Facilitating the Facilitators

Advancing coral reef restoration by considering ecological keystone species

Ewout Geerten Knoester

Propositions

1. Strong positive ecological interactions are a prerequisite for reef restoration to achieve scale.
   (this thesis)

2. Presenting restoration as the best conservation action contributes to coral reef degradation.
   (this thesis)

3. Environmental researchers fearing data theft rob themselves of opportunities.

4. Providing effective compensation for peer review is a responsibility of publishers to improve science.

5. Shifting baselines normalize climate change impacts.

6. To realize change, a picture is worth a thousand scientific papers.

7. Conservation scientists are well-informed activists.

8. NGOs become obsolete when governments become infallible.

Propositions belonging to the thesis, entitled

Facilitating the facilitators: advancing coral reef restoration by considering ecological keystone species

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Advancing coral reef restoration by considering ecological keystone species

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Thesis
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“The way corals change the world – with huge construction projects spanning multiple generations – might be likened to the way that humans do, with this crucial difference. Instead of displacing other creatures, corals support them.”

Elizabeth Kolbert

“*Though human ingenuity may make various inventions which, by the help of various machines answering the same end, it will never devise any inventions more beautiful, nor more simple, nor more to the purpose than Nature does; because in her inventions nothing is wanting, and nothing is superfluous.”*

Leonardo da Vinci

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Summary

The highly biodiverse coral reefs provide important economic and cultural ecosystem services to numerous tropical coastal nations around the world. Yet despite their evident benefits, coral reefs have lost half of their live coral cover in recent decades due to destructive uses and inadequate local management aggravated by global climate change. In addition to urgent climate action and improved local management, coral reef restoration has emerged as a new conservation tool. Coral gardening is a commonly-used restoration technique where coral fragments are first grown in nurseries and then outplanted onto degraded or artificial reefs (ARs). This active manipulation of coral populations is typically applied to accelerate the recovery towards a functional reef and its associated ecosystem services. However, the effectiveness of coral gardening, ARs and the wider practice of reef restoration is not yet well studied and still debated, as restoration efforts have generally been small-scale, costly and hampered by ecological setbacks. For example, coral nurseries commonly require high recurrent maintenance to remove competing biofouling such as macroalgae, while outplanted corals on degraded reefs and ARs often experience high predation pressure by fish and invertebrates. This thesis aims to improve our understanding on the key processes of herbivory and coral predation on natural reefs and use this ecological knowledge to improve the two-step coral gardening approach. Facilitation of ecological processes and keystone species (i.e. facilitating the facilitators) in reef restoration has the potential to reduce ecological surprises, reduce costs and thereby allow upscaling of restoration efforts. Through extensive field experiments in collaboration with an ongoing reef restoration project in Mkwiro, Kenya, the following three investigations were performed: the identification of herbivorous and corallivorous keystone species and their population dynamics on natural reefs (Chapters 2 & 3), the quantification of benefits and costs associated with herbivorous and corallivorous fish interacting with coral nurseries (Chapters 4 & 5) and the determination of how the impacts of keystone species and the performance of outplanted coral fragments in the first years are influenced by AR design (Chapter 6). This thesis concludes with a general discussion in which the research topics are linked, acquired insights synthesized and perspectives on coral reef restoration given (Chapter 7).

Chapter 2 aimed to identify locally important herbivores at six reefs in southern Kenya and empirically quantify their macroalgal removal (i.e. browsing). In addition, the influence of fisheries management on herbivores and their browsing pressure was studied. Video-recorded macroalgae buffet assays were used to identify herbivore species and their browsing activity and these were related to biomass estimates from stationary fish surveys and sea urchins counts. Herbivorous fish biomass was seven-fold higher in no-take zones compared to fished zones and included substantially more browsing unicornfishes and scraping parrotfishes. Macroalgae consumption was nearly three-fold higher in no-take zones and was mainly performed by these larger browsing and scraping herbivorous fishes. In contrast, fished zones with low macroalgae consumption were dominated by damselfishes and sea urchins. This chapter illustrates that fishing restrictions are likely to support reef resilience by increasing the biomass of functionally important herbivorous fishes and their consumption of coral-competing macroalgae.

Chapter 3 explored drivers of invertebrate and vertebrate corallivore populations as well as fish predation on corals. The impact of coral cover and fisheries management on coral predation on both natural coral populations and recently outplanted corals were investigated. At six reefs, coral and corallivore communities were characterized and fish bite marks quantified on natural coral colonies and outplanted fragments. The obligate corallivorous fish that mostly browse coral tissue were strongly associated with coral cover, whereas skeleton-consuming facultative corallivorous fishes such as parrotfishes were most abundant in no-take zones. Corallivorous snails were associated with low coral diversity and corallivorous sea stars were scarce. Bite mark densities (standardized to coral surface area) on natural reefs were clearly highest for branching corals, but did not correlate to coral cover, coral diversity or corallivorous fish densities. Predation pressure was substantially higher on outplanted coral fragments compared to natural coral colonies, especially inside no-take zones. The high predation pressure was associated with low remaining live coral tissue on outplanted fragments. This chapter demonstrates that reefs with low coral cover, often targeted for restoration, do not necessarily experience greater coral predation and that improved outplanting approaches are needed to address high predation pressure on outplanted branching corals. The interplay between fisheries management, reef restoration and corallivory warrants further consideration as high densities of facultative corallivorous fish could hamper restoration efforts.

Chapter 4 quantified the net positive and negative effects of herbivorous and corallivorous fish on coral performance in mid-water nurseries at a primary restoration site at Mkwiro. Coral growth, coral survival, fish bite marks and fouling were compared between caged and uncaged nurseries. Video recordings were used to identify and quantify interactions with herbivorous and corallivorous fish. Caging of nurseries strongly reduced both herbivory and corallivory, resulted in an 800% increase in fouling density, reduced coral growth by 40% and decreased coral survival by 9%. Uncaged nurseries were kept free of fouling primarily by grazing bristletooth tangs and although corals showed a few bite marks their performance was good. This chapter shows that the benefits of fouling control by herbivorous fish clearly outweighs the negative impacts of fish predation in mid-water coral nurseries and therefore recommends placing coral nurseries close to healthy, biodiverse natural reefs.

Chapter 5 aimed to quantify links between herbivorous fish biomass, grazing intensity and coral performance in mid-water nurseries at multiple sites. At six reefs under different fisheries management regimes, herbivorous fish biomass and composition, video-recorded grazing intensity, accumulated fouling, coral growth and coral survival were determined. Grazing intensity was sixfold higher and fouling density fourfold lower in protected areas compared to fished zones, and a high fouling density was strongly associated with reduced coral growth. Interestingly, grazing intensity was not directly associated with fish biomass in general as a single species of bristletooth tang dominated grazing across most studied reefs. This chapter shows that better coral nursery performance in protected areas can be partially linked to higher grazing intensity, which in turn is determined by both fish biomass and local species composition. The importance of key species indicates that species-specific fisheries management may help to maintain ecological processes.

Chapter 6 explored how AR design can influence the recovery of a coral reef community (i.e. corals and associated organisms) when restoring reefs. For two years, outplanted coral survival, coral recruitment, benthic cover and fish and invertebrate communities were monitored across four different AR designs (16 m2), unrestored controls and natural reference patches at Mkwiro. ARs consisted either of concrete disks with bottles, layered concrete disks, metal cages or a combination thereof. Coral survival and coral cover was lowest on concrete-based structures that suffered both from predation by invertebrates and dislodgement by sea turtles, and highest on elevated iron cages that prevented crown-of-thorns sea star predation. In contrast, coral recruitment was moderately high on concrete-based ARs but nearly absent on iron cages. All ARs and the natural reference patches featured nearly twice the fish species richness and about an order of magnitude higher fish abundance and biomass compared to unrestored control patches. AR and natural reference patches were similar in terms of trophic structure of their fish communities, but featured different species compositions. Fish abundance and biomass strongly correlated with coral cover on ARs. Motile invertebrates including gastropods, sea urchins, sea cucumbers and sea stars were present at ARs, but generally more abundant and diverse at reference patches. Taken together, this chapter shows that all studied ecological parameters progressed towards reef recovery, with varying influences of AR design. Although it is important to continue monitoring the succession of reef recovery over at least 10 years, based on the results of these first year's developments, it is recommended to use a combination of metal cages and layered concrete AR designs to promote high coral survival, natural coral recruitment and thereby also support associated reef communities. Future perspectives include optimizing the minimum density of ARs to be placed and outplanted with corals and the optimal diversity of AR-habitats to be provided and for reef rehabilitation in specific locations.

Chapter 7 integrates the identification of keystone herbivores and corallivores (Ch. 2-4), the results of site selection for coral nurseries (Ch. 5) and the effects of AR design on community development during reef restoration (Ch. 6). Here the question is addressed whether we can successfully facilitate the facilitators of reef restoration, thus improving the cost-effectiveness of reef restoration by facilitating specific ecological processes. The grazing of key herbivorous fish could clearly be facilitated by placing coral nurseries nearby natural reefs, with additional benefits to coral performance inside protected areas possibly relating to nutrient cycling by fish. Furthermore, the impacts of invertebrate corallivores could be effectively minimized by using an elevated AR design. Additional ecological integration, such as facilitating herbivores around ARs and reducing the impacts of facultative corallivorous fish on outplanted corals was found to be more complex and can be further explored through pilot restoration studies and improved empirical understanding. The chapter continues centred around a set of themes that place the findings of this thesis in a broader spectrum of coral reef restoration and conservation. These themes include the high potential of ecological facilitation in reef restoration, the complex role of biodiversity in conservation, the reliance on natural succession in restoration and lastly the (in)effectiveness of present-day coral reef conservation. The discussion culminates in a set of practical recommendations and future perspectives to facilitate eco-based and cost-effective coral reef rehabilitation and conservation. The practical recommendations include placing coral nurseries nearby natural reefs to facilitate herbivores, using elevated AR designs to limit coral predation by invertebrates, combining restoration with large no-take zones and establishing long-term socio-ecological monitoring programs. Future studies are recommended to focus on the synergies between restoration and conservation, the costs and benefits of various restoration techniques, the ecological aspects of coral outplanting and the adaptability of corals to climate change.

Chapter 1

General introduction

Coral reef conservation and restoration

Coral reefs are reckoned to support over a third of all marine fish species (Kulbicki et al., 2013) and provide habitat to nearly a million other species (Fisher et al., 2015), while covering less than 0.1% of the ocean floor (Spalding et al., 2002). These impressive and often-cited biodiversity feats are not just biologically interesting, but also support the livelihoods of over half a billion people through food provision, income opportunities and coastal protection (Wilkinson, 2008). The yearly global economic value of coral reefs is estimated to culminate to around ten trillion USD (Costanza et al., 2014). Despite the evident benefits coral reefs provide, only a fraction of their estimated worth is put into reef conservation (ICRI, 2018). Unsustainable use, inadequate local management as well as global climate change have increasingly been threatening reef-building coral species (Carpenter et al., 2008) and disintegrating this delicate ecosystem and the services it provides (Burke et al., 2011; Eddy et al., 2021). Prevalent local stressors include unsustainable and habitat destructive extraction of marine life, including removal of keystone species for ecosystem functioning (Edwards et al., 2014; McCauley et al., 2015), as well as eutrophication due to watershed pollution promoting coral competitors and coral diseases (Norström et al., 2009; Zhao et al., 2021). These persistent stressors erode the resilience of coral reefs to recover from other acute disturbances such as storms and climate-change induced threats and natural coral predation (Anthony et al., 2015). Stressors resulting from climate change include temperature increases above the limits of locally-adapted corals resulting in either direct coral mortality or bleaching, the often fatal breakdown of the symbiosis between corals and their food-providing microalgae (Jokiel & Coles 1990; Sully et al. 2019). Also ocean acidification can impede the formation of the limestone coral skeletons and reef formation (Perry and Alvarez-Filip, 2019; Cornwall et al., 2021). Unable to withstand this myriad of stressors, it is currently estimated that half of the world's live coral cover has been lost since the 1950s (NASEM, 2018; Díaz et al., 2019; Eddy et al., 2021). For some regions the whole ecosystem is even deemed vulnerable to collapse (Obura et al., 2022). Without drastic changes in conservation approaches, the numerous people heavily dependent on coral reefs will have to adapt to the degradation and literal erosion of this ecosystem and the loss of services it used to provide, and the discontinuation of coral-reef associated traditional livelihoods (Rogers et al., 2014; Woodhead et al., 2019).

Traditional management approaches such as the establishment of protected areas, though crucial, have been ineffective or insufficient to prevent the ongoing decline of coral reefs (Ledlie et al., 2007; Anthony et al., 2011; Hughes et al., 2017). Coral reefs and their current ecosystem services can only be sustained if urgent action is taken on three priority areas: reducing global greenhouse emissions, reducing local threats such as overfishing and habitat destruction and investing in active coral reef restoration (Knowlton et al., 2021). The first two priorities have been widely agreed upon within the scientific community, but the role of restoration has remained more controversial (Chou, 1997; Edwards and Clark, 1999). A common restoration objective is to accelerate the recovery of a functioning reef ecosystem and its associated services by actively manipulating reef-building coral populations (Boström-Einarsson et al., 2020; Ferse et al., 2021). The effectiveness of coral reef restoration has been debated for its associated high costs (Bayraktarov et al., 2016), limited spatial extent (Boström-Einarsson et al., 2020) and frequent project failure due to ecological setbacks (Edwards et al., 2010). Furthermore, a disconnect between restoration practitioners and scientific research delays the establishment of effective methods (Boström-Einarsson et al., 2020; Ferse et al., 2021). Nonetheless, substantial progress has been made in development of restoration methodologies (Mcleod et al., 2019; Vaughan, 2021). Initial restoration attempts in the 1980s started by transplanting corals from one site to another (Harriott and Fisk, 1988), often to salvage colonies from planned coastal construction/destruction. To prevent negative impacts on source reefs and to allow upscaling, the two-step coral gardening approach was promoted in the 1990s: this included an initial phase of coral mariculture to create a large stock of corals before outplanting them onto degraded reefs (Rinkevich, 1995). Subsequently, the use of artificial reefs (ARs) for reef restoration was established (Pickering et al., 1999). In the following decade, lessons learned from a growing number of projects were consolidated in various scientific manuals (Precht, 2006; Edwards et al., 2010; Johnson et al., 2010). In recent years, technologically more complex coral culturing methods have emerged (NASEM, 2018), including the use of sexually-reproduced corals to increase the genotypic diversity (Guest et al., 2014), microfragmentation to efficiently culture more stress-resilient massive corals (Forsman et al., 2015) and assisted evolution to advance coral adaptation to increasing anthropogenic stress (van Oppen et al., 2017). A combination of these restoration methods is becoming more accepted as a scientifically-validated conservation tool (Anthony et al., 2017; Abelson et al., 2020; Hein et al., 2021). At the heart of many restoration methods remains the two-step coral gardening approach, which can be effectively combined with more advanced techniques to create a large, diverse and resilient coral stock for restoration (NASEM, 2018; Mcleod et al., 2019).

Coral gardening

The initial nursery phase of coral gardening aims to increase a limited number of small coral fragments into a considerable stock of large colonies. Coral growth in nurseries is faster compared to coral growth on reef substrates, as nurseries provide ample of water exchange and light, while preventing benthic competition and coral predation (Edwards et al., 2010). This approach has two major benefits. First, only a limited (though genotypically diverse) amount of coral has to be collected from natural colonies, limiting the impact on source reefs (Epstein et al., 2001; Lirman et al., 2010). Second, large nursery-grown colonies have higher survival chances than small coral fragments when outplanted, as coral survival scales with size (Forsman et al., 2006; Omori, 2019). Numerous nursery designs exist to mariculture corals, including bottom-anchored tables (Epstein et al., 2001; Soong and Chen, 2003), mid-water suspended nurseries (Shafir et al., 2006a) and even floating structures moving up and down with the tides (Shaish et al., 2008; Levy et al., 2010). Coral nurseries have been highly successful to mass produce corals (Lirman and Schopmeyer, 2016; Omori, 2019) and are implemented by numerous restoration projects around the world and yearly provide tens to hundreds of thousands coral colonies (Vaughan, 2021). At some larger restoration projects, this approach has been used to replant several hectares of reefs, with upscaling plans lying ahead (Vaughan, 2021). The prospect for further upscaling partially depends on the associated costs, which can be high due to underwater maintenance expenditures and especially the SCUBA-diver assisted removal of competing fouling organisms including macroalgae, sponges, tunicates and soft corals (Ferse et al., 2021; Vaughan, 2021). Finding ways to reduce such recurrent maintenance costs could help to upscale coral mariculture and thus reef restoration.

The outplanting of nursery-grown coral colonies onto degraded reefs or ARs, the second phase of the coral gardening process, is anticipated to kickstart coral reef recovery by supporting critical ecosystem processes such as increased structural complexity, the return of keystone species like herbivores and improved coral reproduction and coral recruitment (Hein et al., 2020a). To enable outplanting, numerous methods have been developed to attach corals to hard substrate, including wedging, scattering, gluing, hammering pins, drilling holes, attaching ropes and several more inventive ways (Edwards et al., 2010; Yee et al., 2018). Also the ARs used to mount the corals onto come in an equal diversity of materials and shapes, including sunken boats, vehicles, airplanes or their scrap parts as well as specifically-designed structures consisting typically of concrete, steel, natural rocks or a combination thereof (Ceccarelli et al., 2020; Hylkema et al., 2021; Higgins et al., 2022). All these methods have the same goal: to provide hard substrate at locations where this does not exist anymore. The survival of outplanted colonies (provided they have grown to a substantial size) is generally high when corals are firmly attached onto stable substrate (Bayraktarov et al., 2019; Boström-Einarsson et al., 2020). Though long-term monitoring evaluating coral reef development over many years and associated broad-scale ecosystem effects remains scarce (Ceccarelli et al., 2020), a handful of studies suggest that ecological recovery can be assisted by sustained high coral cover (Hein et al., 2020a), increased coral recruitment (Montoya-Maya et al., 2016) and increased fish species richness and biomass (Hylkema et al., 2020). The outplanting phase, however, is frequently hampered by ineffective AR designs or materials (Hylkema et al., 2021; Higgins et al., 2022) and ecological surprises (Edwards et al., 2010). Commonly encountered ecological problems include predation on recently outplanted coral fragments and high fragment mortality due to negative interactions with benthic competitors (Edwards et al., 2010). Adjustments in AR design and outplanting strategies could potentially help to increase the survival of outplanted fragments and thereby improve the overall effectiveness of reef restoration (Bayraktarov et al., 2019).

Restoration ecology

For coral gardening to become a scalable restoration tool, further improvements are needed in the cost-effectiveness of both the nursery and outplanting phase (Abelson et al., 2020; Boström-Einarsson et al., 2020; Ferse et al., 2021). The integration of ecological knowledge with reef restoration approaches could help to realize such improvements (Shaver and Silliman, 2017; Ladd et al., 2018). In particular, herbivory (the grazing on competing algae) and corallivory (the predation on coral colonies) are two fundamental ecological processes that could strongly influence restoration outcomes (Ladd and Shantz, 2020). These key processes have long been recognized to play important roles in shaping natural reefs (Glynn et al., 1972; Carpenter, 1986), but the integration of these ecological processes into coral reef restoration (i.e. restoration ecology) only gained attention recently (Ladd and Shantz, 2020).

Herbivory is an essential process on coral reefs, which contributes to the dominance of slow-growing hard corals by controlling fast-growing space competitors such as algae (Carpenter, 1986; Steneck, 1988). Keystone herbivorous species such as fish and sea urchins can control macroalgae either through the extensive and indiscriminate foraging, preventing establishment and growth of algal recruits on the reef substrate (i.e. grazing), or the selective consumption of established macroalgae (i.e. browsing). It is well known that a lack of reef herbivores typically leads to drastic increases in fleshy macroalgae, both at an experimental scale in exclusion cages (Thacker et al., 2001; Korzen et al., 2011) and at reef-wide scales due to overfishing and collapsed herbivore populations (Done, 1992; Bruno et al., 2009). Once established, macroalgae can actively compete with corals for space and light through overgrowth, shading, abrasion and allelopathy (Jompa and McCook, 2002) and thereby reduce coral survival, growth, fecundity and recruitment (Box and Mumby, 2007; Hughes et al., 2007a). The importance of herbivores, their population dynamics and ecological functioning are relatively well-studied on natural coral reefs (Hay, 1997; Puk et al., 2016), yet this ecological knowledge is rarely incorporated in restoration approaches (Abelson et al., 2020; Ladd and Shantz, 2020). This mismatch presents untapped opportunities, as coral gardening could benefit from herbivores through both free bio-assisted cleaning throughout the nursery phase (Frias-Torres and Van de Geer, 2015) and control of benthic competitors around outplanted coral fragments (Ladd et al., 2018). Given that only a fraction of reported restoration projects currently consider such ecological facilitation, numerous opportunities remain to improve the success and cost-effectiveness of coral gardening by integrating and facilitating ecological processes such as herbivory (Shaver and Silliman, 2017; Rinkevich, 2019).

Similarly, a better ecological understanding on corallivory could improve restoration outcomes, in this case by limiting the negative impacts of coral predation. On natural reefs, fish and invertebrate corallivores typically target fast-growing coral genera such as branching *Acropora* spp. (Cole et al., 2008; Rotjan and Lewis, 2008). By controlling populations of such competitively-dominant corals, corallivores are deemed important to maintain coral diversity on reefs (Neudecker, 1979; Cox, 1986). However, invertebrate corallivores such as *Acanthaster* spp. sea stars and *Drupella* spp. snails periodically manifest excessive population blooms during which whole reefs can become denuded of live coral (Bruckner et al., 2017; Pratchett et al., 2017). These destructive events appear more common on reefs that already experience other stressors such as lack of predatory fish and eutrophication (Fabricius, 2005; Rice et al., 2019). Such degraded reefs are likely targets for restoration and, indeed, numerous coral reef restoration projects have been hampered by the excessive predation on outplanted corals by these invertebrate corallivores (Omori and Fujiwara, 2004; Shafir et al., 2006b; Johnston and Miller, 2014; Cabaitan et al., 2015). The frequent use of branching corals in restoration can further explain the high invertebrate corallivore predation pressure (Rotjan and Lewis, 2008; Boström-Einarsson et al., 2020), whereas corallivorous fish can severely impact outplanted massive corals (Koval et al., 2020; Rivas et al., 2021). In an early restoration phase, these strong rates of predation do not increase coral diversity, but instead reduce overall live coral cover and hamper further reef development. While manual removal of invertebrate corallivores (Williams et al., 2014) and caging of outplanted corals (Baria et al., 2010) have been attempted to reduce coral predation, such labour-intensive interventions further limit the upscaling potential of reef restoration. Instead, ecological solutions to prevent excessive coral predation could support more cost-effective and successful restoration approaches (Ladd and Shantz, 2020; Seraphim et al., 2020).

Research objectives

Integration of key ecological processes with reef restoration, such as the facilitation of herbivory and control of corallivory around maricultured and outplanted corals, has the potential to improve the cost-effectiveness of the coral gardening approach and thereby support the much-needed upscaling of this conservation tool. The aim of this thesis is to improve our understanding on the role of biological facilitators on natural reefs, explore how this knowledge can be used to facilitate these facilitators in coral mariculture and reef restoration approaches and, ultimately, to improve the efficiency and success of coral gardening. Through extensive field experiments in collaboration with an ongoing community-led reef restoration project in Mkwiro, Kenya, this thesis undertook three investigations that are presented divided over five chapters (Fig. 1): the identification of herbivorous and corallivorous keystone species and their dynamics on natural reefs (*Ch. 2 & 3*), the quantification of benefits and costs associated with herbivorous and corallivorous fish interacting with coral nurseries *(Ch. 4 & 5)* and the determination of how keystone species and the performance of outplanted coral fragments and settlers are influenced by AR design *(Ch. 6).* The five specific research questions for each respective chapter are:

- How does the presence and function of locally identified keystone herbivores differ between reefs, regions and type of fisheries management? (*Ch. 2*)
- How does the presence and function of locally identified key coral predators differ between natural and restored reefs, and does level of fisheries management influence observed patterns? (*Ch. 3*)
- What is the net impact of herbivorous and corallivorous fish on the performance of corals in mariculture? (*Ch. 4*)
- Does a quantitative link exist between herbivorous fish communities, their grazing intensity and the performance of coral in mid-water nurseries? (*Ch. 5*)
- Can identified keystone species, coral fragment performance and coral settlement be facilitated through AR design? (*Ch. 6*)

Following this general introduction (*Ch. 1*), five research chapters are presented in which these research questions are investigated (*Ch. 2 – 6*) and these findings are discussed and future perspectives presented in the general discussion (*Ch. 7*).

Chapter 2 identifies locally important browsing herbivores and quantifies their removal of macroalgae at six reefs in southern Kenya and investigates the impact of fisheries management on herbivory. Through video-recorded macroalgae buffet assays, keystone browsing species and their browsing pressure were determined and related to biomass estimates from stationary fish surveys and sea urchin counts.

Chapter 3 explores corallivore populations and their predation pressure at six reefs in relation to varying levels of coral cover and fisheries management, and investigates the differences between corallivory on natural and outplanted coral colonies. Coral and corallivore communities were characterized and fish bite marks quantified on natural coral colonies and fragments outplanted on small AR structures.

Chapter 4 determines whether the reef-bound fish community has an overall positive or negative effect on coral mariculture, focussing on herbivory and corallivory. The net impact was determined by experimental exclusion of fish from mid-water coral nursery structures and comparing the fouling, coral performance and bite marks in uncaged and caged nurseries at Mkwiro.

Chapter 5 quantifies links between herbivorous fish communities, their grazing intensity and the performance of coral in mid-water nurseries. At six reefs, herbivorous fish biomass and species composition, video-recorded grazing intensity and accumulated fouling densities were studied in relation to coral performance in coral nurseries.

Chapter 6 determines how AR design influences the ecological communities and development of restored reefs by monitoring outplanted coral fragments, coral recruitment and fish and invertebrate communities. Four AR design patches, unrestored controls and natural reference patches in Mkwiro were monitored over a two-year timespan for outplanted coral fragment survival, natural coral recruitment and fish and benthic communities.

Chapter 7 concludes this thesis with a general discussion in which the research questions are linked, acquired insights synthesized and perspectives on coral reef restoration are given.

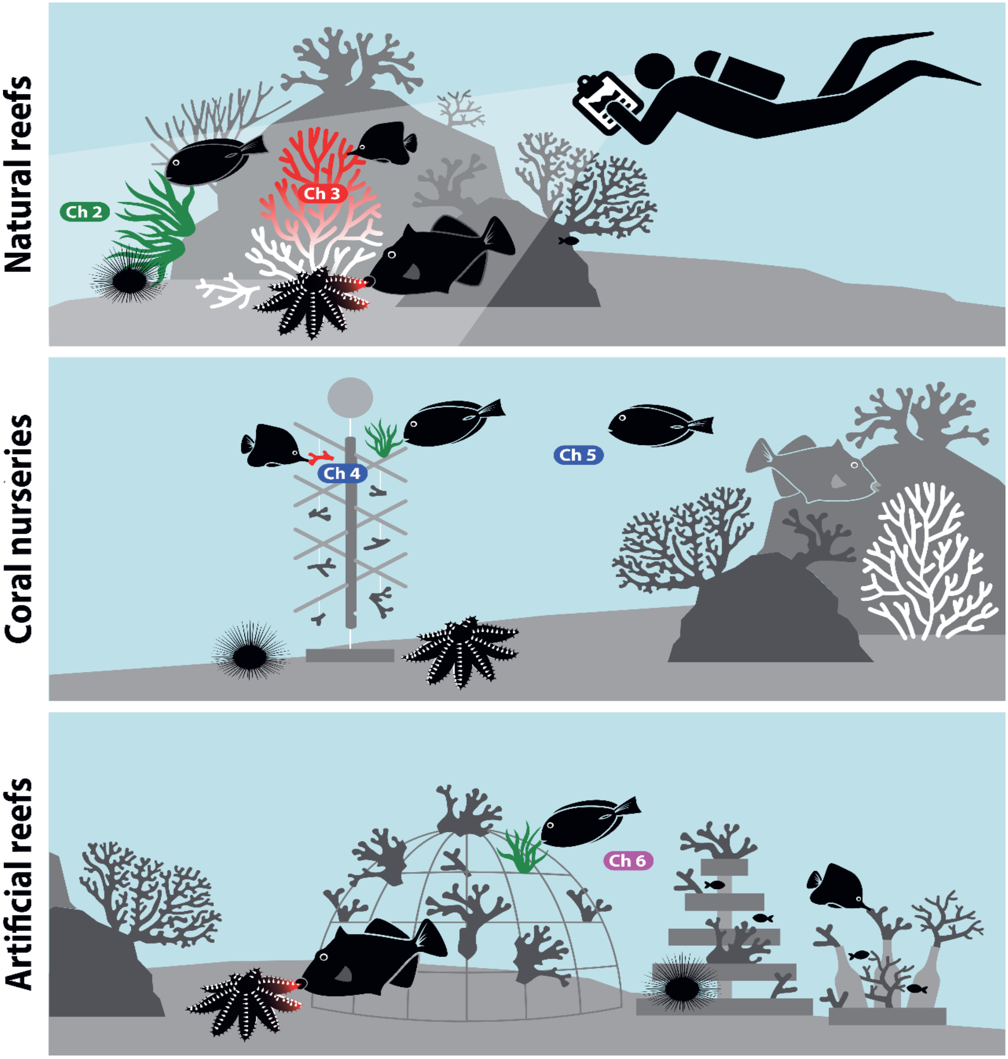

Figure 1 *Conceptual overview of the content of this thesis. Chapter 2 and 3 identify keystone herbivores and coral predators on natural reefs, respectively, and determine drivers of their populations and functional roles. Chapter 4 evaluates the conflicting impact of herbivorous and coral predating fish on coral mariculture, and Chapter 5 quantifies the link between herbivorous fish community and coral mariculture success. Chapter 6 evaluates how artificial reef design can mediate keystone herbivores and coral predators to improve performance of outplanted corals and natural recruits. The general introduction and discussion (Chapters 1 and 7) are not depicted. Artwork by Vrijlansier*

2

Fisheries restrictions and their cascading effects on herbivore abundance and macroalgae removal at Kenyan coral reefs

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Abstract

The increase of macroalgae at degraded reefs impedes several ecosystem services and calls for effective methods to facilitate a return to coral dominance. Removal of macroalgae (browsing) is typically realized by fish, but the role and identity of browsers at the heavily-fished East African coast is still largely unknown. This study investigated how browsing pressure at Kenyan reefs (-4.700, 39.396) related to fisheries management and herbivore community. From October 2018 to January 2019, consumption during 24-h buffet assays using the brown macroalgae Sargassum and Padina was determined and video recorded at six sites: two in fished zones, two in marine reserves (traditional fishing allowed) and two in no-take zones. Herbivorous fish composition, biomass and sea urchin density were also determined. Consumption of Sargassum and Padina was nearly three-fold lower in the fished zones (26% and 28% of macroalgal biomass consumed, respectively) compared to the no-take zones (62% and 82%), with intermediate consumption in the marine reserves (48% and 71%). Herbivore biomass was seven-fold higher in no-take zones and included substantially more browsers (mainly unicornfishes, Naso spp.) and scrapers (scarids), which were associated with the higher browsing pressure. Browsers and scrapers were predominantly responsible for the consumption of macroalgae as determined by video recordings, though key species differed across sites. In contrast, damselfish-dominated fished sites were associated with high sea urchin densities and low browsing pressure. These results indicate that fishing restrictions are likely to support reef resilience by increasing herbivorous fish biomass of key species and thereby promote macroalgae removal.

Key words: Browsers; *Padina*; *Sargassum*; Protected area; Grazers; Reef restoration

Introduction

Important ecosystem services such as coastal protection and sustainable fisheries provision become reduced when coral reefs degrade into seascapes dominated by macroalgae (Pratchett et al., 2014; Rogers et al., 2018). Herbivores, especially fish, play a crucial role in promoting coral over macroalgal dominance (Hughes et al., 2007b; Holbrook et al., 2016) either by preventing the establishment of macroalgal recruits through continuous removal of algal turf (i.e. grazing) or by reversing macroalgal dominance through selective removal of mature macroalgae (i.e. browsing). Grazing of algal turf creates favourable conditions for coral growth and settlement and thereby supports coral dominance (Lefcheck et al., 2019) and consequently reef biodiversity and resilience (Nyström et al., 2008). However, with climate change induced temperature stress weakening the competitive potential of numerous corals (Sully et al., 2019) in combination with overfishing (Edwards et al., 2014) and eutrophication (Norström et al., 2009), impaired grazer communities become increasingly unable to prevent macroalgae establishment. First and predominantly observed in the Caribbean (Done, 1992; Bruno et al., 2009), coral to macroalgae phase shifts are now occasionally reported from Indo-Pacific reefs as well (McClanahan et al., 2001; Ledlie et al., 2007; Chong-Seng et al., 2014). Once established, macroalgae can prevent a return to a coral-dominated state by supressing the survival, fecundity and recruitment of corals (Hughes et al., 2007b; Schmitt et al., 2019). It is thought that reversal of such phase shifts can be achieved mainly through the active removal of macroalgae by browsers (Puk et al., 2016). Therefore, a good understanding on the distribution of key browsing species and the factors influencing their potential to control macroalgae is important.

The use of functional groups has proven helpful to understand the principles of ecological processes and coral reef resilience (Heenan and Williams, 2013). Even though herbivory is a well-studied process on coral reefs, research focussed on browsers specifically has been challenging and results often defy generalization. Identification of key species responsible for macroalgae removal based on their abundance alone has proven difficult for several reasons. Biomass estimates from visual surveys tend to underestimate browser diversity and biomass due to the cautious nature of browsers (Hoey and Bellwood, 2010a; Michael et al., 2013), though the use of video-recorded macroalgae buffet assays have provided a wealth of additional information on browsers (Bennett and Bellwood, 2011). Browsing on macroalgae seems to be commonly done by only a small subset of the diverse browser community due to spatial, temporal and behavioural variation (Bennett and Bellwood, 2011; Lefèvre and Bellwood, 2011; Puk et al., 2016), and is sometimes even dominated by species traditionally not considered as browsers (Bellwood et al., 2006; Chong-Seng et al., 2014; Tebbett et al., 2020). In addition to these various groups of fishes, sea urchins can also contribute to the control of macroalgae (McClanahan et al., 1994) and this has been especially important on Caribbean reefs (Francis et al., 2019). Increasing numbers of sea urchins have become more dominant in macroalgal control at certain overfished Indo-Pacific reefs as well (Humphries et al., 2014), but also contribute heavily to reef erosion through their scraping feeding method (Carreiro-Silva and McClanahan, 2001). The apparent plasticity in functional roles of the browser community complicates the use of browser biomass alone to predict browsing pressure, an indicator deemed relevant for reef resilience (Nyström et al., 2008; Brandl and Bellwood, 2014).

Mismatches between abundance and ecological relevance of browsing species have important management implications, where protection of certain species might not result in the desired coral reef resilience (McClanahan, 2008). A good understanding on which species contribute most to macroalgae removal can enable managers to increase reef resilience and the likelihood of phase shift reversal when restoration towards coral dominance is desired. Although several studies on the well-protected Great Barrier Reef have proven invaluable to identify dominant browsers and potential drivers for the regional variability in browsing pressure (Hoey and Bellwood, 2009; Bennett and Bellwood, 2011; Michael et al., 2013; Streit et al., 2015), the application of this knowledge to other geographical areas and sites with higher fishing pressure may be limited. Indeed, superimposed on geographic differences (Heenan et al., 2016) is the divergent fishing pressure among coastal populations, in which large-bodied fishes such as browsers are often preferred targets (Edwards et al., 2014). The susceptibility of browsers to fishing pressure (see also Froese and Pauly 2015) and their important yet complex role in the coral-algae balance call for a better understanding of these dynamics in general and variability among geographical areas in particular.

This study aimed to further improve our understanding on browsing by expanding the geographic scope and including the impact of fisheries management within the study domain. We provide an identification of key browsers and quantification of their browsing capacity at six Kenyan reefs, which form part of a mostly intensely-utilized fringing reef in the Western Indian Ocean. Here, the enforcement of three distinct fisheries management zones (open access fished zones, marine reserves for traditional fishing only and well-enforced no-take zones) are well suited to investigate the impact of management on the browser community and their influence on reef resilience. Through video-recorded macroalgae buffet assays we identified key browsing species and their browsing pressure and related this to biomass estimates from stationary fish surveys and sea urchin counts. We hypothesised that the increasing levels of fisheries restrictions would result in higher herbivorous fish biomass and more effective control of macroalgae.

Methods

Study sites

The study was performed around Wasini Island in southern Kenya from October 2018 till January 2019 during the dry northeast monsoon. Tidal differences reach over four meters during spring tide and result in moderately strong tidal currents throughout the area. Six study sites were chosen (Fig. 1), equally distributed over three different types of fisheries management. Two study sites are located in a fished zone, where intense and unselective fishing is performed daily by artisanal fishermen using mainly traps, nets, spearguns and hook and line (sites 1 and 2). Two study sites are in the Mpunguti Marine Reserve (11 km^2 established in 1973), where only traditional fishing methods are allowed (i.e. traps and hook and line) and this is enforced by the Kenyan Wildlife Service (sites 3 and 4). Two well-enforced no-take zones were chosen to complete the comparison, each with one study site: Kisite Marine National Park (28 km^2 established in 1973) enforced by the Kenya Wildlife Service (site 5), and the Wasini Community Managed Area (0.31 km^2 established in 2008) enforced locally by the Wasini

Beach Management Unit (site 6). Reef zone was standardized by selecting reef slope habitat across study sites and given differences in visibility, this resulted in different depths per site. Sites 1, 2 and 6 are situated in a sea strait between Wasini Island and the mainland and experience relatively turbid water conditions (average visibility ~7 meters) and therefore exhibit a shallow (up to 8 meters depth) and patchy reef development. These sites had not yet been included in any long-term monitoring program and therefore lack documented data on their habitat such as historical coral cover. Sites 3, 4 and 5, south of Wasini Island, are further offshore and have an average visibility of ~15 meters and fringing reef development up to around 16 meters depth. Sites 4 and 5 have been monitored extensively and have maintained a moderate to high coral cover and diversity (McClanahan et al., 1999), with a decline and subsequent recovery after the 1998 thermal anomaly (McClanahan et al., 2001; Obura et al., 2002). Site 3 has not been included in past monitoring, but given the hard substrate, clear water and moderate depth and exposure one would expect this site to have been historically suitable for hard corals.

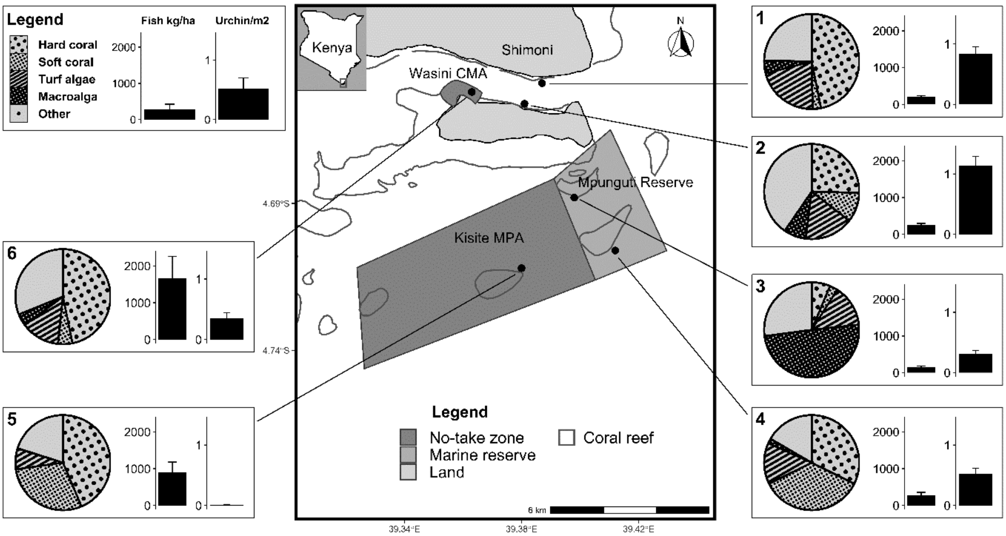

Figure 1 *Map of Kenya showing study area (insert) and detailed map showing the six study sites. Three different fisheries management zones can be identified: unrestricted fished zone (unshaded) including sites 1 (Firefly House Reef) & 2 (Pilli Pipa Restaurant), the Mpunguti Marine Reserve where traditional fishing is allowed (shaded orange) encompassing sites 3 (Lower Mpunguti) & 4 (Dolphin Point) and no-take zones (shaded red) covering sites 5 (Kisite Marine National Park) & 6 (Wasini Community Managed Area). Boxes shows additional information for each study site on benthic cover, total fish biomass and sea urchin density. Bars represent means ± standard error (n = 10 for benthic surveys and n = 11 - 15 for fish surveys). Credit to H. Mwamlavya for compiling the figure*

Benthic and fish surveys

A 20-m point intercept transect with 0.5 m interval was used to map benthic cover in broad categories (hard coral, soft coral, turf algae (< 1 cm), fleshy macroalgae (> 1 cm) and a pooled category ‘other’ including mainly sand, rubble and uncommon sessile invertebrates such as sponges and tunicates (Hill and Wilkinson, 2004). Within a 2 x 20 m^2 belt transect sea urchins were identified to species level and counted to determine their density (Hill and Wilkinson, 2004). A stationary fish census (radius of 7.5 m; surveys were only performed on days when visibility exceeded 8 meters) was used to quantify the composition and abundance of all diurnal, non-cryptic fishes (Bohnsack and Bannerot, 1986). Fish sizes (fork length) were estimated in classes of 5 cm for fishes smaller than 20 cm, and in 10-cm size classes for larger individuals. Per study site, 10 replicate benthic surveys and 11 – 15 replicate fish surveys were performed, covering a stretch of around 200 m at each site. Benthic and fish surveys were performed midway the reef slope at study sites with a fringing reef (depth range: 5 – 9 m) and patch reefs (depth range: 2 – 6 m).

Macroalgae buffet assay

At each study site, browsing pressure was determined by recording consumption from macroalgae buffet assays over 24 h (Fig. 2). Two brown macroalgae were used: *Sargassum ilicifolium* (Turner) C. Agardh, 1820 and *Padina boergesenii* Allender & Kraft, 1983 (henceforth referred to by genus name only). These brown algae were chosen as they are the dominant macroalgae in the area and typical representatives of algal climax communities (Humphries et al., 2014). One day before use, the macroalgae were collected from the shallow reef flat at study site 1 and stored in seawater basins. Before and after deployment, the drip-dry wet weight (shaken 10 times to remove excess water) of each macroalgae was determined. The macroalgae were kept in their natural growth form, resulting in the following average starting weights (mean ± SD): *Sargassum* (38.3 ± 4.6 g) and *Padina* (18.4 ± 2.9 g). The buffet assay also included the seagrass *Thalassia hemprichii* to allow for comparisons with an older buffet assay study from the Kenyan coast (McClanahan, 2008), but these results are discussed separately in the supplementary materials (Fig. S1) as the focus of this report is on macroalgae. For deployment, the three different macrophyte species were strung equidistant and in random order on a 1-m fishing line. The line was weighted with three 10-cm metal pins to enable secure placement on the reef substratum and to provide access to both vertebrate and invertebrate, bottom-dwelling browsers. The macrophytes were transported in basins with seawater and deployed at a similar habitat and depth as where the benthic and fish surveys were performed. One replicate buffet assay consisted of 10 lines, with each line separated approximately 2 meters from the next. Per replicate assay, one additional control line was placed inside a weighted plastic cage of 30 x 30 x 50 cm^3 with 1.3 x 1.3 cm^2 mesh size to exclude all macro-browsers to check for weight loss due to handling, following Seah et al. (2021) amongst others. For each study site, the assays were repeated on five non-consecutive days throughout the 4-month study period.

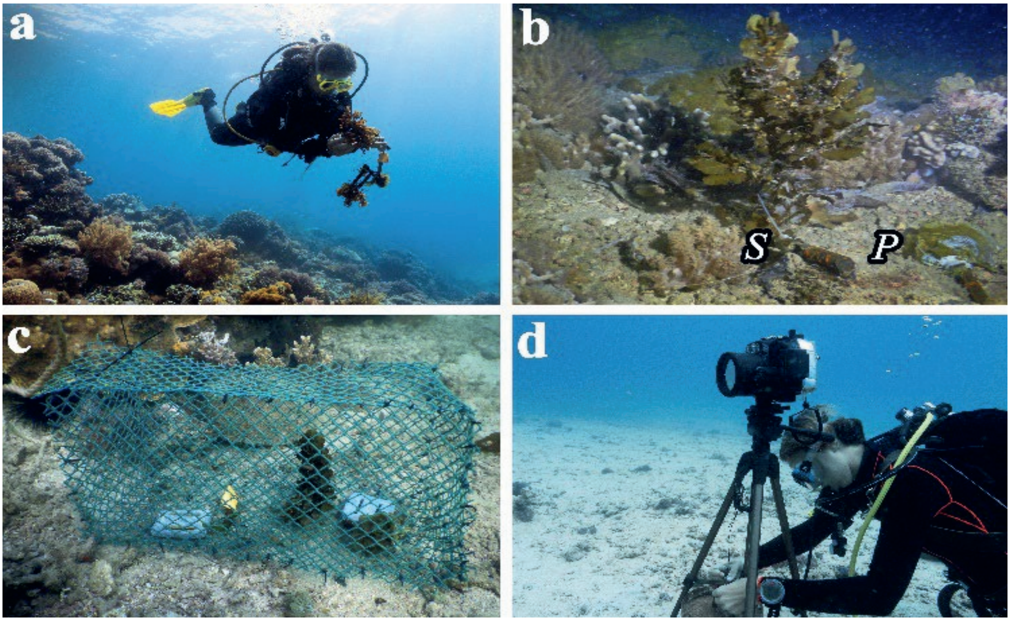

***Figure 2** Experimental setup of the buffet assay. **(a)** Diver placing macroalgae on the reef. **(b)** Close-up of one assay line positioned on the reef, showing* <u>S</u>argassum ilicifolium *&* <u>P</u>adina boergesenii. ***(c)** Close-up of one assay in the control cage. **(d)** Diver preparing the remote underwater video recording. Source a-d: EGK*

Remote underwater video

To identify the species responsible for the reduction in macroalgae biomass and to quantify their browsing activity with minimum disturbance, the first 75 mins of deployment of each buffet assay were recorded on remote underwater video (RUV). A Canon 600D DSLR camera in a Neewer 40M case was placed on a weighted tripod, approximately 2 meters from one randomly chosen line. The camera was programmed to take 10-min clips, with both a starting delay and subsequent interval of 5 min, resulting in a total recording time of 45 min per assay. Recording took place between 1000 h and 1400 h, which coincides with the peak in foraging activity of most roving (i.e. mobile) herbivorous fishes (Hoey and Bellwood, 2009). In total, 30 recordings were made.

