns in the region (Jackson, 2001; Lessios, 2016). Herbivorous fishes that previously competed with *D. antillarum* (Carpenter, 1990) became key grazers of macroalgae (Hay and Taylor, 1985; Robertson, 1991). Parrotfishes (Scaridae; Figure 1), in particular, were identified as playing a primary role in regulating the abundance of macroalgae and turf algae and limiting the development of juvenile macroalgae into larger forms (Frias-Torres and van de Geer, 2015; Adam et al., 2018). However, parrotfishes are also bioeroders of coral reefs. Foraging by species such as *Scarus guacamaia* and *S. coelestinus* leave only superficial scars on the substrate and so are described as 'scrapers' (*sensu* Bellwood and Choat, 1990). But 'excavator' species (*sensu* Bellwood and Choat, 1990), such as *Sparisoma viride*, are important bioeroders because their mode of feeding removes portions of the underlying carbonate reef structure (Clements et al., 2016; Ruttenberg et al., 2019). Recent data from the Pacific suggests that at least some parrotfishes may be microphages that consume reef-bound microorganisms (Clements et al., 2016), but this work has not been replicated in the Caribbean. Despite nuances in the feeding preferences and patterns among species of parrotfish, combined they serve a powerful functional role in removing macroalgae from reefs.

Surgeonfishes (Acanthuridae; Figure 1) are another key family of grazing fishes, although they are much less well-studied than parrotfishes. Surgeonfishes mostly target turf algal assemblages (Duran et al., 2016), although the proportion of energy they derive from turfs, cyanobacteria, and other algae intermixed within the turf algae is unclear. A few species of damselfishes (family Pomacentridae) are also considered herbivorous (e.g., *Stegastes planifrons*), but their presence tends to increase rather than decrease benthic algae communities because they are "gardener species" that create and vigorously maintain small (~0.1 m^2) macroalgal patches on reefs (Sammarco and Carleton, 1982; Klumpp et al., 1987; Santodomingo et al., 2002). Because of their unique role in modifying macroalgal assemblages rather than removing them, we do not consider herbivory by damselfishes further in this review.

The degree of functional redundancy among herbivore fishes is far from clear, but the trophic differentiation, even among congeneric parrotfishes, suggests the importance of a diverse assemblage of species on healthy reefs (Bonaldo et al., 2014; Adam et al., 2015). For example, when both parrotfishes and surgeonfishes are present, benthic algal assemblages are mostly turf algae rather than macroalgae-dominated, which translates into associated benefits to corals (Burkepile and Hay, 2010). Even when targeting different food sources, herbivorous fishes often feed in separate reef areas. For example, some parrotfishes spend most of their time feeding in reef habitats that comprise <20% of the total reef area (Streit et al., 2018). The loss of large-bodied parrotfishes also appears particularly detrimental to the control of macroalgal cover (Steneck et al., 2014; Shantz et al., 2020; but see Kuempel and Altieri, 2017 for an example of the importance of small-bodied herbivores on lagoonal reefs).

One study of purported Caribbean herbivorous fishes suggests that some do not consume macroalgae but instead target epibionts on macroalgae (Dell et al., 2020). That study revealed that only three fishes (surgeonfish, *Acanthurus coeruleus*; red-band parrotfish, *Sparisoma aurofrenatum*; chubs, *Kyphosus* spp.) dominated consumption of experimental outplants of two common species of macroalgae (Dell et al., 2020). Moreover, one of those fishes (chubs) is not generally considered an herbivore. That finding echoes results from an experiment conducted a decade earlier on Australian coral reefs in which the primary consumption of macroalgae was by a "*sleeping functional group*" (Bellwood et al., 2006). Using caging experiments, the authors observed that the rapid reversal from a degraded, macroalgal-dominated reef to a coral- and epilithic algal-dominated state was the result of herbivory by a single batfish species (*Platax pinnatus*), previously considered an invertebrate feeder (Bellwood et al., 2006). Recently, the triggerfish *Melichthys niger* was reported as a consumer of macroalgae in the western Atlantic (Tebbett et al., 2020). More work is needed on the foraging of herbivores, but the multi-faceted dynamics of grazing by reef fishes argues that the restoration of fish herbivory must include a multitude of taxa.

Urchins

Five sea urchin genera (Diadema, Echinometra, Tripneustes, Eucidaris and Lytechinus) are commonly found on Caribbean coral reefs, and they all consume macroalgae (Figure 1). Given its historical high densities (Lessios, 1984) and generalist macroalgal-based diet (Solandt and Campbell, 2001; Herrera-Lopez et al., 2004), *D. antillarum* is considered one of the most important herbivorous sea urchins in the Caribbean. When *D. antillarum* is present in sufficient densities, algal cover declines and coral recruitment improves (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007; Idjadi et al., 2010). After the 1983–84 collapse of *D. antillarum* populations throughout the Caribbean, macroalgae increased (Lessios, 2016). Subsequently, in the few places (e.g., Jamaica, Curacao) where urchins recovered macroalgal cover decreased with positive effects on coral communities (Edmunds and Carpenter, 2001; Debrot and Nagelkerken, 2006). In the decades after the die-off, *D. antillarum* recovery was very slow on many reefs and densities were estimated at 12% of pre die-off densities 2015 (Lessios, 2016). In 2022, a new mass mortality occurred in 25 territories across the Caribbean, resulting in up to 99% mortality (Hylkema et al., 2023). Although the causative agent of the 2022 *D. antillarum* die-off was identified as a scuticociliate (Hewson et al., 2023), it is not known if this micro-organim is invasive or has always been present. Similarly, little is known about the environmental conditions that resulted in the outbreak. As a result of this recent die-off, *D. antillarum* densities have diminished in some areas of the Eastern Caribbean and Greater Antilles but the condition has not been observed in large parts of the Western Caribbean (Hylkema et al., 2023).

At least one species of *Echinometra* (*E. viridis*) is also found in large numbers on coral reefs (up to 35 ind./m^2; Shulman, 2020) and has the capacity to consume substantial amounts of macroalgae (Sangil and Guzman, 2016). However, the foraging range of *E. viridis* is small relative to other grazers (Table 1), rendering high densities necessary to provide significant macroalgae removal. Paired with the observation that high *E. viridis* densities can also negatively impact reefs through bioerosion (Brown-Saracino et al., 2007), questions about the trade-off between herbivory and bioerosion must be addressed before it is a viable candidate for reef restoration efforts. *Tripneustes ventricosus*, another urchin, also occurs on Caribbean reefs where they forage nocturnally on macroalgae at rates exceeding 0.19 g/hr, but their low abundance translates into minimal overall rates of macroalgal removal (Francis et al., 2019). These studies point to urchins as a significant component of the grazer guild on coral reefs and a potential target for inclusion in coral reef restoration. The diets of *D. antillarum*, *E. lucunter*, and *E. viridis* do not overlap appreciably, suggesting niche partitioning of food resources (Rodríguez-Barreras et al., 2016), perhaps driven by interspecific aggression (Shulman, 1990). This partitioning underscores the need for a better understanding of competitive interactions among echinoids so as to develop a co-restocking strategy.

Crabs

Most crabs are not herbivorous and the few that are also consume animal tissue, but herbivorous crabs have emerged as another character in the cast of coral reef grazers. In the Caribbean and western Atlantic, spider crabs (Mithracidae) comprise a diverse guild of macroalgae grazers (Figure 1). Coen (1988a, 1988b) was perhaps the first to recognize the importance of Mithracid crab grazing for coral communities. Working in Belize, he showed that grazing by *Mithraculus* spp. reduced the cover of algae epibionts in *Porites divaricata* thickets from 75% to 10% and suggested that this grazing may have pronounced positive effects on corals. A decade later, studies on *Mithraculus sculptus* revealed a facultative

TABLE 1 A comparison of the estimated mean daily biomass of macroalgae removed per day per m^2 for various Caribbean reef herbivores based on measures of their mean daily consumption of macroalgae, density, and foraging range.

Taxa	Macroalgae Consumption (g C m-2 d-1)	Biomass (g/m^2)	Daily Range (m)	Potential Macroalgae Removal (g/day/m^2)	Data Source
FISH					
Parrotfish	0.3 - 8.2	2 - 20	10 - 500	0.001 – 16.4	Mumby 2006b, Paddack et al., 2006; Adam et al., 2015; Ruttenberg et al., 2019
Surgeonfish	NA	2-12	30	NA	Duran et al., 2019
URCHINS					
Diadema antillarum	3.8 - 9.8	4.5	3	5.7 – 14.7	Carpenter, 1984; Lessios, 1988b; Solandt and Campbell, 2001; Chiappone et al., 2002; Spiers et al., 2021
Echinometra viridis	NA	5.0	0.2	NA	Sangil and Guzman, 2016; Shulman, 2020; Courtney et al., 2013
Tripneustes ventricosus	2.4 - 4.6	0.06	3.7	0.04 – 0.07	Tertschnig, 1989; Francis et al., 2019
CRABS					
Maguimithrax spinosissimus	3 - 9.6	0.007 – 0.05	3 - 100	0.0002 – 0.16	Hazlett and Rittschoff, 1975; Bohnsack, 1976; Butler and Mojica, 2012; Francis et al., 2019

The estimated “potential macroalgae removal” (g/day/m^2) is calculated as: [macroalgae consumption (g/d) * density (#/m^2)]/[daily range (m)].

mutualism between the grazing crabs and their coralline algal hosts (Stachowicz and Hay, 1996). Stachowicz and Hay (1999a) later reported a similar mutualistic relationship between *Mithraculus forceps* and a coral host (*Oculina arbuscula*). The crab attained shelter among the branches of the coral and grew faster in association with natural as compared to artificial corals, presumably by feeding on the lipid-rich coral mucus. The coral in turn benefitted from reduced fouling by algae.

The previously mentioned Caribbean Mithracid crabs are diminutive, but among them exists a "giant" with profound grazing effects and mariculture potentia. The Channel Clinging Crab or Caribbean King Crab (*Maguimithrax spinosissimus*; formerly *Damithrax*, formerly *Mithrax*; Windsor and Felder, 2014; Klompmaker et al., 2015) is the largest crab in the Caribbean and western Atlantic (Figure 1). Large males can weigh more than 3 kg with carapace widths (CW) >190 mm, although adults more typically range in size from 50 to >100 mm CW (Rathbun, 1925; Creswell et al., 1989; Iglehart et al., 1989; Baeza et al., 2012). *Maguimithrax spinosissimus* is widespread throughout the Caribbean Sea, Gulf of Mexico, and tropical and sub-tropical western Atlantic (Rathbun, 1925; Williams, 1984), where they are found in crevice-rich habitats, including coral reefs at depths ranging from <1 m to >200 m. Although edible, there are only a few scattered, mostly artisanal, fisheries for *M. spinosissimus* (Rubino and Stoffle, 1989, 1990; Guzman and Tewfik, 2004), as they are difficult to exploit commercially due to their local scarcity, daytime occupancy deep within rocky crevices, and herbivorous diet which makes them difficult to target with traps.

Maguimithrax spinosissimus graze on a wide variety of macroalgae and algal turfs, including chemically and physically defended macroalgae (e.g., *Amphiroa*, *Halimeda*, *Dictyota*) that most urchin and fish grazers avoid (Adey, 1987; Butler and Mojica, 2012; Spadaro, 2019, but see Adam et al., 2018; Duran et al., 2019). The crabs also opportunistically consume benthic fauna (Wilber and Wilber, 1989; Creswell, 2011), which improves their growth as compared to a diet composed entirely of algae (Wilber and Wilber, 1989, 1991). Their grazing rate exceeds that of urchins and they consume more algae per gram of body mass than nearly all Caribbean parrotfishes (Butler and Mojica, 2012). Although *M. spinosissimus* occurs naturally on coral reefs, their overall grazing effects are diminished by their low density: 0.005 to 0.01 crabs/m^2 (Butler and Mojica, 2012; Francis et al., 2019). However, Francis et al. (2019) estimated that macroalgal consumption achieved by doubling *M. spinosissimus* density on coral reefs in The Bahamas could alone exceed macroalgae production. In two separate experiments in the Florida Keys (Florida, USA), Spadaro and Butler (2021) reported that stocking ~1 crab/m^2 onto coral patch reefs overgrown by macroalgae (primarily *Halimeda* and *Dictyota*) reduced macroalgal cover by 50 to 85%. Furthermore, the crabs maintained a low cover of macroalgae for the entirety of both year-long studies (Spadaro and Butler, 2021). This resulted in a significant increase in the density of juvenile corals and the richness and abundance of reef-associated fishes (Spadaro, 2019; Spadaro and Butler, 2021), demonstrating the potential use of this crab for coral reef restoration.

Restoration of herbivory

Effective approaches to restoring grazing function on coral reefs depend on herbivore identity. The culture and stocking of herbivorous fishes is not a widely advocated solution to restoring grazing on coral reefs (see Rinkevich, 2014; Abelson et al., 2016; Obolski et al., 2016). Restoration of herbivorous reef fish through proper fishery management and enforcement is generally considered a superior approach and has seen some success with respect to parrotfish recovery in places such as Belize and Bermuda (Cox et al., 2013; O'Farrell et al., 2015). Furthermore, in the absence of restocking programs, fish grazers will likely benefit from establishing no-take marine reserves, a widely used spatial management tool (Mumby et al., 2006b). In contrast, mariculture-based solutions show some promise for the recovery of urchins and crabs (Spadaro, 2019; Pilnick et al., 2021; Spadaro and Butler, 2021; Wijers et al., 2023). In this section, the various approaches to recover and sustain herbivores are reviewed.

Herbivorous fishes: management rather than mariculture

The establishment of marine reserves has repeatedly resulted in increases in herbivorous fish, particularly parrotfishes, that can both aid natural reef recovery (Mumby et al., 2007a) and restoration by reducing coral-algal competition and biofouling of structures used for coral attachment (reviewed by Seraphim et al., 2020). For example, meta-analyses demonstrate the benefits of spatial fishing bans to multiple groups of fishes, including herbivores, with a more significant effect where fish are most heavily exploited (Micheli et al., 2004). Similarly, a global analysis of the effect of protection on piscine browsers, scraper/excavators, and grazers demonstrated rapid recovery of their functional roles on reefs (MacNeil et al., 2015). The impact on parrotfishes and their functional role on reefs protected from fishing is clear from a case study in the large, long-established Exuma Cays and Land and Sea Park (ECLSP) in The Bahamas. Despite an increase in predatory groupers, an absence of traps inside the ECLSP led to a significant rise in parrotfish biomass and grazing and a reduction in macroalgal cover (Mumby et al., 2006b). This reduction in macroalgae in turn resulted in increased coral recruitment (Mumby et al., 2007b) and, ultimately, an increase in coral cover (Mumby and Harborne, 2010). By maintaining populations of large-bodied groupers, marine reserves may also benefit populations of herbivorous damselfishes that are susceptible to predation by smaller-bodied groupers (Mumby et al., 2012). However, recent studies in the Pacific suggest that increases in the abundance of grazers may be sensitive to food availability along with a reduction in fishing pressure, meaning that the impacts of marine reserves may be challenging to predict on reefs after disturbance events (Russ et al., 2015; Graham et al., 2020; Fidler et al., 2021).

Although marine reserves simplify the management of reef fisheries, the challenges of their establishment mean that tools such as herbivore-specific fishing bans should also be considered (Rogers et al., 2015), especially with parrotfish fisheries increasing in the Caribbean (Callwood, 2021). For example, in 2009 Belize established a national ban on catching herbivorous fish and, despite some parrotfishes still being found in markets, the ban appears to have reduced harvest (Cox et al., 2013). Parrotfishes have limited susceptibility to hook-and-line fishing and are readily identified by spear fishers so bans on traps, in particular, significantly increase parrotfish populations (O'Farrell et al., 2015). Despite the benefits of management practices for adult fish grazers, concurrent increases in meso-predators may disrupt the expected stock-recruitment relationship (O'Farrell et al., 2015). Moreover, trap bans may not be effective on shallow, highly productive patch reef habitats where other fishing methods predominate (McClanahan and Muthiga, 2020). Implementing changes in fishing methods can be challenging (Agar et al., 2019), but bans on the fishing of herbivores, perhaps in combination with other management tools, could significantly increase the resilience of Caribbean reefs and aid their recovery (Steneck et al., 2019; Mumby et al., 2021b).

In addition to reducing fish abundance and their functional role, over-exploitation of herbivores can have devastating effects on fish reproductive output that persist over generations even among highly fecund species (Sadovy, 2001). For gonochoric, protogynous species where terminal males mate with several females, a reduction in size as a result of overfishing can be particularly detrimental to population sustainability. Hawkins and Roberts (2003) reported order of magnitude declines in terminal male size and even the total absence of *Sparisoma viride* and *Scarus vetula* with increasing fishing across several Caribbean islands. Surgeonfishes might be more resilient to fishing than parrotfishes, given their rapid growth, early maturity, and short life spans (Robertson et al., 2005). Typically, herbivorous fish communities respond quickly to effective fishing regulation (e.g., no-take areas). Their size and number can double in less than five years (Hawkins and Roberts, 2003; O'Farrell et al., 2015) under proper management, which can also reestablish natural sex ratios (O'Farrell et al., 2016). Fish grazing rates are strongly dependent on fish size, therefore maintaining or restoring large fishes to populations can have important consequences on rates of macroalgae removal.

Surgeonfishes and parrotfishes reproduce and recruit year-round and most species display peaks of reproductive activity during the warmest months (Munro et al., 1973), likely related to higher food availability (Clifton, 1995). The pelagic period of the larvae is estimated around 45–70 days for surgeonfishes and 60 days for parrotfishes with some variation depending upon factors such as current speed (Rocha et al., 2002; Valles, 2017). Currently, we are unaware of any attempt to rear surgeonfish or parrotfish for restoration purposes. Anecdotal reports describe aquarist culture of convict surgeonfish (*Acanthurus triostegus*) from wild-spawned eggs, and wild postlarvae capture, culture, and release may hold promise for some reef species (Richardson et al., 2023). There is still much to be done in this field, but the best option appears to be protecting existing stocks from fishing.