Data processing and analysis

Data on benthic cover, total fish biomass and grazing sea urchin density is presented descriptively. Grazing sea urchins include all sea urchin species except the burrowing species *Echinostrephus molaris* which feeds on drifting algae only. Data from stationary visual surveys was used to estimate fish biomass using the midpoint of each size class and published length-weight relationships (Froese and Pauly, 2015). Herbivorous fish biomass was subdivided into the following functional groups: browsers, grazers, scrapers and excavators, based on reported species' functional traits following Green & Bellwood (2009). Two additions were made: *Platax* spp. were also considered browsers (Bellwood et al., 2006) and territorial damselfishes were considered as a separate functional group, including the genera *Amblyglyphidodon*, *Plectroglyphidodon* and *Stegastes.* Average herbivorous fish biomass was compared between the three types of *Fisheries management* using a generalized linear model with Gamma distribution and log-link using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2020). *Reef type* ('Patch' for study sites 1, 2 and 6 and 'Fringing' for sites 3 – 5) was included as factor during model selection to explore potential confounding environmental parameters related to these different habitats, such as depth, water clarity and exposure. The most parsimonious model was selected based on Akaike's Information Criterion (AIC) using a selection threshold of $\Delta AIC > 6$ (Fox et al., 2015). *Study site* was included as random factor to account for non-independence of repeated surveys at each site. Model assumptions were validated by visual inspection of *DHARMa* diagnostic plots for mixed regression models (Hartig, 2021). The Wald Chi-Squared Test from the *car* package (Fox and Weisberg, 2018) was used to determine the significance of fixed factors. Within-level differences between *Fisheries management* were examined using pairwise means comparisons with Tukey adjustment using the *emmeans* package (Lenth, 2020). A similar approach was repeated to test for differences in herbivorous fish biomass between the specific *Study sites*, without the need for inclusion of a random factor here.

The fraction consumption of buffet assays was calculated following Bennett & Bellwood (2011): $\text{Consumption (F)} = 1 - \frac{M_1}{M_0 * (1-C)}$ where M_0 is the initial macroalgal mass, M_1 the remaining mass after 24 h and C the mean fraction of biomass loss at the control treatment (calculated separately for each site and macroalgae). The mean of 10 lines was taken for both macroalgae species to represent a replicate buffet assay. A beta regression model with logit link was used to account for the proportional nature of the consumption data (Douma and Weedon, 2019) using the *glmmTMB* package (Brooks et al., 2017). A mixed-effects model was built to determine the fixed effects of *Fisheries management* and *Macroalgae species* ('Sargassum' and 'Padina') on consumption. *Study site* and *Assay* were included as nested random factors to account for both the non-independence of repeated measurements at each study site and the non-independence of algal species on the same line. Accounting for potential confounding factors, checking model assumptions and performing significance tests were implemented as outlined above. Again, the approach was repeated to specifically test for the effect of individual

Study sites.

All RUV recordings were viewed and for each bite the targeted macroalgae and involved fish species were noted. In addition, fish's fork length was estimated (using the buffet line as reference), transformed to weight using published length-weight relationships (Froese and Pauly, 2015) and multiplied by the number of bites taken to calculate mass-scaled bites (ms-bites) following Hoey and Bellwood (2009). Sums of ms-bites were standardized to hour to correct for slight variations in RUV recording length. Bite impact estimated from RUV is thus expressed as ms-bites in kg h^{-1}. This data is presented descriptively.

A distance-based redundancy analysis (db-RDA; Legendre and Anderson, 1999) was performed using fisheries management, as well as average macroalgae consumption and sea urchin density per study site as (z-score transformed) environmental parameters fitted to a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) on the herbivorous fish species community using the *vegan* package (Oksanen et al., 2022). A main advantage of db-RDA compared to other ordination methods is that it accepts non-Euclidian dissimilarity matrices, such as the ecologically-relevant Bray-Curtis (Ramette, 2007). Significance of the overall db-RDA model and the environmental parameters were assessed using Monte Carlo permutation tests using 999 permutations (Legendre et al., 2011).

Results

Benthos and fish

Average hard coral cover was relatively high across study sites with values ranging between 25 – 47%, except at site 3 where only 6% hard coral cover was found (Fig. 1). In contrast, macroalgal cover was low for all sites (< 8%) except at site 3 where half of the substrate was covered by macroalgae (mainly *Sargassum* spp.). The density of grazing sea urchins (Fig. 1) was highest in the fished zones (0.8 and 1.1 sea urchins m^{-2} at sites 1 and 2, respectively) and lower in the marine reserves and no-take zones (< 0.5 sea urchins m^2 at sites 3 – 6). Total fish biomass was low in the fished zones and marine reserves, with values ranging between 150 – 285 kg ha^{-1} for sites 1 – 4 (Fig. 1). In the no-take zones, total fish biomass was much higher: 898 kg ha^{-1} for site 5 and 1667 kg ha^{-1} for site 6.

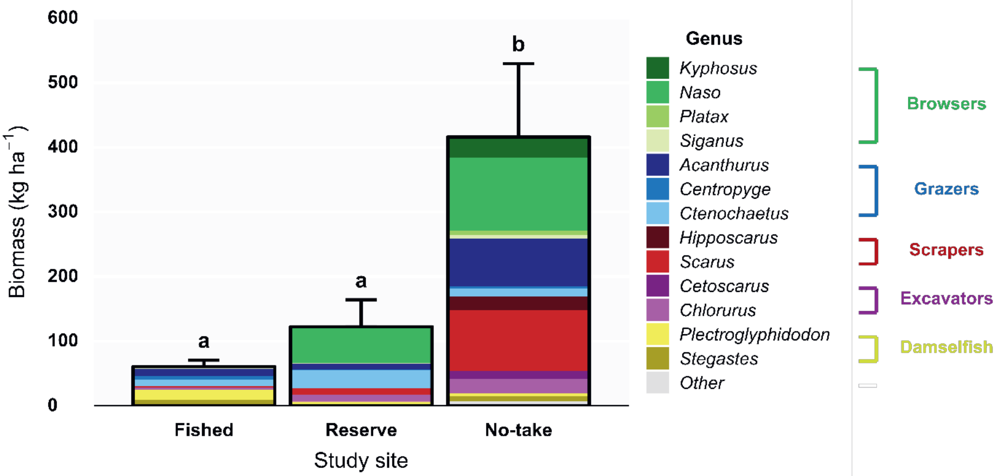

Figure 3 *Herbivorous fish biomass (kg ha^{-1}) per type of fisheries management. Average biomass (n = 21 - 30 fish surveys nested within 2 study sites each) is stacked by genus. Colours indicate functional groups: browsers (green), grazers (blue), scrapers (red), excavators (purple) and territorial damselfishes (yellow), and shades further identify each genus. Error bars denote the standard error of the mean total herbivore biomass and lower-case letters denote significant differences between fisheries management (p < 0.05)*

The biomass of herbivorous fish differed significantly between types of fisheries management ($X^2 = 20.903$, df = 2, $p < 0.0001$; Fig. 3) and was higher in the no-take zones compared to both the fished zones (nearly seven-fold higher, p < 0.0001) and reserves (over two-fold higher, p = 0.0040). The herbivorous fish biomass did not differ significantly between fished zones and reserves. The factor reef type was not included in the final model as it increased the AIC (see Table S1 and Table S2 for model details). There was considerable variation between study sites, with significantly higher biomass at site 4 compared to site 3, both situated in the reserve (Fig. S2). These higher herbivore biomasses at sites 4 - 6 were not only attributable to more herbivores being present, but also due to the presence of larger (> 30 cm) individuals, which were completely absent from sites 1 – 3 (Fig. S3). The composition of functional groups within the herbivorous fish community also clearly differed between types of fisheries management (Fig. 3). Browsers were practically absent from fished sites, while they were well represented in the reserves and no-take zones, mainly due to the presence of *Naso* spp. Grazers were present across all study sites and were relatively more abundant in fished areas. *Acanthurus* spp. dominated the grazer community in the no-take zones, whereas smaller-bodied grazers such as *Ctenochaetus* spp. and *Centropyge* spp. were more commonly found in the fished areas and reserves. Scrapers and excavators (predominantly *Scarus* spp.) were only regularly encountered in no-take zones and even made up more than a third of the herbivorous fish community there. Territorial damselfishes were most abundant in fished zones.

Macroalgae buffet assay

A significant interaction for macroalgae consumption was found between fisheries management and macroalgae species ($X^2 = 10.917$, df = 4, $p = 0.0275$; Fig. 4). Reef type was not included as factor, because the resulting improvement in AIC was marginal (see Tables S1 - S3 for all model output). For *Sargassum,* the consumption was more than two-fold higher in no-take zones (62 ± 11%) compared to the fished zones (26 ± 4%; $p = 0.0064$), with intermediate results for the marine reserves (48 ± 10%) that were not significantly different from the other two management types (Fig. 4). For *Padina*, consumption was comparably low in the fished zones (28 ± 7%) and consumption was over two-fold higher in the marine reserves (71 ± 6%; $p = 0.0002$) and nearly three-fold higher in the no-take zones (82 ± 4%; $p < 0.0001$); the marine reserves and no-take zones were again not significantly different from each other. Across all three protection zones, consumption of *Padina* was higher than for *Sargassum* (Fig. 4). Consumption of *Sargassum* was significantly lower at study sites 3 and 6 compared to sites 4 and 5, respectively (Fig. S4).

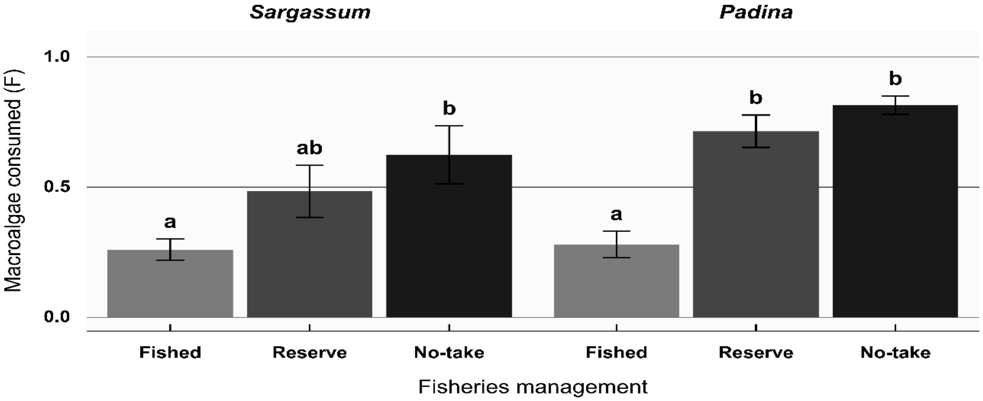

Figure 4 *Fraction of macroalgal biomass consumed in 24 h (F) for both* Sargassum ilicifolium *and* Padina boergesenii, *split between three levels of fisheries management. Bars present mean ± standard error (n = 10 buffet assays nested within two study sites each). Letters above indicate significant differences (p < 0.05) between fisheries management for each macroalgae*

Recorded bites

Mass-scaled bites as recorded on RUV were dominated by a few fish species (Fig. 5). Only three species were recorded taking substantial ms-bites of *Sargassum* (*Naso elegans*, *Hipposcarus harid* and *Zebrasoma desjardinii*). Bites on *Padina* were predominantly taken by a small group of scarids (*Hipposcarus harid*, *Scarus tricolor* and *Calotomus carolinus*) and the unicornfish *Naso elegans*. All ms-bites were recorded at sites 4 – 6, with no recorded bites at sites 1 – 3 (Table S4). At sites 4 – 6, a different species dominated at each site, with *Naso elegans* taking most ms-bites at site 4, *Scarus tricolor* dominating ms-bites at site 5 and *Hipposcarus harid* taking most ms-bites at site 6 (Table S4).

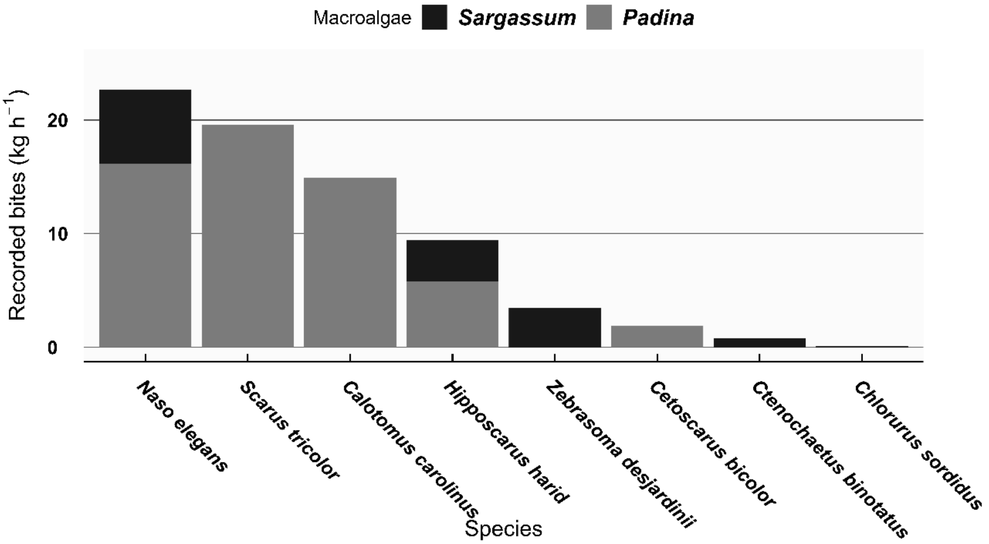

Figure 5 *Recorded mass-scaled bites (kg h^{-1}) on presented macroalgae by fish species recorded on remote underwater video, averaged across all six study sites*

Ordination

The db-RDA model captured 90% of variation in fish species composition (pseudo-F = 2.233, df = 4, p = 0.0278), with the first two axes capturing 65% of the total explained variation (Fig. 6). The overlay vector for reef type was not significant and not included in the final model. The overlay vector for fisheries management (pseudo-F = 2.427, df = 2, p = 0.0389) contributed to the separation of fished sites versus reserves and no-take zones on the first axis, and the separation of reserves and no-take zones on the second axis. The overlay vector for browsing pressure (pseudo-F = 2.524, df = 1, p = 0.0389) was positively associated with the no-take zones and reserves. The overlay vector for sea urchin density, though not significant, was negatively associated with no-take zones, reserves and browsing pressure and instead associated positively with the fished zones. Fish species associating most strongly with reserves, no-take zones and higher browsing pressure included two *Naso* species, various parrotfishes and a kyphosid. In contrast, the fish community associating with the fished zones and high sea urchin densities were predominantly damselfishes.

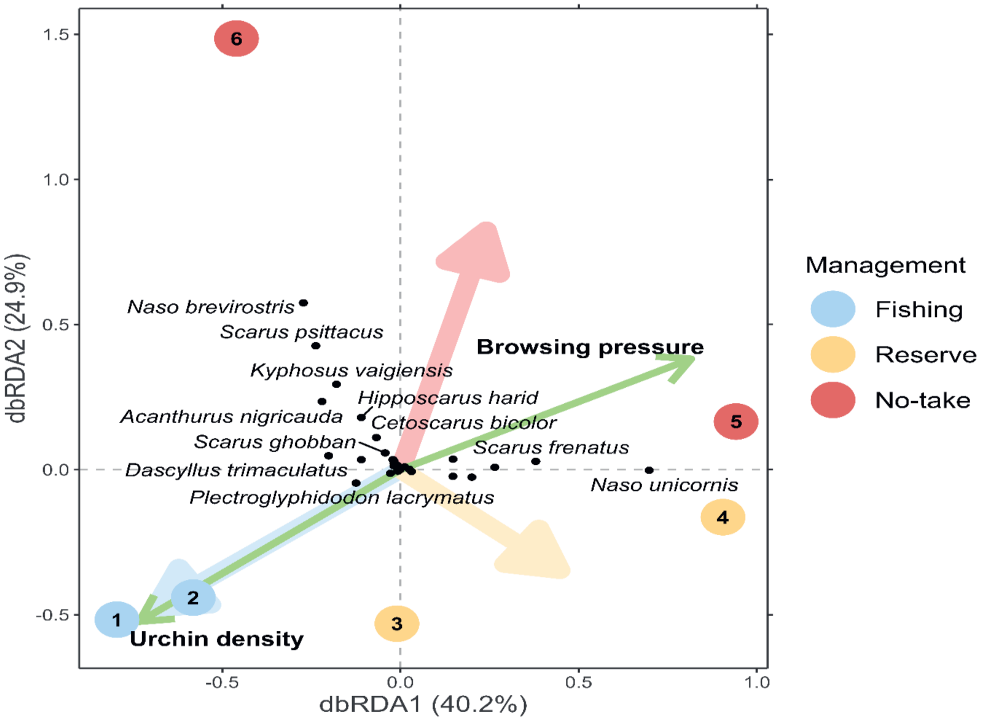

Figure 6 *Distance-based redundancy analysis (db-RDA) plot based on environmental parameters (vectors) per study site (numbered points) fitted to the herbivorous fish community (labelled points). Each point indicates an herbivorous fish species, though only species explaining more than 40% of the variation are shown. Each number represents a study site, their distances based on the Bray-Curtis dissimilarity matrix. Vectors and their length indicate the direction and strength of the parameter effect in the ordination plot. The vectors for fisheries management are coloured according to their level of protection and their widths have been increased to aid visual distinction between overlapping vectors. Monte Carlo permutation tests (999 permutations) showed that browsing pressure and fisheries Management were significant ($p < 0.05$) predictors in the model*

Discussion

A risk to coral reefs and the people dependent on their current services is the phase shift from corals towards macroalgae, promoted by eutrophication and warmer waters and exacerbated by the removal of herbivorous fish by overfishing (Hughes et al., 2007b; Ledlie et al., 2007; Pratchett et al., 2014). Key browsing species, their impact on reefs and the relationships to fisheries management are geographically variable and still largely unknown from the East African coast. We characterized the herbivore community and quantified their browsing pressure at six Kenyan reefs within three distinct fisheries management zones. Browsing pressure on the presented macroalgae was over two-fold greater in areas with partial fishing restrictions and nearly three times higher at fully protected reefs. Biomass of herbivores were respectively two-fold and seven-fold higher in areas with partial and full fishing restrictions compared to fished areas, with substantially higher biomasses of browsing unicornfishes (*Naso* spp.) and scraping parrotfishes. In contrast, sea urchins, damselfishes and small-bodied grazers were dominant in fished areas. In line with previous studies, only a select few dominant browsers were identified to consume the presented macroalgae (Puk et al., 2016), with key species varying strongly across reefs (Cvitanovic and Bellwood, 2009) and also including herbivores not specifically classified as browsers (Chong-Seng et al., 2014). Overall, our results affirm that fishing restrictions can have a strong positive influence on herbivorous fish biomass and highlight how this can be expected to increase reef resilience by supporting higher rates of macroalgae browsing by key species.

Consumption of *Sargassum* in the no-take zones and marine reserves was higher than found in a previously studied community managed area in northern Kenya where only 20% was consumed in 24 h (Humphries et al., 2015), but somewhat lower and more variable than consumption rates (81 – 92% in 24 h) found on the Great Barrier Reef (Hoey and Bellwood, 2010a). *Padina* consumption fell broadly within the ranges previously found (Humphries et al., 2015; Plass-Johnson et al., 2015). It seems that despite widely varying herbivore species compositions across broad geographic scales browsing pressure at unfished reefs can be quite comparable (Tebbett et al., 2020), highlighting the role local drivers such as fisheries management can play in determining browsing pressure. An effect of reef type, such as the combined greater depth and clearer water at offshore sites, was not found to affect fish biomass or browsing pressure in this study. Though the low replications relative to the inherent variation of the data might have obscured some patterns, it is worth highlighting that the effect of fisheries management clearly stood out. Interestingly, consumption at the fish-depauperate and macroalgae-dominated study site 3 was also relatively high. This result contrasts with previous studies where higher densities of macroalgae were associated with lower browsing rates, supposably through feeding dilution (Chong-Seng et al., 2014) or predator avoidance (Hoey and Bellwood, 2011). The combination of both low fish and sea urchin biomass, the absence of browsing recorded on RUV, but relatively high macroalgae consumption at this structurally-eroded and macroalgae-dominated site is indeed surprising. It should be noted that the high consumption was mainly driven by removal of *Padina*, the macroalgae which appeared overall more palatable in this and other experiments (Humphries et al., 2015), compared to *Sargassum*, the macroalgae which dominated this reef and is most often associated with phase shifts (Hughes et al., 2007b). As the stationary survey method likely reduces fish behavioural disturbance (Colvocoresses and Acosta, 2007) and also no browsers were identified through RUV, it appears unlikely that macroalgae removal was driven by (wary) herbivorous fish. Thus, the organism responsible for the high removal of *Padina* at this site remains unidentified and could possibly include overlooked species such as nocturnal crabs (Francis et al., 2019). At the two fished study sites, consumption was higher compared to reports of other overfished or macroalgae-dominated reefs. For example, *Sargassum* sp. removal rates of only 2% in 4.5 h were found on macroalgae-dominated reefs in the Seychelles (Chong-Seng et al., 2014). In the fished areas studied here, macroalgae removal might still be realized by small-bodied grazers and sea urchins.

The differences in the herbivore community and functional absence of browsing, scraping and excavating herbivores found at the fished study sites confirm results found at the central Kenyan coast (Humphries et al., 2015), and potentially undermine the resilience of these reefs (Nyström et al., 2008; Holbrook et al., 2016). Herbivorous fish biomass in the no-take zones and marine reserve (except site 3) was comparable with worldwide averages from protected reefs (Edwards et al., 2014) and this biomass was considerably higher compared to the sites without fishing restrictions. An exception was the macroalgae-dominated study site 3 in the marine reserve, which had an equally low fish biomass as the fished reefs. At this site and at the fished reefs, no large herbivores (> 30 cm) were recorded, indicative of severe overfishing (McClanahan et al., 2008), habitat degradation (Rogers et al., 2018) or both. The observed low biomasses were most striking for large-bodied and functionally important fishes such as browsers, scrapers and excavators. This impact of high fishing pressure on key functional groups has been observed worldwide (Edwards et al., 2014; Humphries et al., 2014) and is remarkably severe along the East African Coast (McClanahan et al., 2008; Humphries et al., 2014). It is therefore promising that the small and recently-established community managed no-take zone of Wasini (study site 6) has been able to sidestep this trend and now boasts the highest fish biomass of all the sites studied here, despite its nearshore location (Johansson et al., 2013). Unlike other young community managed reserves in Kenya where only grazers recovered (Humphries et al., 2015), also browsers and scrapers are abundant at Wasini. Our data suggest that of all herbivorous functional groups, grazers are least impacted by high fishing pressure, with ‘only’ a three-fold lower biomass at fished sites compared to no-take zones and this is conform global trends (Edwards et al., 2014). Sea urchins and territorial damselfishes showed highest densities in fished zones and it is likely that they benefit from reduced competition as well as reduced predation by larger fishes (Ceccarelli et al., 2005; McClanahan, 2008).

The possibility that small-bodied grazers can endure high fishing pressure and control macroalgal establishment could be seen as hopeful (Cernohorsky et al., 2015; Müller et al., 2021), yet there are several reasons to be cautious. First, small herbivorous fishes are likely to be targeting leaves or epiphytes only, without removing the holdfasts of macroalgae (Streit et al., 2015). Second, small herbivorous fishes appear more vulnerable to bleaching events and the ensuing habitat loss of branching coral (Nash et al., 2016). In addition, when bleaching events open up large areas of space, macroalgal settlement and growth is likely to overwhelm the grazing capacity of small herbivores, increasing chances of a phase shift (Williams et al., 2001). We suppose this could have happened at study site 3 during the strong 1998 El Niño (McClanahan et al., 2001), despite the implemented partial fishing restrictions (Williams et al., 2019). Lastly, while increasing numbers of sea urchins might partially compensate for the loss of herbivorous fish (McClanahan, 2014), the intensity of their scraping feeding method can undermine long-term reef development through bioerosion (Carreiro-Silva and McClanahan, 2001) and hinder coral settlement (Humphries et al., 2020). In addition, browsing pressure by sea urchins (at overfished reefs) appears to be relatively small compared to the browsing pressure by herbivorous fish (at protected reefs). Hence, at overfished reefs, small-bodied fishes and sea urchins may partially take over the role of larger herbivorous fishes in controlling macroalgal growth, but such a change in control is likely to undermine reef resilience.

The apparent limited functional redundancy of browsers at the studied protected reefs may also have implications for reef resilience, as the loss of key species can have large detrimental impacts on ecosystem functioning (Cheal et al., 2013; Nash et al., 2016). In accordance with reports from numerous preceding studies using macroalgae buffet assays, browsing in this study was dominated by a few species only (Puk et al., 2016) and with marked variation in dominant species across sites (Cvitanovic and Bellwood, 2009). *Naso elegans* was among the dominant browsers in this study and closely-related species have been identified as dominant browsers across the Indo-Pacific (Hoey and Bellwood, 2009; Humphries et al., 2015; Plass-Johnson et al., 2015; Knoester et al., 2019), highlighting the importance of this genus in macroalgal control across broad geographic scales. Browsing was not only performed by those classified as browsers and this supports several studies that suggest plasticity in functional roles exists (Bellwood et al., 2006; Chong-Seng et al., 2014; Tebbett et al., 2020). Indeed, scraping parrotfishes were recorded taking substantial amounts of bites as has been found in previous studies (McClanahan et al., 1994), but, in contrast to the browsing *Calotomus* spp. (Humphries et al., 2015), these are more likely to have been targeting epiphytes (Lefèvre and Bellwood, 2011; Clements et al., 2017). Interestingly, *Siganus* spp. and *Kyphosus* spp., species frequently identified as dominant browsers in the Central Indo-Pacific and Great Barrier Reef (Michael et al., 2013; Puk et al., 2016), were not recorded biting in this study. *Siganus* spp. were almost exclusively found in dense seagrass beds during this study, likely targeting epiphytes and turf algae which might be a preferred food source for some species (Ebrahim et al., 2020). *Kyphosus* spp. were situated higher in the water column and might have been feeding on drifting algae instead (Ferguson et al., 2017). Though longer RUV recordings would undoubtedly expand the list of identified browsers, these results align with other browsing studies in the Indo-Pacific in that they identify only a select and sometimes surprising group of species responsible for macroalgal removal from the diverse assemblage of potential browsers present. This variability may in part explain the finding that the reef with the highest herbivore biomass in this study did not bolster the highest browsing pressure, and especially consumption of *Sargassum* was relatively low here. Thus, in addition to the biomass of herbivores present, realized browsing pressure is likely also depending on many more factors such as spatial restrictions (Puk et al., 2016), behavioural variation (Bennett and Bellwood, 2011) as well as temporal variation (Lefèvre and Bellwood, 2011; Seah et al., 2021).

The variation in browsing pressure found can be indicative of divergent resilience between the studied reefs (Nyström et al., 2008). Three of the six studied reefs harboured an herbivore biomass that was just above the identified threshold of 50 kg ha^{-1} below which coral reefs might shift to macroalgal dominance (Plass-Johnson et al., 2015; Holbrook et al., 2016). On two of these reefs, coral is still dominant over macroalgae. Nevertheless, reefs like these might be pushed to macroalgae dominance through an external disturbance such as coral bleaching (Williams et al., 2001). The minimum herbivore biomass needed to absorb such increasingly common disturbances remains unknown for the Indo-Pacific (Roff and Mumby, 2012) and likely varies depending on the local community composition given the large influence of key species. In the marine reserve, a coral-dominated and a macroalgae-dominated reef co-exist under roughly equal browsing pressure. This co-existence could possibly be indicative of alternative steady states (Holbrook et al., 2016) and would then illustrate that shifts to alternative stable states can be difficult to reverse even when ambient browsing pressure is relatively high (Schmitt et al., 2019). If such reefs were historically indeed dominated by hard corals, one might consider to combine the protection of herbivorous fish with manual removal of macroalgae and attempt to push the ecosystem back to coral dominance (Ceccarelli et al., 2018; Williams et al., 2019). More effective, however, would be to keep herbivore levels well above potential phase-shift thresholds and prevent macroalgal dominance in the first place (Mumby and Steneck, 2008; Anthony et al., 2015). Our results indicate that fisheries management through marine reserves and no-take zones in particular, even small-scale and community-managed (Bonaldo et al., 2017; Kawaka et al., 2017), have the potential to safeguard the diversity and biomass of functionally important herbivorous fishes. Following effective management, a high level of macroalgal control is realized as especially large-bodied browsing and scraping fishes seem to benefit from fisheries protection. Although reasonable levels of browsing were still realized at fished study sites, the long-term resilience of these fished reefs is uncertain given the eroding nature of sea urchin browsing (Carreiro-Silva and McClanahan, 2001), the high susceptibility of small-bodied herbivorous fishes to coral loss (Nash et al., 2016) and their limited capacity to control sudden increases in macroalgae (Williams et al., 2001; Streit et al., 2015). Therefore, we recommend to continue the establishment of a network of community managed no-take zones to allow for the recovery of herbivorous fish biomass and key species, increase ecosystem resilience, promote local stewardship and move towards sustainable use of coral reefs (Topor et al., 2019). Such local management could help restore and maintain coral dominance and provide heightened resilience against large-scale disturbances during the Anthropocene.

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Conflict of interest: The authors declare that they have no conflicts of interest.

Availability of data and material: The datasets analysed and code used are available as an archived GitHub repository on: https://github.com/ewoutknoester/HerbivoryBrowsing

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Ethical approval: No approval of research ethics committees was required for this observational study. Applicable international guidelines for monitoring on coral reefs were followed.

Supplementary materials

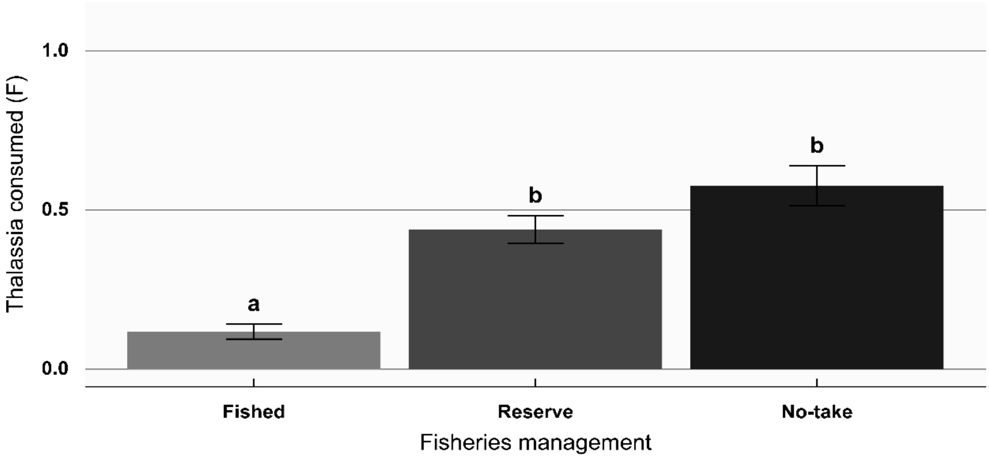


Figure S1 *Fraction of biomass consumed in 24 h of* Thalassia hemprichii *split between three types of fisheries management. Bars present mean ± standard error (n = 10 assays nested in 2 study sites each). Letters above indicate significant differences (p < 0.05) in consumption between fisheries management. The seagrass* Thalassia hemprichii *was included in this macroalgal study to compare herbivory with a previous study along the Kenyan coast (McClanahan, 2008), where it was found that 62% of* Thalassia hemprichii *was consumed per day in no-take zones against 14% in fished zones*

Table S1 *Details on model output of the final models on total herbivorous fish biomass and macroalgae consumption across study sites*

Herbivore biomass ~ Management + (1 | Study site)

Random factors	***Variance***	***Std.dev***
Study site	0.14	0.38
Residual	1.68	1.30

Fixed effects	***Estimate***	***Std.error***	***t value***	***p***
Intercept	4.10	0.30	13.80	< 0.0001
Reserve	0.56	0.42	1.35	0.176
No-take	1.90	0.43	4.46	< 0.0001

Macroalgae consumption ~ Management*Species + (1 | Study site/Assay)

Random factors	***Variance***	***Std.dev***
Assay:Study site	0.18	0.43
Study site	0.15	0.39

Fixed effects	***Estimate***	***Std.error***	***z value***	***p***
Intercept	-1.02	0.32	-3.15	0.0016
No-take	2.55	0.51	5.04	< 0.0001
Reserve	2.01	0.47	4.26	< 0.0001
Sargassum	-0.056	0.20	-0.28	0.78
No-take:Sargassum	-0.83	0.41	-2.04	0.042
Reserve:Sargassum	-0.97	0.33	-2.92	0.0035

Table S2 *Details on model selection regarding the covariate reef type (ReefType). ReefType was set as 'Patch' for study sites 1, 2 & 6, and as 'Fringing' for study sites 3, 4 & 5. Selected models are highlighted in bold. Model information includes degrees of freedom (d.f.), Deviance (Dev), maximum loglikelihood (logLik), Akaike's Information Criterion (AIC) and the difference between AIC of current model versus selected model. Herbivore biomass regards the total herbivorous fish biomass*

Independent variable	Model	d.f.	Dev	logLik	AIC	ΔAIC
Herbivore biomass	**~ Management + (1 | Study site)**	**70**	**888.4**	**-444.2**	**898**	**0**
	~ Management + ReefType + (1 | Study site)	69	887.6	-443.8	900	1.2
Macroalgae consumption	**~ Management*Species + (1 | Study site/Assay)**	**74**	**-130.4**	**65.2**	**-98**	**0**
	~ Management*Species + ReefType + (1 | Study site/Assay)	73	-132.6	66.3	-99	-0.2

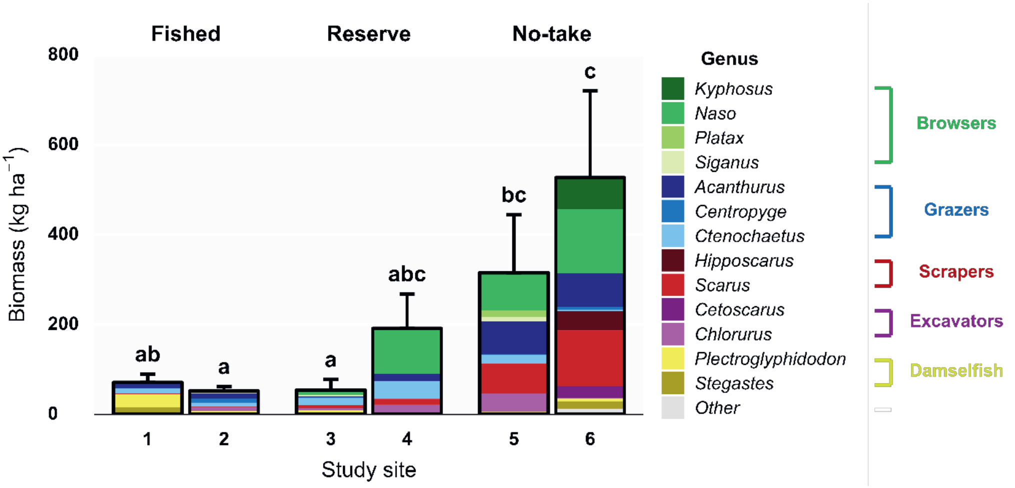


Figure S2 *Herbivorous fish biomass (kg ha^{-1}) per study site. Average biomass (n = 11 - 15 fish surveys) is stacked by genus. Colours indicate functional groups: browsers (green), grazers (blue), scrapers (red), excavators (purple) and territorial damselfish (yellow), and shades further identify each genus. There was a significant difference in herbivorous fish biomass between study sites ($X^2 = 33.361$, $df = 5$, $p < 0.0001$). Error bars denote the standard error of the mean total herbivore biomass and lower-case letters denote significant differences between study sites ($p < 0.05$). Fisheries management is indicated on top*

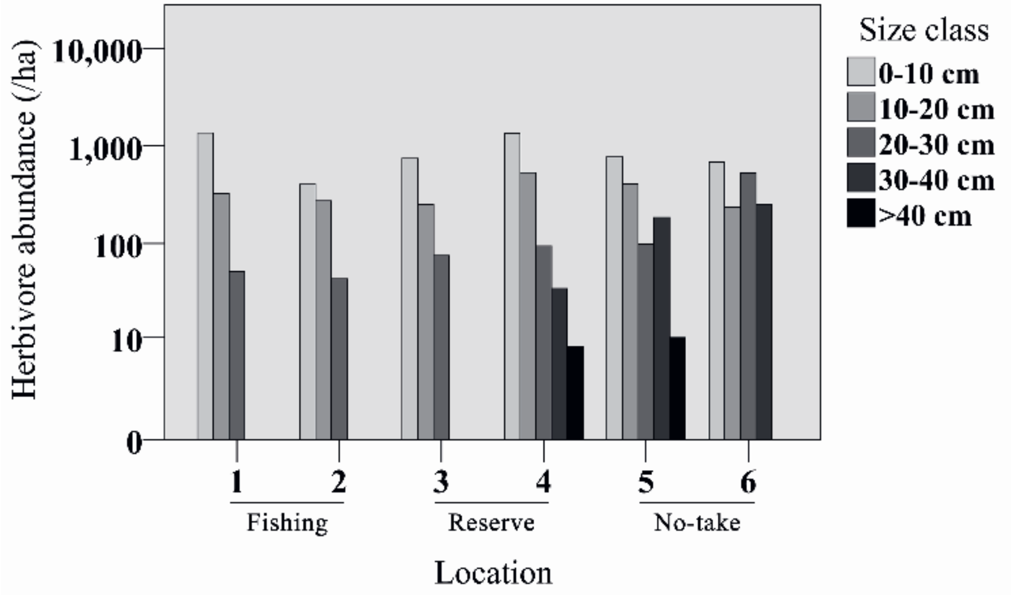


Figure S3 *Mean herbivorous fish abundance (ha^{-1}) split in size classes for each study site (n = 11 – 15 fish surveys). For each of the sites, their fisheries management is indicated below*

Table S3 *Output from Wald Chi-Squared Test of the beta regression mixed-effects model to test for differences in macroalgae consumption between three types of Fisheries management and two Macroalgae species. The model included Study site and Assay as nested random factors*

Fixed factors	**Chisq**	**Df**	***p***
Fisheries management	28.698	2	5.865e-07
Species	76.275	2	2.2e-16
Protection * Species	10.917	4	0.02751

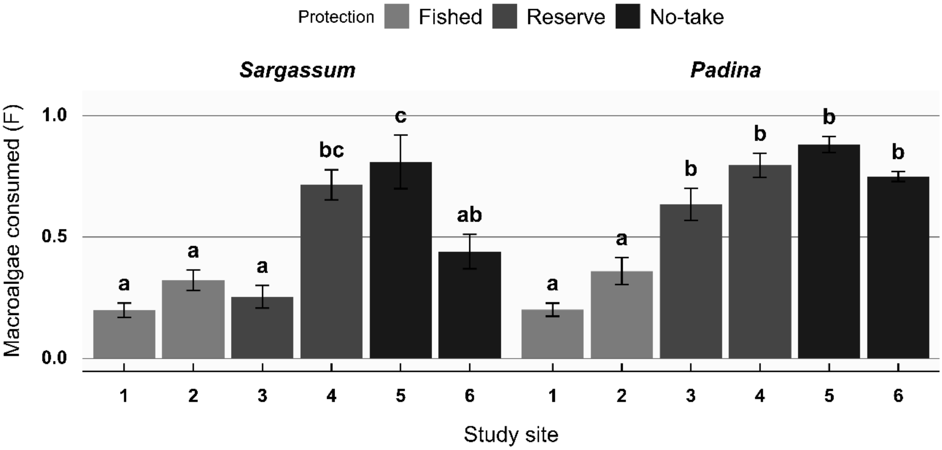
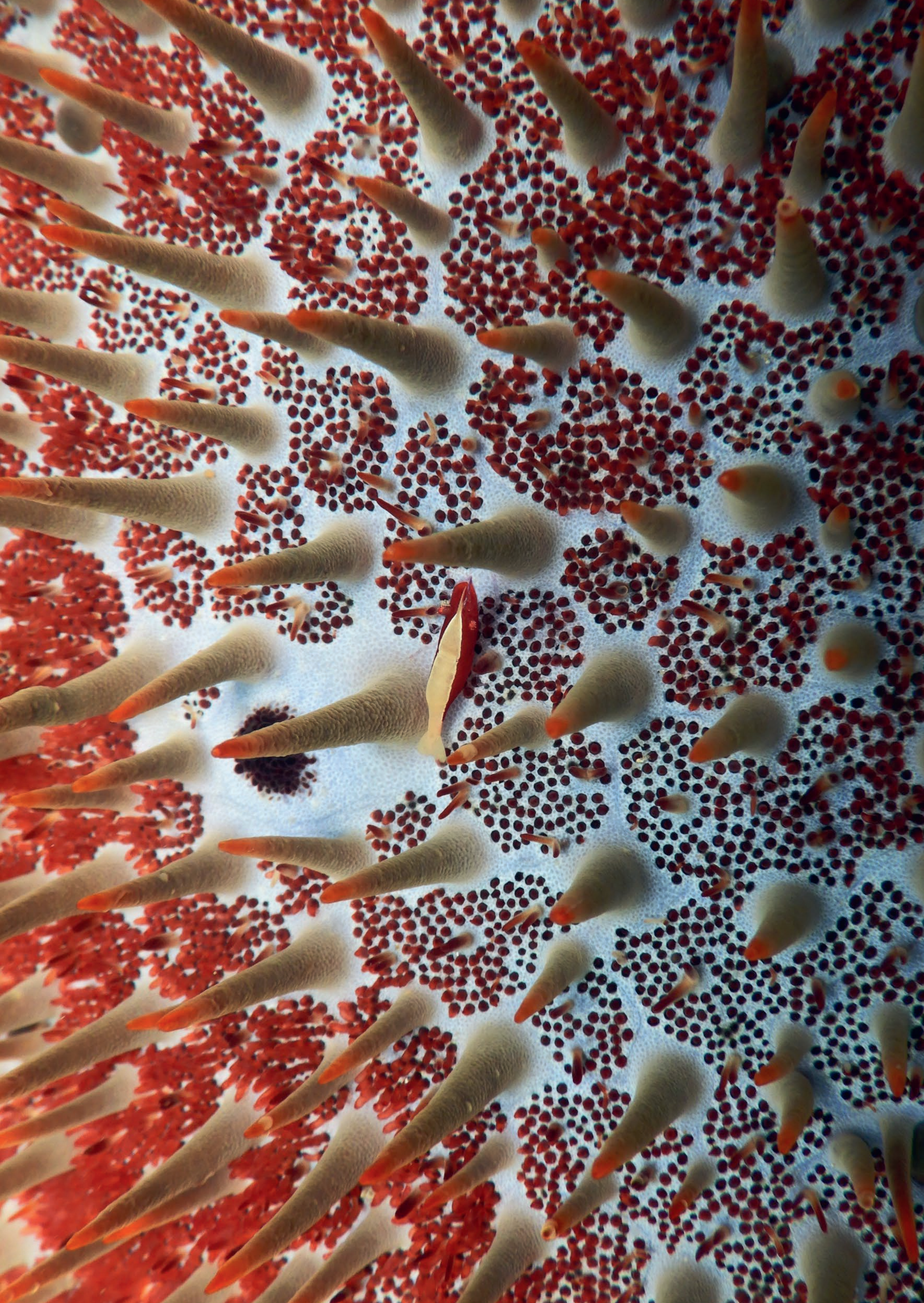


Figure S4 *Fraction of macroalgal biomass consumed in 24 h (F) for* both Sargassum ilicifolium *and* Padina boergesenii*, split between study sites (x-axis) and level of fisheries management (shades). Bars present mean ± standard error (n = 5). There was a significant interaction between Study site and Macroalgae species (X^2 = 30.040, df = 10, p = 0.00084). Letters above indicate significant differences ($p < 0.05$) between study sites for each macroalgae*

Table S4 *Recorded mass-scaled bites (kg h^{-1}) by fish species recorded on remote underwater video split per species, study site and macroalgae.*

Species	**Location**	**Padina**	**Sargassum**	**Sum**
Calotomus carolinus	4			0
	5	72		72
	6	16		16
Cetoscarus bicolor	4			0
	5			0
	6	12		12
Chlorurus sordidus	4			0
	5		1	1
	6			0
Ctenochaetus binotatus	4		5	5
	5			0
	6			0
Hipposcarus harid	4			0
	5			0
	6	34	22	56
Naso elegans	4	94	38	132
	5			0
	6			0
Scarus tricolor	4			0
	5	114		114
	6			0
Zebrasoma desjardinii	4		4	4
	5			0
	6		17	17



3

Coral predation and implications for restoration of Kenyan reefs: the effects of site selection, coral species and fisheries management

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Abstract

Active coral reef restoration is increasingly applied for local reef management, but remains hampered by biological interactions such as coral predation (corallivory). To determine factors that drive corallivory and develop more ecology-based restoration approaches, coral and corallivore communities were characterized and fish bite mark densities quantified on natural coral colonies and fragments outplanted on small artificial structures. Six study sites were distributed equally among three levels of fisheries management at southern Kenyan reefs (fished < reserve < no-take). Obligate corallivorous fish densities strongly correlated with coral cover regardless of fisheries management level, whereas facultative corallivorous fish (mainly parrotfish) were most abundant in no-take zones. High corallivorous snail densities were associated with low coral diversity and corallivorous sea stars were scarce. Bite mark densities on natural reefs were clearly higher for branching corals, but did not correlate to coral cover, coral diversity or corallivorous fish densities. Compared to natural colonies, predation pressure was up to 24-fold greater on outplanted coral fragments and especially fierce inside no-take zones. This high predation pressure correlated with low live tissue cover of outplanted fragments. These results demonstrate that reefs with low coral cover, often targeted for restoration, do not necessarily experience greater coral predation and that improved outplanting methods and species considerations are needed to address high predation pressure on outplanted fragments. The interplay between fisheries management, reef restoration and corallivory warrants further scrutiny: while obligate corallivorous fish are unlikely detrimental to reef recovery, high densities of facultative corallivorous fish could hamper restoration efforts.

Key words: Corallivory; *Drupella*; *Coralliophila*; Coral gardening; Artificial reef; Branching coral

Introduction

Over the past two decades, coral reef restoration has gained momentum to address reef degradation locally (Boström-Einarsson et al., 2020) and to reinforce existing conservation measures for increased reef resilience against global stressors (Anthony et al., 2015; Suding et al., 2015). Through active interventions, reef restoration typically aims to uphold critical services provided by reefs such as food provision and tourism (Hein et al., 2020b). The prevailing restoration approach is two-step coral gardening, where an initial nursery phase is followed by outplanting of corals directly onto degraded reefs or artificial reefs (Rinkevich, 1995). Successful results, albeit small-scale, have been attained using this approach in areas where local human stressors such as pollution and overfishing are kept under control (Hein et al., 2020a). However, numerous instances are known where reef restoration has been set back by biological challenges such as coral predation and algal competition (Precht, 2006; Edwards et al., 2010). Therefore, a good understanding of reef functioning is required to enable a more ecology-based approach in which insights of reef ecology are applied in reef restoration (Ladd and Shantz, 2020).

While reef restoration practitioners have started to develop some ecological tools to improve the coral gardening concept (Rinkevich, 2019), most ecological processes remain unexplored for reef restoration despite their known importance on natural coral reefs (Shaver and Silliman, 2017). For example, effectiveness of reef restoration efforts could be significantly improved by capitalizing on mutualisms by biologically controlling predation on corals or by strengthening the competitive position of corals (Lirman and Schopmeyer, 2016). Such ecologically-inspired methods, however, remain strongly underrepresented in the reef restoration literature (Ladd et al., 2018). Only a handful of ecological reef restoration initiatives have recently emerged, and these mainly focus on mediating coral-algae competition by facilitating natural herbivores or introducing co-cultured herbivores (Toh et al., 2013; Frias-Torres and Van de Geer, 2015; Knoester et al., 2019). Reef restoration practitioners, however, have indicated coral predation (i.e. corallivory) as a more pressing concern hampering their restoration projects (Young et al., 2012). Yet only two studies could be found exploring ecological solutions to reduce corallivory: Delgado and Sharp (2020) introduced a predator of corallivorous snails and Tiddy et al. (2021) used damselfish to fend off corallivorous fish.

A large variety of animals predate on corals (Rotjan and Lewis, 2008), ranging from mucus feeders (e.g. *Trapezia* spp. crabs) and tissue browsers (e.g. *Drupella* spp. snails, *Acanthaster* spp. sea stars and butterflyfish) to scrapers and excavators of coral skeleton (e.g. parrotfishes, pufferfishes and triggerfishes). Their impacts differ: where mucus feeding can be associated with mutualistic gains such as sediment clearing (Stewart et al., 2006), tissue browsing and skeleton consumption present chronic energy drains to the coral (Cole et al., 2012). The loss of tissue and skeleton not only drains coral energy reserves (Henry and Hart, 2005), but can also facilitate the spread of diseases (Williams and Miller, 2005), decrease the coral's competitive ability (Hall, 1997) and increase its susceptibility to other stressors (Rice et al., 2019). On the scale of reefs, the selective feeding of corallivores on fast-growing genera is deemed important for the maintenance of coral diversity (Neudecker, 1979; Cox, 1986). However, severe negative impacts can manifest themselves when corallivore populations promptly increase and their predation outpaces coral regrowth, drastically reducing live coral coverage (Rotjan and Lewis, 2008). Notorious for such outbreaks are the *Acanthaster* spp. crown of thorn sea stars (CoTS; Pratchett et al. 2017) and corallivorous snails of the genus *Drupella* (Bruckner et al., 2017). Such outbreaks are thought to be more common on eutrophic (Rice et al., 2019), overfished (Dulvy et al., 2004) and temperature-stressed reefs (Bruckner et al., 2017). As it is often these disturbed reefs that are targeted for restoration, the potential impact and control of corallivory should be considered when designing a restoration strategy.

Several examples confirm that corallivores can prevent the success of reef restoration projects, including the infestation of coral nurseries by *Drupella* spp. snails (Shafir et al., 2006b), coral fragment detachment by corallivorous fish (Horoszowski-Fridman et al., 2015) and intense predation on outplanted corals by CoTS (Cabaitan et al., 2015), corallivorous fish (Koval et al., 2020) and snails (Johnston and Miller, 2014). This is not entirely surprising, given the prevailing use of fast-growing, branching coral genera for restoration (Boström-Einarsson et al., 2020), which are preferred prey to most corallivores (Rotjan and Lewis, 2008). While manual removal of invertebrate corallivores (Williams et al., 2014) or the caging of coral fragments (Baria et al., 2010) can reduce predation, a better understanding of drivers of corallivory could lead to more ecologically sound and therefore more efficient restoration approaches (Ladd and Shantz, 2020; Seraphim et al., 2020). In this study, we specifically focus on three knowledge gaps. First, it remains unclear whether reefs in need of restoration experience increased coral predation due to their low coral cover. Such a predation pit could be plausible when a decline in coral cover or diversity results in a relative overabundance of corallivores on the remaining coral, as hypothesized, amongst others, by Rotjan & Lewis (2008). Second, it is not well known how predation rates on restored patches relate to predation rates and corallivore communities on nearby natural reefs. The observed predation rates might either be innate to the natural reef system, or be elevated on outplanted fragments due to the frequent use of palatable coral species for restoration (Cole et al., 2008) and other factors related to the transplantation process (Forrester et al., 2012). Third, the net impact of fisheries management on corallivory remains unclear. Increased protection could increase the number of corallivores such as parrotfish and butterflyfish (McClanahan et al., 2005; Bruno et al., 2019; Rice et al., 2019), but also result in stronger predation control on other corallivores, especially invertebrates such as snails and sea stars (McClanahan, 1997; Dulvy et al., 2004; Clements and Hay, 2018).

Here, we present a series of studies that aimed to identify drivers of corallivory on six coral reefs in southeast Kenya. The studies addressed three key questions associated with the aforementioned knowledge gaps: 1) Predation pits: do natural and outplanted coral colonies on degraded reefs experience a greater predation pressure than coral colonies on reefs with higher or more diverse coral cover? 2) Do outplanted corals on restored reef patches experience more predation than natural coral colonies on adjacent reef patches? 3) How does the level of fisheries management influence the observed patterns in corallivory? To address the first question, we assessed coral cover and coral diversity and identified and quantified corallivore communities at each reef. Fish bite mark densities on coral colonies and predation pressure on the most abundant invertebrate corallivores were quantified. It was hypothesized that low coral cover would coincide with high corallivore abundances relative to the amount of coral available and therefore result high predation pressure. To address the second question, bite mark densities on three common branching coral genera were compared between coral fragments outplanted on small artificial structures and natural coral colonies at each reef. We expected higher bite mark densities on outplanted corals, as fragments can become more susceptible to predation due to handling damage and transplantation stress. The third question was addressed by relating the outcomes of the assessments to the type of fisheries management at the studied sites: two sites were located in a heavily fished area, two sites in a marine reserve with restricted fishing and two sites in no-take zones. We hypothesized to find more fish corallivory and less invertebrate corallivory in protected areas.

Methods

Study sites

The study was performed around Wasini Island in southern Kenya from October 2018 till February 2019. Six study sites were chosen, equally distributed over three fisheries management types (Fig. 1). Sites 1 and 2 were located in an unrestricted fishing zone, sites 3 and 4 in a marine reserve (allowing traditional fishing methods only) and sites 5 and 6 each in a no-take zone. Sites 1, 2 and 6 were situated in a relatively turbid sea strait, whereas the other sites were located further offshore. Benthic cover as well as fish and sea urchin densities (Fig. 1) had been assessed in a parallel study (Knoester et al., 2023), which can be consulted for more details on each study site.

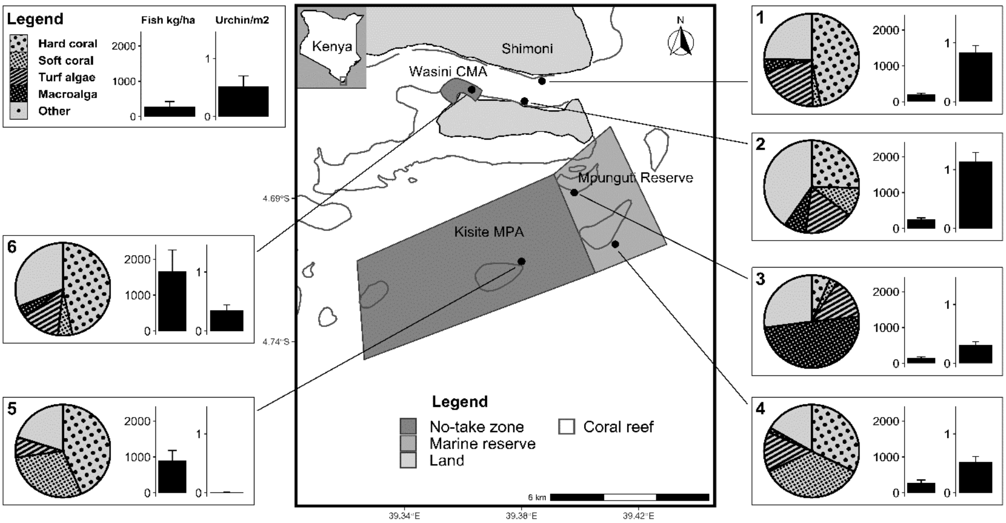

Figure 1 *Map of Kenya showing study area (insert) and detailed map showing the six study sites. Three different fisheries management zones can be identified: unrestricted fished zone (unshaded) including sites 1 (Firefly House Reef) & 2 (Pilli Pipa Restaurant), the Mpunguti Marine Reserve where traditional fishing is allowed (shaded orange) encompassing sites 3 (Lower Mpunguti) & 4 (Dolphin Point) and no-take zones (shaded red) covering sites 5 (Kisite Marine National Park) & 6 (Wasini Community Managed Area). Boxes shows additional information for each study site on benthic cover, total fish biomass and sea urchin density. Bars represent means ± standard error (n = 10 for benthic surveys and n = 11 - 15 for fish surveys). Figure reused from Knoester et al. (2023)*

Benthic surveys

A 20-m point intercept transect was sampled every 0.5 m to map benthic cover in broad categories: hard coral, soft coral, turf algae (< 1 cm), macroalgae (> 1 cm) and a pooled category ‘other’ including mainly sand, rubble and rarer invertebrates such as sponges and tunicates. This general benthic dataset is reused from Knoester et al. (2023), but with the following additions: for each coral colony directly under the 20-m transect line, the total number of fresh and recovering bite marks by fish were counted as a proxy for predation pressure (Littler et al., 1989). A bite mark was defined as a continuous lesion exposing coral skeleton (Fig. 2), see also Woodley et al. (2016). In addition, each coral colony was identified to genus level, its growth form noted and size estimated by simplifying its planar growth form to a circle and estimating the radius of this circle. To determine average bite mark density per survey, the total sum of bite marks was divided by the total coral colony surface area. To allow genus-specific comparisons, bite density was also calculated individually per sampled coral colony (N = 1893, pooled over all surveys). Using genus counts of sampled coral colonies, coral diversity was determined per survey using the Shannon index H’ (Shannon, 1948). Whereas fish bite marks could be readily counted, this was less straightforward for the more cryptic and diffuse predation marks from invertebrates. Therefore, it was decided to use invertebrate population densities as proxy for their predation pressure instead. Along the same 20-m transect, the abundances of corallivorous snails (*Drupella* spp. and *Coralliophila* spp.) were counted within a 1-m wide belt and corallivorous sea stars (*Acanthaster* sp. and *Culcita* sp.) within a wider 5-m belt. The density of corallivorous snails per square meter of coral was calculated by dividing the combined counts of *Drupella* spp. and *Coralliophila* spp. by the coral-covered area per survey (approximated by transect area * percentage hard coral cover). Per study site, 10 replicate benthic surveys were performed.

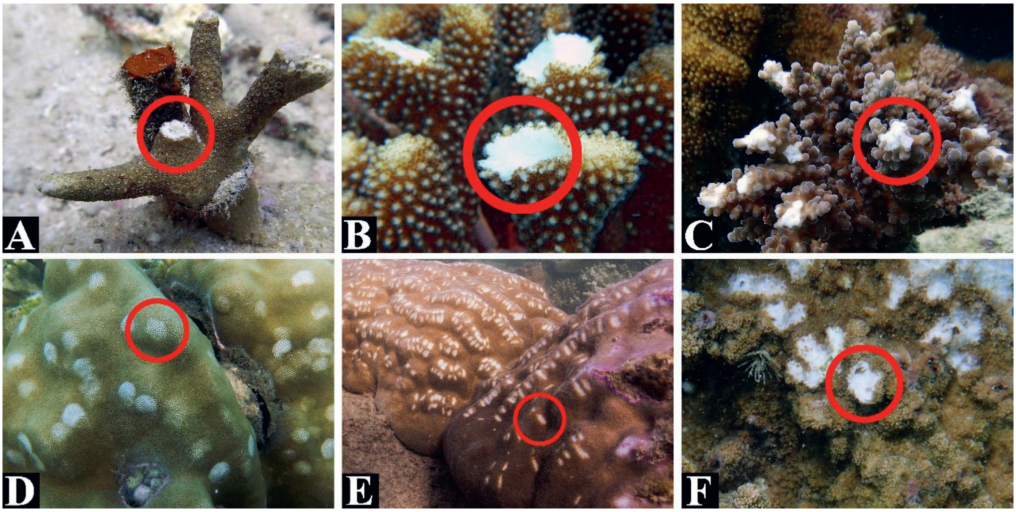

Figure 2 *Examples of fish bite marks. For each picture, the red circle encloses a single bite mark:* ***(A)*** *branching* Porites *with a bite mark,* ***(B)*** Pocillopora *showing bite marks,* ***(C)*** Acropora *showing numerous bite marks,* ***(D) & (E)*** *massive* Porites *showing numerous bite marks,* ***(F)*** *encrusting* Montipora *showing numerous bite marks. Photo credit: EGK*

Fish surveys

A stationary fish census (radius of 7.5 m) was performed diving to quantify the composition and abundance of all diurnal, non-cryptic fish (Bohnsack and Bannerot, 1986). Fish sizes (fork length) were estimated in classes of 5 cm for fishes smaller than 20 cm, and in 10-cm size classes thereafter, so that fish biomasses (kg ha^{-1}) could be estimated using known length-weight relations and the midpoint of each size class (Kulbicki et al., 2005; Froese and Pauly, 2015). Per study site, between 11 – 15 replicate fish surveys were done. The same raw survey data have been used in (Knoester et al., 2023) to determine the herbivorous fish community, but is used here to quantify the corallivorous fish assemblage. Corallivorous species were classified as either obligate corallivores that feed almost exclusively on hard corals or facultative corallivores that supplement their diet regularly with other food sources (Cole et al., 2008; Rotjan and Lewis, 2008).

Snail predation assay

To quantify the predation pressure on corallivorous snails, adult snails (2 – 3 cm shell length) were left exposed on a concrete disk (⌀ 30 cm) and the number of surviving snails were counted after 24 hr. To prevent snails from escaping, a fishing line was used to connect a metal pin on the disk to the aperture of the snail, for which a small hole was drilled at the edge. Per assay, eight *Drupella* spp. snails and eight *Coralliophila* spp. snails collected from study sites 1 and 2 were used. They resembled the species *Drupella cornus* and *Coralliophila violacea* (Richmond, 2002), but given their heavy overgrowth with crustose coralline algae, we will restrict their identification up to genus level. The first hour of each predation assay was recorded on remote underwater video (RUV) to identify potential predators. Per study site, 5 replicate predation assays were performed.

Coral buffet assay

To compare the predation pressure experienced by corals on the natural reef with corals on restored reefs, corals were outplanted onto small artificial reef structures. These structures consisted of a cement disk (⌀ 30 cm) with four metal pins. Each pin would hold a different species: *Acropora verweyi*, *Acropora* sp., *Pocillopora verrucosa* and *Porites cylindrica*, all harvested from coral nurseries at study site 1. These species represent genera that are frequently used in reef restoration projects worldwide (Boström-Einarsson et al., 2020). Per study site, eight artificial reef structures were placed approximately 1 meter from the natural reef and 1 meter from each other. Depth ranged between 3 – 9 m, depending on the extent of reef slope development. Transportation of coral fragments was realized in shaded seawater bins during boat rides of 5 – 50 minutes during which the water was replaced multiple times. Throughout the 4-month study period, bite marks were scored twice a month and the presence of any corallivorous invertebrates was noted. For each fragment, the average counts of bite marks throughout the study period were divided by the average projected surface area to calculate its bite mark density. At the start and end of the study period, the percentage of remaining live coral tissue of each coral fragment was scored.

Data analysis

All analyses were performed in R (R Core Team, 2020). Simple linear models were fitted using the *nlme* package (DebRoy, 2006) to determine the effect of study site on the average hard coral cover (square-root-transformed), coral diversity, bite mark density, snail density and snail predation pressure as well as the (log-transformed) biomasses of obligate and facultative corallivorous fish on natural reefs. For coral cover, fish biomasses and snail density, the distribution of genera making up the totals are presented visually. The number of corallivorous sea stars observed was too low to apply statistical tests, therefore only their average densities are presented. For coral fragments on artificial reef structures, the effects of study site, coral genus and their interaction on (square root transformed) bite mark density were analysed with a linear mixed-effects model from the same *nlme* package, allowing the inclusion of artificial reef structure as random factor to account for the non-independence of multiple fragments on the same disk. To determine the effect of study site, coral genus and their interaction on the live tissue cover of outplanted corals, the *glmmTMB* package (Brooks et al., 2017) was used to fit a generalized linear mixed-effects model with beta distribution, logit link and artificial reef structure as random factor. This model accounted for both the proportional nature of the percentage live tissue data (Douma and Weedon, 2019) and the aforementioned non-independence of multiple fragments on a single structure. As no significant differences were found between the two outplanted *Acropora* species, the *Acroporas* were pooled, the analysis rerun and data presented on genus level (i.e. *Acropora, n = 16*; *Pocillopora,* n = 8; *Porites,* n = 8). All model assumptions were validated by visual inspection of residual plots, using *DHARMa* diagnostic plots in case of the generalized linear model (Hartig, 2021). Wald Chi-Squared Tests from the *car* package (Fox and Weisberg, 2018) were used to determine the significance of the fixed factors for all models and pairwise comparisons with Tukey adjustments were made with the *emmeans* package (Lenth, 2020).

To explore drivers of bite mark density on natural reefs, Pearson correlations were used to relate study-site averages of bite mark density to hard coral cover, coral diversity and facultative and obligate corallivorous fish biomass. Potential genus-specific effects were further investigated by correlating the average bite mark density of each coral genus with its associated (log-transformed) cover. Given the known preference of corallivores for branching corals, this growth form was grouped and analysed separately. Next, drivers of corallivore densities were investigated by correlating the biomass of facultative and obligate corallivorous fish and snail density against coral cover and coral diversity. For corals on the artificial reef structures, a similar set of correlations was performed, but split per genus: bite mark density was correlated again with hard coral cover and facultative and obligate corallivorous fish biomass, but now also with the percentage live coral tissue of outplanted fragments. Throughout the results, the different levels of fisheries management are indicated visually, but given the low number of replicates (n = 2), no statistical analyses have been performed at this level.

Results

Coral cover, diversity and bite marks

Average hard coral cover was significantly different between study sites ($X^2 = 224.05$, df = 5, p < .001), ranging from 4% at study site 3 up to 55% at study site 1 (Fig. 3). Also the diversity of hard coral genera differed significantly among study sites (X^2 = 95.129, df = 5, p < .001). Two sites clearly differed from the other four sites: a significantly lower coral diversity was found at coral-poor study site 3 and *Porites*-dominated study site 5 compared to the other study sites (Appendix A, Fig. S1). Across study sites, bite mark densities differed significantly (X^2 = 27.933, df = 5, p < .001). At nearly 30 bite marks m^{-2}, the average bite mark density was significantly higher at study site 4 compared to nearly all other sites where average bite mark densities did not exceed 10 bite marks m^{-2} (Fig. 4a). Bite mark densities correlated neither with hard coral cover (Fig. 4b), nor coral diversity, nor with the biomass of facultative or obligate corallivorous fish (see Table S1 for details on correlations). Bite mark densities clearly differed across coral genera, with branching genera generally having substantially higher bite mark densities than non-branching corals (Fig. 5). Coral genera with the highest average bite mark densities were: *Pocillopora* (300 bite marks m^{-2}), *Seriatopora* (244), *Isopora* (170), *Stylophora* (151), *Acropora* (80), *Astreopora* (50), branching *Porites* (39), *Montipora* (36) and massive *Porites* (29). Most other genera had fewer than 10 bite marks m^{-2}. For branching genera (triangles in Fig. 5), the higher bite mark densities were related to an exponential decline in the genus' respective coral cover, illustrated by a significant negative correlation between bite mark density and the log-transformed cover of branching coral (Table S1). No significant correlation was found between bite mark density and the cover of corals with other growth forms (Table S1).

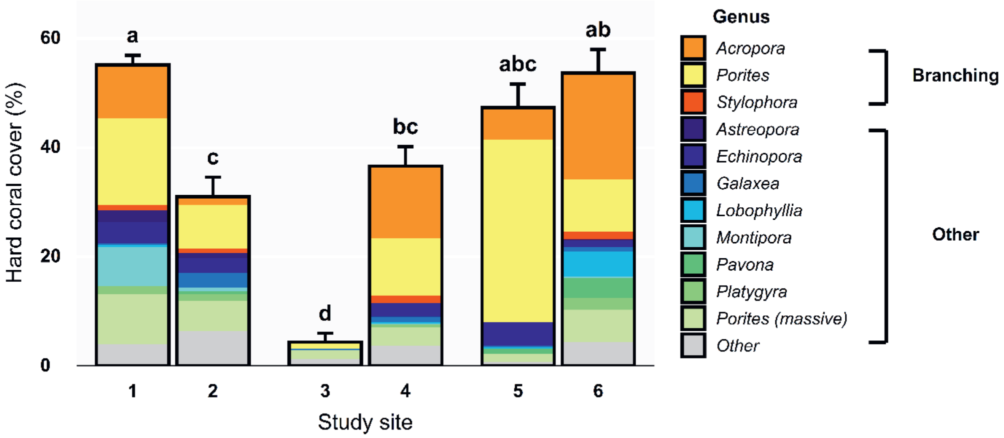

Figure 3 *Average hard coral cover split per genus for each study site. Branching coral genera are grouped separate from corals with other growth forms (mainly massive and encrusting). Note that* Porites *occurs in both groups. The category 'Other' is a collection of 28 genera of various growth forms which each contributed less than 0.5% to total hard coral cover. Differing lower case letters denote a significant (p < .05) difference between study sites in total coral cover (n = 10 surveys). It is indicated whether study sites are situated in an unrestricted fishing zone, a marine reserve (traditional fishing allowed) or no-take zone*

Corallivore densities

In total, 37 corallivorous fish species were recorded across the six study sites (Fig. S2), of which 9 were obligate coral feeders (Fig. S3). The biomass of facultative corallivorous fish differed significantly between study sites (X^2 = 35.887, df = 5, p < .001). The average biomasses of facultative corallivorous fish at study site 5 (143 kg ha^{-1}) and 6 (226 kg ha^{-1}), both located in no-take zones, were higher compared to the four other study sites (5 – 57 kg ha^{-1}), though there was considerable variation per survey (Fig. 4c). Neither hard coral cover nor coral diversity correlated with the biomass of facultative corallivorous fish (Table S1; Fig. 4d). A different pattern was seen for obligate corallivorous fish, whose biomass did correlate significantly with coral cover (Fig. 4f), but not with coral diversity. Average obligate corallivorous fish biomass differed between study sites (X^2 = 30.701, df = 5, p < .001) and was highest at study sites 1, 5 and 6 (Fig. 4e), which also were the sites with highest coral cover.

In total only 4 CoTS were observed, all at study site 4, resulting in an average density of 40 CoTS ha^{-1} for site 4. Single *Culcita schmideliana* sea stars were found at study sites 1, 3 and 6, resulting in average densities of 10 *Culcita* ha^{-1} at these sites. The density of corallivorous snails differed significantly between study sites (X^2 = 43.384, df = 5, p < .001). Study sites 3 and 5 had higher average snail densities of around 3 snails m^{-2}, compared to densities between 0.5 – 1.5 snails m^{-2} for the other four sites (Fig. 4g). *Coralliophila* spp. were markedly more abundant than *Drupella* spp. across all study sites except site 2 (Fig. S4). Hard coral cover did not correlate significantly with snail density (Fig. 4h), but a significant negative correlation was found between coral diversity and snail density (Fig. 4j). Predation on corallivorous snails differed significantly between study sites (X^2 = 17.202, df = 5, p = .0050), but no significant site-specific differences were found by the post-hoc test (Fig. 4i). The average percentage of snails predated across study sites was 13% and though the RUV recordings did not capture any predators in action, the broken and missing shells suggested predation was primarily by fish.

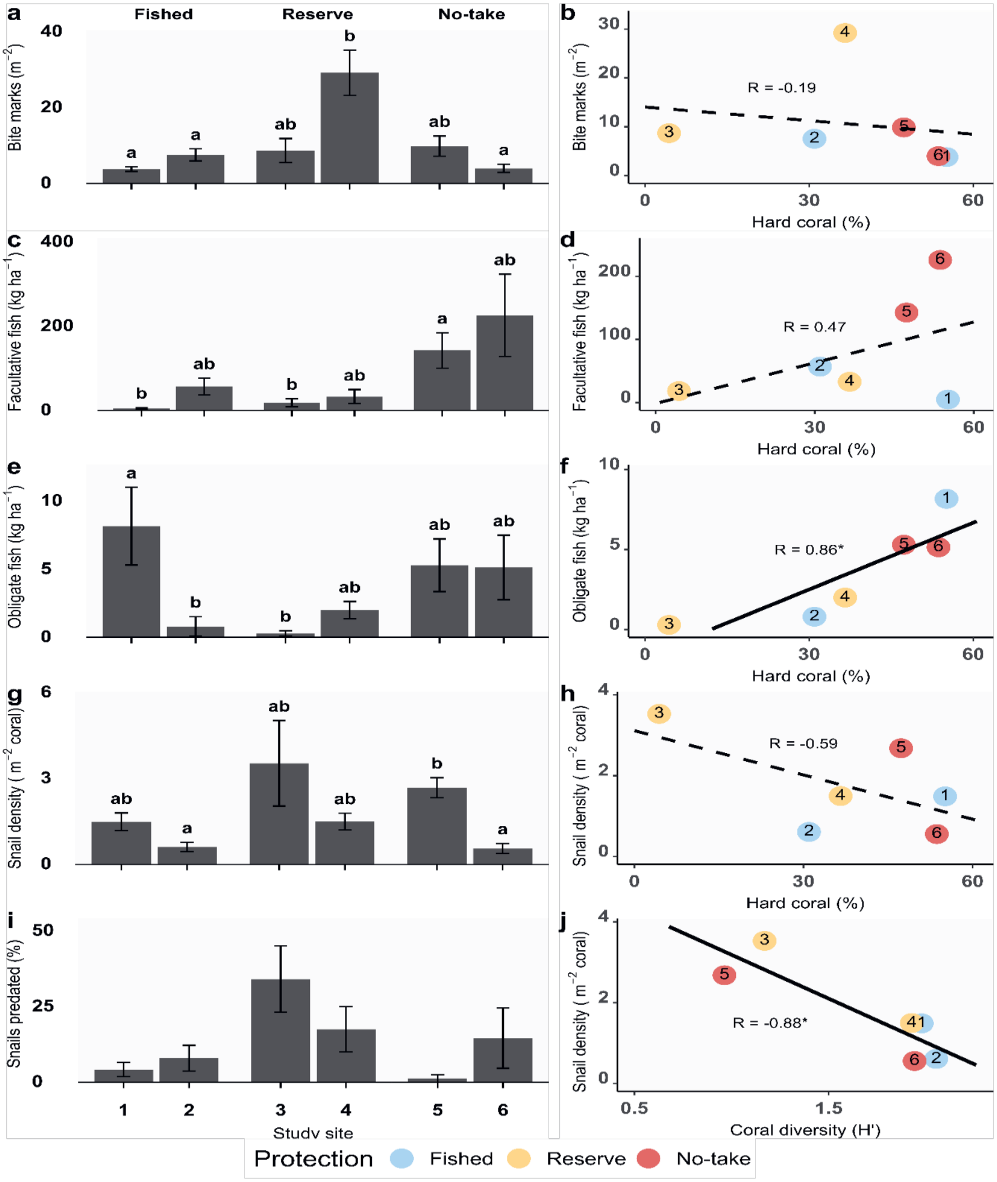

Figure 4 *Overview of bite mark and corallivore densities per study site with correlations against potential driving factors. Differing lower case letters denote significant differences ($p < .05$) and bars show means ± SE. For each study site, it is indicated whether situated in an unrestricted fishing zone, marine reserve or no-take zone. The Pearson's r is noted at each linear trend line and marked (*) when significant (dashed lines are used for non-significant correlations).* ***(a)*** *Bite mark density (bite marks per m^2 of coral) across study sites (n = 10 benthic surveys) and* ***(b)*** *correlated against hard coral cover.* ***(c)*** *Density of facultative corallivorous fish across study sites (n = 11 – 15 fish surveys) and* ***(d)*** *correlated against coral cover.* ***(e)*** *Density of obligate corallivorous fish across study sites (n = 11 – 15) and* ***(f)*** *correlated against coral cover.* ***(g)*** *Corallivorous snail density (combined counts of* Drupella *spp. and* Coralliophila *spp. per m^2 of coral) across study sites (n = 10 benthic surveys) and* ***(h)*** *correlated against hard coral cover.* ***(i)*** *Percentage of snails predated across study sites (n = 5 assays) and* ***(j)*** *average snail density correlated against coral genera diversity (H')*

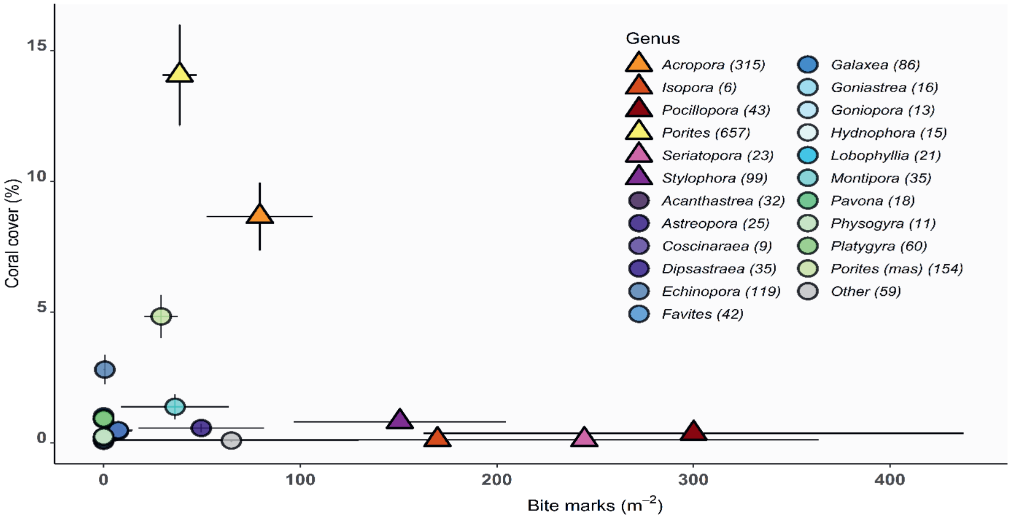

Figure 5 *Bite mark density plotted against hard coral cover per genus. Bite mark density was calculated by dividing the total number of bite marks per colony by the projected coral colony surface. In total, 1893 coral colonies were sampled: the number of colonies sampled per genus is indicated between brackets. Coral genera are grouped into either a 'Branching' growth form (triangles) or 'Other' growth form consisting mainly of massive and encrusting corals (circles). The category 'Other' includes 13 rare (colony count < 5) genera of either growth form that were pooled*

Outplanted corals

For corals on the artificial reef structures, a significant interactive effect on bite mark density was found between study site and coral genus ($X^2 = 50.848$, df = 10, p < .001): all three genera showed higher bite mark densities in the no-take zones, though the exact study site with highest bite mark density varied per genus (Fig. 6a). Overall, bite mark densities were much higher on coral fragments outplanted on the artificial reef structures compared to conspecific coral colonies on the natural reef, ranging from one up to two magnitudes higher (Table S2). *Pocillopora* had the highest average bite mark density on artificial reef structures (1296 bite marks m^{-2}) followed by *Porites* (951 bite marks m^{-2}) while *Acropora* had a considerably lower bite mark density (317 bite marks m^{-2}). The pattern in bite marks across study sites and genera was roughly mirrored in reduced live coral tissue (Fig. 6b). For remaining live coral tissue, also a significant interaction was found between study site and coral genus ($X^2 = 34.145$, df = 10, p < .001) with generally more tissue loss in the no-take zones. A notable exception was *Porites* at site 5, where fragments maintained a high amount of live tissue (Fig. 6b) despite high predation pressure (Fig. 6a). Bite mark density was negatively correlated with the percentage live coral tissue of *Pocillopora*, whereas the negative correlation for *Porites* was not significant and no clear pattern emerged between bite mark density and live coral tissue for *Acropora* (Fig. 7a). For all three genera, a positive correlation was found between their bite mark density and the biomass of facultative corallivorous fish, though these were significant only for *Pocillopora* and *Porites* (Fig 7b). For none of the three genera, the correlations between bite mark density and obligate corallivorous fish biomass or coral cover on the natural reef were significant (Table S1). In addition to the bite marks by fish, several invertebrate corallivores were found to feed on the outplanted coral fragments, including two *Drupella* sp. and one *Coralliophila* sp. feeding on *Acropora* at study site 2, one *Culcita schmideliana* feeding on two *Acropora* fragments at study site 1 and one CoTS consuming three *Acropora* fragments at study site 6.

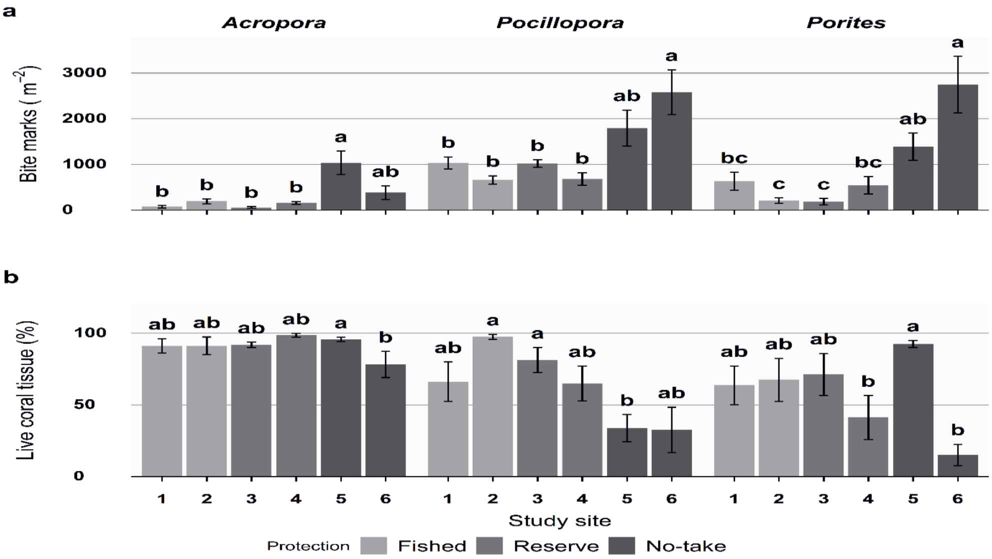

Figure 6 *Average* ***(a)*** *bite mark density and* ***(b)*** *live coral tissue of coral fragments outplanted on artificial reef structures. Bite mark density is averaged over the 4-month study period. Fragments are split over the three used coral genera and six study sites, and fisheries management is indicated by shade. Bars represent means ± SE. Differing lower case letters denote significant differences (p < .05) between study sites for each genus*

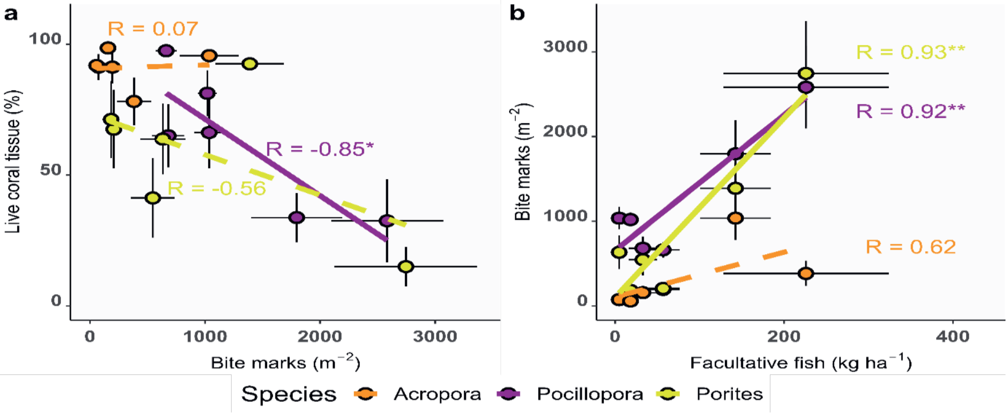

Figure *7 Average bite mark density on outplanted coral fragments per study site correlated against* ***(a)*** *live coral tissue and* ***(b)*** *facultative corallivorous fish biomass. Pearson correlation coefficients (* p < .05, ** p < .01) and linear trend lines are shown and coloured by coral genus. Non-significant correlations are shown by dashed lines. Bite mark density is averaged for the 4-month study period. Error bars denote SE per study site*

Discussion

This study aimed to advance the design of ecological approaches for reef restoration that reduce coral predation. Three potential factors that drive corallivory were explored: 1) the coral cover and coral diversity on reefs targeted for restoration, 2) the corallivore community and their predation pressure at natural reefs compared to outplanted coral fragments and 3) the type of fisheries management established in an area. No evidence for predation pits - higher corallivore densities or predation pressure - was found at reefs with lower coral cover. Instead, the density of obligate corallivorous fish was in equilibrium with coral cover, highest densities of facultative corallivorous fish were found in no-take zones, and high densities of corallivorous snails were associated with low coral diversity instead of low coral cover. On natural reefs, predation pressure differed strongly among coral genera, with highest bite mark densities for branching corals. When corals were exposed as if on an artificial reef for restoration, predation pressure was up to two orders of magnitude higher compared to predation pressure on corals of the same genus on natural reefs. The higher predation pressure notably reduced the percentage live coral tissue of outplanted coral fragments, which indicates that it is the transplantation process rather than the type of coral used for restoration that can cause an increased vulnerability to corallivory. Predation on outplanted fragments was especially strong in no-take zones, possibly due to the higher densities of facultative corallivorous fishes such as parrotfishes. Overall, these results show that reefs with low coral cover, which are often targeted for reef restoration, do not necessarily experience intensive corallivory, that ecological solutions are needed to address the high predation pressure on outplanted branching corals, and that the potential negative effects of facultative corallivorous fish and fisheries management on reef restoration warrants further scrutiny.

Drivers of corallivore densities

No evidence for a predator pit was found across the studied coral cover gradient, as corallivore densities either remained constant or decreased with lower hard coral cover. The scarcity of obligate corallivorous fishes at low coral cover attests the dependence of these fishes on hard coral for shelter and food (Cole et al., 2008). Such an equilibrium also supports that, despite their chronic predation pressure (Cole et al., 2012), obligate corallivorous fishes are unlikely to be detrimental to coral cover (Cole and Pratchett, 2011) and, by extension, restoration success. Facultative corallivorous fish densities did not relate to coral cover, but were highest inside established no-take zones. The fact that their densities were low even inside traditionally-fished marine reserves, suggests a high susceptibility of facultative corallivorous fish, such as parrotfishes, to human exploitation (Cros and McClanahan, 2004). As apex predators such as sharks are hardly present even in the studied no-take zones, the established size of these protected areas might be too small compared to the large home ranges of these predators (MacKeracher et al., 2019). Thus, human fishing pressure on apex predators outside the no-take zones could indirectly be influencing the fish community inside no-take zones: when apex predators become regionally extinct (Cinner et al., 2018; McClanahan et al., 2019), larger facultative corallivorous fish might benefit from low predation rates. High densities of corallivorous snails were associated with low coral diversity. High snail densities are particularly likely to occur when their preferred coral prey species become dominant, as has been shown for both *Drupella* (McClanahan, 1997) and *Coralliophila* (Johnston and Miller, 2014). A high abundance of coral prey species is likely a more important driver of corallivorous snail populations than low coral diversity per se, although plasticity in prey selection could mean abundant, but non-preferred coral species could also support snail populations (Bruckner et al., 2017). Interestingly, predation on the exposed snails was not elevated inside protected areas despite higher densities of potential predatory fish, contrasting previous studies (McClanahan, 1997; Shaver et al., 2020a). It seems that, at least for adult snails (Clements and Hay, 2018), bottom-up control of food availability can be a strong driver as well.

Corallivore populations at the studied sites were thus influenced by divergent drivers and, importantly, no aggregations occurred at low coral cover. The absence of a predator pit contrasts studies that did identify conspicuous aggregations of invertebrate corallivores at low-coral areas (Knowlton et al., 1990; Bruckner et al., 2017). A possible explanation for this disparity could be that predator pits are time dependent: the surplus of corallivores on surviving coral after a large-scale disturbance, such as a hurricane (Knowlton et al., 1990) or a bleaching event (Bruckner et al., 2017), can be expected to dissipate over time through increased mortality and emigration. The duration of a predator pit would then be dependent on the movement and lifespan of the corallivores (Knowlton et al., 1990) and their ability to switch to alternative food sources (Cole et al., 2008). As the last major disturbance in our study area was a bleaching event that occurred more than two decades ago (McClanahan et al., 2005), a predator pit could have potentially aggravated coral losses back then, but plenty of time has passed since for corallivore populations to diverge.

Drivers of bite mark density

In line with the absence of a prevailing predator pit, predation pressure was not negatively related to coral cover, agreeing with findings from the Great Barrier Reef (Bonaldo and Bellwood, 2011) and the Caribbean (Roff et al., 2011). However, high bite mark densities at low coral cover were found at a degraded Caribbean reef with uniquely high parrotfish density (Burkepile, 2012). Additional location-specific variation becomes evident when comparing predation pressure on common coral genera with related studies elsewhere (Jayewardene et al., 2009; Bonaldo and Bellwood, 2011; Burkepile, 2012) and this likely also depends on the local densities of key corallivores and the coral community present. Interestingly, bite mark density found on natural reefs in this study did not relate to facultative corallivorous fish biomass. As these fish are expected to be directly responsible for creating the majority of these bite marks, the absence of a correlation is surprising, yet has been lacking before (Roff et al., 2011; Burkepile, 2012). Possibly, not all facultative corallivorous fish are equally active coral feeders, and some key species may drive the majority of bite marks, much alike how browsing of macroalgae is driven by only a subset of key species (Puk et al., 2016). The species responsible for the observed predation pressure in this study unfortunately remain unidentified and observed predation patterns could not be readily matched to the biomass of any corallivore species. Biomass estimates of key species could misalign with realized predation pressure if corallivory is strongly dependent on seasons (Bonaldo et al., 2012; Horoszowski-Fridman et al., 2015), alternate food sources available (McClanahan et al., 2005), reef zonation (Bonaldo and Bellwood, 2011) or competitive interactions (Cox, 1986). As this complex system seems to defy generalizations, the identification of key species, their predation behaviour and bite mark patterns can be considered a priority to improve our understanding on corallivory.

A closer look at the distribution of bite marks across coral genera revealed that a few branching genera seem to bear the brunt of coral predation, while other growth forms remain largely unscathed. Specifically, branching corals of the Pocilloporidae, Acroporidae and Poritidae families had abundant bite marks per projected colony area, mounting evidence of a preference among corallivores for these families across the Indo-Pacific (Cole et al., 2008; Rotjan and Lewis, 2008). While it should be noted that the surface projection used here (and elsewhere) underestimates the actual surface area of especially branching growth forms (Naumann et al., 2009), bite marks on branching corals are principally targeted at the growing tips around the colony's periphery. Therefore, the used measure is deemed a good estimation of predation pressure on available hard coral substrate. The impact on the coral's energy budget might nevertheless differ between growth forms and bite mark sizes, depending on the ratio of predated and non-predated tissue and this calls for more detailed studies. Branching corals have been shown to recover from high predation pressure through fast regeneration (Hall, 1997; Henry and Hart, 2005). Nonetheless, the identified negative correlation between bite mark density and branching coral cover indicates that corallivory could be a potential determinant of the coral community composition, for example explaining the low abundance of *Pocillopora* spp. Distributional limits of coral through predation have been described before (Frydl, 1979; Neudecker, 1979; Cox, 1986; Littler et al., 1989; Bonaldo and Bellwood, 2011) and could increase overall coral diversity by reducing the competitive advantage of fast-growing genera (Cole et al., 2008). However, when additional stressors such as temperature anomalies or hurricanes disproportionally detriment the same branching genera, their recovery can be seriously impeded leading to the functional disappearance of once-dominant reef builders such as *Acropora* (Knowlton et al., 1990; McClanahan et al., 2005). Understanding and, where needed, remediating the interplay between such natural and anthropogenic stressors is crucial for restoration projects relying heavily on these fast-growing but susceptible corals (Rice et al., 2019).

Implications for reef restoration

Corresponding with the natural reef, no predation pit was found on corals outplanted on reefs with low coral cover, calling for some nuance in voiced concerns about corallivory hampering restoration of reefs in coral poor areas (Ladd et al., 2018; Koval et al., 2020). Also here, temporal and location-specific aspects such as species composition can likely help to explain the presence or absence of predation pits. For example, the predation pit found in Hawaii (Jayewardene et al., 2009) might have been caused by the strong site dependency and prey selectivity of the dominant corallivore, a pufferfish. Regarding reef restoration, the dilution of predation pressure through addition of outplanted coral fragments has been investigated with mixed results: some small-scale studies showed potential predator dilution (Shantz et al., 2011), others found no effect (Kopecky et al., 2021) and even others found corallivore attraction (Johnston and Miller, 2014). While larger experimental setups are needed to test for predation dilution on the relevant reef scale, the identification of location-specific key corallivore species might also help to resolve these conflicting results.

Although invertebrate corallivore densities at some study sites were approaching reported outbreak thresholds (Moran and De'ath, 1992; Bessey et al., 2018), their impact on outplanted corals in our study was limited. In contrast to several other restoration studies in East Africa (Tamelander et al., 2000; McClanahan et al., 2005; Mbije et al., 2013), CoTS predation was not a major impediment. Likewise, predation by snails was limited, though this might be attributed to the relatively short study duration. In clear contrast, heightened fish predation was found on outplanted corals with ensuing decreases in live coral tissue and those findings are in agreement with numerous other restoration studies (Cros and McClanahan, 2004; Horoszowski-Fridman et al., 2015; Koval et al., 2020; Kopecky et al., 2021; Rivas et al., 2021), though corals in nursery structures in the same area remain spared of intensive invertebrate or fish predation (Knoester et al., 2019). Bite mark densities on outplanted corals were highest in the no-take zones, though such increased predation in protected areas was not found on natural reefs in this and a similar study (Jayewardene et al., 2009). As outplanted corals experience stress (Forrester et al., 2012) and stressed fragments are more susceptible to predation (Henry and Hart, 2005; Cole et al., 2008; Hamman, 2018), the outplanting stress can partially explain the increased predation. However, even after caged acclimatization, corallivory can still hamper outplanting success (McClanahan et al., 2005; Rivas et al., 2021). The high predation appears to be caused by a combination of factors besides outplanting stress and the use of susceptible species, and might also relate to the outplanting strategy such as the small coral size and low coral diversity used. On the other hand, high predation does not necessarily lead to reduced live coral tissue (e.g. *Porites* at offshore study site 5), indicating that more factors could be at play such as water quality (e.g. elevated levels of inorganic nutrients), which can make bite wounds more prone to infections (Zaneveld et al., 2016). While corallivory can increase coral diversity on natural reefs, the high predation rates on outplanted corals call for restoration approaches that reduce corallivory and increase outplanting success. The impact of corallivory may be mitigated through outplanting strategies that consider the size (Jayewardene et al., 2009), density (Shaver and Silliman, 2017) and diversity of fragments and their arrangement (Johnston and Miller, 2014; Cabaitan et al., 2015; Koval et al., 2020; Rivas et al., 2021). Additional ecological solutions provided by the reef community also warrant further study, such as the facilitation of corallivore predators (Delgado and Sharp, 2020) and natural coral guardians (Tiddy et al., 2021).

Based on identified corallivore densities, predation pressure and potential driving forces, we outline three recommendations. First, given the unpredictable occurrence of predation pits over time and space, a characterization of corallivore densities is recommended before large-scale outplanting of corals. Pilot studies can provide a quick measure of predation pressure and are especially relevant at recently disturbed areas. If high densities of invertebrate corallivores are found, their manual removal could augment restoration (Williams et al., 2014). Second, the choice of restoration methods and species deserves more scrutiny. Fast-growing branching corals are convenient to mass produce and these pioneer species could, in theory, make reefs suitable for natural recruitment of slower growing and more resistant corals. However, restoring reefs with only a few cultured branching species could render these reef particularly vulnerable to predation by both corallivorous snails and facultative corallivorous fish. If outplanted corals do not survive in sufficient numbers to kickstart reef recovery, the diversity of species and growth forms used, their arrangement, sizes and densities can likely be optimized to reduce predation and this is an avenue for further research. Lastly, even though facultative corallivorous fish such as parrotfish likely have a net positive effect on natural reefs (Mumby, 2009; Bonaldo et al., 2017), these findings are not always consistent (Bruno et al., 2019) and cannot be directly translated to outplanted corals given their higher susceptibility to corallivory (Cros and McClanahan, 2004; McClanahan et al., 2005). The identification of key facultative corallivorous fish species and their impact on outplanted corals are necessary first steps to unravel the effects fisheries management can have on corallivory and reef restoration (Seraphim et al., 2020), and this could be especially important in areas where apex predators remain rare. To conclude, we hope these results and recommendations will inspire more ecology-based reef restoration approaches and research (Shaver and Silliman, 2017; Ladd and Shantz, 2020), increase outplanting success and, ultimately, improve the potential of restoration and conservation to help reefs deal with the pressure of concurrent global stressors (Knowlton et al., 2021).