Urchins and crabs: mariculture to the rescue?

Recent progress in the mariculture and stocking of urchins and crabs provides promise for the restoration of herbivory on coral reefs in the Caribbean. Table 2 summarizes some biological characteristics most pertinent to the mariculture and stocking success of Caribbean herbivorous fishes, urchins, and crabs. The urchin *D. antillarum* has been experimentally spawned from broodstock and reared through settlement in captivity (Pilnick et al., 2021; Wijers et al., 2023). The Caribbean King crab (*M. spinosissimus*) has all of the biological hallmarks for mariculture: the species possesses a short, non-feeding larval period of <1 wk, exhibits rapid growth on a mostly herbivorous diet, and has high post-stocking survival when transplanted at sizes >30 mm CW (Spadaro and Butler, 2021). Researchers have successfully reared *M. spinosissimus* in captivity as a potential seafood product, and new mariculture projects in Florida, Belize, and Mexico are exploring the efficacy of rearing crabs in captivity for release onto coral reefs to manage macroalgal overgrowth. This section reviews the current progress in the mariculture and stocking of herbivorous urchins and crabs on coral reefs.

A. Spawning stocks

Urchins

Adult *D. antillarum* can be maintained in recirculating aquaculture systems (Pilnick et al., 2021; Wijers et al., 2023) and in tropical coastal areas with adequate water quality. Culturists have also had success holding and rearing *D. antillarum* juveniles and adults in systems receiving natural seawater (Sharp et al., 2018; Williams, 2022). For ease of transport and genetic considerations, acquiring animals from local source populations is preferable. However, a Florida Keys-level population study by Chandler et al. (2017) found a homogenous *D. antillarum* genetic structure across the sampled area (Dry Tortugas to Key Biscayne) and good genetic representation in two locally sourced broodstock populations of mixed ancestry. Paired with a lengthy planktonic larval duration (35–90 days; Levitan, 1991; Eckert, 1998), these results suggest that broodstock does not need to originate from the specific reefs that are the restocking target.

Crabs

Most restoration-focused crab mariculture operations rely on the collection of wild ovigerous females rather than both male and female broodstock. However, *M. spinosissimus* will mate and extrude viable clutches of eggs in captivity with appropriate environmental conditions and ample space and food. Spawning stocks are typically collected from reef or backreef habitats by hand and at night. It is possible to collect some gravid females as bycatch in trap fisheries (e.g., Brownell et al., 1977), but catch rates are typically low. For example, Munro (1983) reported landings of ~27 crabs per 1,000 trap nights off Pedro Bank, Jamaica. Husbandry requirements for broodstock are minimal: the crabs require good water quality, appropriate and ample diet, and a low male:female broodstock ratio. Attempts at culturing the species have been carried out either *in situ* in cages (Adey, 1987) or

TABLE 2 A summary of biological characteristics pertinent to mariculture and stocking success of Caribbean herbivorous fishes, urchins, and crabs.

Mariculture Characteristics	Mean Value			Sources
	Fish	Urchins	Crabs	
Time to sexual maturity (mos)	48 mos	6 mos	9 mos	Fish: Robertson and Warner, 1978 Urchins: Randall et al., 1964; Idrisi et al., 2003; Hassan et al., 2022 Crabs: Adey, 1987; Tunberg and Creswell, 1988; Wilber and Wilber, 1989, 1991; Creswell, 2011; Spadaro, pers. obs.
Egg production (# eggs/female/yr)	50,000 – 200,000	> 5,000,000	10,000 – 200,000	Fish: Koltes, 1993 Urchins: Pilnick et al., 2021; Wijers et al., 2023 Crabs: Brownell et al., 1977; Creswell et al., 1989; Creswell, 2011; Glover, 2023
Larval development time (days)	30-45 days	26-90 days	2 - 4 days	Fish: Choat et al., 2003 Urchins: Karlson and Levitan, 1990; Eckert, 1998; Pilnick et al., 2021, Williams, pers Obs. Crabs: Brownell et al., 1977; Provenzano & Brownell, 1977; Gravinese et al., 2022
Larval survival (% of total to competence)	NA	<1.5-90%	40%	Urchins: Pilnick et al., 2021; Wijers et al., 2023 Crabs: Creswell et al., 1989; Butler and Spadaro, pers. obs.
Larval settlement and/or metamorphosis (% of total to 1st juvenile stage)	NA	20-70%	2 - 50%	Urchins: Pilnick et al., 2023; Wijers et al., 2023 Crabs: Creswell et al., 1989; Butler and Spadaro, pers. obs.
Time to grow-out to stocking size (mos)	NA	5-9 mos	3-5 mos	Urchins: Patterson, pers. Obs., Williams, pers. Obs. Crabs: Creswell, 2011; Butler and Spadaro, pers. obs.
Survival during grow-out (% survival from 1st juvenile stage to stocking size)	NA	30-70%	10%	Urchins: Patterson, pers. Obs., Williams, pers. Obs. Crabs: Butler and Spadaro, pers. obs.
Post-stocking survival (% survival 1 yr post- stocking)	NA	0-30%	25%	Urchins: Wynne, 2008; Pilnick et al., 2022b, Crabs: Spadaro and Butler, 2021

in laboratory seawater systems (Brownell et al., 1977; Provenzano and Brownell, 1977; Tunberg and Creswell, 1991; Wilber and Wilber, 1991).

Given the short planktonic larval duration of *M. spinosissimus* (~5 d), larval dispersal is presumably limited suggesting that there should be high levels of genetic differentiation among subpopulations in the Caribbean. Simulation modeling, along with an analysis of molecular variance and pairwise FST values of crabs collected in Costa Rica, Mexico, and the Florida Keys (USA), indeed suggest low, multi-generational or stepping-stone connectivity among natural populations of *M. spinosissimus* (Baeza et al., 2019). With this in mind, it is prudent that broodstock be sourced from populations near the intended release site to avoid genomic mixing of potential subpopulations while still retaining the genomic heterogeneity of wild stocks so as not to limit adaptive potential in response to changing environmental conditions (Texeira and Huber, 2021).

B. Spawning, fertilization, and larval production

Urchins

Echinoids have a complex life history involving the external fertilization of planktonic eggs, development of planktotrophic (feeding) larvae, metamorphosis, settlement, and recruitment of larvae to a benthic habitat followed by maturation of recruits into adults (Smith, 1997). *D. antillarum* reaches sexual maturity at 25–30 mm test diameter (Levitan, 1991). The species spawns throughout the year in much of the Caribbean (Lessios, 1981; Steiner and Williams, 2006; Williams et al., 2009). Settlement studies around Puerto Rico and St. Eustatius revealed peak settlement from May through September (Williams et al., 2009; Hylkema et al., 2022a), indicating that spawning occurs mostly in spring. In the Florida Keys, peak spawning occurs a few months earlier in November (Bauer, 1976).

Spawning in *D. antillarum* can be induced with heat shock (Leber et al., 2009; Pilnick et al., 2021), which is less invasive as compared to the often-used method of injecting a KCl solution into the coelomic cavity (Rahman et al., 2012). Spawning of *T. ventricosus* can be induced by gently rocking or shaking the individual while out of the water (Williams, pers. observ.). If maintained in a stable environment with continuous access to food, urchins can spawn monthly year-round in the laboratory (Pilnick et al., 2021; Wijers et al., 2023).

The mean egg diameter of *D. antillarum* is 72.7 ± 2.4 µm, which is slightly larger than *T. ventricosus* at 61 ± 2 µm (Guete-Salazar et al., 2021). In a hatchery setting, fecundity is high (i.e., several million eggs regularly spawned per female) and fertilization rates are generally >90% with no evidence of polyspermy (see Pilnick et al., 2021). Embryo development proceeds rapidly within a fertilization membrane that disappears in the blastula stage, followed by the prism and early pluteus stages within two days at 27°C (Eckert, 1998). The larvae of *D. antillarum* grow into an echinopluteus (first described by Mortensen, 1921; Figure 2), which is unique to urchins in the Diadematidae family and is a morphology that presents challenges for larviculture.

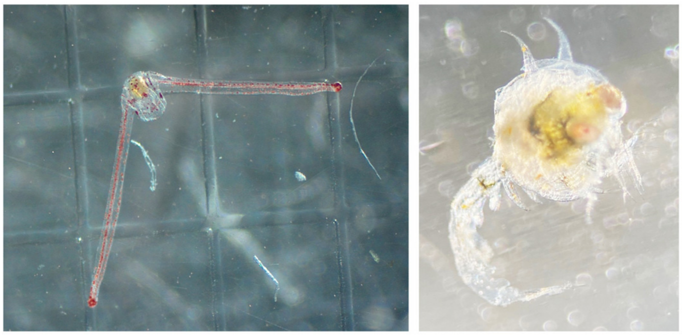

FIGURE 2
(Left) Photo of a *D. antillarum* echinopluteus larva reared in the laboratory (photo credit: *A. Hylkema*). (Right) Photo of a *M. spinosissimus* megalopa larvae reared in the laboratory (photo credit: *L. Cifers*).