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Author contribution statement: EG Knoester: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. N Klerks: Methodology, Investigation, Writing – original draft. SB Vroege-Kolkman: Methodology, Investigation, Writing – review & editing. AJ Murk: Conceptualization, Resources, Writing – review & editing, Supervision. SO Sande Conceptualization, Resources, Writing – review & editing, Supervision. R Osinga: Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration.

Conflict of interest: The authors declare that they have no conflicts of interest.

Availability of data: The datasets and code used for analysis is available as an archived Github repository on: https://github.com/ewoutknoester/PredationPressureRestoration

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Ethical approval: No approval of research ethics committees was required for this observational study. Applicable international guidelines for monitoring on coral reefs were followed. This study was performed under the research license NACOSTI/21/8896.

Supplementary materials

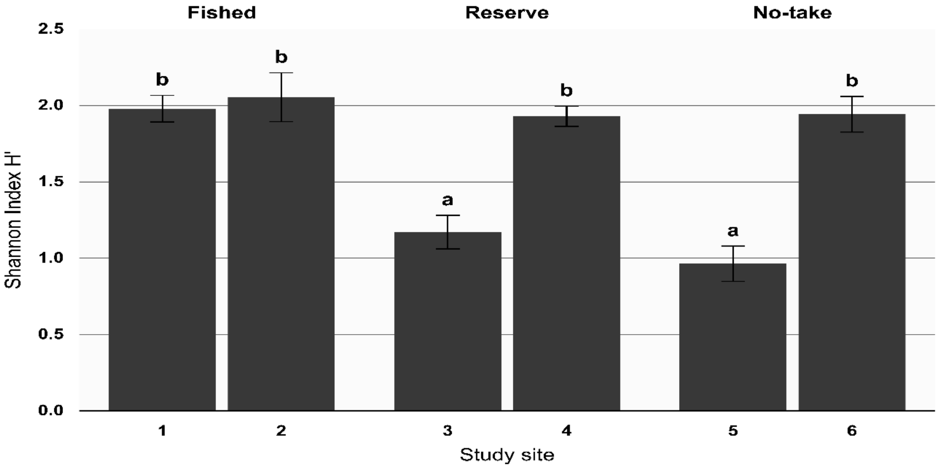

Figure S1 *The diversity of hard coral (on genus level) for each study site expressed as the Shannon Index H'. Differing lower case letters denote a significant (p < .05) difference between study sites in coral diversity (n = 10 surveys). It is indicated whether study sites are situated in an unrestricted fishing zone, a marine reserve (traditional fishing allowed) or no-take zone*

Table S1 *Overview of all Pearson correlations. Correlations are ordered according to position in the manuscript text. Significant (p < .05) correlations are printed in bold. NR = natural reef; AR = artificial reef*

Variable 1	Variable 2	r	df	p
Bite mark density NR	Hard coral cover	-.19	4	.72
Bite mark density NR	Hard coral genus diversity	.05	4	.92
Bite mark density NR	Facultative corallivorous fish biomass	-.29	4	.58
Bite mark density NR	Obligate corallivorous fish biomass	-.39	4	.44
Bite mark density branching genus	**Log(Coral cover branching genus)**	**-.82**	**4**	**.048**
Bite mark density other genus	Coral cover other genus	.13	15	.62
Facultative corallivorous fish biomass	Hard coral cover	.47	4	.34
Facultative corallivorous fish biomass	Hard coral genus diversity	-0.09	4	.87
Obligate corallivorous fish biomass	**Hard coral cover**	**.086**	**4**	**.029**
Obligate corallivorous fish biomass	Hard coral genus diversity	.11	4	.84
Corallivorous snail density	Hard coral cover	-.59	4	.22
Corallivorous snail density	**Hard coral genus diversity**	**-.88**	**4**	**.021**
Bite mark density AR Pocillopora	**Live tissue cover Pocillopora**	**-.85**	**4**	**.030**
Bite mark density AR Porites	Live tissue cover Porites	-.56	4	.24
Bite mark density AR Acropora	Live tissue cover Acropora	.073	4	.89
Bite mark density AR Pocillopora	**Facultative corallivorous fish biomass**	**.94**	**4**	**.005**
Bite mark density AR Porites	**Facultative corallivorous fish biomass**	**.97**	**4**	**.002**
Bite mark density AR Acropora	Facultative corallivorous fish biomass	.62	4	.19
Bite mark density AR Pocillopora	Obligate corallivorous fish biomass	.46	4	.36
Bite mark density AR Porites	Obligate corallivorous fish biomass	.48	4	.33
Bite mark density AR Acropora	Obligate corallivorous fish biomass	.29	4	.57
Bite mark density AR Acropora	Coral cover	.38	4	.46
Bite mark density AR Pocillopora	Coral cover	.49	4	.33
Bite mark density AR Porites	Coral cover	.63	4	.18

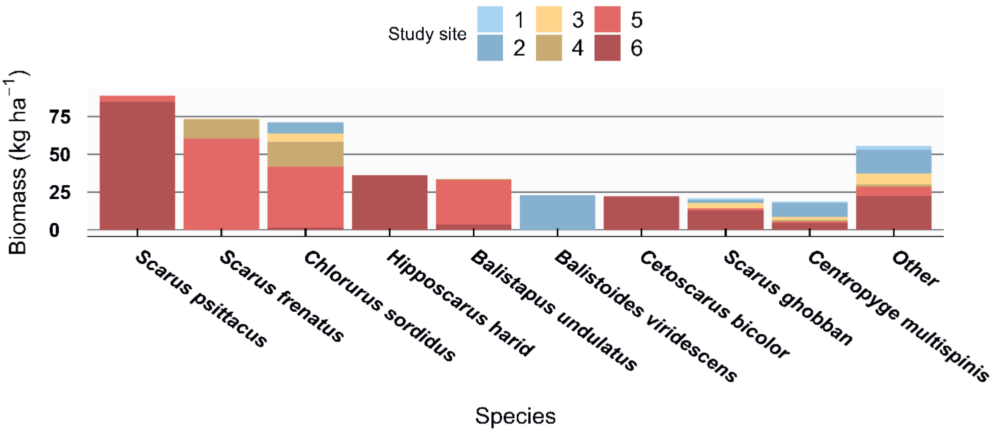

Figure S2 *Average fish biomass of facultative corallivorous fish species across the six study sites as determined by fish surveys (n = 11 – 15). Study sites 1 and 2 were located in an unrestricted fishing zone (blue shades), sites 3 and 4 were located in a marine reserve where traditional fishing methods were allowed (orange shades) and sites 5 and 6 were located in no-take zones (red shades). The category 'Other' includes 19 species that each made up < 3% of the total facultative fish biomass and include the species (in decreasing order):* Chaetodon lunula, Scarus rubroviolaceus, Chaetodon auriga, Arothron stellatus, Gomphusus caeruleus, Arothron hispidus, Chaetodon xanthocephalus, Sufflamen bursa, Sufflamen chrysopterum, Chaetodon kleinii, Pomacanthus semicirculatus, Chaetodon guttatissimus, Canthigaster valentini, Neoglyphidodon melas, Chlorurus atriluna, Scarus niger, Ostracion cubicus, Centropyge acanthops *and* Canthigaster *sp.*

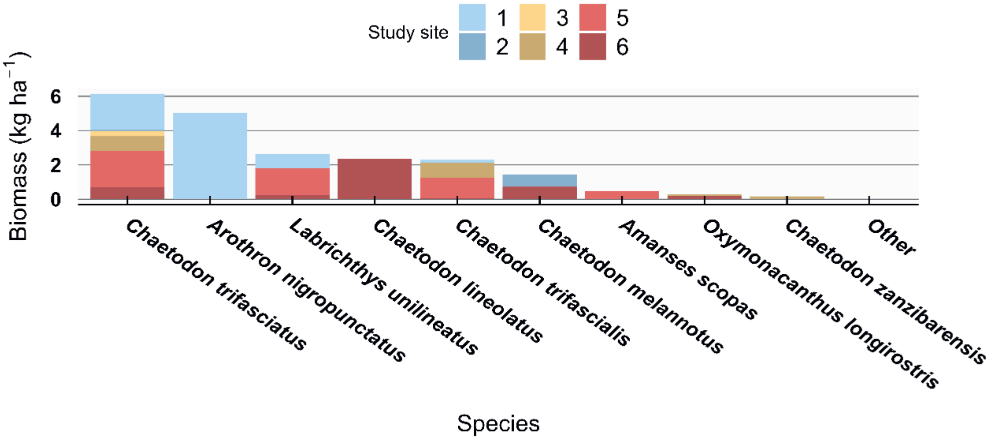

Figure S3 *Average fish biomass of obligate corallivorous fish species across the six study sites as determined by fish surveys (n = 11 – 15). Study sites 1 and 2 were located in an unrestricted fishing zone (blue shades), sites 3 and 4 were located in a marine reserve where traditional fishing methods were allowed (orange shades) and sites 5 and 6 were located in no-take zones (red shades)*

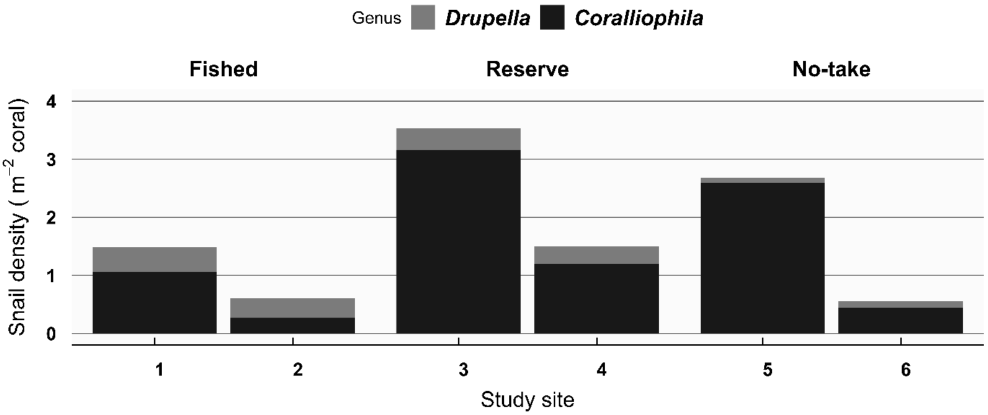

Figure S4 *Average corallivorous snail densities (per square meter of hard coral) across the six study sites, stacked by genus. Data based on 10 replicate benthic surveys per study site*

Table S2 *Comparison between the density of bite marks on the natural reef (NR) against artificial reef (AR) for the three outplanted genera across study sites. Bite marks are expressed per m*^{2} *of coral and the number of sampled colonies is mentioned in brackets. The multiple of bite mark density on the AR compared to NR is noted in the last column (i.e. bite marks AR/ bite marks NR)*

Genus	**Study site**	**Bite marks NR**	**Bite marks AR**	**Difference**
Acropora	1	2 (48)	74 (16)	48
Acropora	2	240 (17)	194 (16)	1
Acropora	3	0 (5)	57 (16)	Inf
Acropora	4	46 (123)	156 (16)	3
Acropora	5	160 (49)	1037 (16)	6
Acropora	6	101 (73)	383 (16)	4
Pocillopora	1	177 (11)	1036 (8)	6
Pocillopora	2	28 (6)	662 (8)	23
Pocillopora	3	134 (4)	1020 (8)	8
Pocillopora	4	366 (12)	680 (8)	2
Pocillopora	5	85 (3)	1796 (8)	21
Pocillopora	6	800 (7)	2582 (8)	3
Porites	1	9 (125)	633 (8)	69
Porites	2	54 (104)	207 (8)	4
Porites	3	57 (24)	184 (8)	3
Porites	4	87 (107)	546 (8)	6
Porites	5	28 (254)	1389 (8)	50
Porites	6	21 (43)	2746 (8)	129

Benefits of herbivorous fish outweigh costs of corallivory in coral nurseries placed close to a Kenyan patch reef

4

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Abstract

Coral mariculture involves time-consuming removal of fouling. On natural reefs, this service is provided by grazers. As natural reefs also harbour corallivores, it is debated whether reef-bound fish have a positive or negative effect on coral maricultured near natural reefs. This study quantified the net impact of herbivorous and corallivorous fish on coral mariculture. Nursery trees either uncaged, caged or as cage-control (15 per treatment) were placed near a patch reef at Wasini, Kenya, each hosting ten *Acropora verweyi* fragments. From April to July 2016, survival and growth of the corals and bite marks on the corals were monitored. Using remote underwater video, bites by herbivorous and corallivorous fish were quantified. Upon termination of the experiment, dry weight of fouling from the nursery trees was determined. Caging of nurseries strongly reduced herbivory and corallivory. Results of cage-controls were not significantly different from uncaged trees. In caged nurseries, coral survival and growth were significantly lower than in uncaged nurseries, respectively 9% and 40% lower. Fouling was nearly 800% higher in caged nurseries. Herbivory was dominated by the surgeonfish *Ctenochaetus striatus*, which was responsible for 77% of the grazing. Monthly assessments showed bite marks on 10% of the uncaged coral fragments. Our study reveals that fouling control by herbivorous fish outweighs the costs of incidental corallivory on the survival and growth of *A. verweyi*. The vigour of unrestricted fouling, its negative impact on coral performance and the scarcity of corallivory justify the recommendation to place coral nurseries in Wasini near the reef.

Key words: Coral reef conservation; Coral gardening; Corallivory; Herbivory; Coral-algae interactions

Introduction

Triggered by the continuous degradation of tropical reefs, coral reef restoration initiatives have rapidly gained support around the turn of the last millennium (Rinkevich 2008). The aim of these active conservation initiatives is to improve the state of degraded reefs and mitigate local anthropogenic impacts to support higher resilience against large-scale disturbances, including climate change (Precht, 2006; Hughes et al., 2007b; Edwards et al., 2010). The practise of coral mariculture and reef restoration is still young and is partially conducted upon a scientific basis and partially upon trial and error. One of the limiting aspects of coral mariculture is the fight against fouling that hampers the performance of coral fragments by overgrowing them. This is not happening on healthy reefs because of the grazing activity of herbivorous invertebrates and fish (Carpenter, 1986; Hughes et al., 2007b). It has been suggested, but not experimentally investigated, to place mid-water coral nursery structures near natural reef formations allowing roving herbivorous fish to visit the structures and consume fouling organisms (Edwards et al., 2010; Johnson et al., 2010). This would reduce the need for human-assisted cleaning efforts and thus project expenses (Shafir et al., 2006b; Frias-Torres et al., 2015). In contrast, other studies advise to isolate mid-water nursery structures from the natural reef in order to eliminate the negative impacts of corallivory (i.e. predation on coral) by fish and invertebrates. Coral nurseries have been isolated from the natural reef ranging from 1 km (Frias-Torres and Van de Geer, 2015), 3 km (Mbije et al., 2010; Horoszowski-Fridman et al., 2011), 5 km (Levy et al., 2010), 8 km (Shafir et al., 2006a) to 13 km (Mbije et al., 2010). Coral nurseries have even been caged to prevent corallivory (Ferse and Kunzmann, 2009). Despite the fact that these reef restoration projects isolated and caged their nurseries to prevent corallivory, no study quantified the actual impact of corallivory on coral mariculture. In addition, no study considered the potentially negative impact of nursery isolation on coral performance through the absence of important reef-associated grazers of biofouling. Hence, quantitative studies on the effects of herbivory and corallivory on coral in mariculture are needed to complement the ample literature on these processes on natural reefs.

Herbivory

Dominant herbivores, such as fish and sea urchins, play a key role in tropical reef health, for their continuous grazing pushes the balance of competitive interactions between fouling organisms and corals towards Scleractinian coral dominance (Carpenter, 1986; Steneck, 1988). From the diverse suite of fouling organisms, macroalgae seem the most widespread threat to Scleractinian corals (Jompa and McCook, 2003). These macroscopic, fleshy and fast-growing algae can compete for space, food and light using several mechanisms, including overgrowth, shading, abrasion and allelopathy (Jompa and McCook, 2002). As a result, the coral colony receives less energy due to shading, polyp retraction and smothering (Tanner, 1995) and becomes more prone to diseases and corallivory (Nugues et al., 2004; Wolf and Nugues, 2013). Experimental exclusion of roving herbivorous fish, the dominant grazers on healthy reefs, has ensued in unrestrained expansion of algal biomass in numerous studies (e.g. Thacker et al. 2001, Fox and Bellwood 2007, Korzen et al. 2011), which, in turn, indeed had negative impacts on coral growth, survival and fecundity (e.g. Tanner 1995, Hixon & Brostoff 1996, Box & Mumby 2007, Hughes et al. 2007). The question remains, however, whether roving herbivorous fish will effectively graze artificial nursery structures. Although grazing by herbivores has been shown an invaluable service to natural coral reefs, the benefit of fish-assisted cleaning to maricultured coral has not yet been quantified.

Corallivory

Dominant corallivores such as certain fish, gastropods and echinoderms inhibit coral growth through the consumption of live polyps and coral skeleton, while also leaving injuries. These injuries make the corals vulnerable to pathogens and fouling, reduce their energy production and increase their energy requirement for regeneration (Hall, 1997). This impact was long considered insignificant, but more recent studies recognize corallivory as a potential important factor shaping coral reefs (Rotjan and Lewis, 2008). For example, corallivory by fish has been shown to limit the local distribution of certain coral species (Neudecker, 1979; Cole et al., 2008; Mumby, 2009) and the main preyed coral species belong to same fast-growing genera (e.g. *Acropora* and *Pocillopora*) that are frequently used in reef restoration projects. In addition, coral in mariculture may be stressed and vulnerable through handling and fragmentation, potentially further increasing corallivory (Cole et al., 2008). Also, large herbivorous fish have been reported to accidently or on purpose scrape young coral fragments (e.g. Miller & Hay 1998, Baria et al. 2010), while other fish have dislodged transplanted coral to reach invertebrate preys (Frias-Torres and Van de Geer, 2015). Corallivory could therefore impede the success of coral mariculture and a reef restoration project. However, until the impact of corallivorous fish on coral mariculture is systematically studied, there is no rational basis for decisions of placing coral nursery structures on isolated locations to limit corallivory.

Research objective

There are conflicting views on site selection for the placement of mid-water coral nursery structures. It remains unclear whether reef-bound fish have an overall positive or negative effect on coral mariculture as experimental studies are lacking. Both herbivory and corallivory have received scientific attention on the natural reef. However, the balance between these two important processes on coral in mariculture has remained unstudied and has been identified as a research priority in a recent review on coral reef restoration (Ladd et al., 2018). This study aims to address this knowledge gap by answering the following research question: What is the net impact of the local, reef-bound fish community at Wasini Island on the performance of corals in mariculture? The net impact was determined by experimental exclusion of fish from mid-water coral nursery structures (coral trees) located at a patch reef at Wasini Island, Kenya, hereby comparing the growth and survival of corals in uncaged and caged nurseries.

Based on the crucial role of herbivorous fish in maintaining Scleractinian coral cover on reefs worldwide and the flourishing of natural reefs despite the presence of corallivorous fish at the study location, it was expected that the benefit of grazing of fouling by herbivorous fish outweighs the cost of coral consumption by corallivorous fish in coral mariculture at this location. Thus, we hypothesize that coral survival and growth will be highest in uncaged nursery structures. The results of this study can be used to identify the best locations for placement of coral nurseries in the waters around Wasini Island.

Methods

Location

The fish-exclusion study was conducted from April to July 2016 at a patch reef north of Wasini Island, Kenya (4°39'34.04"S, 39°22'56.18"E). Wasini Island and the study area (Fig. 1) are separated from the Kenyan mainland by a kilometre-wide channel. Coral patches are haphazardly scattered along the Wasini coastline between 2 to 5 m depth (low tide) and dominated by massive and branching corals from the genera *Porites*, *Acropora*, *Pocillopora, Favia*, *Favites* and *Platygyra*. Tidal difference reaches 4 m at spring tide and spans 2 m at neap tide. Visibility is typically 9 ± 3 m (mean ± SD; n = 45), as measured by horizontal Secchi depth (range: 4 – 15 m). Temperature dropped gradually during the study from 30° Celsius in April to 26° in July. Salinity remained stable at 36 ± 1 ppt (mean ± SD; n = 45).

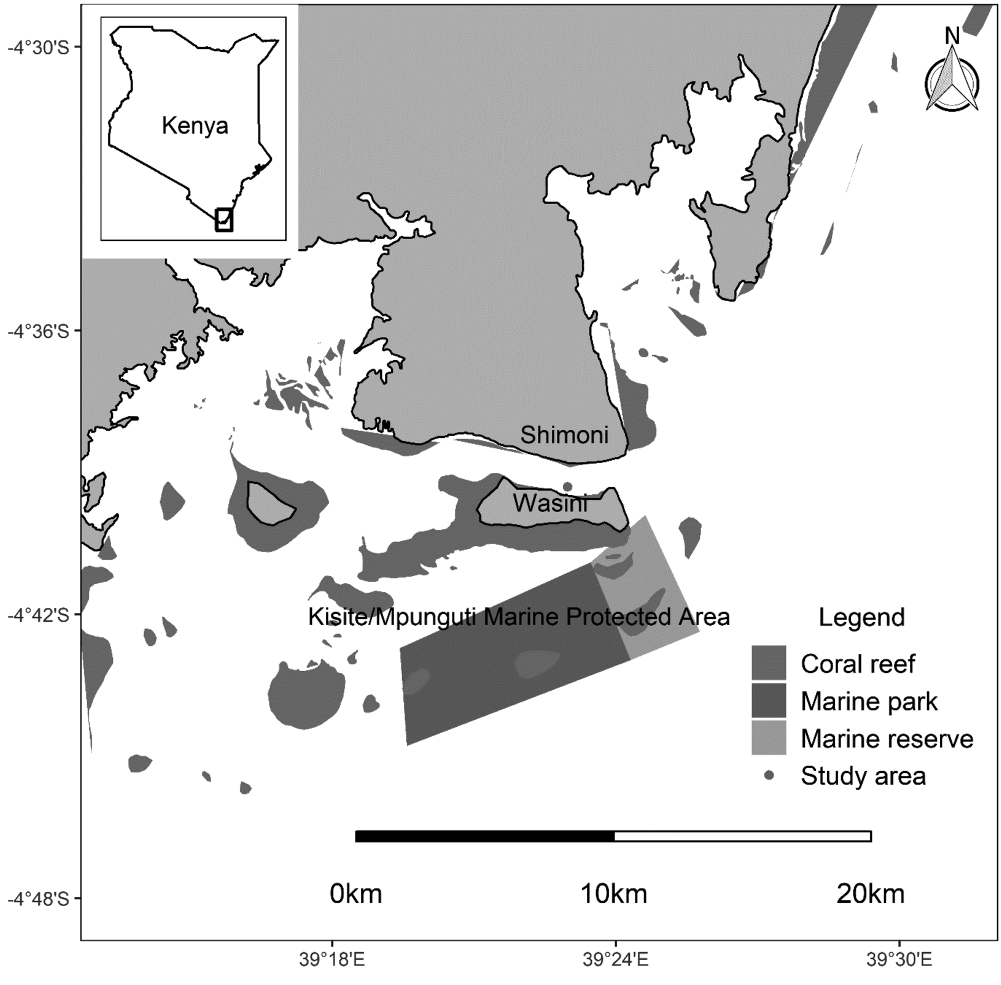

Figure 1 *Map of the study area (●) in the Wasini Channel, located between Shimoni village on the Kenyan mainland and Wasini Island. The study area (4°39'34.04"S, 39°22'56.18"E) consisted of a 100-meter stretch of patch reef*

Experimental design

Three treatments were designed: a caged, uncaged and cage-control coral nursery. The nursery design resembled a small version of the commonly-used 'coral tree' nursery (Nedimyer et al., 2011). Like most coral nursery designs, it hinders access to invertebrates, thereby excluding the impact of herbivorous and corallivorous invertebrates from this study. The caged treatment (Fig. 2a) consisted of four 26 cm PVC pipes (1.3 cm ⌀) forming a cross using two T-joints. A 0.5 x 0.5 x 0.25 m^3 cage made of galvanised monkey wire (1.3 x 1.3 cm^2 mesh size) was attached to the four PVC arms. Two opposite sides of the cage were hinged to enable coral growth measurements. A total of ten clonal *Acropora verweyi* Veron & Wallace, 1984 coral fragments were grown per nursery structure. *A. verweyi* was chosen for three reasons. Fragments were readily available around damaged colonies, the genus is frequently used in restoration projects worldwide (Edwards et al., 2010) and the species had experienced high predation pressure on its axial corallites in mid-water nurseries placed near (5 m) the natural reef of Wasini Island (Knoester pers. obs.). Naturally broken fragments of *A. verweyi* were collected at a patch reef at 4 meters depth (4°39'19.5"S, 39°22'01.7"E) and transported to the study location in seawater bins during a 5-minute boat ride. At the study location, healthy parts of the coral were pruned into linear, thumb-sized fragments of 4.0 ± 0.4 cm (mean ± SD; n = 450) using heavy-duty wire cutters while on SCUBA and hung randomly into fishing-line loops with slipknots. A 1.5-l PET bottle was used as subsurface buoy and a 0.5 m nylon anchor line attached the PVC cross to a 10-kg concrete sinker. The caged treatment excluded access for all fish larger than 12 cm and smaller fish were assumed to exert negligible herbivory and corallivory (cf. Carpenter 1986, Ceccarelli et al. 2005, Fox & Bellwood 2007). The uncaged treatment (Fig. 2b) provided unrestricted access to all fish. Differences in coral survival and growth between the caged and uncaged nursery structures were used to determine whether the fish community had a net positive or net negative impact on coral in mariculture. The cage-control treatment (Fig. 2c) was incorporated to check if any differences in coral survival and growth might be caused by the physical presence of the cage itself. This treatment was analogous to the caged design, but instead of hinged openings it had two sides of the cage completely removed to allow roving fish access to the coral fragments.

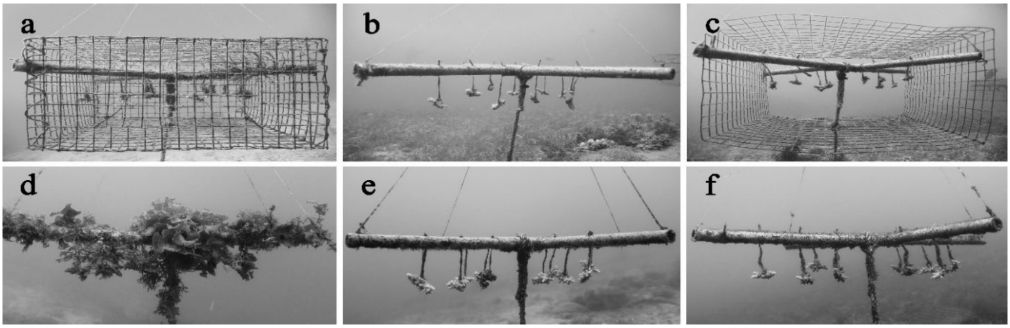

Figure 2 *The three treatment designs deployed in the Wasini Channel (Kenya) at the start and end of the experiment. Top row shows coral nursery structures one week after deployment [**(a)** caged treatment, **(b)** uncaged treatment, **(c)** cage-control treatment] and bottom rows depicts them at the end of the 100-day study to show the development of fouling assemblages [**(d)** caged treatment, **(e)** uncaged treatment, **(f)** cage-control treatment]. The cage and partial cage were removed just before taking the end photographs*

Fifteen replicates for each of the three treatments were deployed on the 8th of April 2016, totalling to 45 structures and 450 coral fragments. To reduce spatial confounding, a homogenous reef stretch of 100 m consisting of 10 coral patches was selected and treatments were assigned a position randomly. The coral patches were between 20 and 30 meters in diameter and between 3 and 6 treatments were placed around each coral patch. All treatments were placed near (i.e. within 1 m) of a coral patch to encourage the interest of reef-bound fish (Frias-Torres and Van de Geer, 2015). Given the narrow depth range in which coral patches naturally occur in the study area, the structures were consequently placed within a narrow depth range of 3.1 ± 0.7 m (mean ± SD; n = 45). Individual structures were separated by at least 2 m. Cages and partial cages were cleaned at least weekly to limit cage artefacts such as shading and water flow reduction due to fouling. The experiment lasted for 100 d.

Measurements and analysis

To test our hypothesis, coral performance (growth and survival) was measured and compared between the three treatments. To link patterns found in coral performance to the activity of grazers, fouling, herbivory and corallivory were also quantified on all three treatments. To characterize the local fish community and thus facilitate comparisons with other study areas, the fish community structure and fish abundance were determined.

Ecological volume (EV) of all coral fragments was determined roughly monthly. EV is defined as the total volume occupied by a coral, including the volume of water between its branches (Shafir et al., 2006b; Levy et al., 2010; Mbije et al., 2010). This volume was approximated by simplifying the form of the whole coral fragment to a cylinder: $EV = \pi \times r^2 \times l$ in cm^3. The increase in EV over the study period was assumed to reflect an exponential function: $EV_t = EV_{t-1} \times e^{SGR \times (t-(t-1))}$, with t in days and SGR being the Specific Growth Rate in d^{-1} (Osinga et al., 2011). SGR was calculated using:

$$SGR = {}^{\ln \frac{EV_t}{EV_{t-1}}} \Big/ {}_{t-(t-1)}$$

Percentage colony survival was estimated approximately monthly for each fragment. Completely healthy fragments were used to start the experiment (100% survival). Coral predation was quantified by identifying all new bite marks approximately monthly and estimating the EV of each removed part by comparing pictures taken during the current and previous measurement.

For each structure, the means for SGR, survival and bite marks were taken of the ten coral fragments and statistical analyses were thereupon carried out with the 45 nursery structures as independent observations. All statistical tests were performed using SPSS version 20. SGR, survival and bite marks were each analysed by a two-way mixed ANOVA with treatment as between-subjects factor (caged, uncaged and cage-control) and time as within-subjects factor (month 1, 2 and 3). Results were further analysed on main effects as none of the interactions between time and treatment were significant. ANOVAs were followed by a Tukey's post hoc.

One aberrant caged treatment was left out of the growth comparison because of strikingly low values (studentized residual values of -5.32 for SGR). This resulted in a sample size of 14 for all three treatments for growth, as an uncaged and cage-control structure were lost through local fishing activity. No other outliers were encountered based on studentized residual values. Approximate normality of data was evaluated by Q-Q plots and transformations were made on survival (arcsine) and bite mark (square root) data to meet this assumption. Further assumptions were met, as confirmed by Levene's test of homogeneity of variance, Box' M test for homogeneity of covariance and Mauchly's test of sphericity.

At the end of the 100-day experiment, fouling was collected from the PVC pipes, monofilament loops and coral fragments. Collected fouling was categorized in the following functional groups: macroalgae, crustose coralline algae (CCA), epilithic algae matrix (EAM) and molluscs. Macroalgae are here defined as large (> 1 cm) and fleshy algae. The EAM is defined as the assemblage of microalgae, filamentous algal turfs, juvenile stages of macroalgae and detrital material, all < 1 cm (sensu Marshell & Mumby 2012). Fouling was sun-dried and weighed on an analytical balance (Sartorius BA 310P). Dry weight was standardized (g m^{-2}) by dividing through the surface area of the nursery structures (0.16 m^2).

A one-way MANOVA with macroalgae, molluscs, CCA, EAM and total fouling as dependent variables was performed with treatments as factor. Data were root-transformed to meet the assumption of normality. Transformed data conformed to the assumptions of univariate outliers (test: Mahalanobis distance), multivariate outliers (studentized residual values), multicollinearity (Pearson correlation) and linearity (scatter plots). The assumptions of homogeneity of covariance (Box' M test) and variance (Levene's test) were not met, thus Pillai's Trace value and a Games-Howell post hoc were used to interpret results. Post hoc test results for each fouling category were interpreted using a Bonferroni adjusted α level of 0.01.

Remote underwater video (RUV) observations were made to identify fish species and quantify their consumption of fouling and predation on coral. At 2 m distance from a nursery structure, divers placed a Canon 600D DSLR camera in a Neewer 40M case on a weighted (10 kg) König tripod (KN-TRIPOD40N). Using the free firmware add-on Magic Lantern, the camera was programmed to take nine 5 min recordings with 10 min intervals. Recordings initiated between 1000 h and 1400 h, to coincide with the peak in foraging activity of most roving herbivorous fish (Hoey and Bellwood, 2009). All structures were first recorded at least once, thereafter additional RUVs were randomly made at the uncaged and cage-control treatments.

For analysis, RUV data was averaged per structure. For all 82 RUVs, the full 45 min of each recording was analysed (62 h of video) by identifying fish species, their size (5-cm size classes) and summing their number of bites directed at fouling organisms (herbivory) and coral fragments (corallivory). As bite size is assumed to scale to fish body mass, number of bites were transformed to mass-scaled bites (bites g) to estimate the impact of feeding (Mantyka and Bellwood, 2007). The weight of each fish was estimated using the length-weight relationship $W = a\ x\ L^b$, with weight (W) in grams, L as total length in cm (mid-point of respective size class) and a and b being estimations for each fish species by least-squares regression available in literature (Kulbicki et al., 2005). These mass-scaled bites were transformed to rates of herbivory and corallivory (bites g min^{-1}) by dividing the mass-scaled bites by the duration of the RUV (45 min). A one-way MANOVA on herbivory and corallivory rates was performed to compare between treatments. Data was square-root transformed to meet the assumption of normality. Further assumptions were met, except for homogeneity of variance and covariance. Hence, the results were interpreted using Pillai's Trace value and Games-Howell post hoc tests.

Fish abundance and composition were quantified by stationary underwater census (Bohnsack and Bannerot, 1986). This method identifies and lists all fish species that enter an imaginary cylinder (7.5 m radius) around a stationary diver for exactly 5 min. After these initial 5 min, the numbers of fish inside the cylinder are counted for all listed species. Time for these surveys averaged at 10 ± 2 min (mean ± SD; n = 51). Surveys were performed with randomly chosen nursery structures (independent of treatment) as mid-points for the surveys. All surveys commenced between 1000 h and 1400 h. The 51 performed surveys were averaged to one value for the overall study location and fish numbers were transformed to density (fish ha^{-1}) by extrapolating the mean number of fish from the survey area to hectare.

Results

Coral performance

All data are presented as mean ± SE, unless stated otherwise. SGR of the coral fragments (Fig. 3A) differed significantly between treatments (two-way mixed ANOVA; $F_{2,\,39} = 18.20$, $p < 0.001$) and over time ($F_{2,\,78} = 34.07$, $p < 0.001$), but no significant interaction was found (Fig. A1). SGR in the caged nursery structure (0.0047 ± 0.0010 d^{-1}) was significantly lower than in both the uncaged (0.0078 ± 0.0010 d^{-1}) and cage-control (0.0099 ± 0.0010 d^{-1}) nursery structures (Tukey; $p = 0.003$ and $p < 0.001$, respectively). The latter two treatments did not differ significantly. Survival of coral fragments differed significantly between the treatments (two-way mixed ANOVA; $F_{2,\,40} = 17.96$, $p < 0.001$). Average survival in caged nursery structures (89 ± 3%) was significantly lower (Tukey; $p < 0.001$) than in both the uncaged (98 ± 2%) and cage-control (99 ± 1%); no significant difference was found between the latter two treatments (Fig. 3B). Over the course of the study, survival significantly declined each month ($F_{2,\,80} = 57.74$, $p < 0.001$), but no significant interaction was found between treatment and time.

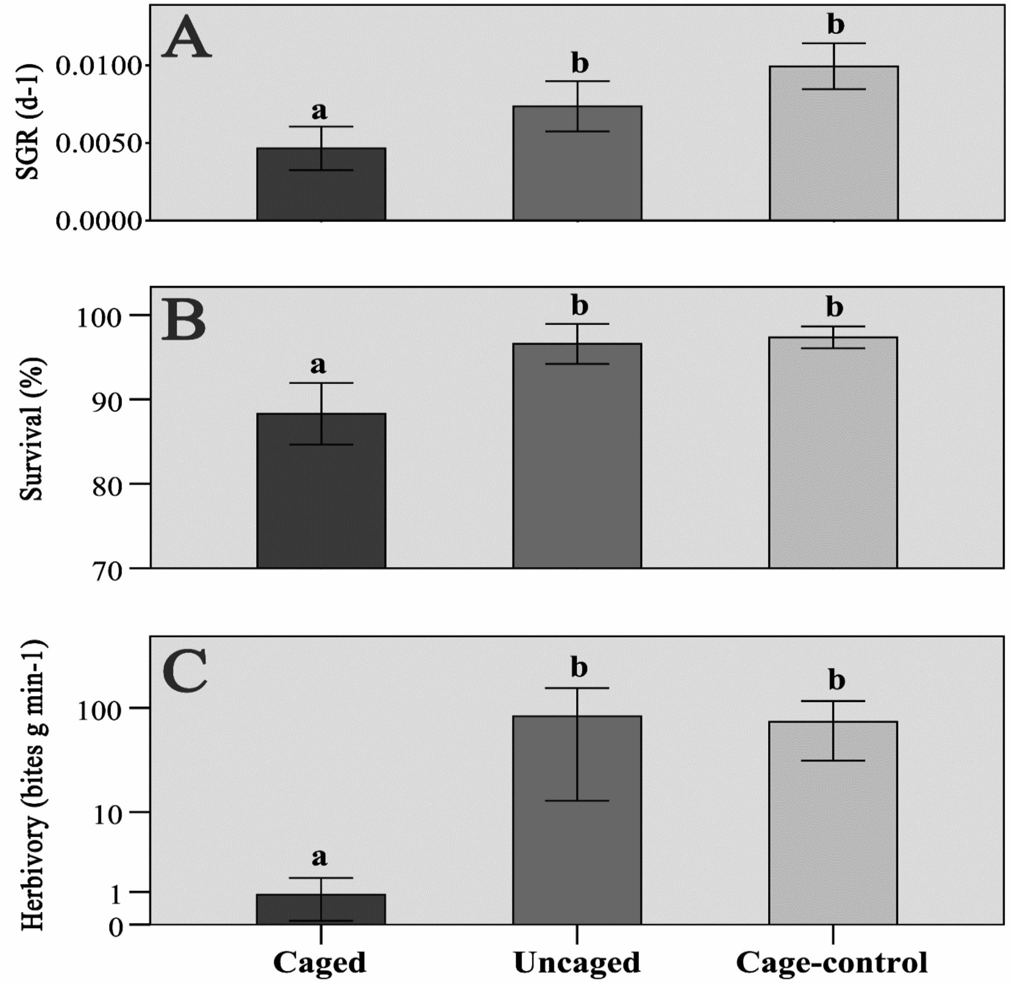

Figure 3 *Coral growth, survival and herbivory at caged, uncaged and cage-control nursery structures.* ***(A)*** *Average specific growth rate (SGR) of* Acropora verweyi *during the 100-day experiment (n = 14 – 15).* ***(B)*** *Average survival (in percentage) of* A. verweyi *fragments at the end of the 100-day study (n = 14 – 15).* ***(C)*** *Average rates of herbivory by fish (in mass-scaled bites per min) as determined by remote underwater video observations in the caged (n = 19), uncaged (n = 31) and cage-control (n = 32) treatments. Bars represent means ± 2 SE. Differing lower case letters note a significant difference (p < 0.05)*

Fouling and herbivory

Development of fouling showed profound treatment effects (Fig. 2d-f and Fig. 4). The following categories of fouling did differ significantly between the treatments: molluscs (MANOVA; $F_{2,36} = 24.23$, $p < 0.001$), macroalgae ($F_{2,36} = 56.99$, $p < 0.001$) and CCA ($F_{2,36} = 6.03$, $p < 0.001$). Also, the total sum of fouling differed significantly between treatments ($F_{2,36} = 71.09$, $p < 0.001$). At 484 ± 43 g m^{-2}, total fouling density was significantly higher (Games-Howell; $p < 0.001$) in the caged treatment than in both the uncaged (61 ± 15 g m^{-2}) and cage-control (78 ± 17 g m^{-2}), the latter two treatments not being different between each other. Fouling by molluscs was dominated by mussels (Family: Mytilidae) and was significantly different between all three treatments ($p < 0.01$), with highest densities in the caged treatment (224 ± 34 g m-2), followed by the cage-control (25 ± 11 g m-2) and then by the uncaged structures (10 ± 7 g m-2) (Fig. 4). Macroalgal density was more than 100-fold higher in the caged treatment (130 ± 21 g m^{-2}; $p < 0.001$) than in the uncaged (1 ± 1 g m^{-2}) and cage-control (1 ± 2 g m^{-2}). Dominant macroalgae were *Padina sp*., *Dictyota sp*. and unidentified red algae (division Rhodophyta). No significant difference in macroalgal density was found between the uncaged and cage-control treatment. CCA was significantly lower ($p < 0.05$) in the caged treatment (2 ± 2 g m^{-2}) compared to both the uncaged (14 ± 5 g m^{-2}) and cage-control (10 ± 5 g m^{-2}), which were not significantly different (Fig. 4). EAM (pooled mean = 35 ± 9 g m^{-2}) did not differ significantly between treatments.

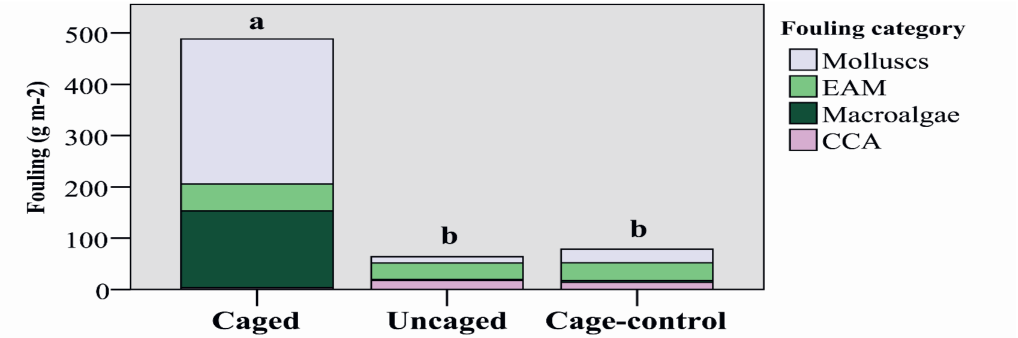

Figure 4 *Mean fouling density (g m^{-2}) of molluscs (grey), epilithic algal matrix (EAM; green), macroalgae (dark green) and crustose coralline algae (CCA; pink) in the caged, uncaged and cage-control treatments (n = 12 - 14) at the end of the 100-day experiment. Differing lower case letters note a significant difference ($p < 0.05$) between the sum of all fouling categories. Fouling density of molluscs differed significantly between the three treatments; EAM did not differ significantly between treatments; macroalgae density was significantly higher in the caged treatment compared to both the uncaged and cage-control; CCA density was significantly lower in the caged treatment compared to both the uncaged and cage-control treatment*

Overall herbivory rates (Fig. 3C) were significantly different between treatments (MANOVA; $F_{2,40} = 11.50$, $p < 0.001$), with rates being substantially lower in the caged treatment (0 ± 1 bites g min^{-1}) compared to the other two treatments (Games-Howell; $p < 0.01$). The uncaged (83 ± 35 bites g min^{-1}) and cage-control (74 ± 21 bites g min^{-1}) treatments did not differ significantly in grazing pressure. Rates of herbivory for the eight most dominant grazers are presented in Fig. 5A. Grazing on the nursery structures was strongly dominated by a single species of surgeonfish, *Ctenochaetus striatus*, which took a sum of 205,096 mass-scaled bites (77% of total standardized bites). Bites of *C. striatus* could clearly be seen after the species visited the experimental structures, indicating removal and likely consumption of EAM by this species. Species composition of the most common herbivorous fish (Fig. 5B) corresponded partly with their contribution to grazing (Fig. 5A). The most common herbivorous fish was the small, territorial damselfish *Plectroglyphidodon lacrymatus* (298 fish ha^{-1}), followed by the dominant grazer *C. striatus* (155 fish ha^{-1}). The third most abundant was the surgeonfish *Naso brevirostris* (140 fish ha^{-1}), which was not recorded grazing.

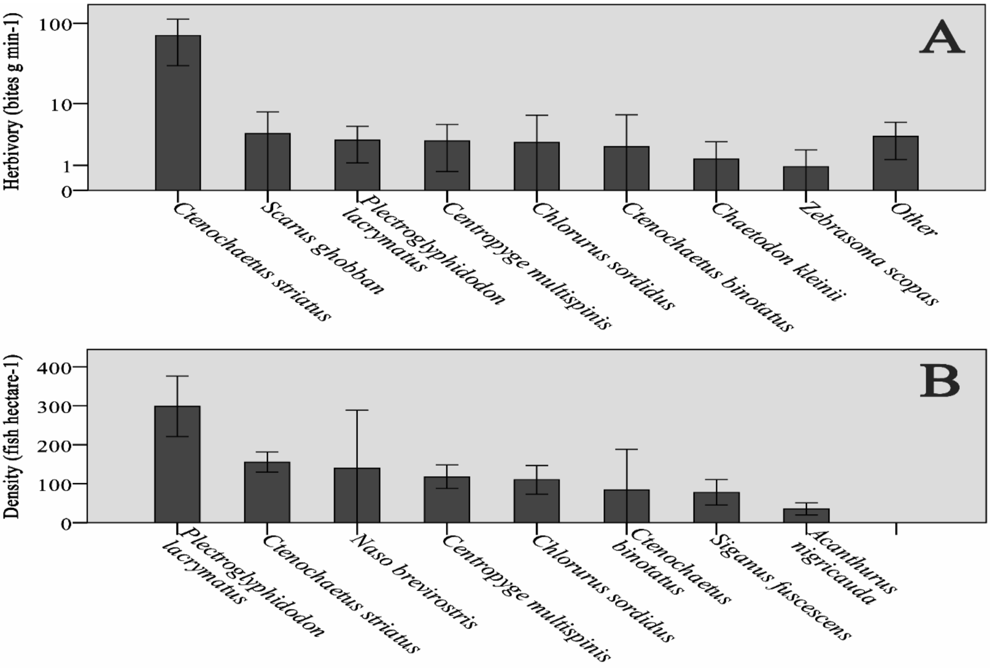

Figure 5 *Herbivory and fish density at the coral nursery structures.* ***(A)*** *Rates of herbivory (in mass-scaled bites per min) for the eight main grazing fish as determined by remote underwater video observations (n = 82). Bites of the less often occurring 24 species is summed under 'Other'.* ***(B)*** *Mean density (fish per hectare) of the eight most abundant roving herbivorous fish as determined by stationary underwater census (n = 51). Summed density of the remaining 132 fish has been omitted. Bars represent means ± 2 SE*

Corallivory

A total of 1450 mass-scaled bites on coral fragments were recorded. There were no bite marks found on coral fragments inside cages. There was neither a significant difference in mean EV of bite marks between the uncaged (0.017 ± 0.006 cm^3) and cage-control (0.023 ± 0.007 cm^3), nor between the first, second and third month. Every month, bite marks were found on average on 10% of the coral fragments. Most of bites targeted axial corallites and growing tips of the fragments. A significant difference in corallivory was found among the treatments (MANOVA; $F_{2,\,40} = 5.35$, $p = 0.009$). The uncaged structures (0.32 ± 0.5 bites g min^{-1}) were subjected to significantly higher (Games-Howell; $p = 0.021$) rates of corallivory than the caged treatment (0 ± 0.16 bites g min^{-1}) and the uncaged treatment did not differ from the cage-control (0.09 ± 0.36 bites g min^{-1}). The eight most dominant corallivorous fish (together responsible for 90% of the 1450 mass-scaled bites) were: *Chlorurus sordidus* (24%), *C. striatus* (23%), *P. lacrymatus* (14%), *Chaetodon melannotus* (9%), *Chaetodon trifasciatus* (7%), *Gomphosus caeruleus* (5%), *Thalassoma lunare* (4%), *Chaetodon kleinii* (4%).

Discussion

The aim of this study was to determine the net impact of the local, reef-bound fish community at Wasini Island on coral in mariculture. We hypothesized that coral survival and growth would be higher in uncaged nursery structures, since the benefits of the fish community through fouling control by herbivorous fish was expected to outweigh the negative impacts of corallivorous fish. Here, first the methodology of the study is discussed. Following this evaluation of the experimental set-up, the role of herbivorous and corallivorous fish at Wasini Island on coral in mariculture will be discussed. The discussion concludes with a recommendation on the placement of nurseries at Wasini Island, general management recommendations and future perspectives for coral mariculture projects in other areas of the world.

Methodological considerations

The coral tree nursery design chosen in this study excluded access of grazing invertebrates. Though inclusion of invertebrates would make the study more complete, it is believed that such nursery designs are less advantageous, because both algal proliferation and corallivory have been reported to be much higher in such designs (Edwards et al., 2010). As our goal is to further increase the efficiency of nurseries, the focus on the preferable, invertebrate-excluding coral trees is justified. The uncaged and cage-control treatments generated equivalent results on nearly all aspects, strongly indicating that secondary cage artefacts have not confounded the results of this study, which, according to Steele (1996), is a potential pitfall for cage exclusion studies. The large mesh size and weekly cleaning apparently minimised alterations in light and current, resulting in equal coral growth, coral survival and the development of a similar fouling community between the uncaged and cage-control nursery structures, except for fouling by molluscs. The intermediate effect found for molluscs was likely caused by the partial cage partially precluding the bulky, mollusc-devouring triggerfish *Balistoides viridescens* (Frias-Torres and Van de Geer, 2015). Deterrence of corallivorous fish by partial cages, as found in some studies (e.g. Miller & Hay 1998, Baria et al. 2010), was not detected here and bite marks were equally distributed between uncaged and cage-control treatments. The spatially complex reef has likely prevented the use of partial cages as additional refuge (Carpenter, 1986) and rates of herbivory were therefore equal between uncaged and cage-control structures. However, it was observed during cleaning dives that the large mesh size did allow access to small (<12 cm total length) and slender fish such as juvenile *Scarus ghobban* and *Thalassoma lunare* inside caged treatments, but this resulted only in insignificant amounts of herbivory given the seemingly unconstrained growth of macroalgae inside these caged treatments Thus, the design of the cages has proven successful in practically excluding herbivory and corallivory, without generating secondary cage artefacts.

The combination of RUV and stationary underwater census have ascertained what fish were the dominant daytime grazers of the nursery structures and that any differences found in the caged treatment are principally due to the exclusion of fish. Though herbivory is captured well, 62 h of RUV revealed not a single fish consuming coral skeleton. Nonetheless, bite marks on the coral fragments were found each month. The identity of the fish species responsible for these bite marks thus remains unknown. For some species, such as the obligate corallivores

Chaetodon melannotus and *Chaetodon trifasciatus*, the bites recorded on RUV likely reflect actual cases of tissue corallivory, leaving the coral skeleton intact: they are known to predate on individual coral polyps (Cole et al., 2008). For other herbivores and omnivores such as *Chlorurus sordidus, Ctenochaetus striatus* and *Plectroglyphidodon lacrymatus*, it is more likely that they targeted minute algae and other fouling growing on the coral. In conclusion, the recorded bite marks accurately quantify predation on coral skeleton, though the perpetrator remains unknown, and tissue predation is likely performed only by a subset of the 'corallivorous' species recorded on RUV.

Positive effects of herbivores

C. striatus, responsible for 77% of all mass-scaled bites*,* and other grazing fish forestalled the development of an abundant fouling community on the uncaged and cage-control nursery structures. Some authors have proposed that profuse increases in algal biomass, and an eventual shift from coral to algal dominance on reefs, could be a peculiarity of overfished Caribbean reefs only (Roff and Mumby, 2012). At the end of this 100-day study on the East African coast, however, macroalgal density was 100-fold higher in caged structures compared to uncaged structures and showed no sign of recession. After an initial bloom of EAM, Phaeophyta and Rhodophyta quickly took over and formed a climax community. Such profound increases in macroalgal biomass appear to be the common development in absence of fish, also outside the Caribbean (Rasher et al., 2012), and attest the importance of fish in controlling standing stock of algae by their continuous grazing, consuming up to 90% of the daily algal production (Carpenter, 1986). On the other hand, the continuous grazing by fish on the uncaged and cage-control nursery structures supported the formation of a CCA crust. These early-successional CCA keep the substrate free from macroscopic fouling and also enhance natural settlement of coral larvae (Belliveau and Paul, 2002). Thus, while the importance of herbivorous fish in structuring the benthic community and favouring CCA and Scleractinian coral dominance at natural reefs has long been established, now their potential role in controlling algal biomass on coral nursery structures has been clearly demonstrated as well.

SGR of coral fragments in the uncaged (0.0078 d^{-1}) and cage-control (0.0099 d^{-1}) structures were comparable to growth rates of branching coral found in previous (restoration) studies (e.g. Shafir et al. 2006, Levy et al. 2010, Osinga et al. 2011). Survival after 100 d was reputably high for the uncaged (98%) and cage-control fragments (99%). Considering the seemingly intense competition between coral and fouling in caged structures, with most fragments fully overgrown and barely visible (Fig. 2d), coral survival (89%) and growth (0.0047 d^{-1}) were still respectable in the caged treatment. Surprisingly, the decrease in coral survival and growth in the caged treatment were not accelerating over time compared to the other treatments, despite an ever-increasing quantity of fouling. Nevertheless, 9% higher survival and a 40% increase in SGR in the uncaged treatment indicate very meaningful advantages of growing coral near natural fish communities. In particular, the presence of macroalgae is likely to have a direct negative impact on coral. An earlier exclusion study on herbivory and corallivory on a natural reef found no net impact of the fish community on coral recruit survival, but did observe a shift from predation-induced mortality of uncaged recruits towards morality caused by competing turf algae for caged recruits (Penin et al., 2011). The observed decreases in survival and growth of caged coral in this study are most likely also directly attributable to competitive mechanisms of fouling organisms, such as overgrowth, shading and abrasion, in particular by macroalgae (Jompa and McCook, 2002; Box and Mumby, 2007). Though mollusc weight was also elevated in caged structures, their presence is unlikely to have been detrimental to the coral as their shells represent much of the weight, and the molluscs themselves occupied relatively small surface areas. In addition, mollusc density was more than twice as high in the cage-control compared to uncaged structures, but growth and survival did not differ between these two treatments. Our results support previous studies on natural reefs and show that favourable conditions for coral survival and growth, also on artificial structures, is largely due to grazing fish preventing macroalgae from outcompeting coral.

Negative effects of corallivores

Advantages for coral in the uncaged and cage-control treatments created by grazing herbivorous fish could have been reduced by direct predation on coral by corallivorous fish. One study reported that the negative effect of corallivores completely offset the positive effect of herbivores (Miller and Hay, 1998). In this present study, however, only 10% of coral fragments showed bites marks each month representing only very small absolute volumes of consumed coral. Nonetheless, the majority of bites were targeted at axial corallites and the removal of these growing tips is likely to retard coral growth (Lirman et al., 2010). Furthermore, predation has been shown to increase the susceptibility of coral to diseases (Sheridan et al., 2013). Though on an individual basis corallivory can have a grave impact on the survival and growth of a coral fragment, the rarity of such events has rendered its overall negative effect rather small, especially compared to the positive effects of herbivory by fish. Also, the arborescent growth form of the *Acropora* genus is known for its high regenerative capabilities (Hall, 1997) and this might have mitigated partly the negative impact of corallivory. The potentially increased corallivory on stressed fragments (Cole et al., 2008) was not seen in this study. Corallivory remained constant over the experimental period and was not higher in the initial month when corals may have been stressed due to handling or fragmentation. This study on *Acropora verweyi* maricultured near natural reefs shows some negative impact of corallivory on growth of coral fragments, but this is not offsetting the beneficial effects of herbivory, as reflected by the better growth and survival in the uncaged and cage-control nurseries. These results correspond well with studies that examined the merits of herbivory versus corallivory on the natural reef (Mumby, 2009). Interestingly, none of the fish captured on RUV targeting the coral fragments are known to be consumers of coral skeleton and are more likely to have been targeting coral tissue only. Future studies with longer RUV recordings or detailed in-field observations might reveal the identity of the skeleton-consuming fish.

Limited functional redundancy

The control of fouling through continuous grazing was dominated by a single species, although 18 roving herbivorous fish were censused. *C. striatus* kept the nursery structures clean by regularly grazing early successional stages of fouling (see also Marshell & Mumby 2012) and was solely accountable for 77% of all mass-scaled bites taken during the experiment. Such apparent limited functional redundancy at highly diverse reefs seems common and single-species dominance in herbivory has been encountered in various other studies, for example by

Siganus rivulatus (Fox and Bellwood 2007), *Platax pinnatus* (Bellwood et al., 2006) and *Naso unicornis* (Bellwood et al., 2003). Though fish from the Acanthuridae family are recognized as important herbivores and detritivores, no preceding study could be found in which *C. striatus* is the dominant grazer. This is surprising, given the wide distribution and generally high abundance of *C. striatus* in the Indo-Pacific (Marshell and Mumby, 2012). *C. striatus* used to be considered a detritivore only consuming detritus without impacting algae, but new research by Marshell & Mumby (2012) has shown that *C. striatus* actually removes algae as well: a conclusion supported by this study. Other species frequently recorded on RUV are considered herbivores, such as *Centropyge sp.*, *Zebrasoma sp.* (Clements et al., 2017) and *Plectroglyphidodon sp.* (Jones et al., 2006), whereas *Scarus sp.* and *Chlorurus sp.* might only target microorganisms living in or on the EAM and macroalgae (Clements et al., 2017). Shifts in dominance among the common species between different areas remains inexplicable, though this variability is likely dependent on their relative abundance, the food availability, food palatability and seasonal variation (Hoey and Bellwood, 2009) and perhaps also on selective removal of certain herbivorous species by fishing. In the aforementioned studies, the dominant macroalgal grazers were, surprisingly, often not the numerically dominant herbivores. In this current study, however, the dominant grazer *C. striatus* was also the most abundant roving herbivore. For the studied location, this facilitates the selection of nursery sites, which can simply be based on the local species composition and abundance as determined by fish surveys. In short, despite the presence of a diverse assemblage of herbivorous fish, grazing was dominated by *C. striatus*, locally the most common roving herbivorous fish.

Conclusions

The vigour of unrestricted fouling organisms, their negative impact on coral growth and survival through competition, and the scarcity of corallivory justify the recommendation to place coral nursery structures near natural fish assemblages in the Wasini Channel. As hypothesised, the advantage of having biological fouling control by herbivorous fish is shown to outweigh the negative impacts of incidental corallivory on the survival and growth of *A. verweyi*. Coral that was easily accessible to the natural fish assemblage attained very high levels of survival and good coral growth without the need of human-assisted cleaning for a period of 100 d. Nonetheless, the balance between herbivory and corallivory will depend on the site-specific fish assemblage and can be difficult to predict due to a potential discrepancy between fish abundance and functional impact. Also, roving herbivorous and coralivorous fish might visit isolated nursery structures (Shafir et al., 2006a), thus it is possible that structures away from the natural reef receive some bio-assistance or suffer from predation as well. A deeper understanding between the abundance of herbivorous and corallivorous fish and their functional role will greatly enhance our capabilities to identify and use beneficial fish assemblages for mariculturing coral. The approach presented in this study, through monitoring and comparing small fish-exclusion nurseries to uncaged and cage-control nurseries on coral survival and growth, development of fouling, occurrence of bite marks and herbivory and corallivory, is recommended to be used at other reef restoration projects to evaluate the net impact of their local fish communities on coral mariculture. In addition, it is recommended that future research directly compares isolated nurseries with nurseries placed near natural reefs, to quantify the effects of isolation. Given the apparent limited functional redundancy of herbivorous fish found in this and previous studies, it is recommended to consider and protect functionally important key species in fisheries management. This study at the patch reefs of Wasini Island indicated that its fish assemblage favours coral survival and growth. Such free animal-assisted cleaning not only promotes coral survival and growth, but also reduces human cleaning time and thus project costs, ultimately benefitting the restoration of reefs.

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Ethical approval: No approval of research ethics committees was required for this observational study. Applicable international guidelines for monitoring on coral reefs were followed.

Supplementary material

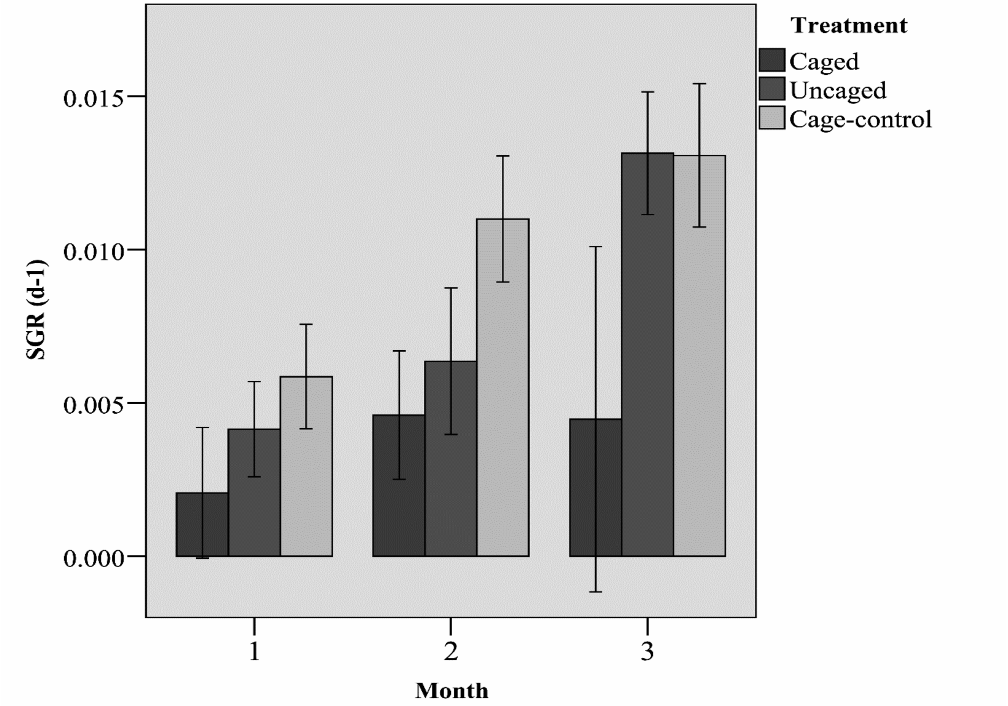

Figure A1 *Average specific growth rate (SGR) of* Acropora verweyi *for each month in the caged (dark red), uncaged (blue) and cage-control (light blue) treatments (n = 14 – 15). Bars represent means ± 2 SE. SGR differed significantly between the treatments (two-way mixed ANOVA, p < 0.001) and increased significantly over time (p < 0.001), but no significant interaction was found*

5

Biomass of key grazing herbivorous fish species is an important determinant of fouling control and coral growth in coral nurseries

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Abstract

Restoration is an emerging tool for coral reef conservation, yet despite small-scale successes there are concerns about high costs and ecological setbacks. Integration between reef ecology and restoration could help address such concerns. A prime example is the use of grazing herbivores to reduce coral nursery cleaning costs. However, the relation between herbivore communities and cleaning benefits remains unquantified. This study aimed to measure links between herbivorous fish communities, grazing intensity and coral nursery performance. Six reefs were selected in southern Kenya, equally divided across three levels of fisheries management (fished < reserve < no-take). Fish surveys determined herbivorous fish biomass and composition, and remote underwater videos recorded grazing intensity on coral nurseries. Accumulated fouling and coral growth were measured at the end of the 4-month study. Grazing intensity was sixfold lower and fouling density fourfold higher in the fished areas compared to protected zones. Higher fouling correlated strongly with lower coral growth: exponential growth constants in fished areas were respectively twice and three times as low compared to marine reserves and no-take zones. Across study sites grazing was dominated by bristletooth tangs (*Ctenochaetus* spp.), except where these were outcompeted by territorial damselfish. Thus, better coral nursery performance in protected areas can be partially linked to higher grazing intensity, which in turn is determined by both fish biomass and local species composition. We recommend protecting herbivorous fish species and placing coral nurseries in areas with high biomass of key grazers to improve coral nursery performance and reduce maintenance costs.

Key words: Coral gardening; *Ctenochaetus striatus;* Fisheries management; Marine protected area; Nursery cleaning; Reef restoration ecology

Introduction

Restoration is establishing itself as a supporting coral reef conservation tool (Rinkevich, 2019), complementing traditional measures and climate action to maintain coral reef ecosystem functions and services under present-day stressors (Anthony et al., 2017; Mcleod et al., 2019). The appropriate use of coral gardening, a commonly-used restoration technique where corals are first grown in nurseries before being outplanted on the reef (Rinkevich, 1995, 2005), has been outlined in several science-based guidelines (Edwards et al., 2010; Johnson et al., 2010; Shaver et al., 2020a). This two-step coral gardening technique has realized substantial increases in hard coral cover locally (Hein et al., 2020a) and the adaptability of this low-tech concept allows for easy implementation in emergent regions such as East Africa (Mbije et al., 2010, 2013). However, the majority of coral reef restoration projects around the world are still small and costly, featuring a median restored area of just 100 m^2 (Boström-Einarsson et al., 2020) at a median project cost of roughly 400,000 US$ ha^{-1} (Bayraktarov et al., 2019). If reef restoration aspires to have an impact on socio-ecological meaningful scales, further improvements in the cost-effectiveness and scalability of techniques are imperative.

A considerable cost for numerous reef restoration projects is the maintenance of coral nurseries. Bio-fouling such as macroalgae, tunicates and molluscs can settle onto nursery structures and reduce the performance of nursery-grown corals (e.g. Dehnert et al. 2022) due to shading, abrasion, overgrowth and allelopathy (McCook et al., 2001). To reduce these competitive interactions, frequent and time-consuming cleaning of nurseries is common practice (Precht, 2006; Edwards et al., 2010; Johnson et al., 2010; Ferse et al., 2021). Fortunately, a closer integration between reef restoration and reef ecology is afoot (Ladd et al., 2018). The importance of herbivores on natural reefs has been established long ago (Carpenter, 1986; Hay, 1997), but only since more recently has herbivory gained appreciation in the process of reef restoration as well. For example, temporal (Frias-Torres et al., 2015) or permanent (Knoester et al., 2019) placement of coral nurseries nearby fish communities of natural reefs or the co-culturing of grazing gastropods (Toh et al., 2013) have all demonstrated the benefits of free bio-control of fouling. Still, only just a fraction of restoration publications examine such facilitative opportunities (Abelson et al., 2020; Ladd and Shantz, 2020), despite the great potential such ecological integration could have to improve the effectiveness and reduce the costs of reef restoration efforts (Ladd et al., 2018, 2019).

The shortage of ecological knowledge could stall restoration progress and, even though awareness on the importance of herbivory is growing (Rinkevich, 2019; Seraphim et al., 2020), there are no tangible guidelines. For example, the positive interactions between herbivorous fish and mid-water coral nurseries have been demonstrated (Frias-Torres and Van de Geer, 2015; Knoester et al., 2019), yet specific site criteria such as a minimum recommended fish biomass or presence of key species for effective herbivory are lacking. To establish such guidelines, the quantification of site-specific herbivorous fish communities and their effect on coral nursery performance are needed (Shaver and Silliman, 2017). This study aimed to determine the links between herbivorous fish communities, their grazing intensity and the performance of coral in mid-water nurseries. Herbivorous fish biomass and species composition were determined at six study sites in southern Kenya, two per level of fisheries management (fished < reserve < no-take). At each study site, remote underwater videos were used to record grazing intensity exerted on coral nurseries and accumulated fouling density and coral growth were also measured. We hypothesized that placing nurseries in areas with higher fish biomass would result in higher grazing intensity by a diverse assemblage of herbivorous species, less fouling and better coral performance. The identification and quantification of such ecological links can be used to develop a more ecologically-integrated and cost-effective reef restoration approach (Abelson et al., 2020; Boström-Einarsson et al., 2020).

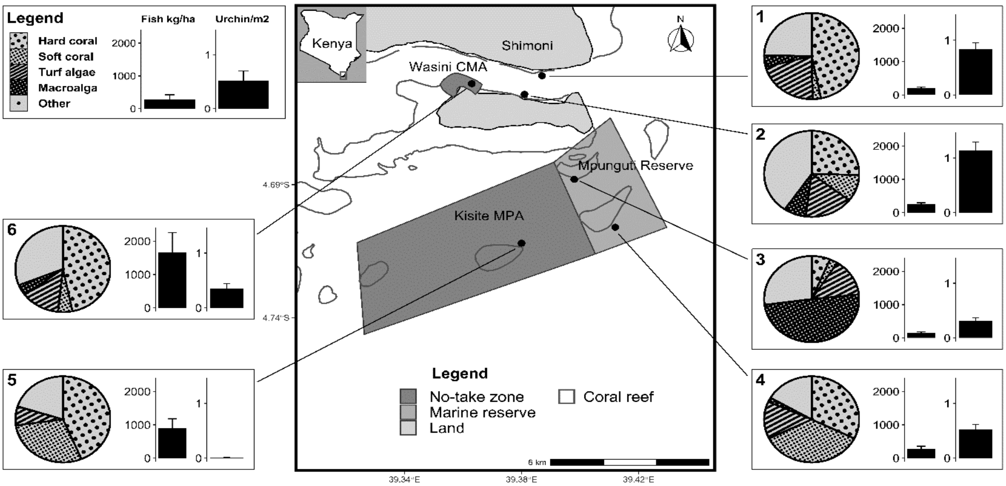

Figure 1 *Map of Kenya showing study area (insert) and detailed map showing the six study sites. Three different fisheries management zones can be identified: unrestricted fished zone (unshaded) including sites 1 (Firefly House Reef) & 2 (Pilli Pipa Restaurant), the Mpunguti Marine Reserve where traditional fishing is allowed (shaded orange) encompassing sites 3 (Lower Mpunguti) & 4 (Dolphin Point) and no-take zones (shaded red) covering sites 5 (Kisite Marine National Park) & 6 (Wasini Community Managed Area). Boxes shows additional information for each study site on benthic cover, total fish biomass and sea urchin density. Bars represent means ± standard error (n = 10 for benthic surveys and n = 11 - 15 for fish surveys). Figure reused from Knoester et al. (2023)*

Methods

Study sites

The six study sites were located around Wasini Island in southern Kenya (Fig. 1) and were equally distributed over three levels of fisheries management. Study sites 1 and 2 were located in a fished zone, where artisanal fishing was both intense and unselective. Sites 3 and 4 were located in the Mpunguti Marine Reserve (11 km^2 established in 1973), where only the traditional fishing methods of basket traps and handline were officially allowed by the Kenyan Wildlife Service. The remaining two sites were situated inside well-enforced no-take zones: study site 5 in Kisite Marine National Park (28 km^2 established in 1973 and enforced by the Kenya Wildlife Service) and study site 6 in the Wasini Community Managed Area (0.31 km^2 established in 2008 and enforced locally by the Wasini Beach Management Unit). Study sites 1, 2 and 6 were situated in a sea strait between Wasini Island and the Kenyan mainland and experience relatively turbid water conditions (average visibility of ~7 meters) and therefore exhibit a shallow (up to 8 meters depth below Mean Lower Low Water) and patchy reef development. Sites 3, 4 and 5 were situated around small coral islands further offshore that featured an average visibility of ~15 meters and fringing reef development up to around 16 meters depth (see Table S1 in Appendix A for details). Tidal differences across all study sites were significant, reaching over four meters during spring tide.

Experimental setup

From November 2017 to March 2018, largely coinciding with the dry northeast monsoon, eight replicate coral nurseries were placed and monitored at each study site. This study looked at the first four months of coral performance in nurseries, as the initial small fragments are deemed most responsive to the effects of fouling and grazing by fish. The structures (Fig. 2) closely resembled the design by Knoester et al. (2019): a plastic (PPR) cross holding 8 coral fragments in monofilament loops, kept afloat 1 meter from the sea bottom by a 2-l glass bottle and anchored by a 10-kg concrete sinker. This design is adapted from the commonly-used and effective coral tree nursery design (Nedimyer et al., 2011) and prevents access by bottom-dwelling herbivorous and corallivorous invertebrates, which were therefore not relevant for this study. Coral nurseries were placed on sand or rubble approximately 1 meter from either a coral patch or a fringing reef. Depth varied per study site and depended on the extent of reef slope development and light availability: nursery placement was shallower in the turbid sea strait compared to the offshore islands (Table S1) so that irradiance levels were estimated to be roughly similar among study sites. Replicate nurseries were separated 2 meters from each other and placed parallel to relatively homogenous stretches of reef. Following Knoester et al. (2019), all nurseries were filled with healthy, thumb-sized (range: 3.9 – 4.5 cm) clonal coral fragments of *Acropora verweyi*, which were harvested from a large coral nursery at study site 2. Transportation to other study sites was realized in shaded seawater bins during boat rides of 5 – 50 minutes during which sea water was replaced multiple times. No visible signs of stress

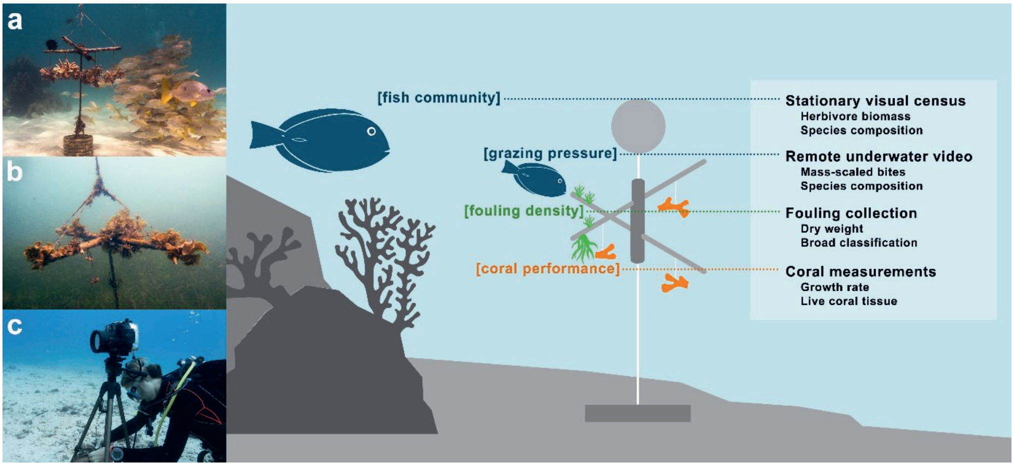

Figure 2 *Schematic representation of the experimental setup with inset photos showing* ***(a)*** *coral nursery structure,* ***(b)*** *a close-up of a nursery structure with some fouling and* ***(c)*** *a diver preparing a remote underwater video recording. Artwork assisted by: Vrijlansier, photo sources a-c: EGK*

were noticed on the coral fragments (e.g. no excess mucus production or bleaching) and in the first month after deployment no fragment mortality was observed.

Measurements

The composition and abundance of all diurnally-active, non-cryptic fishes were determined by a stationary underwater census with a 7.5-m radius and 5-min initial time slot, following Bohnsack and Bannerot (1986). Fork length was estimated for each fish in classes of 5 cm for fishes smaller than 20 cm and in 10-cm size classes thereafter. Estimation of fork lengths was practiced before commencing the surveys. Per study site, between 11 – 15 non-overlapping, replicate surveys were performed around the coral nurseries, covering a stretch of roughly 200 m per site. Fish abundance was transformed to biomass using the midpoint of each size class and published length-weight relationships of species (Froese and Pauly, 2015). Herbivorous fish biomass was further subdivided into the following functional groups: grazers (targeting turf algae < 1 cm), browsers (targeting macroalgae > 1 cm), scrapers, excavators and territorial damselfish, based on reported species' functional traits following Green and Bellwood (2009).

Remote underwater video (RUV) was used to identify key grazers and their grazing intensity with minimal diver disturbance. A Canon 600D DSLR camera with Neewer 40M case was positioned approximately 2 meters from a coral nursery on a weighted tripod (Fig. 2c). The camera started recording after a 12-min delay and took five 10-min recordings with 12-min intervals, thus the 2-hr deployment resulted in a total recording time of 50 min per replicate video. After installing the camera, divers would either leave the water or move at least 50 m away. Recording usually took place between 10:00 h and 14:00 h, coinciding with the peak in foraging activity of most roving herbivorous fishes (Hoey and Bellwood, 2009). Each coral nursery was recorded once, resulting in 8 replicate recordings per study site. All RUV recordings were viewed and each bite targeting the PPR frame, monofilament loops or coral fragments was counted and the fish species noted. In addition, fish's fork length was estimated (using the nursery structure as size reference), transformed to weight and multiplied by the number of bites taken to calculate mass-scaled bites (ms-bites), following (Hoey and Bellwood, 2009). Sums of ms-bites were standardized per hour to correct for slight variations in RUV recording length. Grazing intensity on nurseries is thus expressed as ms-bites in kg h^{-1}.

At the end of the 4-month experiment, fouling was collected from the PPR pipes, monofilament loops and coral fragments. Collected fouling was categorized in the following broad functional groups: turf algae (< 1 cm), macroalgae (> 1 cm), crustose coralline algae (CCA), shelled animals (including both molluscs and barnacles) or others (consisting mainly of tunicates and sponges). Fouling was sundried and dry weight was standardized to fouling density by dividing through the nursery surface area (0.16 m^2). Coral growth measurements were taken right at the start and end of the experiment. Using scaled photographs, the ecological volume (Shafir et al., 2006b) was determined using ImageJ and the live coral tissue was quantified visually as a percentage. The specific growth rate of healthy fragments (live coral tissue >= 80%) was determined using the same formulas as Knoester et al. (2019) and references therein.

Analyses

All analyses were performed in *R* (R Core Team, 2020) and data presented as means ± standard error. A generalized linear model with Gamma distribution and log-link from the *stats* package (R Core Team, 2020) was used to compare average herbivorous fish biomass and grazing intensity between study sites. The distribution of functional groups and genera is presented visually. Simple linear models were fit using the *nlme* package (DebRoy, 2006) to determine the effect of study site on each fouling group separately and the log10-transformed sum of fouling. A linear mixed-effects model was fit using the *nlme* package to determine the effect of study site on the specific growth rate of coral fragments. Nursery structure was included here as a random factor to account for the non-independence of multiple coral fragments in the same nursery. To determine the effect of study site on percentage live coral tissue, a beta regression model with logit link was used using the *glmmTMB* package (Brooks et al., 2017), as this accounts for the proportional nature of the live coral tissue data (Douma and Weedon, 2019). All model assumptions were validated by visual inspection of residual plots, using *DHARMa* diagnostic plots in case of generalized linear models (Hartig, 2021). Wald Chi-Squared Tests from the *car* package (Fox and Weisberg, 2018) were used to determine the significance of the fixed factor study site for all models. Pairwise comparisons with Tukey adjustments were made with the *emmeans* package (Lenth, 2020). Lastly, Pearson correlation analyses were performed to explore potential links between herbivorous fish biomass, grazing intensity, fouling development and coral performance. As nursery depth varied across study sites, nursery depth was correlated against all above variables to check for any effects of nursery depth on these key processes (Table S2).

Results

The total biomass of herbivorous fishes differed significantly between study sites ($X^2 = 34.355$, $df = 5$, $p < .001$) and mostly increased with stricter levels of fisheries management (Fig. 3). Herbivorous fish biomass was low in the fished zone at site 1 (58 ± 11 kg ha^{-1}) and site 2 (34 ± 8 kg ha^{-1}), low to moderate in the marine reserve at site 3 (41 ± 16 kg ha^{-1}) and site 4 (162 ± 70 kg ha^{-1}) and clearly higher in the no-take zones at site 5 (248 ± 105 kg ha^{-1}) and site 6 (391 ± 154 kg ha^{-1}). Appreciable numbers of browsers, scrapers and excavators were only observed in the protected areas, whereas grazers and damselfishes were relatively more abundant in fished zones (Fig. 3). Overall, grazers (predominantly represented by *Acanthurus* and *Ctenochaetus*) were common across study sites, comprising two-thirds of the herbivorous fish biomass at site 2, one-third at sites 3 – 5 and around a fifth at sites 1 and 6.

Grazing intensity on nursery structures differed significantly between study sites ($X^2 = 23.538$, $df = 5$, $p < .001$) and was significantly higher at sites 2 – 6 compared to site 1 (Fig. 4), where grazing was practically absent (ms-bite rate of 0.6 ± 0.3 kg h^{-1}). The grazing intensity experienced at site 2 (8 ± 3 kg h^{-1}) and site 6 (10 ± 7 kg h^{-1}) was less than half that of sites 3, 4 and 5 (24 ± 16, 34 ± 14 and 28 ± 11 kg h^{-1}, respectively), though these differences were not significant likely owing to the high variation in grazing intensity within study sites. The dominant grazers at site 2 (*Centropyge multispinis*) and site 6 (*Amblyglyphidodon indicus*) differed from sites 3 – 5, where *Ctenochaetus* spp. were dominant (see Fig. 4 for genera and Table S3 for species-specific details). Taken together over all study sites, *Ctenochaetus* spp.

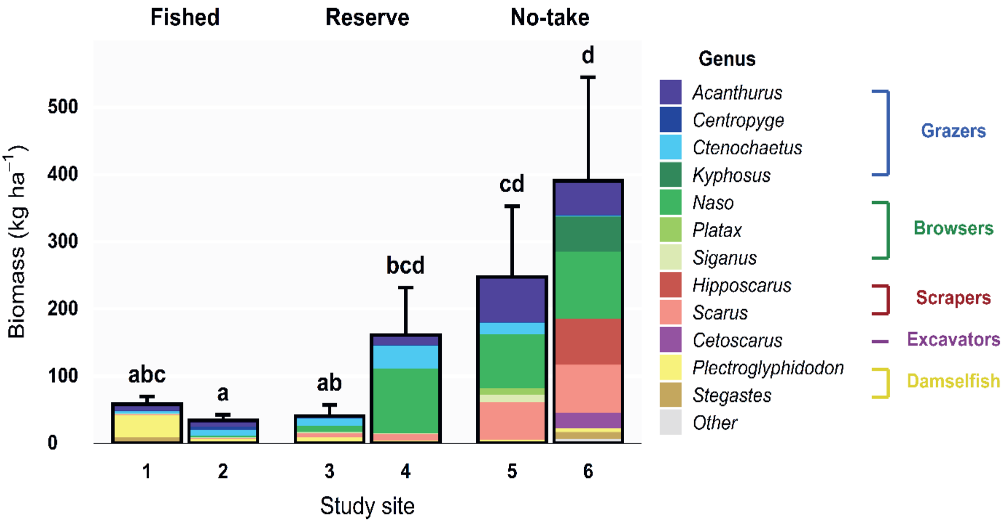

Figure 3 *Herbivorous fish biomass (kg ha^{-1}) per study site and type of fisheries management. Average biomass (n = 11 - 15 fish surveys) is stacked by genus. Colours indicate functional groups: grazers (blue), browsers (green), scrapers (red), excavators (purple) and territorial damselfish (yellow), and shades further identify each genus. The group Other includes a mixture of uncommon herbivorous fish. Error bars denote the standard error of the mean total herbivore biomass and lower-case letters denote significant differences between study sites ($p < 0.05$)*

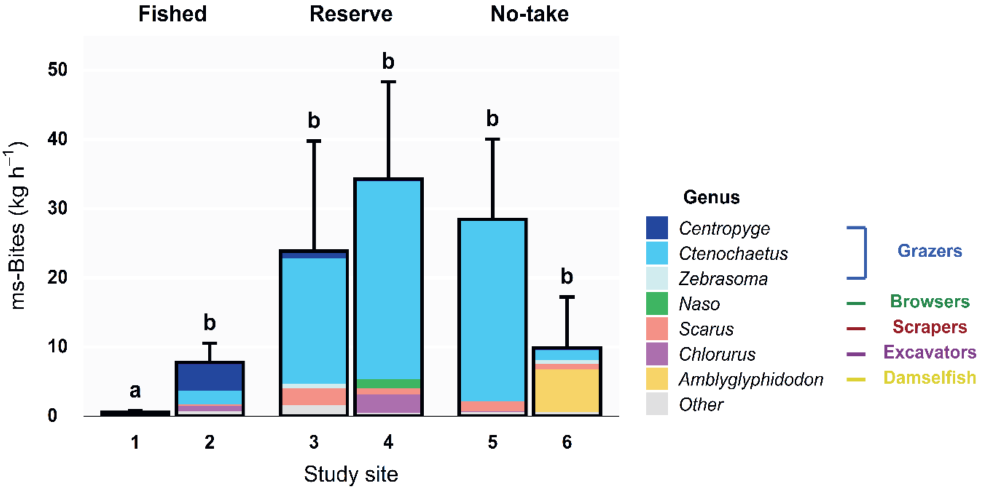

Figure 4 *Average + SE numbers of mass-scaled bites per hour (kg h^{-1}) on coral nursery structures (n = 8) per study site, split by fish genus and functional group. Colours of the genera match those in Fig 3. The group 'Other' contains 30 species of non-herbivorous fish, which were recorded taking infrequent bites (Table S3). Study sites are grouped according to level of fisheries protection, as indicated on top. Study sites not sharing any lower-case letters experienced significantly different ($p < 0.05$) average number of mass-scaled bites*

(mainly *Ctenochaetus striatus* and *Ctenochaetus binotatus*) were the dominant grazers on nursery structures, accounting for 73% of all recorded ms-bites, followed by the genera *Amblyglyphidodon*, *Centropyge* and *Scarus*, which were each contributing 6% to the total of ms-bites. The remaining 9% of ms-bites were recorded from a diverse group of 48 other species (Table S3). The grazing intensities observed at the study sites were neither found to correlate with the total herbivorous fish biomass at each site (Fig. 5a), nor with the biomass of grazing herbivorous fishes specifically (Fig. 5b). Grazing intensity did correlate with *Ctenochaetus* spp. biomass, the identified key grazer on RUV ($r = 0.86$, $p = .029$; Fig. 5c).

Total fouling density accumulated on the nursery structures over the 4-month study (Fig. 6) differed significantly between sites ($X^2 = 97.304$, $df = 5$, $p < .001$) and was clearly higher at site 1 (289 ± 53 g m^{-2}, mean ± SE) and site 2 (130 ± 32 g m^{-2}) compared to sites 3 – 6 (all below 60 g m^{-2}). In addition to an accumulation of molluscs, barnacles and turf algae at the sites in the fished zone, even macroalgae (predominantly brown algae of the genera *Padina* and *Dictyota*) became established on the nurseries at study site 1 (see also Fig. 2b). In stark contrast, the little fouling accumulated at study sites 3 – 6 consisted primarily of crustose coralline algae (see also Fig. 2a). For details on significant differences between study sites for all fouling groups, see Table S4. Herbivorous fish biomass and grazing intensity were correlating negatively but not significantly with fouling density (Fig. 5d-e).

Lastly, also coral performance differed among study sites, regarding both the percentage of coral live tissue ($X^2 = 53.332$, $df = 5$, $p < .001$) and coral growth ($X^2 = 394.4$, $df = 5$, $p < .001$). Live coral tissue at the end of the study was high at all study sites (>90% live coral tissue), except for study site 3 where live coral tissue was 83% (Fig. S1). This lower average at study site 3 can be attributed to a relatively large share of fragments that died (i.e. had 0% live coral tissue): out of all 384 coral fragments at the start of the study, 14 did not make it to the end and 8 of those were at site 3. A different pattern was seen for coral growth (Fig. 7), which increased stepwise from very poor at site 1 (mean specific growth rate of 0.001 d^{-1}) to superb at site 5 (0.012 d^{-1}) and 6 (0.014 d^{-1}), with intermediate growth values for sites 2, 3 and 4 (0.006, 0.008 and 0.010 d^{-1}, respectively). A strong positive correlation between herbivorous fish biomass and coral growth was found ($r = 0.83$ $p = .040$; Fig. 5f), though the positive correlation between grazing intensity and coral growth was not significant (fig. 5g). Percentage live coral tissue did not correlate with fouling density. A very strong negative and significant correlation ($r = -0.91$, $p = .0073$) was found between fouling density and coral growth (Fig. 5h). It is worthwhile to point out here that, despite comparably low fouling densities in both the marine reserve and no-take zone (Fig. 6), substantially higher coral growth rates were found for study sites in the no-take zone (Fig. 7 and Fig. 5h).

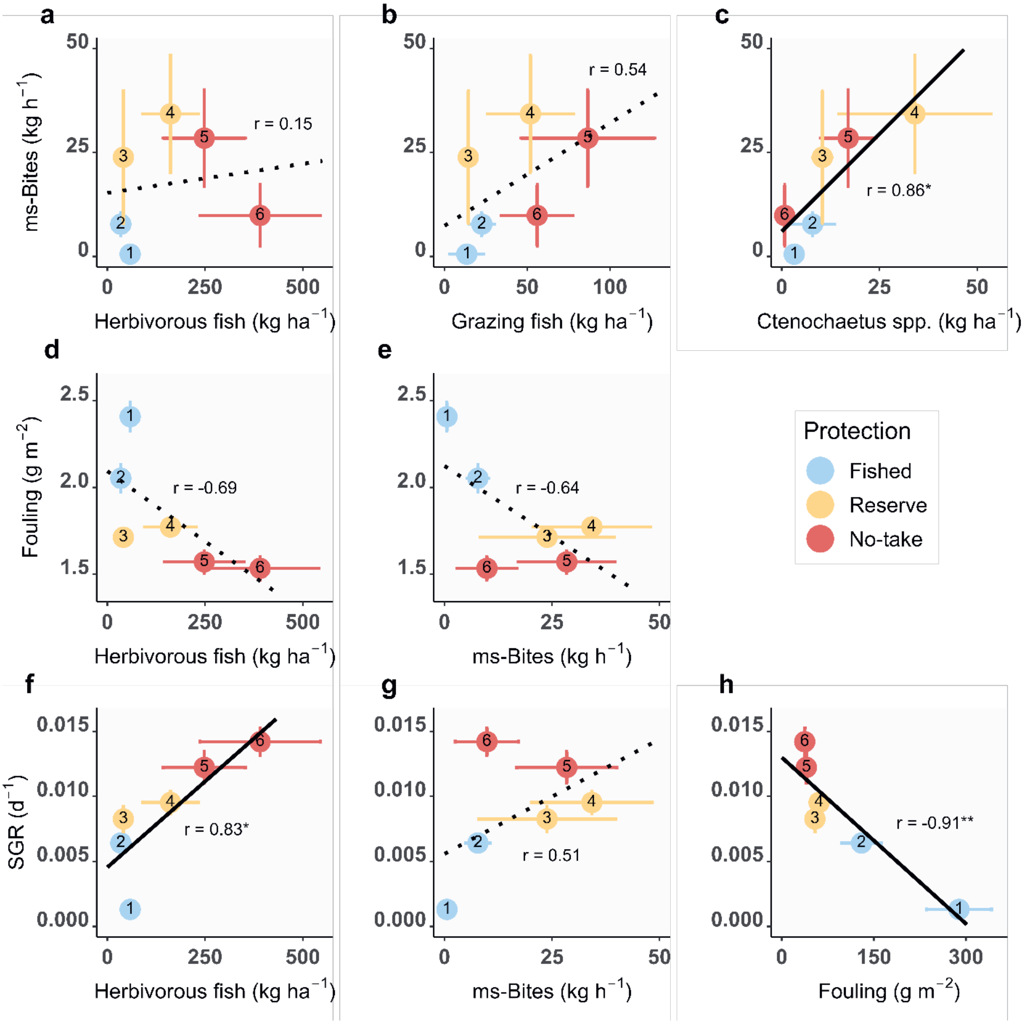

Figure 5** Correlations between study site averages of the biomass of **(a)** all herbivorous fish, **(b)** grazing herbivorous fish specifically and **(c) Ctenochaetus *spp. against the rate of mass-scaled bites (i.e. grazing intensity) on coral nursery structures. The (log10-transformed) accumulated fouling density present on nursery structures is correlated against **(d)** the biomass of herbivorous fish and **(e)** grazing intensity. Coral growth rate (expressed by the exponential specific growth rate constant) is correlated against **(f)** the biomass of all herbivorous fish, **(g)** grazing intensity and **(h)** fouling density. Linear trend lines are added with their associated Pearson correlation coefficient (r) and significance indicated (*p < 0.05, **p < 0.01; non-significant correlations are drawn as dotted lines). Each study site is indicated by its number and coloured according to fisheries protection level. Standard errors are shown for each data point to depict the variation in fish surveys (n = 11 – 15) and bite rate, fouling and coral growth measurements (all n = 8, except for study site 5 which has n = 4 due to damaged structures). Correlations were performed on site averages to avoid pseudo-replication*

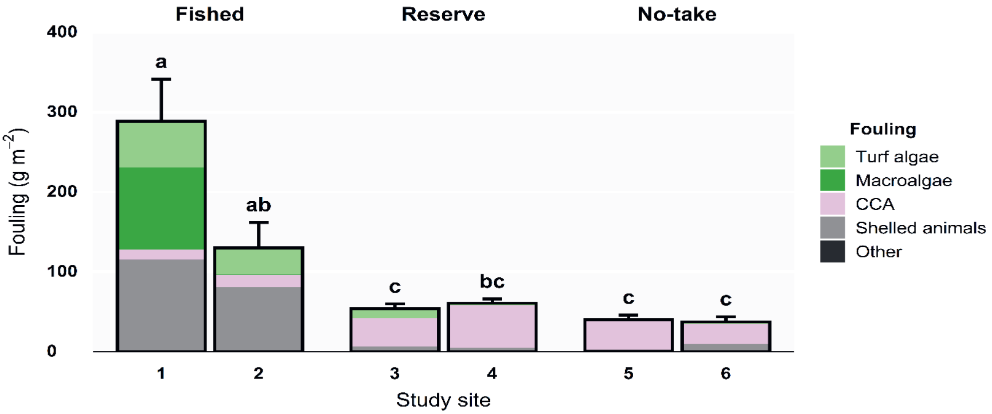

Figure 6 *Average + SE density of total fouling (g m^{-2}) on coral nursery structures (n = 8, except for study site 5 which has n = 4 due to damaged structures) per study site, split by type of fouling. Turf algae are categorized as a multi-species assemblage of benthic algae that are smaller than 1 cm in height, Macroalgae include brown, red and green fleshy algae, CCA are crustose coralline algae and Shelled animals include both bivalves and barnacles. The group 'Other' contains remaining uncommon benthic groups consisting predominantly of sponges and tunicates. Study sites are grouped according to level of fisheries protection, as indicated on top. Study sites not sharing any lower-case letters have significantly different ($p < 0.05$) average density of total fouling. See Table S4 in supplementary material for the statistical results for each fouling type separately across study sites*

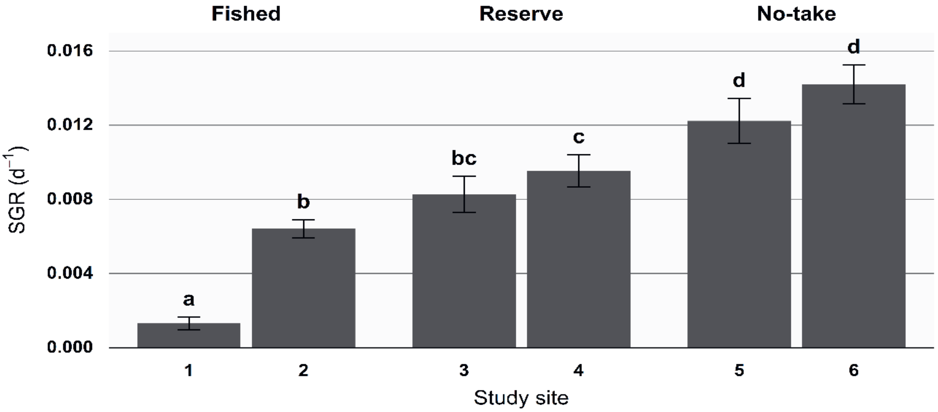

Figure 7 *Average growth rates per study site of the coral* Acropora verweyi *in nursery structures (n = 8, except for study site 5 which has n = 4 due to damaged structures) during the 4-month study period. Growth rates are expressed as a constant growth factor (Specific Growth Rate in d^{-1}) of the exponential increase in coral volume over time. Study sites are grouped according to level of fisheries protection, as indicated on top. Study sites not sharing any lower-case letters have significantly different ($p < 0.05$) average growth rates*

Discussion

This study aimed to determine the links between levels of fisheries management, herbivorous fish communities, grazing intensity and the performance of early-stage coral performance in mid-water nurseries. Clear differences in nursery coral growth were found across study sites and higher growth rates strongly coincided with lower fouling accumulation. Coral growth was faster in no-take zones than in marine reserves despite equally low fouling densities, suggesting there might be additional benefits of a healthy fish stock besides grazing, such as nutrient recycling (Shantz et al., 2015). The majority of ms-bites were taken by *Ctenochaetus* spp. and overall grazing intensity correlated strongly with the biomass of this key species. A high abundance of *Ctenochaetus* spp. could as such be indicative for locations where nurseries need little human-assisted cleaning (e.g. sites 3, 4 and 5). The links between total herbivorous fish biomass, bite marks and fouling were less clear, and may have been confounded by the presence or absence of territorial damselfish (site 6). These feisty fish prevented other grazers access to nurseries within their territory, yet grazing by certain damselfish species also resulted in low fouling accumulation and good coral performance. A relatively low herbivorous fish biomass appeared sufficient to keep coral nurseries free of fouling (e.g. sites 2 and 3), though nurseries placed in areas with low fish biomass that also lacked key grazers were quickly overgrown with macroalgae (site 1). Overall, these results indicate that fish communities can facilitate coral nursery performance in various ways and that especially at low overall herbivorous fish biomass densities, successful facilitation likely depends on the presence of site-specific key species.