Larval functional performance depends on larval size and shape, which influence susceptibility to predation (Eckert, 1998), swimming speeds (Emlet, 1983), metabolic requirements (McEdward, 1984), and clearance capacity (Hart and Strathmann, 1995). The pluteus arm span of *D. antillarum* is larger than most tropical echinoid larvae and can grow to over 4.5 mm long for a total arm span of over 9 mm (Eckert, 1998). Eckert (1998) stated that with this large arm span, *D. antillarum* larvae may not be as vulnerable to predators as other echinoid larvae. Also, larvae with larger arm lengths may maximize the capability of locomotion and feeding (Hart and Strathmann, 1994). However, in the culture environment these long arms are fragile and subject to physical damage, which may lead to energetic expenditure for repair and/or opportunistic infection.

Eckert (1998) was the first to successfully culture *D. antillarum* from eggs to a few juveniles. More small-scale cultures followed (Idrisi et al., 2003; Nedimyer and Moe, 2006; Leber et al., 2009; Pilnick et al., 2021), but large-scale culture has not yet been achieved. Larval *D. antillarum* are extremely sensitive to many environmental parameters, bacterial infection, and are described by Bielmyer et al. (2005) as among the marine organisms most sensitive to dissolved metal toxicity. The larvae of *D. antillarum* need constant, gentle water movement during culture because they are negatively buoyant (Leber et al., 2009; Pilnick et al., 2021; Wijers et al., 2023). The microalgae *Rhodomonas* (either *R. lens* or *R. salina*) seems essential for rearing *D. antillarum* at a larval density between 0.1 and 2 larvae/mL (Eckert, 1998; Nedimyer and Moe, 2006; Pilnick et al., 2022a; Wijers et al., 2023). Improving survival of urchins during their sensitive planktonic larval and early benthic juvenile stages will be necessary for large-scale production of juvenile *D. antillarum* for restoration.

Crabs

There are no published data on mating dynamics or fertilization success in *M. spinosissimus*, but crabs in nearshore habitats of the Florida Keys attain sexual maturity at ~45 mm CW in males (Baeza et al., 2012) and 50–70 mm CW in females (Baeza et al., 2012; Glover, 2022). They are reproductively active year-round in the Caribbean (Munro, 1974; Craig et al., 1989; Iglehart et al., 1989), with females producing successive clutches from a single mating approximately every three to six weeks (Adey, 1987; Creswell, 2011). Clutches are incubated for 2–3 weeks before hatching, and fecundity estimates vary widely from tens of thousands (Brownell et al., 1977; Creswell et al., 1989) to ~100,000 eggs/clutch (Creswell, 2011; Glover, 2022). Egg mortality in females held under laboratory conditions varies widely (0%–100%) but is unrelated to female body size (Baeza et al., 2015).

Provenzano and Brownell (1977) were the first to describe the early life history and culture of *M. spinosissimus* and to successfully rear larvae; in their case within static containers with daily water changes of natural seawater. A new description of the larval development was recently published by Turini et al. (2021). After hatching, larvae spend a short time in the plankton with two swimming zoeal stages lasting 8–24 hours each, followed by a single benthic post-larval megalopa stage lasting 3–4 days (Brownell et al., 1977; Provenzano and Brownell, 1977; Tunberg and Creswell, 1988; Gravinese et al., 2022) (Figure 2). Both zoeal larval stages and the post-larval megalopa stage are lecithotrophic (non-feeding) (Creswell, 2011). As with many taxa, the larvae are sensitive to water quality and require well-oxygenated seawater for successful development. However, Gravinese et al. (2022) report that larval and juvenile *M. spinosissimus* are tolerant to seawater conditions associated with climate change predictions.

C. Grow-out

Urchins

D. antillarum requires ~1 year to grow from settler to reproductive adult. However, growth rates depend on the space available for the urchin to grow and the amount and type of feed provided. Feed used for grow-out includes macroalgae such as *Ulva* sp. and *Dictyota* sp., but also dried nori or pellets marketed for herbivorous fish (Hassan et al., 2022). Idrisi et al. (2003) found an average growth rate of 3 mm/mo for juveniles (Figure 3) reared in a flow-through seawater system and fed solely with the macroalgae *Gracilaria ferox*. Under ideal circumstances, higher growth rates can be expected, as Randall et al. (1964) reported growth rates of up to 6.7 mm/mo for caged juveniles in field experiments. In a laboratory recirculating seawater system, Hassan et al. (2022) measured average increases in test diameter of up to 8.3 mm/mo over six weeks for hatchery-propagated juvenile urchins at an

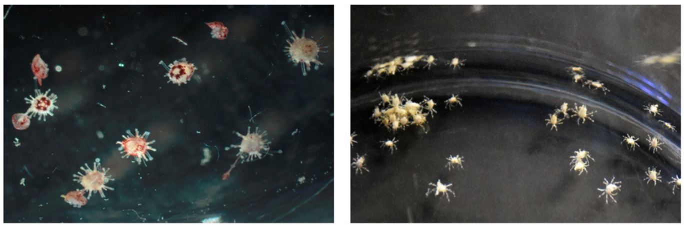

FIGURE 3
(Left) Photo of recently settled *D. antillarum* juveniles hatched in the laboratory (photo credit: *T. Wijers*). (Right) Photo of recently settled *M. spinosissimus* hatched in the laboratory (photo credit: *AJ Spadaro*).

average starting test diameter of 5.5 mm. By both test diameter and live weight metrics, Hassan et al. (2022) observed improved growth in animals fed dried nori rather than an equivalent weight of a commercial herbivore pellet.

Crabs

Early juveniles of *M. spinosissimus* feed primarily on filamentous turf algae and benthic diatoms (Brownell et al., 1977; Tunberg and Creswell, 1988; Lellis, 1992) (Figure 3). Wilber and Wilber (1989) reported that juvenile growth and survival both increased significantly with the addition of animal protein to the diet. The crabs have been successfully reared *in situ* within mesh cages fouled by algal turfs and moored in backreef habitats (Adey, 1987), as well as under controlled laboratory settings (Tunberg and Creswell, 1988, 1991; Gravinese et al., 2022). Tunberg and Creswell (1988) noted that, when provided with good water exchange, early benthic juvenile crabs could be maintained at a high stocking density (>22,500 ind./m^2), whereas Wilber and Wilber (1989, 1991) found that survival and growth were both directly correlated with holding space and inversely correlated with crab density. In the laboratory, Provenzano and Brownell (1977) reared *M. spinosissimus* to a CW of 20 mm in 175 days after hatch, whereas Creswell (2011) reared them to ~30 mm CW in about 180 days. Based on juvenile growth trajectories, Adey (1987) estimated that crabs could be cultured to marketable adult size (~140 mm CW) in just over 400 days.

Adult *M. spinosissimus* consume algae and animal protein (Winfree and Weinstein, 1989). Recent physiological evidence suggests that the gut chemistry of *M. spinosissimus* changes through ontogeny, with protein increasing in importance in the diet of adult crabs (Chávez-Rodríguez et al., 2020). Nevertheless, Mithracid crabs are hearty consumers of macroalgae. In laboratory feeding trials conducted by Coen (1988a), two crabs related to *M. spinosissimus* (*Mithraculus sculptus* and *M. coryphe*) ate corticated (e.g., *Laurencia, Acanthophora*) and leathery (e.g., *Padina*, *Lobophora* ruffled form) macroalgae, except where algal secondary metabolites reduced consumption (e.g., *Lobophora* decumbent form, *Stypopodium*). Crab feeding preferences were negatively correlated with measures of algal quality, perhaps reflecting their aversion to high caloric but chemically defended macroalgae. Later studies with *M. spinosissimus* (Butler and Mojica, 2012; Spadaro, 2019) show that, unlike its congeners, the species consumed a wide range of macroalgae, including chemically defended algae (e.g., *Dictyota* sp; *Laurencia* sp.) as well as physically defended macroalgae (e.g., *Halimeda* spp.) but diet preferences were weak, suggesting that the species is a generalist grazer.

D. Post-release mortality, growth, and emigration

Urchins

Out-planting smaller (juvenile) *D. antillarum* is expected to be more cost effective than out-planting adults, but with the possible trade-off of higher post-stocking mortality. It is therefore important to determine the best size for restocking to optimize cost and retention. The size of restocked *D. antillarum* may affect retention, as size determines the use of shelters and avoidance of predation. Restocking experiments with *D. antillarum* have been conducted throughout the Caribbean and the Florida Keys (Table 3). Studies have differed greatly in methodology, duration, reef type and size, and *D. antillarum* size and source and so cannot be easily compared; yet some general conclusions are possible.

Overall, predation (7 out of 10 studies) and emigration (6 out of 10 studies) were the main explanations for low retention of restocked urchins. High predation pressure and low shelter availability appear to be the two main factors determining predation rates (The Nature Conservancy, 2004; Chiappone et al., 2006; Nedimyer and Moe, 2006; Burdick, 2008; Wynne, 2008; de Breuyn et al., 2023), whereas emigration seems most dependent on the size of the restocked *D. antillarum* and shelter availability (Maciá et al., 2007; Wynne, 2008; Williams, 2018; Pilnick et al., 2022b). Retention of stocked *D. antillarum* on reefs varies greatly among studies, from 0% (The Nature Conservancy, 2004; Burdick, 2008; Dame, 2008) to as much as 20%–75% after one year (Chiappone et al., 2006; Nedimyer and Moe, 2006; Nedimyer and Moe, 2006; Maciá et al., 2007; Wynne, 2008; Delgado and Sharp, 2021; Pilnick et al., 2022b). Most restocking studies were performed on relatively shallow reefs (<10 m), the two restocking studies that were performed on deeper reefs had low retention that was attributed to high predation pressure (Burdick, 2008; de Breuyn et al., 2023). In the Florida Keys, Delgado and Sharp (2021) found that adult *D. antillarum* (60 mm test diameter) had significantly higher survival when tethered with artificial crevice structures on a severely degraded reef previously devoid of appropriately scaled natural shelter. Any effort to stock *D. antillarum* on reefs must consider habitat quality, which is location-specific and can be susceptible to natural disturbances (Kobelt et al., 2019),and must either target sites with appropriate shelter for the urchins or artificially enhance shelter prior to stocking to reduce post-stocking predation.

TABLE 3 Comparison of stocking results for *D. antillarum* and *M. spinosissimus*.

Diadema antillarum

Location	Source	Number Released	Retention (%)	Study Duration	Reef alterations	Urchin loss attributed to	>References
Florida Keys, US	Wild	N/A	33	3 - 6 months	Enclosed	Predation	The Nature Conservancy, 2004
	Cultured		0	Several weeks	None		
	Cultured		100	Several months	Enclosed		
Florida Keys, US	Wild	693	30	1 year	None	Fish predation and storm	Nedimyer and Moe, 2006
Jamaica	Wild	508	40	6 weeks	None	Emigration	Maciá et al., 2007
			26	28 weeks			
The Bahamas	Wild	~79	0	5 - 12 months	Macroalgae removed	Predation or lack of shelter	Burdick, 2008
Curaçao	Wild	36	47	3 weeks	Artificial shelter	Predation or emigration	Dame, 2008
		36	0	1 day	None		
Anguilla	Wild	348	50	6 – 12 months	None	Predation or emigration	Wynne, 2008
Puerto Rico	Cultured settlers	150	44-52	1 month	Enclosed	Emigration	Williams, 2018
		150	5 - 6		Open top		
Puerto Rico	Wild	N/A	N/A	6 months	Enclosed	N/A	Olmeda-Saldaña et al., 2021
Puerto Rico	Cultured settlers	480	27	2 months	Enclosed	Emigration and predation	Williams, 2022
		276	26				
Saba	Wild	16	31	10 days	Artificial reefs	Predation	de Breuyn et al., 2023
	Cultured settlers	16	25				

Maguimithrax spinosissimus

Location	Source	Number Released	Retention (%)	Study Duration	Reef alterations	Crab loss attributed to	References
Florida Keys, US	Wild	84	20	1 year	None Algae removed	Emigration and predation	Spadaro and Butler, 2021
Florida Keys, US	Wild	360	3	2 years	None	Emigration and predation	Butler and Evans, unpub. data
Mexico	Cultured	85	?	?	None	Emigration and predation	McField et al., unpub. data

Juvenile *D. antillarum* are preyed upon by many fishes, including: queen triggerfish (*Balistes vetula*), Spanish hogfish (*Bodianus rufus*), pudding wife (*Halichoeres radiatus*), black margate (*Anisotremus surinamensis*), Spanish grunt (*Haemulon macrostomum*) and jolthead porgy (*Calamus bajonado*) (Randall et al., 1964). Spiny lobsters (*Panulirus argus*, *Panulirus guttatus*) also consume *D. antillarum* of many sizes (Butler and Kintzing, 2016), and chemical odors from *P. guttatus* elicited shelter seeking behavior and reduced foraging in *D. antillarum* in the laboratory (Kintzing and Butler, 2014). The batwing coral crab (*Carpilius corallinus*) and helmet shells (*Cassis* spp.) also prey on *D. antillarum* (Randall et al., 1964; Sharp and Reckenbeil, 2022). The presence of damselfish that tend algae gardens, especially the three-spot damselfish, also reduces retention of *D. antillarum* (Williams, 2022). Damselfish do not prey on *D. antillarum*, but they induce the urchins to flee by pecking at their spines (Williams, 2022).

Stocking of herbivores is only useful if their density is high enough to reduce macroalgae cover and, in the case of *D. antillarum*, optimal restocking density depends on the rugosity of the reef, which affects urchin movement and predation (Olmeda-Saldaña et al., 2021; Pilnick et al., 2022b). Burdick (2008) suggests avoiding small patch reefs (<8 m^2) when restocking urchins because larger reefs improve retention and reduce emigration by providing more shelters. Two studies, one conducted on large patch reefs (44 to 96 m^2) and another on contiguous reefs, arrived at similar estimates of *D. antillarum* retention (23%–30%) after 267–365 days (Wynne, 2008; Pilnick et al., 2022b). Olmeda-Saldaña et al. (2021) showed that for more rugose reefs, the optimum density for stocking *D. antillarum* is about 2–5 urchin/m^2. Pilnick et al. (2022b) noted a significant decline in macroalgae cover (~27%) on reefs stocked with *D. antillarum* when urchin densities were above 0.15 urchin/m^2 but observed no effect on macroalgae at urchin densities of 0.04 urchin/m^2.

Crabs

Stachowicz and Hay (1999b) postulated that high site fidelity and predation risk are associated with a broad generalist diet and compensatory feeding in marine crabs. Still, only three studies have been published on the movement of *M. spinosissimus* in the wild. Using external tags, Hazlett and Rittschoff (1975) followed the daily movement of a wild population of crabs living along the sides of a man-made canal in the Florida Keys for four months. In that essentially linear expanse of continuous rocky crevice habitat, adult *M. spinosissimus* generally moved <10 m/d with the majority remaining within just a few meters of their daytime crevice den. Male crabs moved further from their site of capture (58 m) than females (32 m) and, when at higher density, crabs moved further. Bohnsack (1976) also conducted a mark-recapture study with externally tagged crabs in two rocky canals in the Florida Keys. During the 12-month study, Bohnsack (1976) recovered over 50% of the tagged crabs within the 100 m long survey areas and noted that crabs often used the same daytime den repeatedly over time. Spadaro and Butler (2021) found that tagged crabs stocked on coral patch reefs (~3 to 5 m diameter) that were isolated by expanses (~10 m) of sand and open hardbottom typically remained on the patch reefs where they were released, with 40% remaining after 6 months and 25% after a year. More detailed studies on the factors that influence crab movement and home range in more contiguous and architecturally complex coral reef habitats are needed to develop appropriate, perhaps context-dependent stocking densities for reef restoration.

Tethering of various sizes of crabs (10–90 mm CW) on coral reefs and other habitats (e.g., saltwater quarries, coastal hardbottom) indicates that crab mortality is highest among small crabs on coral reefs (Spadaro and Butler, 2021; Glover, 2023). Male and female crabs appear to suffer similar rates of mortality, but mortality declines precipitously once crabs reach ~30 mm CW, representing a potential target size at which crabs can be stocked in the field with substantially lower risk of predation. Analysis of the stomach contents of the reef-dwelling spotted spiny lobster (*Panulirus guttatus*) confirms that a large portion of their diet is small juvenile crabs (Butler and Kintzing, 2016). Spadaro and Butler (2021) reported a strong effect of *M. spinosissimus* on macroalgae cover (50%–85% removal) and coral reef community composition with a stocking density of 1 crab/m^2, but optimal restocking densities for *M. spinosissimus* have yet to be determined. Similarly, optimal restocking sex ratios are unknown. Large male *M. spinosissimus* appear to be territorial and defend a harem of females against other large males (Bohnsack, 1976). This territoriality will likely present a challenge to restocking efforts aimed at maintaining crab density through time. Table 3 summarizes data on the attempts to release and monitor the persistence of urchins and crabs on coral reefs.

E. Captivity-related genomic or behavioral selection?

Urchins

Animals cultured and raised in captivity often exhibit traits that are suboptimal for survival in the wild (Näslund, 2021). Wild *D. antillarum* flee from predator chemical cues (e.g., Kintzing and Butler, 2014) and largely remain in shelter during the daytime, a behavior typical of individuals under predation pressure, whereas hatchery-produced urchins may not. Sharp et al. (2018) suggested that hatchery-produced *D. antillarum* possess innate predator recognition and that shelter-seeking behavior could be increased by laboratory-based habituation. Indeed, refinements in grow-out conditions of newly-settled, cultured *D. antillarum* (e.g., natural light cycles, access to appropriately scaled shelters, and reduced handling; Sharp et al., 2018; Pilnick et al., 2021) have resulted in individuals that exhibit diurnal shelter-seeking behavior similar to that of wild individuals (Hassan et al., 2022; Sharp et al., 2023).

In Florida, resource managers require the development of a veterinarian health certification protocol for any captive reared animals to be released in the wild. Accordingly, a framework has been adopted for the culture and release of *D. antillarum* in Florida based upon the development of diagnostic methods for the comprehensive health assessment for the species (Francis-Floyd, 2020) and a description of its captivity-related genomics (Chandler et al., 2017).