Biomasses of functionally important herbivorous fishes such as scrapers, browsers and large-bodied grazers were low outside protected areas, affirming the known impacts of fishing pressure (Edwards et al., 2014; Heenan et al., 2016; Knoester et al., 2023). In contrast, the biomass of small-bodied grazing fishes such as *Ctenochaetus* spp. appeared unaffected by the level of fisheries management, supporting previous studies that found these detrivorous surgeonfishes to be more affected by bottom-up processes such as resource availability (Miller et al., 2012; Robinson et al., 2020). Indeed, unlike the majority of reef fishes, detrivorous surgeonfishes can benefit from large-scale disturbances that reduce live coral cover (Russ et al., 2018) and thrive on overexploited reefs as long as sufficient structural complexity remains (Nash et al., 2016; Obura et al., 2017). Also the high biomass of damselfishes in one of the fished areas is conform global trends, and likely relates to both reduced predation and competition (Edwards et al., 2014; Seraphim et al., 2020).

Total herbivorous fish biomass was not correlated with fish grazing intensity on nursery structures, indicating a more refined approach is advisable that discriminates the functional diversity (e.g. grazers, browsers, scrapers) within the broad group of herbivores (Heenan and Williams, 2013). However, even the biomass of grazing herbivores specifically did not correlate with grazing intensity. Instead, in accordance with the findings of similar study nearby (Knoester et al., 2019), grazing intensity was driven by a select group of key species, principally *Ctenochaetus* spp. The limited impact of fishing pressure on these species in combination with high grazing rates found for small-bodied and juvenile herbivores (Cernohorsky et al., 2015; Robinson et al., 2020) could explain the unexpected high grazing intensity found on nursery structures located in study sites with overall low fish biomass (e.g. site 3). While other differences in biological or physical properties between study sites might impact grazing intensity, the difference in abundance of this key species is likely the main driver. As *Ctenochaetus* spp. are among the most abundant surgeonfishes throughout the Indo-Pacific (Marshell and Mumby, 2015), feature a high bite rate (Marshell and Mumby, 2012) and target early-successional stages of turf (Hamilton et al., 2014; Kelly et al., 2016; Tebbett et al., 2017), the importance of these fishes for bio-assisted cleaning of nursery structures can conceivably be more widespread. Interestingly, another identified key grazer was a territorial damselfish species, A*mblyglyphidodon indicus*, which were also able to prevent the build-up of macroalgae and this indicates other species might take up grazing when *Ctenochaetus* spp. is uncommon (i.e. functional redundancy). The potential role of macroalgae control by damselfishes where grazing herbivores are rare has been identified at the Great Barrier Reef (Ceccarelli et al., 2011) and contrasts the negative effects of damselfishes often found at Caribbean restoration efforts (Ladd and Shantz, 2020).

The high grazing intensity by key herbivorous fish species even at depauperate fish communities can be crucial for restoration projects as these generally target degraded and overexploited reefs. Nonetheless, caution is warranted. A system reliant on key species, especially in the absence of functional redundancy, can be vulnerable to variation in grazing intensity due to for example seasonal changes (Paddack et al., 2006; Lefèvre and Bellwood, 2011; Seah et al., 2021) or community shifts following additional disturbances such as coral bleaching (Cheal et al., 2010; Nash et al., 2016). Furthermore, reef restoration is a two-step process and grazing intensity on nursery structures is unlikely to be directly translated to grazing intensity around outplanted corals. The higher diversity and complexity of natural reef substrates likely requires complementary feeding by a broader assemblage of herbivore species (Burkepile and Hay, 2008; Fox and Bellwood, 2013; Brandl and Bellwood, 2014, 2016; Kelly et al., 2016; Lefcheck et al., 2019). Furthermore, the grazer community might vary depending on the exact habitat being restored (Bonaldo and Bellwood, 2010; Hoey and Bellwood, 2010a; Roff et al., 2019) and will also include invertebrates such as sea urchins that especially graze nearby the seafloor (Carreiro-Silva and McClanahan, 2001). Altogether, this means that for successful reef restoration a more diverse herbivore community is likely needed than was found sufficient for grazing of mid-water suspended coral nurseries in this study. Indeed, a study in central Kenya using plates positioned on the seafloor found macroalgae accumulation within a few months despite an herbivorous fish biomass of 180 kg ha^{-1} (Humphries et al., 2014).

Accumulation of macroalgae on the studied nurseries here only happened at the reef (site 1) with the lowest biomass of roving herbivorous fish (16 kg ha^{-1}), of which grazers constituted 14 kg ha^{-1}. This fits within the grazing fish biomass range of 10 – 20 kg ha^{-1} which Robinson et al. (2018) identified as critical threshold below which Pacific coral reefs become (turf) algae dominated. A corresponding threshold for grazing intensity as determined in this study might lay around 10 ms-bites h^{-1}, with higher grazing intensities effectively keeping coral nurseries free of fouling. Interestingly, the natural reef at this studied site with a grazing intensity below this threshold was still coral dominated, suggesting a fragile state in which newly opened substrate can quickly become colonized by algae, a threat also described for other exploited Kenyan reefs (Humphries et al., 2014). Invertebrate and nocturnal herbivores such as sea urchins can partially substitute the grazing role of diurnal herbivorous fish (Humphries et al., 2014), but were found to have limited capacity for macroalgae control at this specific site (Knoester et al., 2023) and furthermore can contribute to reef erosion (Carreiro-Silva and McClanahan, 2001). The effective fouling control on other nurseries in this study at a roving herbivorous fish biomass as low as 31 kg ha^{-1} might relate again to the simple grazable surface of mid-water nursery structures as opposed to natural reef substrate. The accumulation of bivalves and barnacles on nursery structures is not expected to influence coral performance, as explained by Knoester et al. (2019). Another interesting finding was that grazing intensity at a macroalgae-dominated reef (site 3) was sufficiently high to prevent the accumulation of algae on nursery structures. Besides factors discussed above, this might also be explained by a past disturbance such as the 1998 bleaching event opening up a large area for algal settlement (McClanahan et al., 2001) and subsequent maturation of an unpalatable algae community that is difficult to reverse (Humphries et al., 2014; Schmitt et al., 2019).

In line with previous studies, coral growth was negatively associated with the accumulation of fouling, especially macroalgae (Hughes et al., 2007b; Knoester et al., 2019). The observed lower coral growth rates at site 1 can be explained by direct macroalgal competition (McCook et al., 2001), while reduced live coral tissue in absence of direct macroalgal contact (at study site 3) could possibly be inflicted through allelopathy by the dense *Sargassum* community there (Smith et al., 2006). Besides through the control of algal competitors, the fish community can also facilitate reef restoration in other ways (Seraphim et al., 2020). Indeed, while featuring equally low levels of biofouling, coral growth rates were higher in no-take zones compared to the reserves. An explanation could be the delivery of beneficial nutrient pulses by the abundant fish community around nursery structures in the no-take zones (Burkepile et al., 2013; Shantz and Burkepile, 2014; Shantz et al., 2015). In light of these benefits, suggested potential negative effects of a diverse and abundant fish community on coral nursery performance (e.g. coral predation) appear negligible (Knoester et al., 2019). Additional variables that might have influenced coral performance across study sites seem limited, but remain to be studied. Substantial differences in algal production due to bottom-up processes such as nutrient availability are not expected based on previous research along the Kenyan coast (Humphries et al., 2020) and are generally considerably less important than grazing intensity (Belliveau and Paul, 2002; Burkepile and Hay, 2006). Potential differences in light availability are assumed to be minimal as deeper sites were chosen because these locations featured better visibility than shallower sites. Indeed no correlations were found between water depth and coral performance.

This study aligns with earlier work that found effective fouling control on coral nurseries by herbivorous fishes (Frias-Torres and Van de Geer, 2015; Frias-Torres et al., 2015) and corroborates an earlier study that related the grazer-induced reduction in fouling to improved coral performance (Knoester et al., 2019). Such free bio-assisted cleaning bypasses costly human cleaning and thereby facilitates upscaling of restoration activities (Bayraktarov et al., 2016; Shaver and Silliman, 2017; Abelson et al., 2020; Ladd and Shantz, 2020). Interestingly, a relatively low diurnal fish grazing pressure appeared sufficient to keep nurseries clean of fouling. In this study area, a minimum grazing herbivorous fish biomass of around just 20 kg ha^{-1} was sufficient to keep coral nurseries macroalgae free, though potential functional redundancy among grazing species might quickly erode below that threshold. Given the apparent greater importance of key species compared to overall herbivore biomass found here and elsewhere (Humphries et al., 2015; Plass-Johnson et al., 2015; Ruttenberg et al., 2019; Knoester et al., 2023), this threshold will likely vary depending on the region and the local species community and therefore limits the formulation of simple site selection guidelines regarding a minimum recommended herbivorous fish biomass. Instead, the identification of suitable nursery sites with sufficient grazing pressure by local herbivorous key species is recommended through small pilot studies. Lastly, while a marginalized fish community could suffice to keep coral nurseries free of fouling, the protection of the full fish community will likely provide additional benefits for reef restoration including nutrient recycling, increased functional redundancy and more effective grazing pressure around outplanted corals. Therefore, we consider the integration of restoration and protection the most effective way forward to rehabilitate and preserve functional coral reefs locally, while global stressors are being addressed simultaneously (Knowlton et al., 2021).

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Availability of data and material: The data and code used for analysis is available as an archived Github repository on: https://github.com/ewoutknoester/HerbivoryGrazing.

Supplementary materials

Table S1 *Details on study sites and coral nursery placement. Patch reefs are discontinuous and interspersed with rubble or sand, whereas fringing reefs are running undisrupted parallel to the coast. Average visibility are diver's estimates, and depth range given for the eight replicate nurseries in meters below Mean Lower Low Water*

Study site	Reef type	Average visibility	Nursery depth (m)
1	Patch reef	6	2 - 3
2	Patch reef	8	5 - 6
3	Fringing reef	12	5 - 6
4	Fringing reef	14	8 - 9
5	Fringing reef	14	10 - 11
6	Patch reef	7	4 - 5

Table S2 *Results of Pearson correlations between coral nursery depth and key variables of this study. Significant ($p < 0.05$) correlations are highlighted with an asterisk (*)*

Variable 1	Variable 2	r	p
Depth	Herbivore biomass	0.26	.62
Depth	Grazer biomass	0.79	.06
Depth	*Ctenochaetus spp.* biomass	0.73	.10
Depth	Grazing intensity	0.86	.03*
Depth	Fouling density	-0.66	.15
Depth	Specific growth rate coral	0.57	.24
Depth	Coral condition	0.34	.51

Table S3 *Species-specific details on mean number of mass-scaled bites (ms-Bites in kg h^{-1}) targeted at coral nursery structures (n = 8) per study site, split per functional group*

Study site	**Functional group**	**Species**	**ms-Bites (kg h^{-1})**
1	Grazers	*Ctenochaetus striatus*	0.18
1	Territorial damselfish	*Plectroglyphidodon lacrymatus*	0.21
1	Omnivores	*Abudefduf sparoides*	0.00
1	Omnivores	*Canthigaster valentini*	0.01
1	Omnivores	*Dascyllus aruanus*	0.02
1	Omnivores	*Paraluteres prionurus*	0.01
1	Invertivores	*Cantherhines pardalis*	0.02
1	Invertivores	*Cheilinus oxycephalus*	0.00
1	Invertivores	*Labroides dimidiatus*	0.00
1	Invertivores	*Sufflamen chrysopterum*	0.09
1	Invertivores	*Thalassoma lunare*	0.01
1	Invertivores	*Canthigaster bennetti*	0.01
2	Grazers	*Centropyge multispinis*	4.06
2	Grazers	*Ctenochaetus sp.*	1.33
2	Grazers	*Ctenochaetus striatus*	0.66
2	Scrapers	*Scarus ghobban*	0.18
2	Excavators	*Chlorurus sordidus*	0.87
2	Territorial damselfish	*Plectroglyphidodon lacrymatus*	0.05
2	Planktivores	*Chromis lepidolepis*	0.00
2	Planktivores	*Thalassoma amblycephalum*	0.01
2	Invertivores	*Chaetodon lunula*	0.00
2	Invertivores	*Cheilinus chlorourus*	0.01
2	Invertivores	*Cheilinus sp.*	0.03
2	Invertivores	*Cheilinus trilobatus*	0.04
2	Invertivores	*Gomphosus caeruleus*	0.12

Study site	Functional group	Species	ms-Bites (kg h^{-1})
2	Invertivores	*Thalassoma hebraicum*	0.00
2	Invertivores	*Thalassoma lunare*	0.23
2	Piscivores	*Lutjanus fulviflamma*	0.08
2	Piscivores	*Plectorhinchus gaterinus*	0.11
3	Grazers	*Centropyge multispinis*	1.02
3	Grazers	*Ctenochaetus binotatus*	6.98
3	Grazers	*Ctenochaetus sp.*	9.90
3	Grazers	*Ctenochaetus striatus*	1.29
3	Grazers	*Zebrasoma scopas*	0.60
3	Browsers	*Siganus luridus*	0.59
3	Scrapers	*Scarus frenatus*	2.35
3	Scrapers	*Scarus psittacus*	0.06
3	Territorial damselfish	*Plectroglyphidodon lacrymatus*	0.12
3	Omnivores	*Chaetodon kleinii*	0.22
3	Omnivores	*Pomacentrus baenschi*	0.02
3	Planktivores	*Chromis dimidiata*	0.00
3	Planktivores	*Meiacanthus mossambicus*	0.00
3	Planktivores	*Thalassoma amblycephalum*	0.01
3	Invertivores	*Anampses twistii*	0.01
3	Invertivores	*Cantherhines pardalis*	0.05
3	Invertivores	*Chaetodon guttatissimus*	0.03
3	Invertivores	*Chaetodon melannotus*	0.01
3	Invertivores	*Cheilinus oxycephalus*	0.01
3	Invertivores	*Gomphosus caeruleus*	0.00
3	Invertivores	*Labrichthys unilineatus*	0.00
3	Invertivores	*Labroides dimidiatus*	0.01
3	Invertivores	*Oxycheilinus digramma*	0.01

Study site	Functional group	Species	ms-Bites (kg h^{-1})
3	Invertivores	*Parupeneus macronemus*	0.03
3	Invertivores	*Sufflamen chrysopterum*	0.48
3	Invertivores	*Thalassoma hebraicum*	0.05
3	Invertivores	*Thalassoma lunare*	0.00
3	Piscivores	*Plagiotremus tapeinosoma*	0.00
4	Grazers	*Centropyge multispinis*	0.34
4	Grazers	*Ctenochaetus binotatus*	15.66
4	Grazers	*Ctenochaetus sp.*	9.56
4	Grazers	*Ctenochaetus striatus*	3.10
4	Grazers	*Ctenochaetus truncatus*	0.23
4	Browsers	*Naso annulatus*	1.35
4	Scrapers	*Scarus ghobban*	0.21
4	Scrapers	*Scarus niger*	0.30
4	Scrapers	*Scarus psittacus*	0.41
4	Excavators	*Chlorurus sordidus*	2.66
4	Omnivores	*Dascyllus trimaculatus*	0.04
4	Invertivores	*Chaetodon trifascialis*	0.19
4	Invertivores	*Hemigymnus melapterus*	0.05
4	Invertivores	*Neoglyphidodon melas*	0.17
5	Grazers	*Acanthurus tennenti*	0.33
5	Grazers	*Ctenochaetus binotatus*	1.38
5	Grazers	*Ctenochaetus sp.*	18.05
5	Grazers	*Ctenochaetus striatus*	6.87
5	Browsers	*Calotomus carolinus*	0.12
5	Scrapers	*Hipposcarus harid*	0.13
5	Scrapers	*Scarus frenatus*	0.23
5	Scrapers	*Scarus ghobban*	0.60

Study site	Functional group	Species	ms-Bites (kg h^{-1})
5	Scrapers	*Scarus niger*	0.49
5	Scrapers	*Scarus psittacus*	0.09
5	Excavators	*Chlorurus sordidus*	0.13
5	Omnivores	*Dascyllus trimaculatus*	0.01
6	Grazers	*Acanthurus nigricauda*	0.05
6	Grazers	*Acanthurus sp.*	0.28
6	Grazers	*Centropyge multispinis*	0.31
6	Grazers	*Ctenochaetus sp.*	0.63
6	Grazers	*Ctenochaetus striatus*	0.78
6	Grazers	*Zebrasoma scopas*	0.56
6	Scrapers	*Scarus ghobban*	0.55
6	Scrapers	*Scarus psittacus*	0.30
6	Territorial damselfish	*Amblyglyphidodon indicus*	6.18
6	Omnivores	*Dascyllus trimaculatus*	0.03
6	Omnivores	*Paraluteres prionurus*	0.02
6	Planktivores	*Chromis atripectoralis*	0.01
6	Planktivores	*Chromis viridis*	0.01
6	Invertivores	*Bodianus axillaris*	0.02
6	Invertivores	*Chaetodon trifascialis*	0.01
6	Invertivores	*Gomphosus caeruleus*	0.00

Table S4 *Post hoc for fouling densities per study site. Compact Letter Display (CLD) summarizes the statistical results at* $p < 0.05$

Type of fouling	**Study site**	**Density (g m^{-2})**	**Standard error**	**CLD**
Turf algae	1	57.7	9.3	a
Turf algae	2	33.0	5.4	ab
Turf algae	3	11.6	5.9	bc
Turf algae	4	2.0	0.5	c
Turf algae	5	1.4	0.3	c
Turf algae	6	2.5	0.6	c
Macroalgae	1	102.6	36.2	a
Macroalgae	2	0.3	0.2	b
Macroalgae	3	0.2	0.2	b
Macroalgae	4	0.8	0.3	b
Macroalgae	5	0.2	0.2	b
Macroalgae	6	0.1	0.1	b
CCA	1	12.9	2.9	ab
CCA	2	15.2	1.5	a
CCA	3	35.9	4.6	cd
CCA	4	53.2	4.0	d
CCA	5	36.1	4.4	cd
CCA	6	25.2	2.4	bc
Shelled animals	1	114.5	30.2	a
Shelled animals	2	81.2	33.0	ab
Shelled animals	3	5.7	2.3	c
Shelled animals	4	2.7	1.4	cd
Shelled animals	5	0.1	0.1	d
Shelled animals	6	9.5	4.7	bc

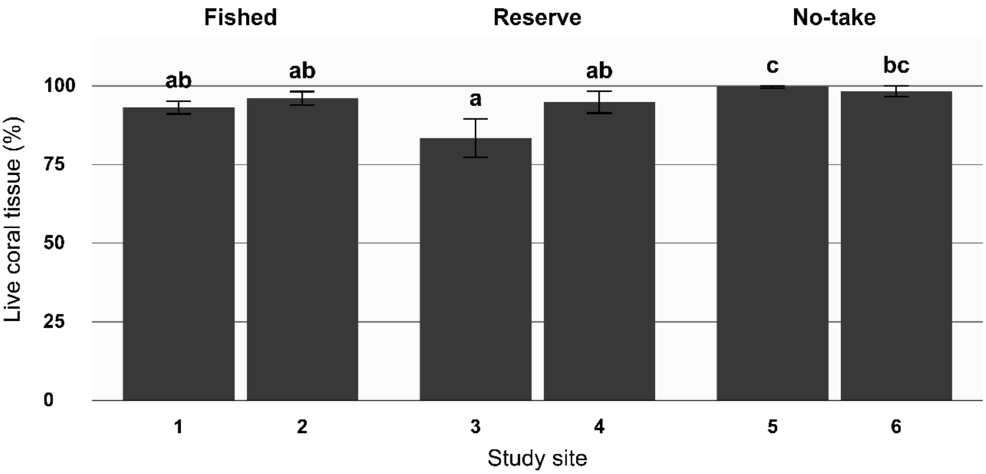

Figure S1 *Average percentage live coral tissue per study site for the coral* Acropora verweyi *in nursery structures (n = 8 for all expect Study site 5 where n = 4 due to detached structures) at the end of the 4-month study period. Study sites are grouped according to level of fisheries protection, as indicated on top. Study sites not sharing any lower-case letters had significantly different ($p < 0.05$) percentage live coral tissue at the end of the experiment*

Community-managed coral reef restoration in southern Kenya initiates reef recovery using various artificial reef designs

6

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Abstract

Monitoring of reef restoration efforts and artificial reefs (ARs) has typically been limited to coral fragment survival, hampering evaluation of broader objectives such as ecosystem recovery. This study aimed to determine to what extent AR design influences the ecological recovery of restored reefs by monitoring outplanted coral fragments, benthic cover, coral recruitment and fish and invertebrate communities for two years. Four AR designs (16 m^2), unrestored controls and natural reef patches as reference ($n = 10$) were established in Mkwiro, Kenya. ARs consisted either of concrete disks with bottles, layered concrete disks, metal cages or a combination thereof. A mixture of 18 branching coral species (mainly *Acropora* spp.) was outplanted on ARs at a density of 7 corals m^{-2}. After two years, 60% of all outplanted fragments had survived, already resulting in coral cover on most ARs comparable (though *Acropora*-dominated) to reference patches. Coral survival differed between ARs, with highest survival on cages due to the absence of crown-of-thorns sea star predation on this design. In total, 32 coral genera recruited on ARs and recruit densities were highest on reference patches, moderate on concrete ARs and low on cages. ARs and reference patches featured nearly twice the fish species richness and around an order of magnitude higher fish abundance and biomass compared to control patches. Fish abundance and biomass strongly correlated with coral cover on ARs. AR, reference and control patches all had distinct fish species compositions, but AR and reference patches were similar in terms of trophic structure of their fish communities. Motile invertebrates including gastropods, sea urchins, sea cucumbers and sea stars were present at ARs, but generally more abundant and diverse at natural reference patches. Taken together, all studied ecological parameters progressed towards reef ecosystem recovery, with varying influences of AR design and material. We recommend a combination of metal cages and layered concrete ARs to promote high fragment survival as well as natural coral recruitment. Ultimately, a longer period of monitoring is needed to fully determine the effectiveness reef restoration as conservation tool to support coral reef ecosystem recovery.

Key words: *Acropora*; Coral gardening; Coral predation; Coral recruitment; Fish community; Keystone invertebrates; Long-term ecological monitoring; Structural complexity

Introduction

Coral reefs have been deteriorating worldwide due to local human impacts such as overfishing and pollution (Burke et al., 2011) and declines are rapidly worsening with climate change (Heron et al., 2017). In the Western Indian Ocean, coral reefs and coastal communities are especially vulnerable due to the high dependence and utilization of reefs by people for their livelihoods, including artisanal fishing and tourism (Obura et al., 2022). Reef managers – unable to influence climate change – aim to strengthen reef resilience locally to reduce impacts of large-scale disturbances beyond their control (Nyström et al., 2008; Anthony et al., 2011, 2015; Graham et al., 2013). In addition to the crucial reduction of local threats (Anthony et al., 2017; McLeod et al., 2019), active interventions such as restoration of damaged and deteriorated reefs are now deemed necessary to reverse the ongoing loss of biodiversity and reef resilience (Suding et al., 2015; Rinkevich, 2019; Duarte et al., 2020). Alongside with climate action on an international level, such active local reef management might give reefs a better chance to resist or recover from disturbances whilst providing crucial ecosystem services and buying time for coral adaptation to increasing temperatures (Hein et al., 2020b; Knowlton et al., 2021).

A commonly used and recommended method for reef restoration is the two-phase coral gardening approach in which coral fragments are first cultured in nurseries and then outplanted onto degraded reefs or artificial reef (AR) structures (Rinkevich, 1995). The nursery phase of coral gardening has been well established: high coral growth rates (Lirman et al., 2010) in combination with low costs (Levy et al., 2010) have made this an effective way to generate considerable coral stock, especially when integrated with natural processes such as herbivory to maintain coral health (Frias-Torres and Van de Geer, 2015; Knoester et al., 2019). The outplanting phase remains more costly and is not always successful in effectively increasing coral cover (Omori, 2019), partially due to ineffective AR design (Hylkema et al., 2021; Higgins et al., 2022) and a lack of understanding of ecological processes that determine coral survival such as coral predation and competition among benthic species (Ladd and Shantz, 2020). Although it is the ambition to substantially upscale restoration efforts (Vaughan, 2021), scientifically documented projects are currently still both small in size and high in costs (Bayraktarov et al., 2016, 2019). Furthermore, projects often (cl)aim to restore ecosystem functionality and ecosystem services, but monitoring generally lacks clear aims and mostly tracks item-based successes such as outplanted coral fragment survival (Boström-Einarsson et al., 2020; Hein et al., 2020b). Improved monitoring is needed to evaluate both AR design as well as the broader ecosystem impact of reef restoration as this could create the scientific credibility needed to further upscale restoration efforts (Abelson et al., 2020).

Traditionally, ARs have been widely used to exploit rather than restore marine ecosystems (Higgins et al., 2022). AR monitoring studies have therefore mainly focused on optimizing fisheries yields for a select group of commercial species by adjusting the design, site selection and management of ARs (Bohnsack and Sutherland, 1985; Baine, 2001). Studies that include the development of the whole reef community around ARs in comparison to natural reference reefs are needed to evaluate ecosystem restoration success, however such studies remain scarce (Carr and Hixon, 1997; Ceccarelli et al., 2020; Hylkema et al., 2021). Nonetheless, structural complexity has been identified as a driving factor supporting fish and invertebrate communities on both natural reefs (Graham and Nash, 2013) and ARs (Baine, 2001; Hunter and Sayer, 2009). In return, accommodated reef communities can facilitate reef restoration by providing ecological functions such as herbivory or top-down control of coral predators that benefit coral survival and growth (Ladd and Shantz, 2020). Thus, monitoring how the development of ecological communities is influenced by AR design and complexity has the potential to improve the cost-effectiveness of reef restoration by evaluating to what extent critical ecological processes are re-established that drive ecosystem recovery (Horoszowski-fridman and Rinkevich, 2016). Since most reef restoration projects intend to initiate reef recovery (not to rebuild the entire reef) by using pioneer coral species such as branching *Acropora* spp., key indicators of a functional ecosystem need to be monitored including benthic cover, coral diversity, coral recruitment and the fish and invertebrate community (Boström-Einarsson et al., 2020; Ferse et al., 2021). Ultimately, monitoring at the relevant ecological scales (as opposed to item-based monitoring) allows for the appropriate evaluation of the central restoration goal of re-establishing self-sustaining reefs (Hein et al., 2020b; Ferse et al., 2021).

To restore a self-sustaining coral reef ecosystem that ultimately provides ecosystems services, ecological recovery on three levels is required (NASEM, 2018): individual coral colonies (survival and growth), coral population (reproduction and recruitment) and reef community (functional diversity). This study evaluated whether the outplanting of pioneer coral species onto ARs could initiate recovery on these three levels and to what extent recovery is influenced by AR design (Fig. 1). Detailed benthic and fish surveys were performed on four different types of AR patches, unrestored control patches and natural reference reefs over a period of two years to answer three research questions (RQs). RQ1: How does AR design influence the extent to which outplanted corals survive and grow sufficiently to establish themselves and outperform benthic competitors? RQ2: How does AR design affect coral recruitment? RQ3: How do the community composition and ecological functionalities of fish and invertebrates that develop on different AR designs compare to those communities on surrounding natural reefs? We expected to observe 1) Differences between growth and survival of corals among ARs due to the impact of AR design on associating reef communities such as benthic competitors, coral predators and herbivores; 2) Intermediate coral recruitment on ARs compared to control and references reef patches due to the addition of moderately complex substrate, with further specific differences between ARs due to design, materials and associated communities; 3) Early stage ARs supporting the establishment of a moderately diverse fish and invertebrate community, with diversity of species and dietary guilds increasing with increasing complexity of AR designs.

Methods

Area description

The study area (-4.659, 39.381) covered a 1.6-km stretch of coastline between the villages of Mkwiro and Wasini on the north coast of Wasini Island, Kenya (Fig. 2A). A kilometre-wide sea strait separated the study area from a headland of the Kenyan mainland featuring the central village Shimoni. Extensive mangrove forests surrounding two river mouths envelope both sides of the headland. The sea strait is subjected to semi-diurnal tides that cause differences in seawater surface levels of up to 4 m. Due to this specific combination of environmental settings, the study area experienced moderately strong currents, relatively low visibility (8 m yearly average) and moderate wave exposure (max significant wave height of ~1.5 m during the NE monsoon). Long-term average sea surface temperature range from 25˚ C in August to 29˚ C in April (NOAA, 2022). During the study period, however, water temperatures peaked above 30˚ C in April 2019 and again in April 2020, culminating in a temperature stress of respectively 6 and 10 degree heating weeks in those two years (Liu et al., 2006).

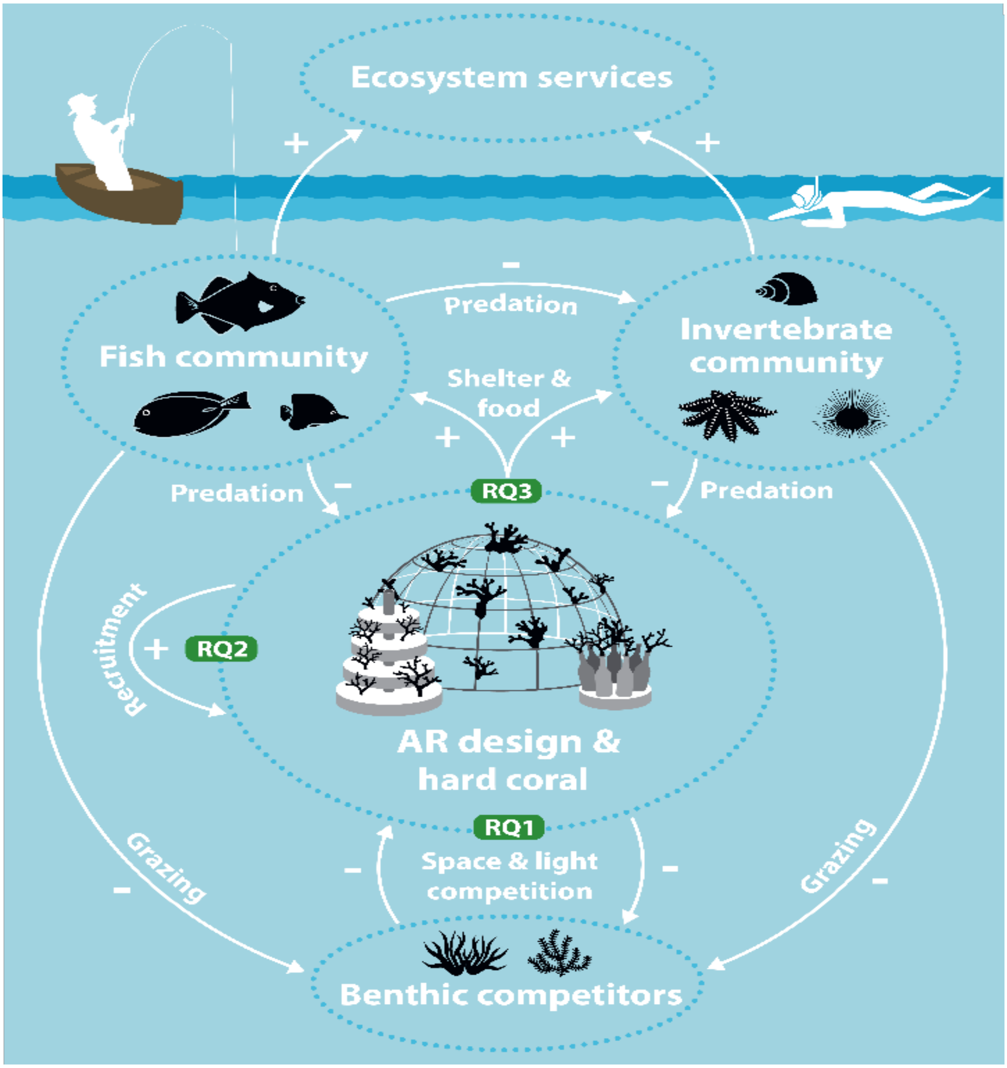

Figure 1 *Schematic overview of the study, research questions (RQs) and wider socio-ecological setting. Growth and survival of hard corals outplanted onto artificial reefs (ARs) was evaluated and compared to benthic competitors (RQ1). The effect of AR design on coral recruitment was monitored (RQ2). The development of fish and invertebrate communities and their functions on different AR designs was compared (RQ3). A functional fish community can graze on benthic competitors, predate on invertebrates and predate on corals. A functional motile invertebrate community can also graze on benthic competitors and impact coral through predation. Both the fish and invertebrate community can also support ecosystem services such as artisanal fishing and tourism. Artwork by Vrijlansier*

Natural coral reefs in the study area were limited to a narrow strip (2 to 5 m depth at low tide) of discontinuous patches interspersed with extensive fields of unconsolidated rubble, which were occasionally overgrown by sheets of soft coral. Seagrass and macroalgae typically formed dense canopies in shallower water, whereas a diverse assemblage of soft corals and sponges covered the sandy slope into deeper water. The patch reefs had moderately high and diverse coral cover, with remaining hard substrate largely covered by macroalgae and sessile invertebrates such as sponges, hydroids, soft corals and tunicates. Encrusting and (sub)massive hard corals prevailed, but extensive heaps of rubble indicated that branching corals and especially *Acropora* spp. once were more common. Throughout the region, *Acropora* populations had been dominant (McClanahan et al., 1999) until diminished by the severe 1998 temperature anomaly (McClanahan et al., 2001). *Acropora* and other temperature-sensitive genera have not recovered since (McClanahan, 2014). Recovery of these predominantly branching and delicate corals is further hampered by ongoing destructive fishing practices such as the use of beach seines (Samoilys et al., 2017).

Study context: reef restoration in Mkwiro

The study area falls within the waters of Mkwiro village, which is heavily dependent on its marine resources for fishing and, increasingly, tourism (Arthurton and Korateng, 2006). To promote community participation in the sustainable management of marine resources, Mkwiro Beach Management Unit (BMU) was established in 2007 as a local fishery stakeholder association under the State Department of Fisheries (Kawaka et al., 2017). In 2018, Mkwiro BMU started a collaboration with the REEFolution Foundation (the Netherlands) to improve the status of their reefs. The REEFolution Foundation, currently represented by an independent Kenyan branch named REEFolution Trust, aims to train and educate coastal communities to restore and protect their coral reefs and thus safeguard local livelihoods. The REEFolution Trust collaborates with Wageningen University and Research (WUR) to develop scientifically validated and effective restoration methods. A co-management plan was drafted in which restoration and protection of a protected community managed area (CMA) for Mkwiro were proposed. Implementation of the co-management plan started in 2019 with the training of community members and students, coral gardening activities and demarcation of the Mkwiro CMA, though enforcement of the no-take zone has been largely lacking. As part of this collaboration between Mkwiro BMU, REEFolution Foundation, REEFolution Trust and WUR, the current experiment was set up under research license NACOSTI/P/21/8896.

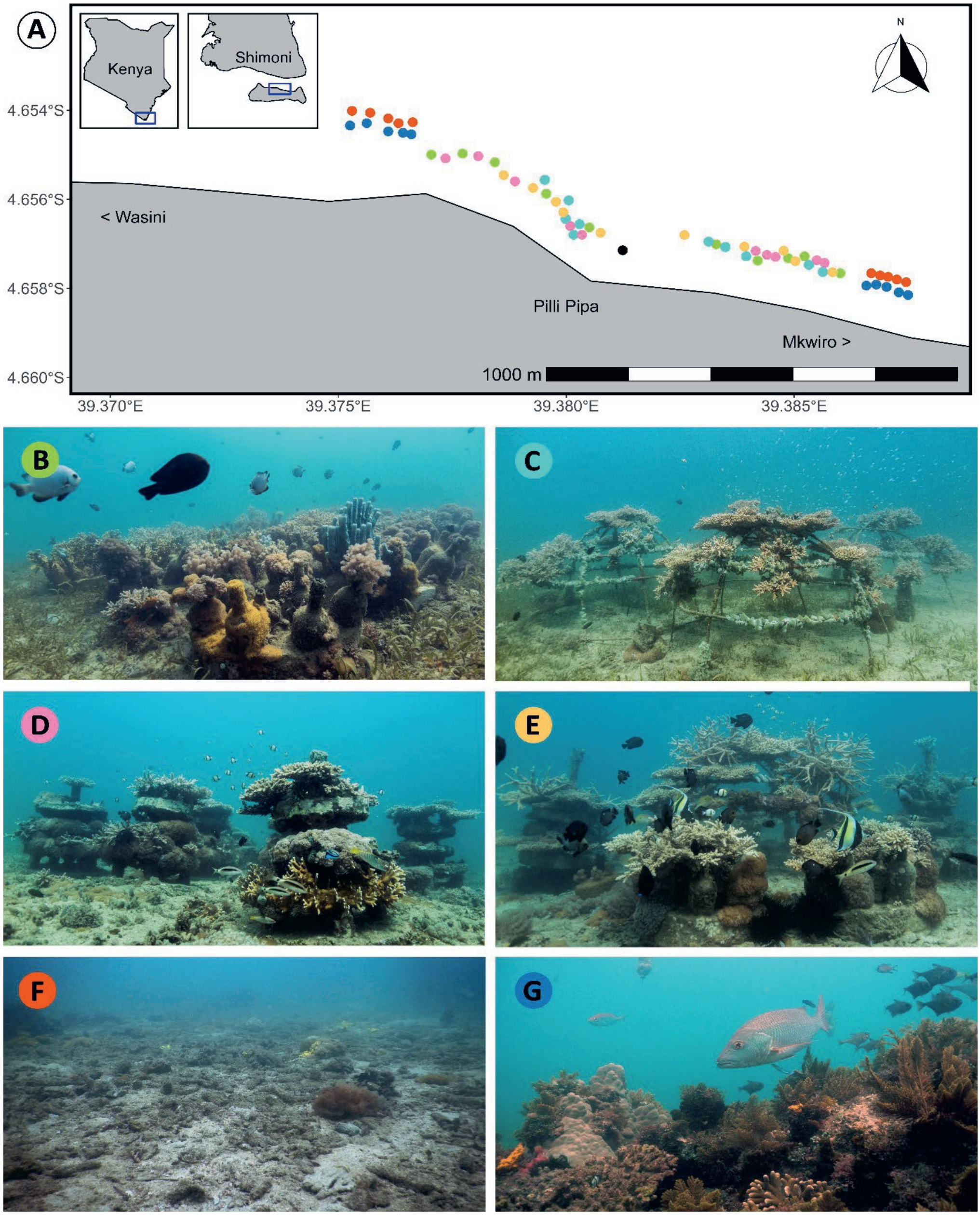

Figure 2 ***(A)*** *Map of the study area (insets showing position within Kenya) and representative pictures of the six treatment patches two years after starting the experiment:* ***(B)*** *Bottle patch consisting of 16 bottle modules,* ***(C)*** *Cage patch consisting of 4 metal cages,* ***(D)*** *Cake patch consisting of 8 layered cakes,* ***(E)*** *Compound patch consisting of 4 bottle modules, 1 metal cage and 2 layered cakes,* ***(F)*** *Control patch that was not restored and* ***(G)*** *Reference reefs that retained natural structural complexity. Each coloured point on the map represents a patch (n = 10 per treatment) and matches with the treatment colour (B-G). The black point indicates the coral nursery. The land marker of Pilli Pipa Restaurant (also known as Panga Tatu) is indicated, as are the directions of the nearby villages of Mkwiro and Wasini*

Experimental setup

A total of 40 AR patches were deployed and filled with coral fragments between April and November 2019. Each AR patch covered approximately 16 m^2, resulting in a total restored reef areal dimension (sensu Goergen et al., 2020) of 640 m^2. Four different types of AR patches were created (n = 10): Bottle patches, Cage patches, Cake patches and Compound patches combining all AR types (Fig. 2B-E). In addition, 10 rubble fields were left unrestored as Control patches (Fig. 2F) and 10 natural reef patches that retained moderate structural complexity were chosen as Reference patches (Fig. 2G). The AR patches were separated by at least 50 m from the Control and Reference patches (Fig. 2A). The distance (measured from edge to edge) between adjacent AR patches was 12 ± 5 m (mean ± SD) and the distances between AR patches and any nearest natural reef structure was and 14 ± 5 m. The distance between Control patches and natural reef was 13 ± 6 m. The depth of control patches (8 ± 2 m) and AR patches (8 ± 1 m) was greater than for Reference patches (5 ± 1 m). The Control and AR patches were positioned slightly deeper for two reasons: 1) natural reef patches were smaller (< 16 m^2) and spaced more widely in deeper waters, leaving extensive fields of rubble where deployed AR patches could be considered independent of each other and the natural reef and 2) it was expected that deeper restored patches would be less impacted by temperature anomalies, benefitting the long-term objectives of the ongoing restoration project. Details on the exact placement of each patch can be found in the Supplementary data, Table S1.

The following modules were used to build each AR patch: Bottle patch (16 bottle modules), Cage patch (4 cages), Cake patch (8 layered cakes) and Compound patch (4 bottle modules, 1 cage and 2 layered cakes). A bottle module consisted of a concrete disk with about eight glass bottles (Fig. 2B). A cage was made of metal and consisted of three vertical crossbows and four horizontal rings (Fig. 2C). A layered cake consisted of four concrete disks, each separated from the next by PVC pipes and held together by a central PVC pipe (Fig. 2D). Details on exact dimensions of modules can be found in Table S2. Coral fragments (10 – 15 cm length) were attached using tie-wraps (4.8 x 300 mm) to bottle necks, metal intersections on cages and PPR pins that were embedded in both the top and third layer of cakes. Coral fragments were sourced from coral nursery trees (Nedimyer et al., 2011) in the study area (Fig. 2A), which had been filled with naturally broken coral fragments (corals of opportunity) one year earlier. Coral species have not been confirmed, but a presumed 19 branching species of five genera have been outplanted: 12 *Acropora* spp., 2 *Millepora* spp., 2 *Pocillopora* spp., 1 *Porites* sp. and 2 *Stylophora* spp. Since fragments were collected as corals of opportunity, a high genotypic diversity is expected, but this remains unconfirmed. An outplanting density of 7 corals m^{-2} was realized at the start of monitoring, totalling to 4256 outplanted fragments (3580 *Acropora* spp., 201 *Millepora* spp., 107 *Pocillopora* spp., 145 *Porites* sp. and 223 *Stylophora* spp.). Species were haphazardly outplanted on AR patches. After outplanting, no maintenance (e.g. predator or fouling removal) was performed.

Monitoring

To monitor the survival of outplanted fragments, all AR modules were photographed at the start (Dec 2019) and near the end of the study (Dec 2021). Throughout the study, AR patches were visited at least quarterly to identify recent or ongoing causes of coral mortality. Benthic surveys were performed just after the start (Feb – Mar 2020) and at the end of the study (Feb – Mar 2022) to monitor benthic cover and motile invertebrates. To avoid sampling excessive amounts of rubble around the small AR patches, two perpendicular 5-m point intercept lines were used (crossing in the middle). This approach was used to monitor all AR, Control and Reference patches. The lines were sampled every 0.25 m and benthic cover divided into the following categories: hard coral to genus level (including the reef-building hydrozoan *Millepora*), soft coral, macroalgae (fleshy algae > 1 cm), hard substrate (including bare substrate, crustose coralline algae and turf algae < 1 cm), soft substrate (rubble, sand and seagrass) and other (mainly sponges, tunicates and hydroids). Motile invertebrates were sampled in a circle around the intersecting survey lines, with the radius depending on the size of the invertebrates: corallivorous snails (*Drupella* spp. and *Coralliophila* spp.) were counted within a 2.5-m radius (i.e. sampling area of 20 m^2), sea urchins were identified and counted within a 3.6-m radius (40 m^2) and larger invertebrates such as sea cucumbers, sea stars, large (> 5 cm) gastropods, octopus and lobsters were identified and counted within a 5.6-m radius (100 m^2). Each patch was surveyed once in 2022, but due to COVID-19 fewer patches were sampled in 2020. At the end of the study (Mar 2022), coral recruits (1 – 10 cm diameter) were counted and identified to genus level where possible. At AR patches, coral recruits on each AR module were counted, the material type noted (glass, concrete, iron, PPR or PVC) and for recruits on concrete the orientation (horizontal or vertical) was noted as well. At each Control and Reference patch, coral recruits were sampled within 16 replicate 1 m^2 quadrats.

Fish surveys were performed just after the start (Feb – Mar 2020) and at the end of the study (Dec 2021 – Mar 2022). A stationary fish census with standard 5-min initial sampling period was used to quantify the composition and abundance of all diurnal (surveys were performed between 0800 h and 1400 h), non-cryptic fish (Bohnsack and Bannerot, 1986). The radius of the fish census was typically 7.5 m, but lower when visibility was below average (to a minimum radius of 6 m). Surveys were performed about two meters distance from AR patches, and the large radius was chosen so that wary fish could be observed as well. Fish sizes (fork length) were estimated in classes of 5 cm for fishes smaller than 20 cm, in 10-cm size classes up to 50 cm and in 50-cm bins for larger fishes (i.e. trumpetfishes, cornetfishes and morays), so that fish biomasses (kg ha^{-1}) could be estimated using known length-weight relations and the midpoint of each size class (Froese and Pauly, 2015). At each of the 60 patches, two to three fish surveys were performed in 2022, but not all patches were sampled in 2020 due to COVID-19 disruptions. Control and Reference patches had also been also surveyed in Apr – Jun 2019, before large-scale deployment of AR patches started. Surveys were performed by various observers, but always trained and tested by EGK on species identification and size estimation. A number of surveys were conducted by two observers (EGK and JJR) simultaneously on the same patch and comparisons did not show significant differences in observed fish richness, abundance or biomass.