Crabs

There is no published information on captivity-related effects on *M. spinosissimus* genomics or behavior. This presents a challenge to restocking efforts and is a substantial knowledge gap, but researchers and resource managers are currently developing a health certification protocol for *M. spinosissimus.*

F. Reproductive success of stocked individuals and potential for self-recruitment?

Urchins

Following the Caribbean-wide disease-induced mass mortality of *D. antillarum* in the 1980’s, recovery has been restricted in part by low fertilization success at low population density (Lessios, 2005; Chiappone et al., 2013; Feehan et al., 2016), so stocking may be necessary to reestablish viable spawning populations. *Diadema antillarum* exhibits lunar periodicity in spawning (Bauer, 1976; but see Levitan, 1988) and aggregation during spawning is posited as an adaptation to increase fertilization success (Randall et al., 1964; Bauer, 1976; Younglao, 1987). An advection-diffusion and fertilization-kinetics model was used to estimate *D. antillarum* fertilization success as a function of various site-specific biophysical factors (Feehan et al., 2016). The model indicated that fertilization success varies indirectly with current velocity and directly with urchin density, urchin aggregation size, and the linear extent of the population in the direction of mean flow (Feehan et al., 2016). This information provides a reference point for assessing how stocking density, the subsequent survival and behavior of stocked individuals, and local physical characteristics may affect reproductive output and the potential for post-stocking self-recruitment. An understanding of the broadscale source-sink population dynamics of *D. antillarum* across the Caribbean, which is currently lacking, also will be important for understanding future population growth.

Natural recruitment of *D. antillarum* at stocked sites may act to supplement stocked populations if sites contain appropriate settlement habitat. Given the relatively long planktonic larval duration of *D. antillarum*, larval dispersal could in theory occur at scales of up to 1000s of km (Feehan et al., 2019). However, biophysical dispersal models for many taxa demonstrate the strong effects of regional oceanography and larval behavior on dispersal that often increase retention (Cowen et al., 2006; Williams et al., 2009; Butler et al., 2011; Feehan et al., 2019). Moreover, the settlement of larval *D. antillarum* around the Caribbean and in specific regions is highly variable in space and time (Hernández et al., 2006; Miller et al., 2009; Williams et al., 2010; Hylkema et al., 2022a).

The relationship between larval supply and recruitment can be decoupled by larval and post-settlement mortality. For example, on reefs in the Florida Keys, larval settlement on artificial substrate did not translate into measurable recruitment to the benthic population, likely due to a lack of appropriate natural settlement substrate or habitat structure to protect from predators (Feehan et al., 2019). The spine canopy of adult *D. antillarum* can provide a local refuge to juveniles from predators (Miller et al., 2007). Hence, adult urchin restocking could enhance the post-settlement survival of natural recruits and is an area for future research.

Crabs

The extraordinarily brief planktonic larval duration of *M. spinosissimus* portends a high probability of limited dispersal and self-recruitment, which is supported by population genetics information and connectivity modeling (Baeza et al., 2019). Therefore, it stands to reason that increasing breeding stocks by an order of magnitude or greater through stocking could increase local larval supply. As an example of local recruitment, populations of *M. spinosissimus* have been discovered in land-locked saltwater quarries in the Florida Keys that are physically isolated from the sea. Those crab populations have reproductive patterns and fecundity identical to those in wild habitats and, therefore, are almost certainly self-recruiting (Glover, 2023). Furthermore, unpublished data indicate that crab populations in quarries are genetically distinct from nearby wild populations and are consistent with a "founder effect" genetic structure (Whitaker, 2023). Despite the potential for self-recruitment, wherever *M. spinosissimus* occurs naturally their density is low suggesting either limited larval supply or high larval and post-settlement mortality (Butler and Kintzing, 2016), so studies that disentangle those explanations will shed light on the possibility of enhancing local recruitment through stocking.

G. Enhancement of natural recruitment

Urchins

Many species of sea urchins respond to bare substrate or those with new biofilms as cues for settlement (Bak, 1985; Pearce and Scheibling, 1991; Rahim et al., 2004; Williams et al., 2011), but the spatiotemporal patterns of settlement by *D. antillarum* vary appreciably among locations (Bak, 1985; Miller et al., 2009; Vermeij et al., 2010; Williams et al., 2010, 2011; Feehan et al., 2019; Maldonado-Sánchez et al., 2019; Hylkema et al., 2022a). Recent laboratory experiments by Pilnick et al. (2023) and Wijers et al. (2024) revealed a lack of settlement by competent *D. antillarum* larvae exposed to a sterile seawater control, but settlement rates increased to ~50% in response to two types of calcareous macroalgae (Pilnick et al., 2023; Wijers et al., 2024) and to natural biofilms (Wijers et al., 2024). If settlement hotspots are identified it is possible to collect high numbers of *D. antillarum* settlers during certain months of the year (Williams et al., 2010, 2011; Hylkema et al., 2022a; Klokman and Hylkema, 2024). Settlement collectors are preferably deployed in mid-water (Williams et al., 2010; Hylkema et al., 2022a) at a depth of around 9 m (Williams et al., 2011). They have been constructed of many materials (e.g., plastic doormats; bio balls; rope; artificial turf) but plastic doormats and bio balls appear best (Williams et al., 2010; Hylkema et al., 2022a). The collection of *D. antillarum* postlarvae appears to be a viable option for naturally enhancing populations given the difficulties in rearing *D. antillarum* larvae in the laboratory. For example, over 6500 *D. antillarum* juveniles collected from the field have been successfully reared in the laboratory and restocked to multiple reefs in Puerto Rico (Williams, 2022).

Hylkema et al. (2022b) introduced a new approach of *D. antillarum* restoration, termed "*Assisted Natural Recovery*" (ANR) in which settlers are not collected, but their recruitment facilitated on the reef. Strings of plastic bio balls, which are normally used in aquaculture filters but also work well as *D. antillarum* settlement collectors (Hylkema et al., 2022a), were attached to the reef at the onset of the settlement season to provide additional settlement substrate and shelter availability. Without further modifications and without the need to raise urchins *ex situ*, reefs with bio ball streamers had significantly more *D. antillarum* recruits than control reefs without the urchin larval collectors after six months, showing that a lack of settlement substrate is one of the factors constraining natural recovery. However, in that same study, subsequent recruit retention was relatively low, which was attributed to high predation pressure (Hylkema et al., 2023).

Crabs

There have been no assessments of post-stocking reproductive success for *M. spinosissimus* nor mention of *in situ* larval collection of *M. spinosissimus* in the literature. Although culture of wild larvae collected in the field is theoretically feasible, the cost (labor and time) involved in obtaining and separating *M. spinosissimus* larvae from the plankton would likely outweigh the potential benefits. Natural settlement and recruitment of early benthic phase *M. spinosissimus* has not been reported, but their density is likely limited due to high larval and post-settlement mortality (Butler and Kintzing, 2016; Spadaro and Butler, 2021; Glover, 2022).

Similarly, there have been no published studies on settlement patterns or habitat preference for the various life stages of the species. Identifying the cues and conditions that limit or promote settlement and recruitment of *M. spinosissimus* are of obvious importance. Such studies may also offer insight into physical or chemical interventions that can be made to restoration sites to improve the likelihood of crab settlement and recruitment, thus reducing the potential need for repeated stocking events.

Cost of herbivore restoration?

Estimating the cost of large-scale restoration efforts is imprecise and changes with economic conditions (e.g., labor, utilities, and materials costs). In the case of coral reef restoration, costs are largely unknown because few if any large-scale programs have been completed and, therefore, actual expenses incurred are undetermined (but see Bayraktarov et al., 2016 for estimated costs of various forms of marine coastal restoration). Perhaps the most thorough estimation of the cost of large-scale coral reef restoration was crafted by NOAA for the "Mission: Iconic Reefs" restoration project in the Florida Keys (NOAA, 2021). For each of the seven reef areas to be restored, estimates were made of the daily effort and cost required for site preparation, coral additions, grazer additions, monitoring, maintenance, and adaptive management. This process arrived at an overall cost of approximately \$97M US spread over a 10-year timeframe to restore about 27 hectares of coral reef habitat. Stocking >400,000 grazers (*D. antillarum* and *M. spinosissimus*) on those 27 hectares is expected to cost approximately \$14M US or an estimated \$35 per grazer (compared to \$259 per restored coral). Grazer additions account for only about 7% of the estimated total cost of restoration and represent only about 10% of the estimated cost of reintroducing corals (~\$61M US). How accurate such *a priori* estimates may be is unknown and most of the funding for the project is yet to be acquired.

Unintended or non-beneficial effects of increasing grazers on coral reefs

One of the aims of coral out-planting is to 'kick start' natural coral reproduction and larval settlement. A potential concern of increasing herbivore populations during the early stages of restoration efforts is that they may negatively affect other ecological processes on coral reefs. For example, parrotfishes eat juvenile corals, either deliberately or while grazing for other food sources, so increasing their abundance may increase the mortality of small corals. Still, the evidence suggests that the positive effect of parrotfishes in reducing macroalgal cover outweighs any negative impacts on coral demographics (Mumby, 2009). Herbivores may also increase the mortality of outplanted corals either directly via predation or through increases in algal gardens by territorial damselfishes (Schopmeyer and Lirman, 2015; Koval et al., 2020).

When urchins form unnaturally large populations or dense aggregations in the absence of predators (e.g., triggerfishes, spiny lobsters), they can increase the mortality rates of coral recruits, damage established coral colonies (Bak and van Eys, 1975; Sammarco, 1980), and increase reef bioerosion (Ogden, 1977; Bak, 1994; Brown-Saracino et al., 2007). However, we anticipate that most restoration efforts will be paired with some level of protection of fishes and, thus, unnaturally large populations of Caribbean urchins are unlikely because of the presence and conservation of their predators. Indeed, the effectiveness of Caribbean fish predators has been invoked as one reason why urchin populations have not recovered naturally (Lessios, 1988a; Harborne et al., 2009).

There are no known negative effects of increasing the density of Mithracid crabs on coral reefs. Indeed, some Mithracid crabs dwell symbiotically with corals and improve coral growth and health by removing detritus and algae from their coral hosts (Coen, 1988a; Stachowicz and Hay, 1996, 1999a). The positive indirect effects of crab consumption of macroalgae on coral growth and recruitment are also well documented (Coen, 1988a; Spadaro and Butler, 2021). But crabs also consume small, soft-bodied benthic fauna opportunistically (Wilber and Wilber, 1989; Creswell and Tunberg, 2000; Chávez-Rodríguez et al., 2020). As described earlier, juvenile Mithracid crabs are prominent in the guts of one species of reef-dependent spiny lobster (*P. guttatus*; Butler and Kintzing, 2016) and the discarded remnants of the exoskeletons of larger crabs are frequent evidence of octopus and triggerfish predation (Spadaro, 2019). However, the implications of these predatory interactions on coral reef food webs are unknown.

The question of how restocking herbivores will affect the wider food webs at restored sites is difficult to predict. Reef food webs are complex and typically contain a large number of weak trophic links (Bascompte et al., 2005). If the aim is the restoration of grazers to approximate 'natural' levels of macroalgae abundance, any negative effects on reef trophodynamics are likely to be modest or nil. Still, the long-term implications of restoring grazers on reefs represents a challenging knowledge gap. Looking ahead to large-scale coral reef restoration efforts whose plans include the simultaneous stocking of corals and different grazer species (e.g., "Mission: Iconic Reefs" program in Florida Keys) though desirable from a restoration perspective, will not alone permit assessment of the unintended effects of grazer reintroductions on coral reef ecosystems. Ferraro et al. (2023) argue that natural resource management, including restoration, be conducted in an experimental format so as to simultaneously fill-in important knowledge gaps. We believe this is sound advice as it pertains to the restoration of coral reef herbivores. For example, the "Mission: Iconic Reefs" restoration program mentioned above would benefit from a design that includes further *in-situ* and modeling research on trophic networks under different restocking scenarios.

Ramifications of climate change for the restoration of herbivores

Higher levels of CO_2 expected under near-future climate change is likely to increase the growth of macroalgae, further exacerbating the present overgrowth of macroalgae on coral reefs (Fong and Paul, 2011). But the effects of climate change on grazers is unclear. Bodmer et al. (2017) caution that predator avoidance behavior by *D. antillarum* may be compromised under near-future ocean warming scenarios due to reduced function in the light-detecting melanophores of urchins at elevated temperatures, leading to less spine movement in response to predator shadows. In the closely related sea urchin *D. africanum*, reduced pH resulted in lower fertilization and development rates, which were partially ameliorated by higher temperatures (García et al., 2018). Similarly, reduced pH resulted in a lower skeleton density, weaker spines, and increased predation on stocked *D. africanum* (Rodríguez et al., 2017). For other sea urchins, ocean acidification reduces fertilization success (Havenhand et al., 2008) and has negative effects on larval development (Sheppard Brennand et al., 2010), settlement, and post-settlement survival. Wittmann and Pörtner (2013) reviewed all existing studies on the subject and concluded that most sea urchin species were negatively affected by moderate climate change scenarios although much will be dependent on the speed and extent of global warming and ocean acidification.

In general, fish size – especially for tropical fishes – is predicted to decline in response to the higher temperatures and lower oxygen concentrations expected with climate change (Cheung et al., 2013), and there is empirical evidence in support of this. Comparisons of reef fish assemblages in the Persion Gulf and Gulf of Oman between sites that differ in the effects of climate change suggest that overall fish abundance, richness, biomass, and size are likely to decrease when subject to climate change (Feary et al., 2010). However, there is evidence that the abundance of small herbivorous fish in particular may increase on reefs subject to climate change due to the proliferation of macroalgae (Feary et al., 2010; Thibaut et al., 2012; Graham et al., 2020).

Diseases in decapod crustaceans are generally expected to rise in response to elevated temperatures, acidification, and salinity change which are all host stressors associated with climate change (Shields, 2019). However, no diseases have been described in *M. spinosissimus*, which also appears relatively robust to climate change. Laboratory experiments exposing larval and juvenile *M. spinosissimus* to the elevated temperatures and lower pH revealed that the crabs are tolerant to changes associated with climate change (Gravinese et al., 2022). The tolerance of *M. spinosissimus* to such climate stressors suggests that it could be particularly beneficial to restoration efforts aimed at making coral reefs more resilient to increasingly warm and acidic seas.

Guiding principles for herbivore restoration

Coral reef restoration has largely focused on out-planting a few species of framework-building corals with the aim of reestablishing sufficient coral populations to rebuild reef architecture and reestablish lost biodiversity and ecological function. The goal is lofty considering the ecological headwinds posed by climate change, disease, and habitat degradation fueled by eutrophication, siltation, and the proliferation of macroalgae. The latter problem is the one most tractable at local scales given emerging capacities for rearing and stocking native grazers, the promise of which is reviewed here.

As one might expect, Caribbean fish, urchin, and crab herbivores differ appreciably in life histories, which confer advantages and disadvantages in the ease of their mariculture (Table 2) and their suitability for specific restoration scenarios. As noted by others (Burkepile and Hay, 2009; Mumby, 2021a), studies of herbivory on coral reefs have repeatedly taught us that reliance on just one or a few species creates ecosystem instability. Even taxa with seemingly similar ecological functions are rarely identical (e.g., diet preferences, reproductive periodicity, resistance to disease, mobility) and their respective populations fluctuate. This variability implies that a restoration approach that embraces functional redundancy and complementarity in the management and restoration of grazing function, coupled with the enhancement of coral abundance, diversity, and recruitment is likely to be the most effective.

Macroalgal coverage targets

Using grazers as part of a reef restoration plan begs the question of what is the target in terms of a reduction in macroalgae on reefs? Restoration targets for macroalgae abundance could be based on historical data for a region assuming those data exist and there is a clear indication of how far back to reset the ecological clock. However, a historical approach to setting such a baseline ignores the myriad of environmental changes that have occurred since then that influence the coral-algae relationship. Therefore, addressing the dilemma of "how much grazing is enough" in the modern context requires consideration of two additional questions:

(1) *At what level of abundance does macroalgae negatively affect corals?*

(2) *Which and how many herbivores are needed to keep reefs below this threshold?*

With respect to question one, data (Butler; unpublished data) from 29 coral reefs surveyed (by divers using 0.25m^2 photo-quadrats) throughout the Florida Keys in 2021 suggest a negative relationship between total macroalgae abundance and coral abundance (both expressed as % cover), but the correspondence breaks down when macroalgae cover falls below about 25% cover at which point coral cover varies widely (Figure 4A). This suggests that below this threshold or "tipping point", coral community dynamics may be driven by other factors unrelated to macroalgae abundance. If so, this represents a logical target for the reduction of macroalgae that can be accomplished through the stocking of grazers. Yet, such relationships – if they exist – are likely to be idiosyncratic to ecoregions because of the importance of local driving factors. This appears to be the case in the Florida Keys. A separate data set (Butler; unpublished data) focusing on a similar number of survey sites conducted within a smaller ecoregion (Lower Florida Keys) in 2021 still implies that there is a tipping point where macroalgae cover hampers coral cover. But at this smaller scale the tipping point is reached at a higher level of macroalgal cover of approximately 55% (Figure 4B).