Analyses

All analyses were performed in R (R Core Team, 2020). The comparison of fragment survival between AR patches included only the genus *Acropora* (representing 84% of outplanted fragments) due to the unequal distribution of the other genera among patches. Fragment survival was averaged per patch and compared between the four AR patch types using a generalized linear model with beta distribution from the *betareg* package (Cribari-Neto and Zeileis, 2010), thereby accounting for the proportional nature of the survival data. Model assumptions were validated by visual inspection of residual plots. A Wald Chi-Squared Test from the *car* package (Fox and Weisberg, 2018) was used to determine significance, and pairwise comparisons with Tukey adjustments were made using the *emmeans* package (Lenth, 2020). Putative causes of fragments mortality were summarized descriptively per AR patch type and per coral genus.

Coral recruits were summed per patch and divided by the projected area (i.e. 16 m^2) to determine recruit density. Recruit density was log-transformed and compared between all six treatment patches with a linear model using the *nlme* package (DebRoy, 2006). Checking model assumptions and performing significance tests were implemented as outlined above. Genus-specific recruit densities were summarized descriptively. For AR patches specifically, recruit densities were explored further by material type and orientation. To get material-specific recruit densities, recruits were summed per material type and divided by the respective materials' surface area per patch. For orientation-specific recruit densities the same procedure was repeated, but only concrete was sampled due its clear horizontal – vertical distinction. In addition, these results were further split by coral genus. As surface area and replicate numbers varied substantially for material type and orientation, these results are presented descriptively only.

Hard coral cover was compared between the six treatment patches using a generalized linear model with beta distribution as described above. Hard coral genera were summarized descriptively, as were data on other benthic categories. Given the similar patterns across years but limited number of replicates for 2020, the focus has been put on the more recent and complete 2022 data. Densities of motile invertebrates were all square-root transformed and compared between treatment patches using linear models of the *nlme* package as described above. The richness within each group was presented descriptively on either genus or family level. Due to their limited numbers found across all surveys, octopuses (9) and lobsters (5) were not included in the analysis. To explore the association between coral cover and recruit densities, a Pearson correlation was performed using AR module averages.

Fish communities were compared between treatment patches on three parameters: species richness, abundance and biomass. As for benthic communities, the focus has been put on the final 2022 data. Surveys performed simultaneously by two observers at the same patch were averaged. Silversides (*Atherinomorus* spp.) were excluded due to their highly variable abundance. Depth and distance to nearest AR or natural reef patch were evaluated as covariates in model selection based on Akaike's Information Criterion (AIC) using a threshold of ΔAIC > 6 (Fox et al., 2015). For all three parameters, mixed-effects linear models were fitted using the *lme4* package (Bates et al., 2015) with patch as random factor to account for non-independence of repeated surveys. Abundance and biomass were log-transformed and checking assumptions and performing significance tests were implemented as outlined for the models described above. The procedures were repeated for survey-area corrected abundance and biomass data: to get an estimate of how much fish there could be if the entire surveyed area had been restored, abundance and biomass values were divided by patch size (i.e. 16 m^2) instead of the whole survey area (177 m^2). Furthermore, for Control and Reference patches, the effect of year (2019, 2020 and 2022) on all three (uncorrected) parameters was compared using the mixed-effects linear model approach just described. Pearson correlation tests between average AR patch hard coral cover against fish species richness, abundance and biomass were performed. Lastly, fish community composition was compared between and within treatment patches using Bray-Curtis dissimilarity matrices based on average fish biomass per patch on both species and dietary guild level, following Morais & Bellwood (2020) for diet categories. Community differences were statistically evaluated using multivariate permutation tests (PERMANOVA) with Bonferroni adjustment and visually presented with non-metric multidimensional scaling (NMDS) plots using the *vegan* package (Oksanen et al., 2022).

Results

Benthic cover, fragment survival and coral recruitment

Hard coral cover was largely similar across AR patches at the start of the study (averaging 19%) and differences appeared over time (Fig. 3). Reductions or increases in hard coral cover on AR patches were frequently mirrored by reciprocal increases or reductions in soft coral cover (mainly *Cespitularia* spp. and *Rhytisma* sp.), whereas macroalgae (mainly *Dictyota* sp. and *Sargassum* spp.) were only commonly seen at Reference patches (Fig. 3). Benthic cover on Control and Reference patches remained largely unchanged throughout the study (Fig. 3). At the end of the 2-year study, hard coral cover differed significantly between the six treatment patches (Fig 4; $X^2 = 373.43$, df = 5, $p < 0.001$). Control patches remained devoid of hard coral (1%), whereas Cake (18%), Cage (32%) and Compound patches (29%) featured moderately high coral cover, comparable to Reference patches (26%); Bottle patches featured intermediate and therefore rather low coral cover (9%). Genus-level coral richness differed greatly between treatments (Fig. 4): all AR patches were dominated almost exclusively by *Acropora* (though Cake patches featured several additional genera at low cover), whereas Reference patches showed a moderately diverse assemblage of genera (with very limited *Acropora* cover).

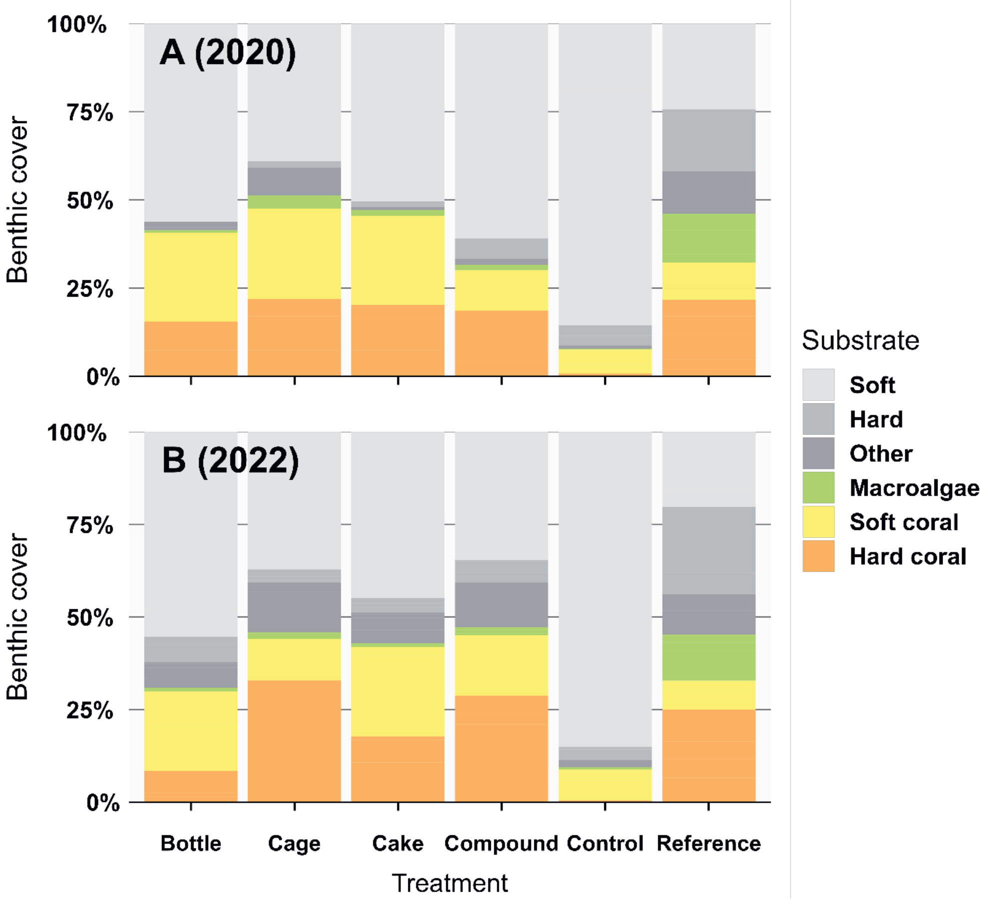

Figure 3 *Percentage benthic cover* ***(A)*** *a few months and* ***(B)*** *two years after deployment of artificial reef patches, compared to unrestored Control patches and natural Reference reefs (n = 3 – 10 for 2020; n = 10 for 2022). Benthic substrate was divided into the following groups: Soft substrate (including sand, rubble and seagrass), Hard substrate (including bare rock and rocky substrate covered by crustose coralline algae or turf algae < 1 cm), Macroalgae (fleshy algae > 1 cm), Soft coral, Hard coral and the group Other including rarer sessile invertebrates such as sponges, tunicates and hydroids*

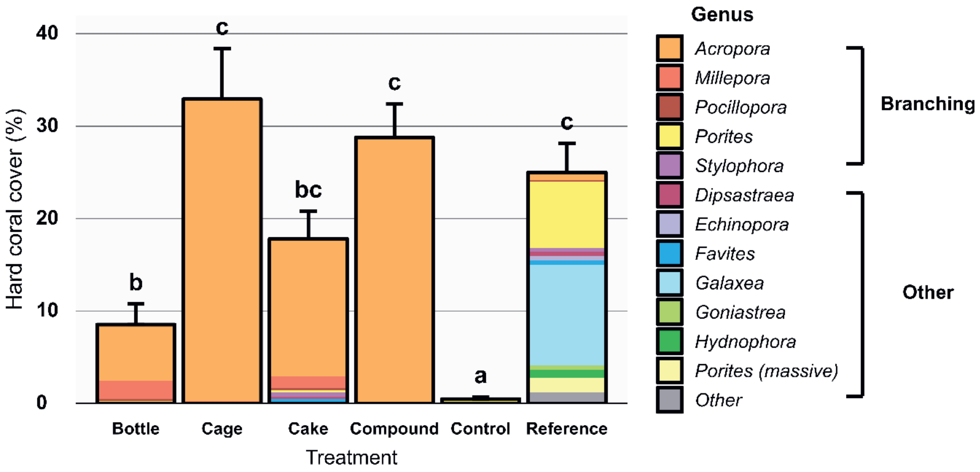

Figure 4 *Percentage hard coral cover (including the hydrozoan* Millepora*) on artificial reef patches two years after deployment, unrestored Control patches and natural Reference patches. Error bars denote SE (n = 10) and treatments not sharing lowercase letters differ significantly ($p < 0.05$). Colours represent coral genera, split between branching corals and other growth forms*

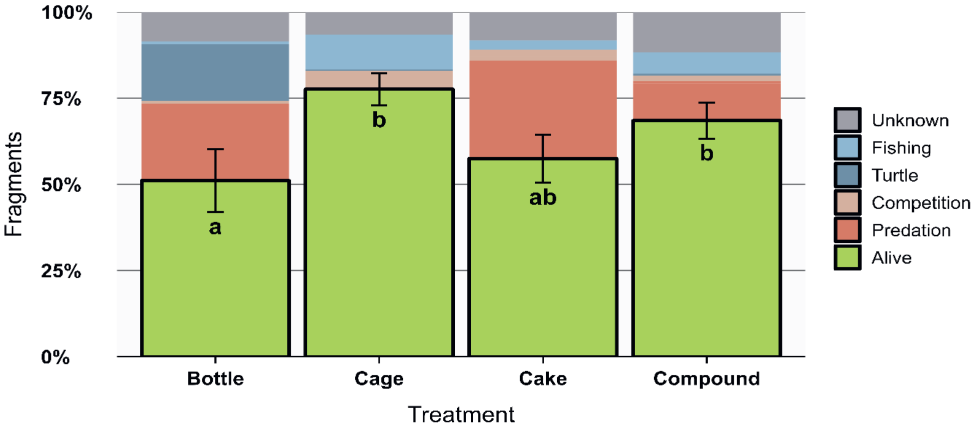

Figure 5 *Survival of* Acropora *spp. coral fragments (N = 3580 fragments) two years after outplanting onto four different types of artificial reef patches (n = 10 per treatment). The percentage of surviving fragments are outlined in black with SE noted by error bars. Patches not sharing lowercase letter differ significantly ($p < 0.05$) in percentage of surviving fragments. The remainder of fragments did not survive and their putative mortality causes have been indicated: bleaching (mortality due to above-average water temperatures), fishing (detachment due to entanglement in fishing gear), turtle (detachment due to interaction with sea turtles), competition (mortality due to competing benthic organisms such as tunicates, sponges and soft coral), predation (consumption by* Acanthaster *sp. sea stars or* Drupella *spp. snails) or unknown cause of death*

Of all 4256 outplanted coral fragments, 2552 remained alive for two years (60%), 1300 died (31%) and 404 were dislodged (9%). Survival of *Acropora* fragments differed significantly between AR patches ($X^2 = 15.35$, df = 3, $p = 0.0015$) and was higher on Cage and Compound patches compared to Bottle patches, with intermediate results for Cakes (Fig. 5). Across all fragments and genera, crown of thorns sea stars (CoTS; *Acanthaster* sp.) were chiefly responsible for predation mortality (14% of outplanted fragments), with the remainder of predation mortality caused by *Drupella* spp. (1%). Other mortality causes included: dislodgement due to turtles (*Eretmochelys imbricata* and *Chelonia mydas*) scraping their carapace (5%), detachment after entanglement with fishing gear (4%) and benthic competition with neighbouring hard corals, sponges, tunicates or soft corals (2%). Bleaching caused the demise of 2% of coral fragments. For the remainder of dead coral fragments (10%), no clear cause could be identified; no symptoms of diseases were observed throughout the study. Identified mortality causes for *Acropora* were distinct between AR patches (Fig. 5): predation caused substantial losses at all patches except Cages, which suffered more from detachment by fishing gear. Only Bottle patches suffered substantial dislodgement by sea turtles. Clear differences could also be observed between coral genera, both in terms of survival and mortality causes (Fig. S1). Across all patches, survival was highest for *Millepora* spp. (85%) and *Acropora* spp. (64%), with much lower survival for *Stylophora* spp. (29%), *Pocillopora* spp. (16%) and *Porites* sp. (12%). All genera except *Millepora* suffered from predation, *Acropora* and *Millepora* suffered relatively little from competition, only *Pocillopora* was impacted by bleaching and for *Porites* the mortality causes remained largely unknown (Fig. S1).

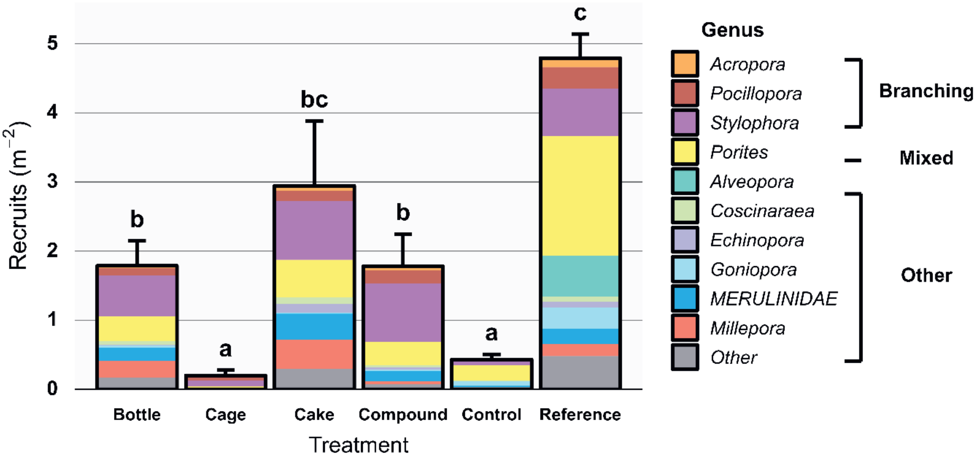

Figure 6 *Hard coral recruit density (colonies 1 -10 cm diameter, including hydrozoan* Millepora*) two years after deployment at restored patches, compared to unrestored Control patches and natural Reference reefs. Error bars denote SE (n = 10) and treatments not sharing lowercase letters differ significantly (p < 0.05). Colours represent coral genera, split between branching corals and other growth forms*

Hard coral recruit density differed significantly between the six treatment patches ($X^2 = 148.62$, df = 5, $p < 0.001$). Recruit density was very low at both Control (0.4 m^{-2}) and Cage patches (0.2 m^{-2}), significantly higher at Bottle (1.8 m^{-2}), Compound (1.8 m^{-2}) and Cake patches (2.9 m^{-2}) and highest at Reference patches (4.8 m^{-2}; Fig. 6); differences between Cake and Reference patches were not significant. Genus-level richness of coral recruits mirrored this pattern (Fig. 6), with highest number of genera found on Reference reefs. Recruits of *Stylophora* and *Porites* were dominant across patches. In total, 1401 recruits were observed on the ARs. Concrete featured both highest recruit densities (7 recruits m^{-2} versus < 4 recruits m^{-2} on all other material types) and genus-level richness (Fig. S2). Nearly all of the 32 coral genera that settled onto concrete preferred to settle on vertical surfaces, which typically featured three-fold higher recruit densities than horizontal surfaces (Fig. S3). Only *Porites*, *Coscinaraea*, *Leptastrea* and genera from the Merulinidae family (*Favites*, *Dipsastraea, Cyphastrea* and *Goniastrea*) were found in roughly equal densities on both orientations (Fig. S3). Recruit densities were not correlated to hard coral cover on AR modules (r = 0.025, df = 868, p = 0.46).

Fish and invertebrate communities

There were significant differences between the six treatment patches in terms of fish species richness ($X^2 = 47.57$, df = 5, $p < 0.001$), fish abundance ($X^2 = 54.90$, df = 5, $p < 0.001$) and fish biomass ($X^2 = 69.46$, df = 5, $p < 0.001$). Depth was a significant covariate in the model for fish species richness (deeper patches showed lower species richness: mean ± SE of beta estimate -2.3 ± 0.44 species m^{-1}) and therefore depth-corrected values for richness are shown (Fig. 7A). Patterns across treatment patches were similar for all three parameters: Control patches featured significantly lower fish species richness, abundance and biomass than all other patches, which did not differ among each other (Fig. 7A-C). At Control patches, fish species richness (13 species) was just over half that of other patch types (21 – 24 species). Both the abundance (0.1 fish m^{-2}) and biomass (8 kg ha^{-1}) at Control patches were between five to twelvefold lower compared to all other patch types (abundance: 0.45 – 1.2 fish m^{-2}; biomass: 38 – 92 kg ha^{-1}). When standardized to actual area restored (i.e. excluding the unrestored but surveyed rubble areas surrounding the patches), all AR patches except Bottle patches featured significantly higher abundances (three to eightfold higher) and biomasses (two to sixfold higher) than natural Reference reefs (Fig. S4). Coral cover on AR patches was positively correlated with fish abundance (r = 0.71, df = 38, p < 0.001) and fish biomass (r = 0.54, df = 38, p < 0.001), and a trend was seen for species richness (r = 0.31, df = 38, p = 0.055; Fig. S5). The abundance and biomass of fish remained constant on both Control and Reference patches before and after restoration (Fig. S6), though average fish richness increased (from 7 to 10 species on Control patches and from 19 to 27 species on Reference patches).

Fish species composition was significantly different between the six treatment patches (F = 2.77, df = 5, p < 0.001), see Table S3 for the Bray-Curtis dissimilarity matrix. The fish community at Control and Reference patches were different from each other (p < 0.001) and both were different from AR patches (all p < 0.05; Fig. 8A). AR patches were similar to each other, except Bottle patches, which differed from Cage (p = 0.011) and Compound patches (p = 0.0077), and a significant difference between Cage and Cake patches (p = 0.024). The total number of fish species encountered was higher on Reference patches (145 species) than Bottle

(108), Cage (103), Cake (101), Compound (113) and Control patches (72). Fish community composition on dietary guild level also differed between treatment patches (F = 3.49, df = 5, p < 0.001; Table S4), but now Reference patches were similar to all AR patches, while Control patches remained distinct (all p < 0.01; Fig. 8B). The similar dietary guilds but different species compositions among restored and reference patches can be highlighted by some common planktivorous and omnivorous species such as *Dascyllus trimaculatus* and *Dascyllus carneus* (common on AR patches) compared to *Plectroglphidodon lacrymatus* and *Chromis dimidiata* (common Reference patches). Control patches hosted a fish community consisting mainly of invertivores, whereas herbivores were more associated with both Reference and AR patches. Some larger predatory fish (e.g. *Diagramma pictum* and *Lutjanus fulviflamma*) were more associated with Cage patches, though not significantly so.

Motile invertebrates were generally more abundant and diverse at Reference patches compared to other patches, but patterns varied among key invertebrate groups (Fig. 9A-E). Significant differences were found in abundances of corallivorous snails ($X^2 = 56.52$, df = 5, $p < 0.001$) and sea urchins ($X^2 = 78.26$, df = 5, $p < 0.001$) between treatment patches. Both groups were significantly more abundant at Reference patches compared to all other patches (Fig. 9A&B). In addition, highest genus richness was found on References patches as well for these two invertebrate groups. Sea stars showed a similar pattern (Fig. 9C), but differences were not significant. CoTS were rarely encountered, but some were seen on Bottle patches. No clear patterns nor statistical differences were seen for sea cucumbers (Fig. 9D). Average abundance of gastropods did not differ significantly between Reference and AR patches, but family-level richness was higher at Reference patches. In contrast, AR patches were dominated by Cypraeidae gastropods (mainly *Cypraea tigris),* which were rarely encountered on Reference patches.

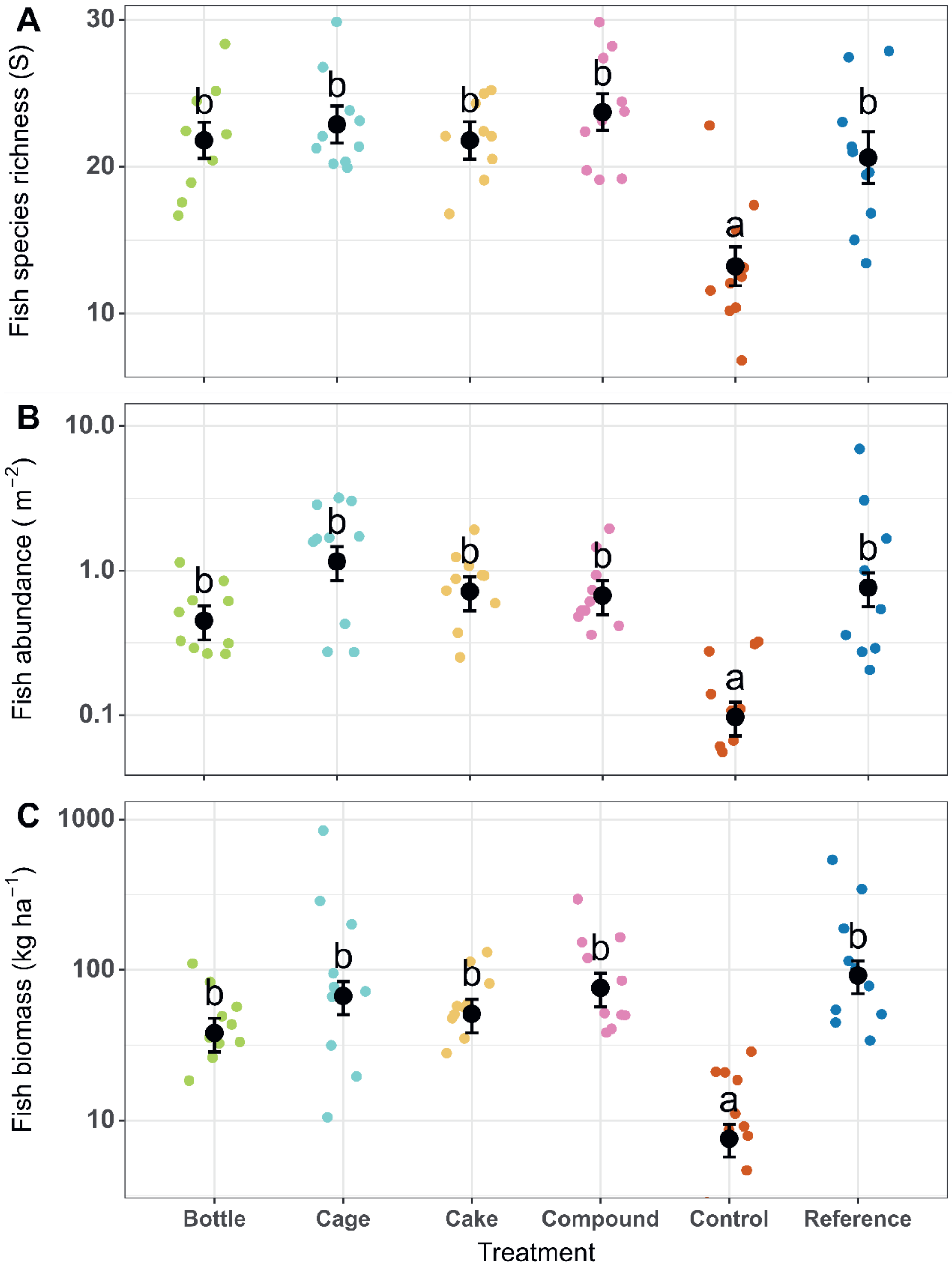

Figure* 7 *A *Fish species richness per survey (corrected for depth),* ***B*** *Fish abundance and* ***C*** *Fish biomass two years after deployment of restored patches, compared to unrestored Control patches and natural Reference patches. Error bars denote SE (n = 10) and treatments not sharing lowercase letters differ significantly ($p < 0.05$). Coloured points indicate values for replicate patches within each treatment type*

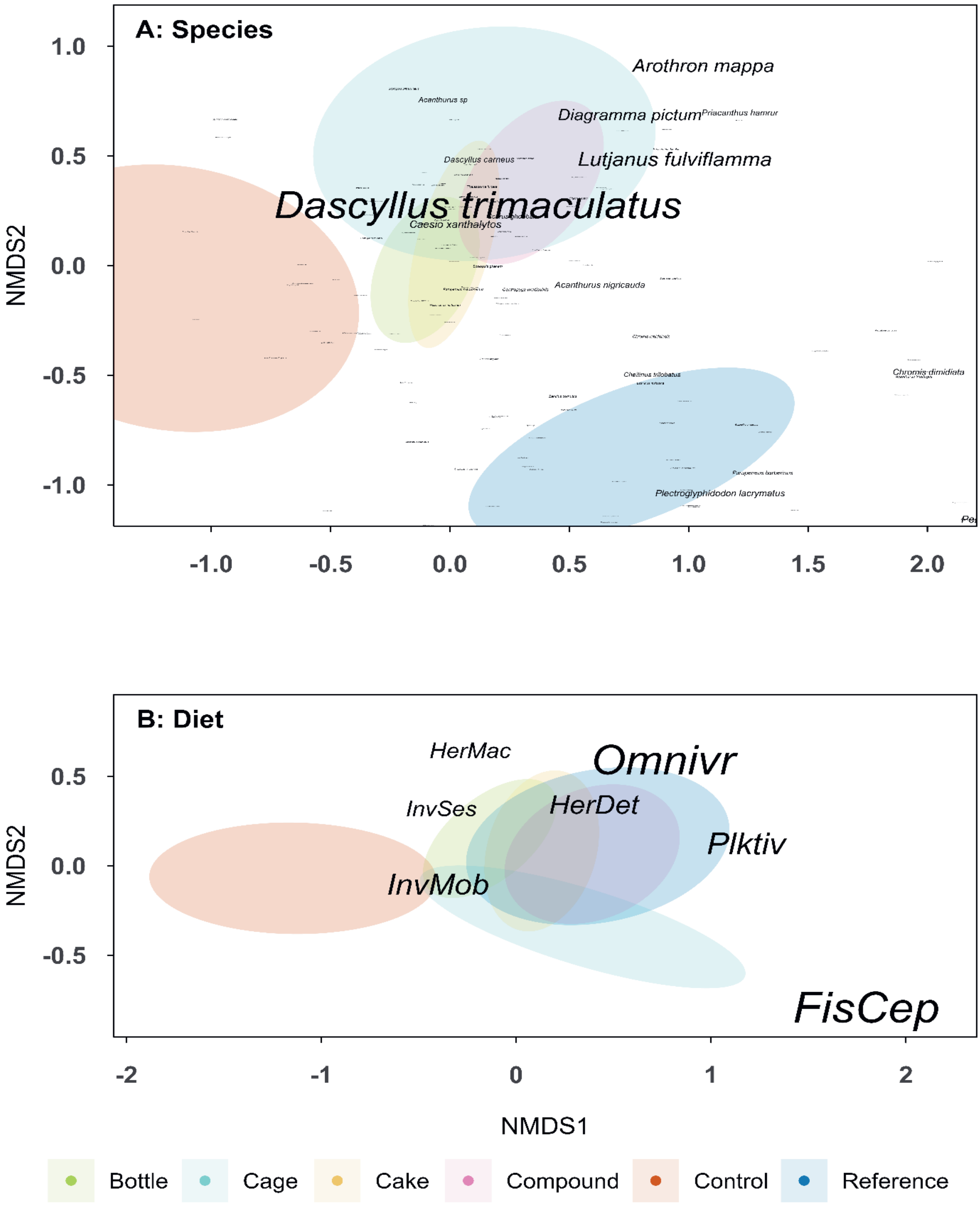

Figure 8 *Non-metric multidimension scaling (NMDS) plots based on Bray-Curtis dissimilarity matrices on* ***(A)*** *fish species (2 dimensions, stress: 0.199) and* ***(B)*** *fish diet (2 dimensions, stress: 0.138). Font sizes increases with fish abundance. Data based on 10 replicate patches of four different types of artificial reef, unrestored Control patches and natural Reference patches (as indicated by colours). Data on the fish community was collected two years after deployment of the artificial reef patches. Ellipses show a 99% confidence interval around the centroid for each treatment. Diets are as follows: FisCep = fish and cephalopod predators, HerDet = herbivores/detritivores, HerMac = herbivores/macroalgivores, InvMob = invertivores (motile prey), InvSes = invertivores (sessile prey), Omnivr = omnivores, Plktiv = planktivores*

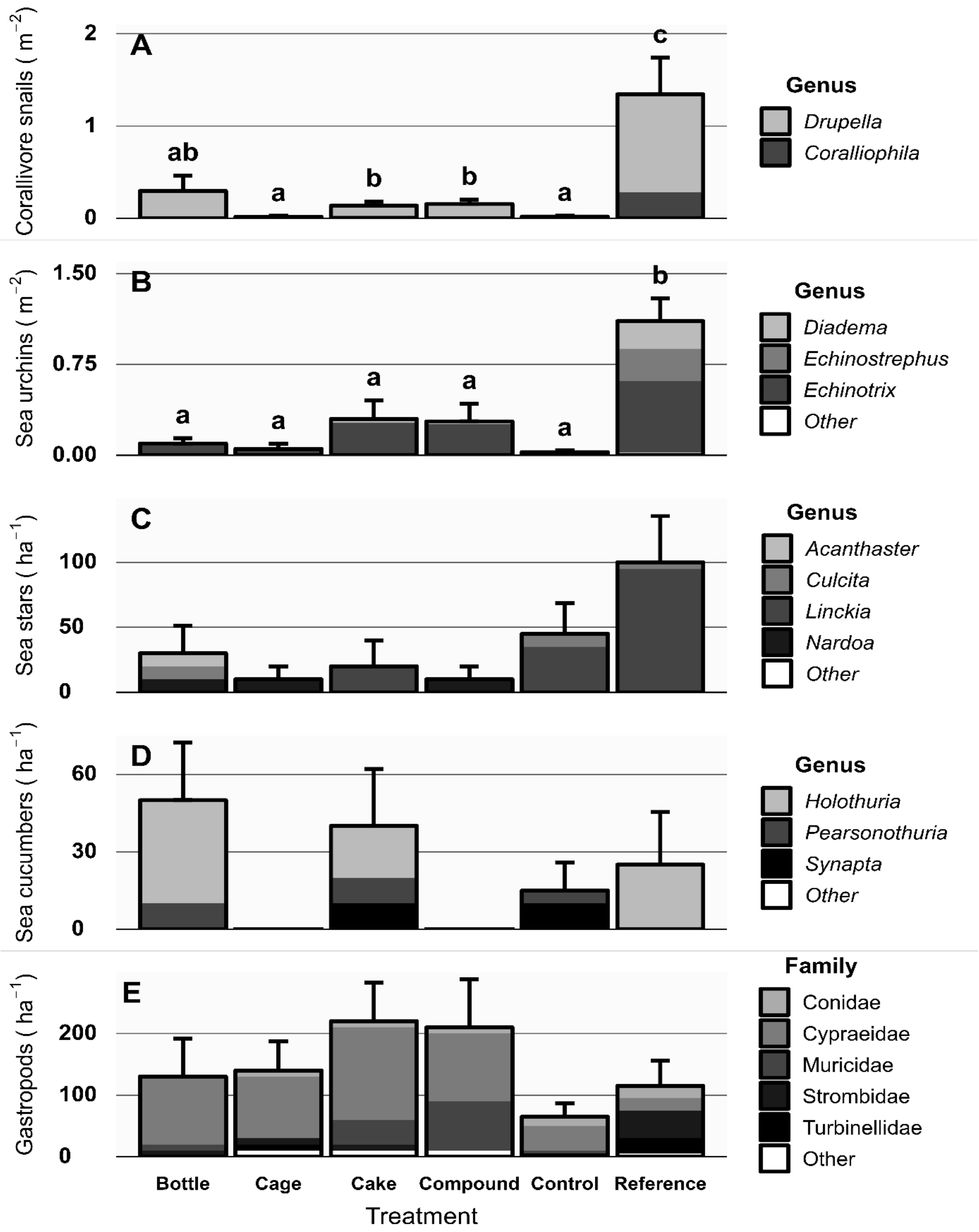

Figure 9 *Densities of key motile invertebrates at artificial reef patches two years after deployment, unrestored Control patches and natural Reference patches. Key groups shown are* ***(A)*** *Corallivorous snails* m^{-2}*,* ***(B)*** *Sea urchins* m^{-2}*,* ***(C)*** *Sea stars* ha^{-1}*,* ***(D)*** *Sea cucumbers* ha^{-1} *and* ***(E)*** *Large (> 5 cm) gastropods* ha^{-1}*. Error bars denote SE (n = 10) and treatments not sharing lowercase letters differ significantly (p < .05). No significant difference between treatment patches were found for sea stars, sea cucumbers and large gastropods. Octopus and lobsters were rarely observed and not included here. Shades represent genera or families that make up the invertebrate communities*

Discussion

This study aimed to determine to what extent AR design influences the recovery of restored reefs using a uniquely broad ecological approach (Hein et al., 2020a) that monitored the development of outplanted coral fragments, coral recruitment and fish and invertebrate communities. Two years after their deployment, the AR patches with outplanted corals have shown positive development towards recovery of reef ecosystem functionality. Coral fragment survival was on par with reported global averages (Bayraktarov et al., 2019; Boström-Einarsson et al., 2020), but clearly differed between AR designs. Metal cages featured highest fragment survival and coral cover by preventing access to invertebrate coral predators, whereas a combination of predation by CoTS and dislodgement by sea turtles reduced fragment survival and increased soft coral cover on (especially low-set) concrete ARs. In contrast, coral recruitment was negligible on metal cages and moderately high on concrete ARs. Thus, metal cages featured high coral cover which remained dominated by outplanted branching corals (principally *Acropora* spp.), whereas concrete ARs featuring lower coral cover showed higher potential to increase coral diversity through natural recruitment. Fish abundance and biomass were similar across all AR designs, and were already after two years comparable to natural reference reefs. Abundance and biomass of fish are even expected to surpass levels of reference reefs when larger areas are restored, since these parameters already exceeded levels detected at reference reefs when unrestored areas around AR patches were excluded from the census counts. Fish species richness and trophic composition were also similar between all AR designs and reference reefs, though exact species compositions remained distinct between natural and restored reefs. Motile invertebrate communities remained less abundant and less diverse on AR patches and might need more time or specific habitat to get established. Taken together, all studied ecological parameters progressed towards reef recovery, with unique and varying influences of AR design. We recommend reef restoration with a combination of metal cages and layered concrete ARs to promote high fragment survival as well as natural coral recruitment. Further considerations on AR design, ecological facilitation and restoration recommendations are discussed below.

AR design

AR design clearly affected the performance of outplanted coral fragments by mediating the effects of reef organisms causing coral predation and detachment. CoTS predation was less intense than reported by earlier restoration studies in the region (Tamelander et al., 2000; Mbije et al., 2013), but was still causing substantial coral mortality on bottle and cake patches despite low observed densities of the sea star. CoTS were not able to climb metal cages, which explains the higher fragment survival on these ARs. Similarly, predation by corallivorous snails can be reduced using cages, especially when recruitment by snail larvae from the water column is low and colonization of ARs would have to happen by ground-dwelling adult snails (Williams et al., 2014). Coral predation can increase hard coral diversity by selectively targeting fast growing genera (Neudecker, 1979; Cox, 1986), but extensive predation might also induce overgrowth of coral colonies and even full ARs by benthic competitors such as macroalgae (Rice et al., 2019) and soft corals (Bruno et al., 2009; Norström et al., 2009). In this study, fragments that died due to predation were quickly overgrown by soft corals. This space occupation by soft corals can prevent hard coral recruitment, succession and reef recovery (Sammarco et al., 1985;

Norström et al., 2009). Remarkably, also sea turtles hampered efforts to increase hard coral cover by dislodging fragments when scraping the underside of their carapaces on bottle modules. This, in combination with high predation on the same modules, has rendered the bottle design least successful for coral survival. Besides AR design, coral genus was also an important determinant of fragment survival with clear genus-specific mortality causes such as predation (*Acropora* and *Stylophora*) and bleaching (*Pocillopora*). The high but unexplained mortality of *Porites* sp. could possibly indicate that for this species, larger fragment sizes could be needed for outplanting (Seebauer, 2001).

Hard coral recruitment on concrete ARs was moderately high and diverse compared to references reefs and falls within the range of regional averages of around 2 – 8 recruits m^{-2} (Obura et al., 2008; Visram et al., 2009), highlighting the potential of ARs and reef restoration to support key ecological processes (Montoya-Maya et al., 2016; Hein et al., 2020a). The finding that recruit densities on concrete approached densities on natural reef substrates demonstrates that concrete is a suitable substrate for coral recruitment, especially when vertically oriented. Sufficiently high coral recruitment (Graham et al., 2014b) and high outplanted fragment densities (Ladd et al., 2016) can prevent shifts to benthic competitors which could otherwise inhibit reef recovery (Norström et al., 2009; Ladd et al., 2018). The absence of an association between coral cover and recruit densities on AR modules, though, suggests that other factors than nearby hard corals per se are important for coral settlement and survival, such as provision of suitable hard substrate (Hata et al., 2017). Nonetheless, over time, outplanted corals are expected to contribute to reproduction (Horoszowski-Fridman et al., 2011) and local recruitment (Montoya-Maya et al., 2016). For the moment, common recruits mainly included opportunistic brooding genera such as *Pocillopora* and *Stylophora* and the stress-tolerant genus *Porites* (sensu Darling et al., 2012), and it remains unclear if outplanting of once dominant competitive species such as broadcasting *Acropora* will assist their recruitment and comeback in absence of natural recovery (McClanahan et al., 2001, 2014; McClanahan, 2008).

AR design did not affect the composition of fish or invertebrate communities that developed around the restored patches. This contrasts earlier studies, as both AR design (Bohnsack and Sutherland, 1985; Hylkema et al., 2020) and structural complexity (Graham and Nash, 2013) have been shown to be determinants of fish communities (Seraphim et al., 2020). The levels of structural complexity provided by the various studied ARs likely differ and quantification of this structural complexity could help explain the different impacts on reef communities. Provision of fine-scale habitat and food by corals is likely the main driver for development of fish and invertebrate communities on these ARs, as indicated by the association between AR coral cover and fish abundance and biomass in this study. This suggests that hard coral cover is more crucial for reef fish communities than artificially created structural complexity (Coker et al., 2014; Pratchett et al., 2014). Follow-up factorial studies that separate the effects of ARs and outplanted corals on reef communities can help to clarify the benefits of each restoration approach. Interestingly, fish species richness appeared unrelated to both AR design and coral cover, implying that these factors are less important if restoration of fish species richness is the only goal. The difference in fish species composition between AR patches and reference reefs is commonly observed (Higgins et al., 2022), and likely relates to the different coral species composition (Berumen and Pratchett, 2006) and probably additional factors such as AR material, complexity, relative size or age (Hylkema et al., 2021). On a level of dietary guilds, however, the similarity between ARs and reference reefs shows that restored fish communities can support similar trophic roles as natural fish communities (in agreement with Paxton et al., 2020). The effects of AR patch size and condition of the direct surroundings remain to be tested, but extrapolation (Fig. S4) indicates that substantial potential exists for AR patch size to further enhance fish communities, especially in combination with hierarchical spatial arrangement (Bohnsack et al., 1994). The absence of clear patterns for invertebrates might relate to their natural low abundances and high variability (McClanahan, 1989) and comparisons and interpretation are further complicated by the lack of data on this diverse functional group in restoration projects (Hylkema et al., 2021; Higgins et al., 2022).

Ecological facilitation

Fish and invertebrate communities can improve reef recovery when mediating ecological processes in favour of hard cover growth and recruitment (Shaver and Silliman, 2017; Ladd et al., 2018). For example, herbivores can prevent the establishment of macroalgae and thereby create a competitive advantage for corals (Hughes et al., 2007b). Local herbivorous key species such as grazing surgeonfish (Knoester et al., 2019), sea urchins (Humphries et al., 2020) and browsing unicornfish (Knoester et al., 2023) might indeed have controlled macroalgae on ARs in this study, but sessile benthic invertebrates became more abundant over time compared to natural reefs, including contentious competitors of hard coral such as soft corals, tunicates and sponges (Stobart et al., 2005; Bruno et al., 2009). The current grazer community around ARs (despite high abundances of, for example, the sponge and soft-coral eating gastropod *Cypraea tigris*) might not be able to provide sufficient top down control on these often toxic sessile invertebrates (La Barre et al., 1986; Pawlik et al., 2018), which might additionally benefit from elevated nutrient levels in the relatively turbid study area (Pastorok and Bilyard, 1985; Norström et al., 2009). Pre-emptive space occupation by outplanting more hard corals and thereby intensify grazing pressure on smaller areas of remaining open substrate could help to prevent the establishment benthic competitors, but requires outplanting corals at appropriate densities and subsequent high fragment survival (Ladd et al., 2016). Outplant densities used in this study appear sufficiently high to sustain coral cover, except for the Bottle AR that suffered high predation and dislodgement.

Additional ways of ecological facilitation include control of corallivores through predation or for example nutrient cycling by fish (Shaver and Silliman, 2017; Ladd et al., 2018). Natural control of coral-predating invertebrates is important to prevent pest-like outbreaks (Rotjan and Lewis, 2008; Rice et al., 2019), especially as restoration projects generally use coral species susceptible to predation (Cole et al., 2008). As broad trophic roles of the fish community in this study were similar among ARs and reference reefs this could indicate that such functions are being re-established, but more detailed and empirical data on key species would be needed to confirm this. Also, top-down control on adult CoTS was not sufficient to prevent substantial coral predation. To maintain sufficient coral cover on recently established ARs, reducing coral predation directly through AR design or outplanted species selection appears more effective than attempting to regulate corallivore populations indirectly by facilitating their predators.

This suggestion applies in particular to larger adult corallivores, which are less sensitive to predation (Cowan et al., 2017; Shaver et al., 2020b). Excess nutrient inputs by humans are generally detrimental to reef functioning and could promote corallivores (Shantz and Burkepile, 2014; Pratchett et al., 2017), but nutrient recycling by fish communities has been shown to benefit corals on natural reefs (Shantz et al., 2015) and might help to facilitate recovery of degraded reefs (Ladd and Shantz, 2020). For example, the colonization of outplanted corals by planktivorous damselfish can be expected to enhance coupling of pelagic nutrients to restored reefs (Seraphim et al., 2020) and schooling predatory fish can create nutrient hotspots (Shantz et al., 2015). A better understanding of such processes could further improve reef restoration effectiveness (Shaver and Silliman, 2017; Ladd et al., 2018).

Methodological considerations

This study provides a more holistic evaluation of reef ecosystem restoration performance than item-based monitoring only (Bayraktarov et al., 2019; Abelson et al., 2020). For future work, three further methodological improvements are recommended. Firstly, two years is a short time in ecology and this study therefore only represents the early successional stage of reef recovery, although longer than most reef restoration studies (Bayraktarov et al., 2016). Over time, when coral recruits grow, outplanted corals become fertile and benthic cover further increases complexity, AR communities are expected to become more diverse and resemble natural reefs more closely (Thanner et al., 2006), while likely still remaining distinct (Hylkema et al., 2021). Long term monitoring (> 5 – 10 years) will therefore be vital to track succession (Hein et al., 2020b), understand ecological interactions (Seraphim et al., 2020) and ensure functional reefs which continue to provide ecosystem services (Abelson et al., 2020; Hein et al., 2021). Secondly, the long-standing debate on relative contributions of attraction versus production of fish and invertebrates around ARs needs to be clarified (Pickering and Whitmarsh, 1997), especially if the restoration goal is to support sustainable exploitation (Lima et al., 2019; Hylkema et al., 2021). On the studied ARs, the high abundance of damselfish species not regularly encountered on nearby reefs indicate that local production of these small planktivorous fishes is likely, which might in turn support production on higher trophic levels. Abundance and biomass of fishes at nearby natural reefs did not decrease, despite the substantial addition of ARs, which further suggests that ARs were supporting local production. Of course, the relative size of the restored area compared to the surroundings and distance to healthy reefs will be of great influence on this. Incorporation of age cohort monitoring over time will provide more certainty on this aspect (Brickhill et al., 2005). Thirdly, biases in the used methodologies should be noted: observer bias might explain the observed increase in fish species richness over the different years on control and reference patches and this could be addressed by monitoring methods using artificial intelligence (Barbedo, 2022), and the discrepancy between small AR size and large surveyed area for fishes as well as the small areal coverage for benthic surveys ideally are solved by upscaling restoration efforts rather than through adjusted monitoring methodologies.

Restoration recommendations

Concluding, we highlight several recommendations with broader relevance. Firstly, as clearly outlined in restoration guidelines (Precht, 2006; Edwards et al., 2010), causes of coral decline need to be addressed for restoration to be successful. During the current study, fishing efforts still interfered with restoration efforts both directly by dislodging fragments and likely indirectly by affecting the community composition of fish – also on natural reference reefs (McClanahan et al., 2008). Continued efforts to align restoration with protection are therefore crucial (Hylkema et al., 2021). Secondly, at least equally important, adaptation to climate change impacts must be considered. To address this potential threat to restoration success, we used, where possible, presumed temperature-resilient corals (outplanted *Acropora* spp. and other corals that had survived previous bleaching episodes) and we placed ARs slightly deeper to reduce combined heat and light stress. This might have contributed to the low bleaching mortality among most outplanted corals despite significant heat stress during the study. However, the bleaching mortality of *Pocillopora* spp. and the anticipated ever-increasing temperatures clearly show more research is needed to combine ongoing restoration efforts with new techniques such as assisted evolution (van Oppen et al., 2017; NASEM, 2018; Rinkevich, 2019). There should be no doubt, however, that long-term success of coral reef conservation ultimately depends on how soon global greenhouse gas emissions are curbed (Knowlton et al., 2021). Thirdly, the clear effects of AR design and species selection on coral survival highlight the importance of these factors for reef restoration success. A combination of AR designs with species-specific outplanting strategies is recommended to realize high coral cover and diversity: predation-sensitive genera such as *Acropora* can be placed on elevated structures such as cages, whereas predation-resilient corals such as *Millepora* and *Porites* can be put on concrete structures such as layered cakes. In this way, coral cover can be increased quickly using pioneer species while coral recruitment is also facilitated, supporting the development of a more diverse and resilient coral community, which can in turn support the fish community (Horoszowski-fridman and Rinkevich, 2016). Low concrete structures such as bottle reefs are not recommended for coral outplanting, but could be placed specifically to create turtle hangouts in the studied area. Further improvements in coral performance are likely possible by varying outplant density (Ladd et al., 2018) and species composition (Cabaitan et al., 2015). Altogether, considerations of these ecology-based processes have the potential to improve outplanting success even further (Shaver and Silliman, 2017; Ladd et al., 2018). Ultimately, monitoring at socio-ecological relevant scales will determine if reef restoration can support the recovery of coral reefs and their services and thus can be considered an effective, efficient and engaging conservation tool (McDonald et al., 2016; Goergen et al., 2020).