As the above example demonstrates, despite the known negative effects of macroalgae on corals the relationship between their

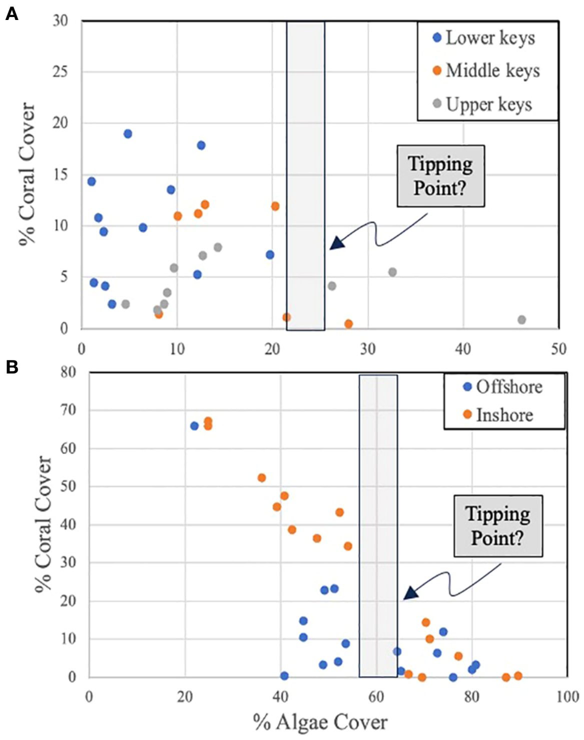

FIGURE 4
(A) Plot of percent coral cover versus percent macroalgae cover on 28 coral reef sites surveyed in 2021 throughout the lower, middle, and upper Florida Keys, Florida (USA). **(B)** Plot of percent coral cover versus percent macroalgae cover on 32 coral reef sites within the lower Florida Keys, Florida (USA) surveyed in 2021. The green bar in both graphs represents an inflection in the data that may represent a "tipping point" in the relationship. Graphics in Figure 4 are adapted with permission from the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

respective abundances on a particular reef is far from precise (hence the variance in Figure 4) and fraught with complexity. All macroalgae are not the same in terms of their effects on corals, coral species or individuals differ in their susceptibility to the insults posed by macroalgae, and casting this question so simply ignores other important considerations such as coral larval supply, the effects of climate change, coral diseases, and so on.

More sophisticated approaches to predicting how much grazing is 'enough' to ensure a reef's resilience have been proposed based on estimates of coral cover and grazing intensity (Mumby et al., 2007a) and such calculations have been made for mid-depth forereefs using fish grazers (Mumby et al., 2006a; Mumby, 2006b; Mumby et al., 2007a). For example, there are algorithms for calculating the grazing intensity of parrotfishes based on species identity, life phase, and size (e.g., Mumby, 2006b; Ruttenberg et al., 2019) that when combined with estimates of density, allow for the quantification of grazing intensity, which is a key input into models of reef resilience (Mumby et al., 2007a).

With proper parameterization, such models could be extended to other piscine herbivores (e.g., surgeonfishes; Duran et al., 2019) as well as invertebrate grazers (i.e., urchins, crabs). Important herbivore inputs to such models include size- or phase-specific grazing rates, algal preference, and foraging areas such as those summarized in Table 1. But to extend the generality of this approach, those models must also be modified to account for physical aspects of reefs (e.g., depth, wave exposure, water quality) that modify herbivory and algal growth rates (Mumby et al., 2006a; Mumby and Hastings, 2008; Graham et al., 2015). Synergistic (e.g., grazing complementarity), inhibitory (e.g., inter-specific competition), and non-consumptive interactions (e.g., behavioral modification of grazing) are also possible with multi-species stocking – even likely – which mandates careful empirical studies and model accommodation of these unknown consequences of multi-species stocking of reef grazers. Again, sufficient data at an appropriate local scale may not be available to make such an approach practical at the multitude of localities around the Caribbean where reef restoration is desired. Is a more basic "blueprint" possible that can help guide restoration practitioners in situations where quantitative data and historical records are lacking?

A grazer restoration decision framework

Developing a decision framework for restoration practitioners to estimate which and how many grazers need to be stocked to make their targeted reefs more resilient represents an important advance for increasing the effectiveness and cost-efficiency of reef restoration work.

In Figure 5, we present a decision tree that can help guide the implementation of a grazer stocking plan based on the general attributes of the reef system in question. This framework lacks recommendations for the stocking density of grazers, which may be idiosyncratic to local conditions. For example, more isolated reefs surrounded by open sand bottom But that issue can be addressed based on consideration of the details we provide in terms of rates of herbivory and foraging areas of fish, urchins, and crabs contained in this review.

Restoration of grazer assemblages is expected to yield the most durable outcome for the management of macroalgae on Caribbean coral reefs. Hence, we recommend restoration of multiple invertebrate grazers for which mariculture is presently considered feasible: the Long-Spined Sea Urchin *D. antillarum* and the Caribbean King Crab *M. spinosissimus*. Yet, there will be circumstances in which stocking success is unlikely for one or both species and efforts should be focused on other locations or the one species deemed most likely to succeed.

Prior to initiation of such a program, we recommend that baseline monitoring of the proposed sites be conducted to identify characteristics of the target reefs that are key to the successful stocking of grazers. We also assume that stocking of herbivores will be an on-going task, at least until (or if) local increases in grazer recruitment and survival are demonstrated by a stock-recruitment relationship. It is also important that grazers be stocked at sizes large enough to minimize post-release predation, which may vary with local predator assemblages. Other relevant factors to consider when reaching a stocking decision include: the availability of shelters for urchins and crabs, the dominant coral

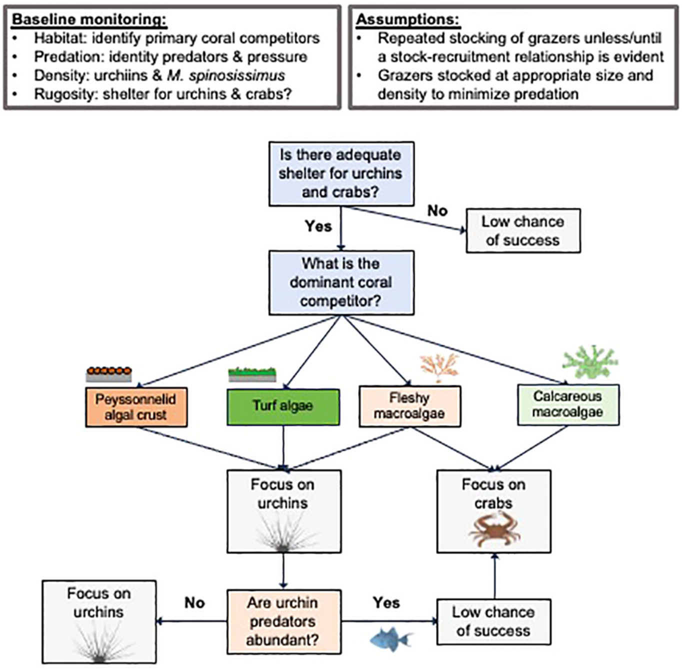

FIGURE 5
Decision tree specifying which reef herbivore type is recommended for a given coral reef restoration effort depending upon shelter availability, type of macroalgae overgrowth, and predation pressure.

competitor present, and the types of predators that are locally abundant. The availability of shelters of the right dimension for use by stocked grazers is crucial to reduce predation that can decimate stocked invertebrates. The type of nuisance macroalgae that is locally abundant is another important factor to consider because their palatability to urchins and crabs differs, as will the desired grazing effect of each herbivore.

Conclusions

Whether coral reefs as humans have appreciated, studied, and exploited them for tens of thousands of years will survive the Anthropocene in their current or diminished state is a matter of conjecture (Norström et al., 2016; Bellwood et al., 2019). Reefs in the Caribbean are particularly in peril. Restoration of corals lost on reefs has been successful in some cases and a miserable failure in others, owing largely to the background conditions into which corals are out-planted. Along with climate change and disease, the over-abundance of macroalgae is a common culprit in the degradation of coral reefs and a persistent roadblock to the return of corals to their former prominence. The large-scale mariculture and stocking of native herbivores onto reefs to counterbalance the proliferation of macroalgae will require a herculean effort. But doing so is feasible and early studies indicate that it can be an effective means of restoring coral reefs to some semblance of their previous state. There are gaps, identified here, in our knowledge of some of the best practices needed for successful coral reef habitat restoration by stocking grazers. However, the biggest challenge is the funding necessary to scale-up the mariculture and stocking of grazers from its current research development stage to the level necessary for meaningful coral reef restoration.

We conclude by acknowledging that any conservation measure must be considered within the context of climate change, and the restoration of herbivores is no different. It is clear that unless significant steps are taken to reduce the use of fossil fuels, coral reefs are one of the most threatened ecosystems on the planet and no amount of restoration will maintain coral dominance without constant outplanting (Bellwood et al., 2019). While global solutions remain challenging it is clear that local actions, such as restocking or managing herbivores, can at least 'buy time' for reefs and make them more resilient to temperature induced mortality events (Kennedy et al., 2013). Over the short term, this makes research into the relative impacts of increased temperatures on macroalgal growth rates versus the physiology and energetic demands, and hence grazing rates, of all herbivores all the more critical. But we must recognize that the reduction or removal of major stressors to coral reefs underpins the long-term future of reefs and must allocate conservation resources accordingly.

Author contributions

MB: Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization. AD: Writing – review & editing, Investigation. CF: Writing – review & editing, Investigation. ARH: Writing – review & editing, Investigation. AH: Writing – review & editing, Investigation. JP: Writing – review & editing, Investigation.

WS: Writing – review & editing, Investigation. AS: Writing – review & editing, Investigation. TW: Writing – review & editing, Investigation. SW: Writing – review & editing, Investigation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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