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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.

Author contributions: EG Knoester: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. JJ Rienstra: Methodology, Investigation, Formal analysis, Writing – review & editing. QJF Schürmann: Methodology, Investigation, Writing – review & editing. AE Wolma: Methodology, Investigation, Writing – review & editing. AJ Murk: Conceptualization, Resources, Writing – review & editing, Supervision. R Osinga: Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration.

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Data Availability Statement: The datasets analysed and code used are available as an archived GitHub repository on: https://github.com/ewoutknoester/SurveysAR

Supplementary data

Table S1 *Details on positioning of treatment patches. Reef.dist is the distance to the nearest significant reef feature (i.e. natural coral patch with diameter > 8 m^2 - half the size of the treatment patches). AR.dist is the distance between an artificial reef patch and the nearest neighbouring artificial reef patch. Distances were measured edge to edge. Depth_abs is the depth of a patch, expressed in meters below Mean Low Water*

Treatment	Transect	Reef.dist (m)	AR.dist (m)	Depth_abs (m)
BOTTLE	NT-BRU-1	7.3	11.4	4.5
BOTTLE	NT-BRU-2	23.4	8.1	6.6
BOTTLE	NT-BRU-3	10.0	9.3	6.5
BOTTLE	NT-BRU-4	14.4	15.0	5.7
BOTTLE	NT-BRU-5	9.5	7.0	5.4
BOTTLE	F-BRU-1	12.3	13.5	6.0
BOTTLE	F-BRU-2	7.3	9.5	4.5
BOTTLE	F-BRU-3	17.5	8.5	5.6
BOTTLE	F-BRU-4	9.2	15.5	5.7
BOTTLE	F-BRU-5	8.2	23.1	3.7
CAGE	NT-CAGE-1	6.4	7.7	4.4
CAGE	NT-CAGE-2	9.3	8.1	5.2
CAGE	NT-CAGE-3	8.2	10.7	5.9
CAGE	NT-CAGE-4	6.1	7.0	5.5
CAGE	NT-CAGE-5	3.9	7.5	5.8
CAGE	F-CAGE-1	16.1	6.5	7.1
CAGE	F-CAGE-2	30.8	9.1	4.9
CAGE	F-CAGE-3	9.9	8.0	4.1
CAGE	F-CAGE-4	32.3	11.0	8.2
CAGE	F-CAGE-5	18.1	9.5	8.0
CAKE	NT-CAKE-1	11.7	10.3	4.9
CAKE	NT-CAKE-2	11.4	9.3	6.5
CAKE	NT-CAKE-3	20.1	11.3	7.3
CAKE	NT-CAKE-4	9.7	10.7	7.1
CAKE	NT-CAKE-5	16.2	50.0	6.7
CAKE	F-CAKE-1	10.1	13.5	6.0
CAKE	F-CAKE-2	20.2	9.1	4.4
CAKE	F-CAKE-3	7.6	8.7	5.0
CAKE	F-CAKE-4	15.5	10.7	8.2
CAKE	F-CAKE-5	17.2	13.5	4.3
COMPOUND	NT-COMP-1	18.5	7.7	5.6
COMPOUND	NT-COMP-2	12.4	9.9	5.9

Treatment	Transect	Reef.dist (m)	AR.dist (m)	Depth_abs (m)
COMPOUND	NT-COMP-3	6.4	11.3	5.6
COMPOUND	NT-COMP-4	13.9	15.0	6.3
COMPOUND	NT-COMP-5	14.5	22.7	6.8
COMPOUND	F-COMP-1	16.7	6.5	4.9
COMPOUND	F-COMP-2	16.2	10.8	4.2
COMPOUND	F-COMP-3	10.6	13.5	6.8
COMPOUND	F-COMP-4	11.3	8.5	6.5
COMPOUND	F-COMP-5	8.3	23.1	3.6
CONTROL	NT-R-1	20.7		6.1
CONTROL	NT-R-2	11.5		6.1
CONTROL	NT-R-3	19.3		5.5
CONTROL	NT-R-4	13.8		5.7
CONTROL	NT-R-5	6.2		5.7
CONTROL	F-R-1	8.1		8.3
CONTROL	F-R-2	12.2		9.3
CONTROL	F-R-3	12.7		7.9
CONTROL	F-R-4	8.7		4.7
CONTROL	F-R-5	21.3		5.2
REFERENCE	(NT-R-1)			2.2
REFERENCE	(NT-R-2)			2.0
REFERENCE	(NT-R-3)			2.9
REFERENCE	(NT-R-4)			2.6
REFERENCE	(NT-R-5)			2.6
REFERENCE	(F-R-1)			3.0
REFERENCE	(F-R-2)			1.7
REFERENCE	(F-R-3)			3.3
REFERENCE	(F-R-4)			2.3
REFERENCE	(F-R-5)			0.9

Table S2 *Surface area (m^2) per reef module available for hard coral recruitment. A bottle module consisted of a concrete disk (⌀ 0.5 m; height 0.1 m) filled with on average 8 glass bottles (⌀ 0.075 m; available surface area of 0.043 m^2 per bottle) and a 20-cm iron handle (⌀ 12 mm). An iron (⌀ 12 mm) cage module consisted of three 3-m crossbows, a lower ring of 4.2 m, a middle ring of 3 m and a top ring of 1.8 m length (the base ring was placed in rubble, thus not suitable for recruitment). A layered cake module consisted of four concrete disks (0.1 m height each): the bottom two were of similar size (⌀ 0.6 m) as were the top two disks (⌀ 0.4 m). Disks were separated using 4 PVC pipes (⌀ 51 mm): the lower disks separated by 10 cm and both sets of disks on top separated by 5 cm. It was assumed that only the concrete area receiving direct incident light straight from above (with an additional 5-cm 'shadow' margin) would be available for coral recruitment. The cake's top and second disk from below each had eight 5-cm PPR pipes for attachment of outplanted corals*

	Concrete (top)	Concrete (side)	Glass	Iron	PPR	PVC
Bottle	0.16	0.16	0.34	0.01	-	-
Cage	-	-	-	0.68	-	-
Cake	0.48	0.63	-	-	0.04	0.15

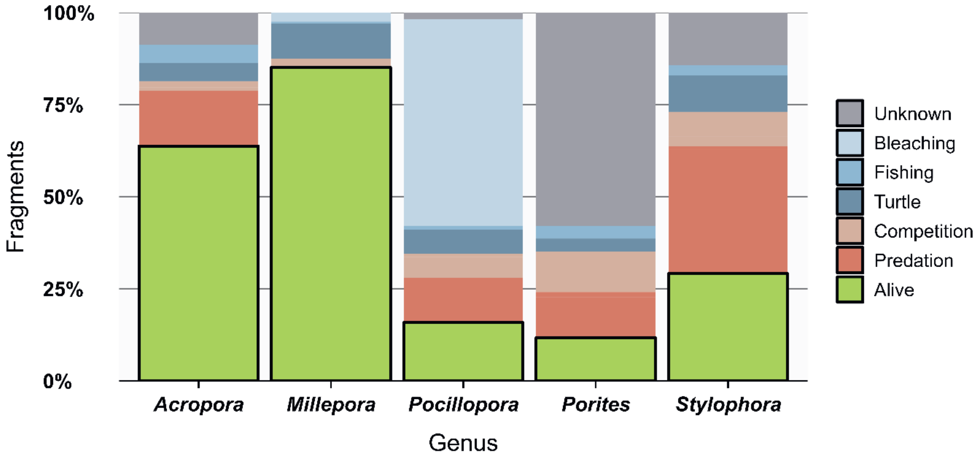


Figure S1 *Survival of coral fragments (pooled across treatment patches, N = 4256 fragments) two years after outplanting, split per genus (*Acropora *spp. n = 3580,* Millepora *spp. n = 201,* Pocillopora *spp. n = 107,* Porites *sp. n = 145 and* Stylophora *spp. n = 223). The percentages of surviving fragments are outlined in black. The remainder of fragments did not survive and their putative cause of death has been indicated: bleaching (mortality due to above-average water temperatures), fishing (detachment due to entanglement in fishing gear), turtle (detachment due to interaction with sea turtles), competition (mortality due to competing benthic organisms such as tunicates, sponges and soft coral), predation (consumption by crown of thorns sea stars or* Drupella *spp. snails) or unknown cause of death*

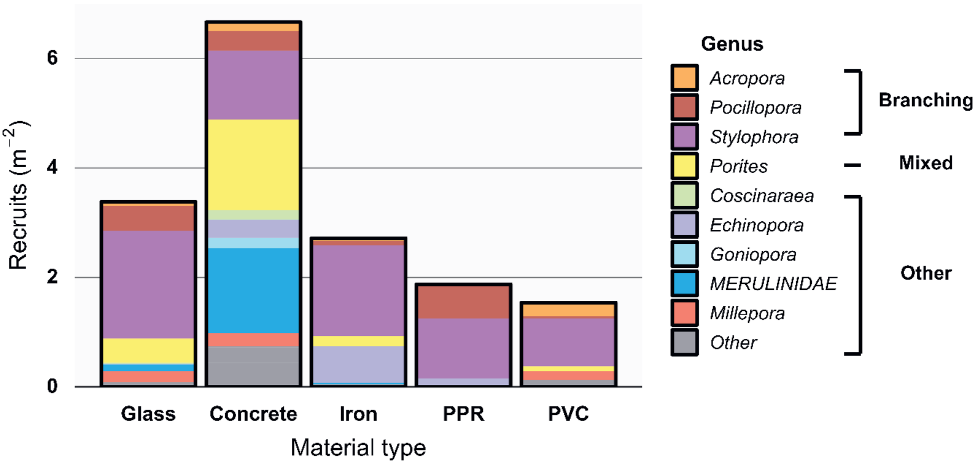


Figure S2 *Hard coral recruit density (colonies 1 - 10 cm diameter, including hydrozoan* Millepora*) two years after deployment of restored patches, split per material type. Average densities were calculated per material per patch (Bottle n = 20, Concrete n = 50, Iron n = 50, PPR n = 20, PVC n = 20). Colours represent coral genera, split between branching corals and other growth forms. NB: PPR and PVC were used to support outplanted corals and concrete disks of the Cake design, respectively, and were therefore more shaded than the other material types*

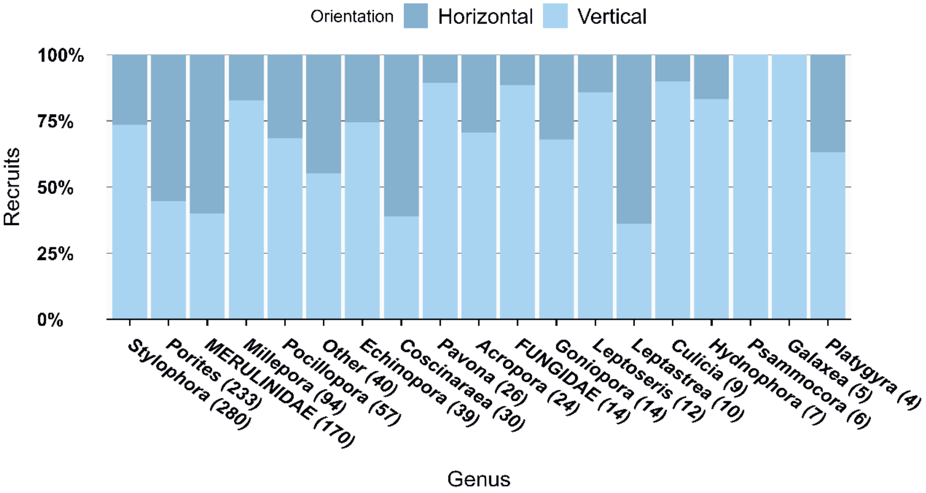


Figure S3 *Percentage of hard coral recruits (based on recruit densities) between 1 – 10 cm size that settled either on horizontal or vertical sides of concrete used across artificial reefs. Data is shown for the most common genera; numbers in brackets note total number of recruits for each genus. The group Other includes 17 genera that were each observed less than 3 times*

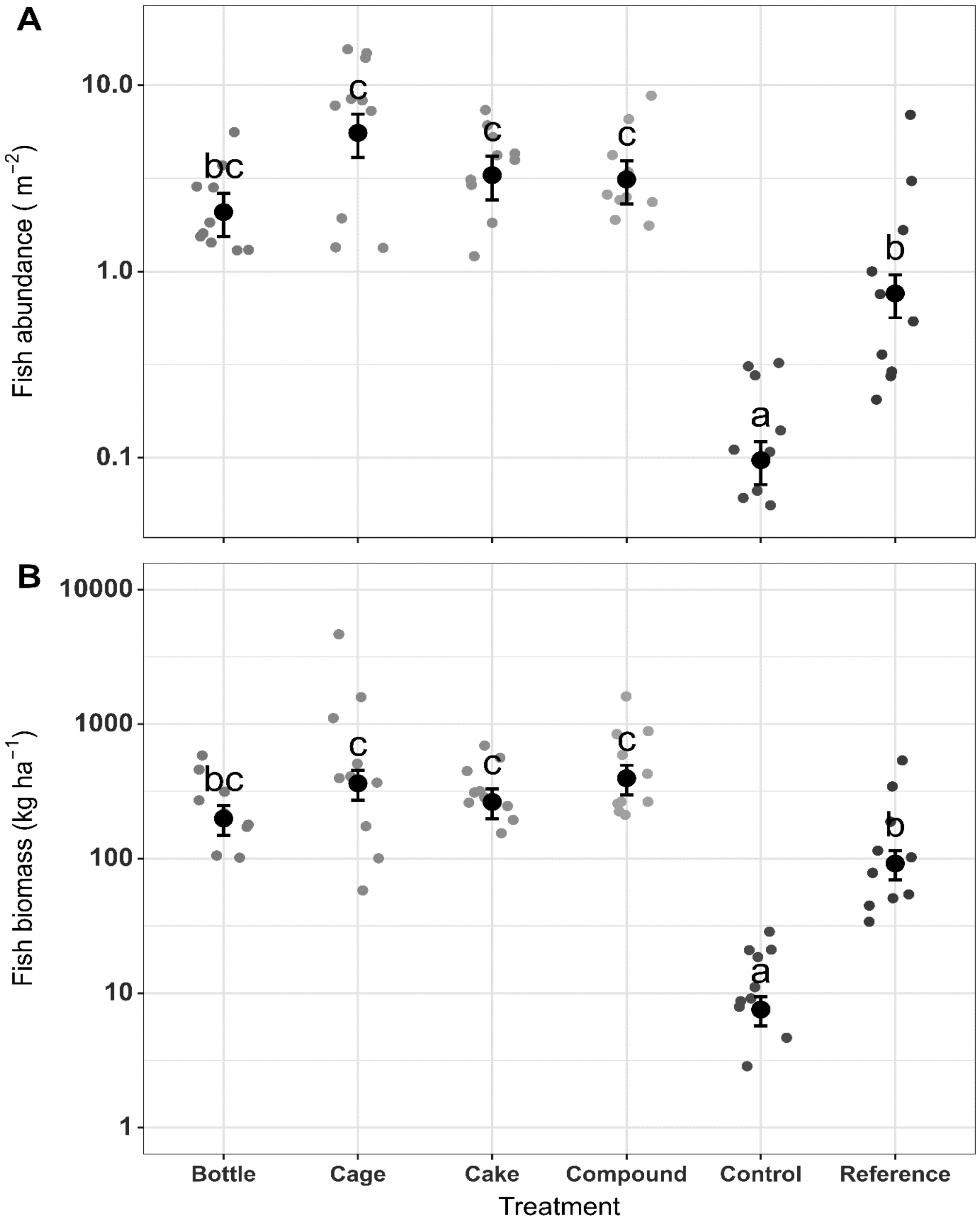


Figure S4 (A) *Estimated fish abundance and* ***(B)*** *estimated fish biomass two years after deployment of restored patches, compared to unrestored Control patches and natural Reference patches. To calculate the estimated abundance and biomass on the four types of artificial reefs (each 16 m^2), the values were not divided by the total survey area (~177 m^2), but by a smaller area actually restored of 16 m^2. These results are therefore a rough indication what might be expected in terms of fish abundance and biomass if the entire survey area had been filled with artificial reefs. Error bars denote SE (n = 10) and treatments not sharing lowercase letters differ significantly ($p < 0.05$). Coloured points indicate values for replicate patches within each treatment*

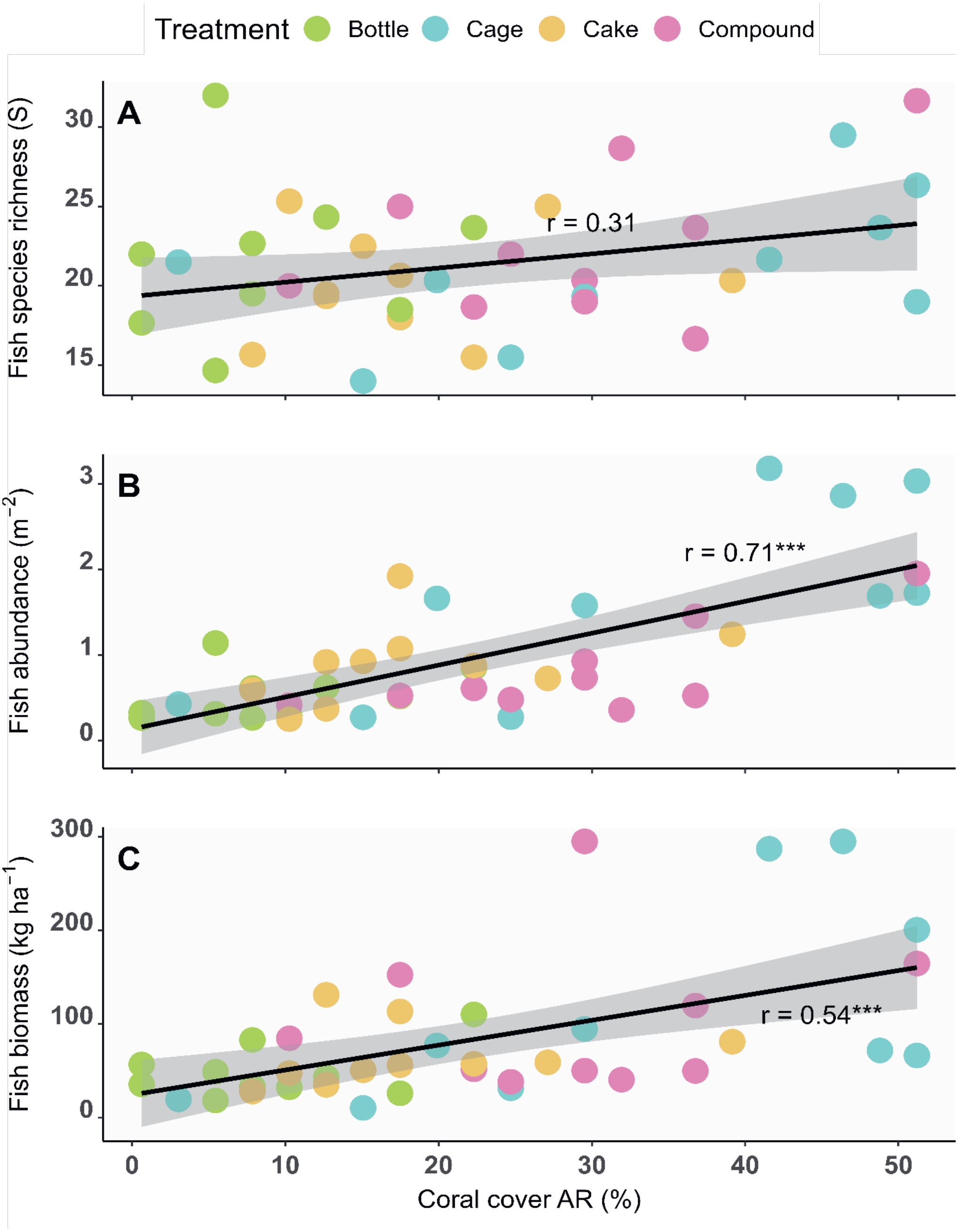


***Figure S5** Pearson correlations between percentage hard coral cover on artificial reef patches and **(A)** fish species richness **(B)** fish abundance and **(C)** fish biomass. The four different types of artificial reef patches (n = 10) are coloured. Linear trend lines and their 95% confidence interval are added and their associated Pearson correlation coefficient with significance is indicated (*p < 0.05, **p < 0.01, ***p < 0.001)*

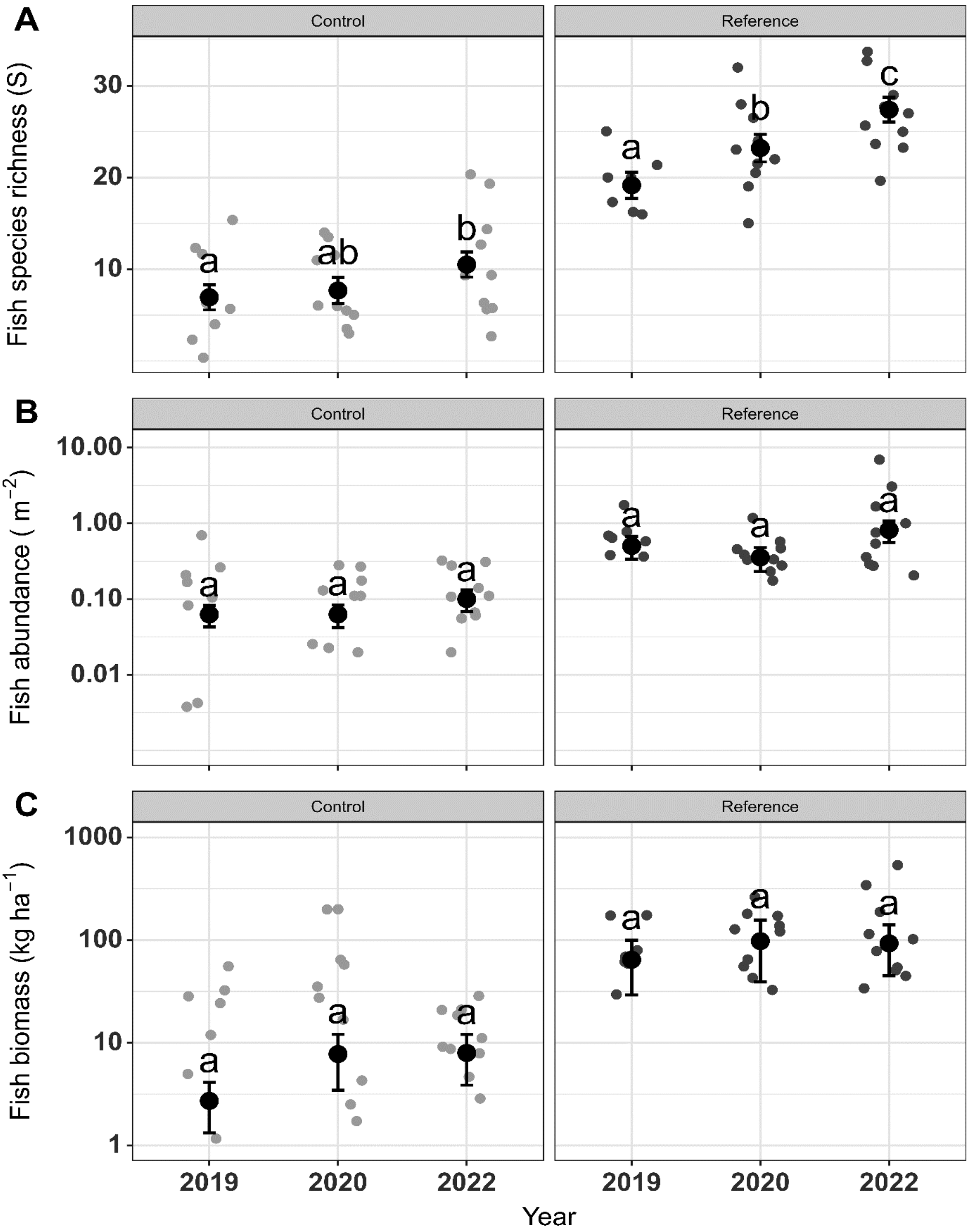


Figure S6 *(A) Fish species richness* ***(B)*** *Fish abundance and* ***C*** *Fish biomass at unrestored Control patches and natural Reference patches over time. Both Control and Reference patches were situated at least 50 m from restored patches, which were restored after the 2019 surveys. Coloured points indicate values for replicate patches within each Year. Error bars denote SE (n = 7 - 10) and treatments not sharing lowercase letter differ significantly ($p < 0.05$). A significant interaction between treatment and time was found on species richness ($X^2 = 6.71$, $df = 2$, $p = 0.0349$)*

Table S3 *Bray-Curtis dissimilarity matrix of fish species community composition between restored patches, unrestored Control patches and natural Reference patches, all n = 10. Higher values indicate greater dissimilarity, with 1 indicating completely different fish communities and a 0 indicating exact similar fish communities. Values below 0.5 are coloured green and values above 0.5 are coloured red, with darker tones indicating greater similarity/dissimilarity*

	Bottle	**Cage**	**Cake**	**Compound**	**Control**	**Reference**
Bottle	0.69					
Cage	0.82	0.82				
Cake	0.70	0.81	0.69			
Compound	0.75	0.77	0.73	0.72		
Control	0.82	0.88	0.86	0.88	0.81	
Reference	0.88	0.92	0.90	0.90	0.93	0.87

Table S4 *Bray-Curtis dissimilarity matrix on fish species' diet level composition between restored patches, unrestored Control patches and natural Reference reefs, all n = 10. Higher values indicate greater dissimilarity, with 1 indicating completely different fish communities and a 0 indicating exact similar fish communities. Values below 0.5 are coloured green and values above 0.5 are coloured red, with darker tones indicating greater similarity/dissimilarity*

	Bottle	**Cage**	**Cake**	**Compound**	**Control**	**Reference**
Bottle	0.49					
Cage	0.63	0.65				
Cake	0.52	0.62	0.53			
Compound	0.58	0.61	0.53	0.53		
Control	0.64	0.75	0.73	0.76	0.58	
Reference	0.62	0.67	0.62	0.61	0.79	0.64

Chapter 7

General discussion

This thesis aims to improve our understanding on the role of biological facilitators on natural reefs, explore how this knowledge can be used to facilitate these facilitators in coral mariculture and reef restoration approaches and, ultimately, to improve the efficiency and success of coral gardening. This final chapter starts with a summary of the main findings, which will be further discussed in specific subsections.

Several keystone species from the diverse reef community were identified that fulfil important functional roles on the studied natural reefs, coral nurseries and restored patches. Bristletooth tangs (*Ctenochaetus* spp.) were the principal grazing herbivorous fish that kept biofouling from establishing on coral nurseries and thereby improved coral growth and survival (Ch. 4 & 5). This species was particularly important in areas where overall herbivorous biomass was low. Facultative corallivorous fishes such as parrotfishes (Subfamily Scarinae) were associated with considerable predation on recently-outplanted corals (Ch. 3). Parrotfishes were also identified as important herbivores consuming macroalgae on natural reefs and, together with unicornfishes (*Naso* spp.), these browsers can insure macroalgae control in case grazing pressure becomes compromised (Ch. 2). The dual herbivorous and corallivorous role of parrotfishes highlights some of the ecological complexities on coral reefs (Mumby, 2009). Ecological complexities were further exemplified by territorial damselfishes. These feisty fishes only consumed low absolute amounts of macroalgae on otherwise fish-depauperate natural reefs (Ch. 2), yet were also found capable of preventing macroalgae establishment on coral nurseries (Ch. 5). Identified keystone species were observed at all restored reef types and were not strongly associated with any specific AR design. The overall trophic structure of fish communities at the restored reefs was similar to that of natural reference reefs (Ch. 6). At several restored patches, high outplant densities of pioneer corals (mainly *Acropora* spp.) attracted another keystone species: the coral-devouring crown-of-thorns sea star (*Acanthaster* sp.), which consumed a substantial amount of outplanted corals (Ch. 6). Whereas the ecological roles of some of the identified keystone species such as parrotfishes, unicornfishes and crown-of-thorns sea stars were already known (Puk et al., 2016; Pratchett et al., 2017), other functional roles such as grazing by bristletooth tangs and territorial damselfish were more surprising (Hoey and Bellwood, 2010b; Tebbett et al., 2017). Altogether, this highlights the value of empirically identifying keystone species and quantifying their functional roles, which can be either locally unique or globally comparable.

Although the exact composition of keystone species was unmistakably site-specific, the broad functional roles fulfilled by the keystone species allow for at least two ecological generalizations that might universally benefit coral gardening approaches. First, the free bio-assisted cleaning of coral nurseries by herbivorous fishes can be facilitated by placing nurseries close to functional natural reef patches and thereby benefit coral performance (Ch. 4). These benefits will be especially strong when coral nurseries are positioned within a marine protected area, reinforcing herbivory and possibly additional key ecological processes such as nutrient cycling by fish (Ch. 2 & 5). Second, the high predation on outplanted corals by invertebrate corallivores can be effectively prevented by using elevated AR designs to limit accessibility (Ch. 3 & 6). Other ecological processes still remain too equivocal to allow for general guidelines. The top-down control of benthic competitors such as soft corals appeared limited around outplanted hard corals, and potential facilitative keystone species that constrained the soft coral outgrowth were either not identified or were not clearly associated with any particular AR design (Ch. 6). The opposing impacts of parrotfishes and damselfishes on coral performance complicate the unambiguous establishment of their roles in restoration and conservation (Ch. 3 & 5). Biological top-down control of invertebrate corallivores by fish or invertebrate predators was neither evidently related to fisheries management nor to AR design (Ch. 3 & 6). While it may not be easy to unravel some of these ecological processes and pathways in the highly complex coral reef system (Delgado and Sharp, 2020), the strong effects of several keystone species indicate that a greater understanding could be worth pursuing. Comparable to the optimized coral nursery strategy, the identification and quantification of the role of these keystone species in the reef recovery ecology and the effects of fisheries management can all help to find ecological solutions that facilitate grazing and reduce predation around outplanted corals.

While further improvements are likely to come with increased ecological understanding, applying presently learned lessons can already improve restoration outcomes right now. Using the bio-assisted cleaning services of herbivorous fish around coral nurseries, human-assisted cleaning costs can be reduced or even completely omitted whilst coral survival in nurseries remains far above benchmark values of 80% (Schopmeyer et al., 2017). By applying difficult to access, elevated AR designs, outplanted corals performed appreciably better than survival benchmark values of 75% for outplanted corals (Schopmeyer et al., 2017). This coral performance was considerably better compared to corals in treatments that did not benefit from such ecological facilitation and is, notably, also well above globally reported restoration averages of around 60% survival for outplanted corals (Boström-Einarsson et al., 2020). In terms of coral recruitment and fish and invertebrate communities establishing around restored patches, levels comparable to reference reefs were quickly achieved without any noticeable reductions on surrounding natural reefs. These are all clear examples that important resilience indicators of functional corals reefs such as complexity, community composition, coral cover and coral recruitment can be positively influenced by local restoration efforts (Anthony et al., 2015) and, in return, restoration efforts benefit by the existence of ecologically healthy surrounding environments. This latter finding confirms the recently suggested, but largely untested, assertions that integration of ecology with reef restoration practices can improve the success and cost-effectiveness of restoration efforts (Shaver and Silliman, 2017; Ladd et al., 2018). Additional improvements using new ecological insights are undoubtedly possible (Omori, 2019) and further work can build upon the gained insights and remaining questions of this thesis.

The remainder of this general discussion will focus on a set of themes that place the results of this thesis in the broader spectrum of coral reef restoration and conservation. These themes include the high potential of facilitation in reef restoration, the complex role of biodiversity in conservation, the reliance on natural succession in restoration and lastly the effectiveness of present-day coral reef conservation. This discussion will culminate in a set of practical recommendations and future perspectives.

Facilitating the facilitators

Coral nurseries have proven to be a valid and practical way to mass produce coral colonies (Lirman and Schopmeyer, 2016; Vaughan, 2021). Especially mid-water nursery designs are effective as they hamper access by ground-dwelling corallivores, while still allowing herbivorous fish to control biofouling (Frias-Torres and Van de Geer, 2015). In addition, corallivory by fish in mid-water nurseries was found to be limited. Still, some restoration projects have experienced mid-water nursery infestations by small invertebrate corallivores such as *Drupella* spp. snails (Shafir et al., 2006b) and *Phestilla* sp. flatworms (Dehnert et al., 2021), which likely recruited as larvae from the water column. Ecological solutions to such infestations can be sought through site selection: nurseries near natural reef patches might not only allow herbivorous fish to visit nurseries, but could also invite invertivorous fish to exert predation control on such invertebrate pest species (Shaver and Silliman, 2017). In this thesis, the limited impact of fish predation, the lack of invertebrate corallivore recruitment yet the satisfactory levels of herbivory all demonstrate that nursery placement close to a functional natural reefs can improve nursery performance. An additional benefit of close proximity to natural fish communities could include nutrient cycling by fish (Huntington et al., 2017). Excess nutrient inputs by humans are generally detrimental to reef functioning, but the type and frequency of nutrient pulses excreted by fish can be beneficial to corals (Shantz & Burkepile 2014; Shantz et al. 2015). Also co-culture of corals with symbiont crabs (Dehnert et al., 2022) or herbivorous invertebrates such as sea urchins (Serafy et al., 2013) or gastropods (Toh et al., 2013) could potentially further improve nursery success. Thus, mid-water nurseries are already highly effective to mass produce corals and cleaning maintenance costs may approach zero when site selection facilitates natural herbivores. Yet, even further improvements in coral growth and survival are possible by including additional mutualistic ecological interactions (Shaver and Silliman, 2017; Ladd and Shantz, 2020).

The scope for improvements is considerably greater for the second phase of coral gardening, as outplanting of corals is invariably associated with both higher costs and lower survival (O'Donnell et al., 2017; Omori, 2019). The use of ARs may be inevitable when solid substratum is absent, but increases costs further. When well designed, however, ARs can also provide additional - yet still poorly quantified - benefits (Ceccarelli et al., 2020; Higgins et al., 2022). Two major impediments that frequently hinder the successful establishment of outplanted corals are corallivory by fish or invertebrates (Tamelander et al., 2000; Mbije et al., 2013; Cabaitan et al., 2015; Horoszowski-Fridman et al., 2015; Page et al., 2018) and competition with for example macroalgae, soft corals, sponges and tunicates (Higgins et al., 2022). As shown in this thesis, a poorly accessible, elevated AR design can effectively limit predation by invertebrate corallivores. To reduce coral predation on the more durable ground-based ARs such as layered cakes and to limit the impact of corallivorous fish, the identification of additional ecological levers are needed. Avenues worth exploring include outplanting a mixture of palatable and unpalatable coral species (Cabaitan et al., 2015; Rivas et al., 2021), adjusting coral densities (Ladd et al., 2016) and sizes (Jayewardene et al., 2009), smartly choosing the outplanting season (Horoszowski-Fridman et al., 2015) or facilitating corallivore's enemies (Delgado and Sharp, 2020; Tiddy et al., 2021). For benthic competition, no clear AR design effects were observed and fouling communities were broadly comparable across different structures and materials. Indirect effects of AR design that could facilitate top-down control of benthic competitors were not evident either, as all studied ARs hosted functionally similar fish communities and invertebrate densities. Furthermore, identified keystone herbivores were not closely associated with any AR design. Nonetheless, macroalgae were sparse and other benthic competitors such as soft corals mainly followed opportunities (i.e. occupying spaces that were left open) rather than caused hard coral declines through direct competition. Thus predation exceeded competition in terms of impact on coral performance in this thesis, though the influence of benthic competitors could grow over time (Perkol-Finkel and Benayahu, 2005), especially when reducing hard coral recruitment. To improve the performance of outplanted corals and evaluate the effectiveness of ARs, additional experiments to reduce coral predation and long-term monitoring (> 10 y) of benthic community development are both needed (Ladd et al., 2018; Hylkema et al., 2021). The appearance of recruits of several species of hard corals on some of the AR designs is promising in this respect, as this could indicate that the benthic community might stabilize and more closely resemble that of healthy natural reef patches over such longer periods.

One feature of AR design that has the potential to influence a broad range of facilitative ecological interactions is structural complexity. On natural reefs, structural complexity mainly results from the continuously opposing forces of accreting reef organisms such as hard corals against biological and physical erosion, and this complexity is what largely underpins the biodiversity and functioning of coral reefs (Pratchett et al., 2008; Graham and Nash, 2013; Emslie et al., 2014; Darling et al., 2017). Reef complexity supports biodiversity by providing refuges of different sizes against predation, creating environmental gradients that allow for niche development and moderating density-dependent competition (Ceccarelli et al., 2020). Similarly, structural complexity of ARs can support diverse communities (Seraphim et al., 2020) that can further support coral performance and coral recruitment (Yanovski and Abelson, 2019). From this thesis and several of other studies (e.g. Rogers et al. 2018; Graham 2014), it is evident that structurally-eroded reefs cannot accommodate a functional reef community and coral rubble hampers reef recovery. Reef restoration can help to return this complexity by using ARs. A relatively limited amount of structural complexity might already be sufficient to support a large share of the fish community (Rogers et al., 2018). More important even, as shown in this thesis, is the addition of corals such as branching *Acropora* spp. providing fine-scale complexity to further assist community recovery by providing habitat and food for juvenile and specialized species (Feary et al., 2007; Coker et al., 2014; Pratchett et al., 2014). Zooming out, complexity on a seascape level can be created by varying the size and configuration of ARs and spaces in between that allow habitat heterogeneity, and this might further improve reef resilience by increasing reef connectivity and, possibly, reef biodiversity (Horoszowski-fridman and Rinkevich, 2016). Follow-up studies have ample of opportunities to further explore this by better quantification of a broader range of complexities, ranging from individual AR structures and their texture to spatial plot design and seascape heterogeneity.

Biodiversity blowback

The role of biodiversity in providing resilience to ecosystems has been long debated and remains ambiguous for coral reefs (Mora et al., 2011; Tilman et al., 2014; Duffy et al., 2016).

A high biodiversity can be expected to provide resilience through a high diversity of feedback responses to a disturbance as well as a high redundancy in species' functional roles (Nyström et al., 2008). The presence of a limited number of keystone species makes ecosystem functioning vulnerable as resilience largely depends on a few key species whose essential functions might not simply be replaced by other species (Bellwood et al., 2003; Mouillot et al., 2013). The ecological role of keystone species can also be replaced by species that only partially fulfil the original functions, and sometimes bring unwanted consequences. For example, sea urchins that can replace macroalgae consumption by herbivorous fish can also contribute to reef erosion (Carreiro-Silva and McClanahan, 2001). The identification of keystone species is therefore important to understand and to manage functioning reefs, but further complicated by spatial, temporal and behavioural variation of species (Bennett and Bellwood, 2011; Lefèvre and Bellwood, 2011; Puk et al., 2016). In addition to biomass estimates of potential keystone species, therefore, the empirical determination of functional processes is crucial (Nyström et al., 2008; Bellwood et al., 2019). The identification and conservation of key functional species and roles might be more realistic given current day stressors than attempting to maintain the full diversity of coral reefs (Brandl et al., 2019). While the reliance on a few species for crucial ecosystem functions can be vulnerable to disturbances, it also provides opportunities: the identification and support of a few species could help to assist reef recovery. Only when sufficient studies have empirically established the connection between species composition and functional processes such as herbivory and predation, then simpler surveys might suffice to determine the suitability of a site for restoration. As our understanding on the complex links between biodiversity, keystone species and coral reef recovery is still limited (Bellwood et al., 2019), pilot studies will remain decisive for restoration projects to see if the local species composition is supportive of recovery before upscaling should be considered (Edwards et al., 2010). The studies presented in this thesis provide a useful template for the execution of such pilot studies.

Succession and success

The coral gardening approach crucially depends on natural succession to achieve ecosystem recovery (Horoszowski-fridman and Rinkevich, 2016). It is not realistic to establish an entire functional reef at once (Edwards et al., 2010), but instead to kick-start recovery processes by taking advantage of positive feedback loops and facilitative interactions by keystone species. For example, outplanting of pioneer coral species like *Acropora* spp. can increase herbivory rates by providing habitat for herbivores and also improve coral recruitment by providing settlement cues and increasing the adult coral stock (Ladd et al., 2018). The density or diversity of corals needed to effectively initiate these recovery processes remains largely unknown and likely depends on the local reef community composition. Furthermore, outplant density involves a trade-off between restoration costs and recovery rate: higher densities of coral presumably reduce recovery time, but at increased costs. Identifying the minimum threshold of outplanted corals that can survive, grow, stimulate recruitment and thus prevent a shift to benthic competitors can help identify a most cost-effective restoration approach. In this thesis, an outplanting density of 7 corals m^{-2} successfully stimulated these processes, with varying responses per AR reef type. Pervasive benthic competitors that can undermine this approach and reef resilience in general have received considerable scientific attention, especially macroalgae and the herbivores controlling them (Carpenter, 1986; Hughes, 1994; Williams et al., 2019). However, at the restoration site studied here, not macroalgae but soft corals were quick to dominate open space, indicating that these and other understudied but ubiquitous benthic competitors warrant more attention (Bruno et al., 2009; Norström et al., 2009). Even though soft corals did not appear to actively outcompete established hard corals, their quick occupation of bare substrate and dead coral skeletons prevents recruitment of new hard coral and may hamper coral diversification. It is not yet known whether soft corals will effectively halt succession towards reef recovery or whether a gradual shift will occur towards coral dominated reefs over the years. Information lacks on factors that could control the often toxic soft coral populations (La Barre et al., 1986) and this knowledge would further support options for implementation of new ecological solutions. Investigation of the relative importance of both top-down control by predators or grazers and bottom-up processes such as food provision by strong currents on soft coral populations are suggested first steps (Fabricius, 1997; Fox et al., 2019). Interestingly, soft corals were barely recruiting on coral nurseries due to continuous grazing on these smooth surfaces by herbivorous fish, whereas the microtopographic complexity of ARs provided refuges for soft coral settlement. Nonetheless, depending on AR design, this complexity also facilitated hard coral recruitment and corals that were not predated increased the overall coral cover. This shows that despite some predation and competition setbacks the coral gardening approach with moderate density and diversity of pioneer species on certain ARs can support initial reef recovery processes.

Recently, a number of restoration projects have increased the diversity of outplanted coral species and growth forms in an attempt to skip the initial stages of succession and directly install a more diverse and resilient coral community (Horoszowski-fridman and Rinkevich, 2016). A key technique that enabled this shift is microfragmentation (Forsman et al., 2015): breaking corals into small species of a few polyps that show high growth rates and this substantially reduces the nursery time needed to culture slow-growing, massive corals. Adding massive corals to the mix of currently mostly outplanted branching corals could help to increase the resilience of restored reefs against common stressors such as predation, diseases and temperature anomalies (Darling et al., 2013). However, the incurred costs and required infrastructure to culture massive corals are higher too (Boström-Einarsson et al., 2018). Monitoring and comparisons of the costs and long-term ecological success between these pioneer and diversity approaches are critically needed to identify which method is most cost-effective under what circumstances. Much work remains to be done here, and similar comparisons are needed for other developing restoration techniques such as substrate stabilization (Ceccarelli et al., 2020) and coral larval attraction enhancement (dela Cruz and Harrison, 2017). Each approach has its specific benefits and associated price tag (Bayraktarov et al., 2019) and reef restoration will mature as a conservation tool when reef managers can decide with reasonable certainty, based on the status of their reefs and the desired timeline of recovery, which approach will be most cost-effective.

Choosing an appropriate restoration approach also depends crucially on the restoration aims and therefore the desired endpoint: when is a reef deemed restored? Following a strict definition, restoration is “the act of bringing a degraded ecosystem back into its original condition" (Edwards et al., 2010). Even if one would consider the condition of reefs in the pre-industrial era as original (which is debatable given the long history of artisanal fishing; McCauley et al. 2015), a return to this condition is not possible given the ongoing multiple, continuous and sometimes synergistic local and global human impacts on the environment (Graham et al., 2014a; McClanahan et al., 2019). Even reefs that have managed to recover naturally from acute disturbances without restoration interventions often demonstrate substantial community shifts (Berumen and Pratchett, 2006; Cheal et al., 2008). Rather than pushing for the unrealistic return to pristine reefs, a more appropriate restoration course would be to discuss, identify and pursue local goals and aims together with relevant stakeholders. For the studied project as well as many other reef restoration projects, this entails the already challenging task of maintaining or returning a self-sustaining reef that continues to provide relevant ecosystem services throughout the next decades (Hein et al., 2020b). This means that those restored reefs most likely will look different than former reefs (Rinkevich, 2015; Hylkema et al., 2021) , but they may become comparable to the inevitably changing natural reefs in the same area. It is imperative, however, that clear goals for reef restoration are formulated and that long-term monitoring is pursued at relevant ecological, social and economic scales to evaluate project progress (Hein et al., 2017, 2020b). Without clear goals or appropriate monitoring, reef restoration will not gain the credibility it needs as a conservation tool (Hein et al., 2020b; Ferse et al., 2021) and could instead become an easy target for promotional or even greenwashing projects that do not achieve real benefits (Bruno, 2021).

Restoring reefs

The ongoing monitoring and comparisons of reef restoration approaches across projects will contribute to the development of more cost-effective and scientifically-validated restoration techniques. However, without controlling both local and global stressors any reef restoration effort will ultimately fail (Anthony et al., 2011). A hierarchy can be distinguished in these intertwined conservation prerequisites: control of global stressors is needed for successful long-term local coral reef conservation (Heron et al., 2017; Hughes et al., 2017) and effective local conservation is a prerequisite for successful restoration efforts (Edwards et al., 2010). In other words, reef restoration can neither replace nor succeed without strong conservation actions such as enforced fisheries management and pollution control. In addition, urgent climate action is needed at global scale. Both restoration and local conservation actions have the potential to increase the resilience and persistence of reefs while global challenges are being tackled (Anthony et al., 2015; Knowlton et al., 2021). The globally modest yet locally important role of reef restoration is to assist recovery of degraded reefs that are limited in natural coral recruitment or suitable substrate (Possingham et al., 2015; Rogers et al., 2015; Rinkevich, 2019; Duarte et al., 2020). Attained benefits from locally restored ecosystem services and even the persistence of coral reefs globally can be extended if such restoration happens in identified climate refuge areas (Beyer et al., 2018). Such holistic views and management efforts in which various conservation actions are simultaneously applied are crucial in today's ecosystems where human impacts are ubiquitous (Abelson et al., 2020). These numerous and complex linkages, like in the reef ecosystem itself, also provide opportunities: the small-scale restoration efforts and associated educational opportunities could for example serve as a catalyst that stimulates local marine protection among involved communities and inspire climate action among visiting tourists (Lirman and Schopmeyer, 2016). The web of human impacts has evidently resulted in the large-scale destruction of coral reefs; using this connectedness to harmonize solutions is a daunting yet worthwhile path to reef recovery.

Fisheries management has traditionally been and will remain a central local management tool as basis to conserve coral reefs (Bellwood et al., 2004; Burke et al., 2011; Graham et al., 2011). Synergies with restoration include the protection of keystone herbivores (Edwards et al. 2014; this thesis), regulation of corallivore species (Dulvy et al. 2004; this thesis) and prevention of overharvesting around ARs (Hylkema et al., 2021). Regarding herbivory, the restriction of fishing activities has stimulated algal removal on some studied reefs (Mellin et al., 2016; Bonaldo et al., 2017), but not on others (Ledlie et al., 2007). The discrepancy could be explained by numerous factors including differences in the effectiveness, size, habitat complexity or age of protected areas (Edgar et al., 2014). Furthermore, as found in this thesis and other studies (Graham et al., 2014b), a relatively low abundance of herbivores appear already sufficient for algal control at some reefs and circumstances and some sustainable harvesting seems possible. The results from protection of top predators to control of corallivores are not yet clearcut and this might relate to the higher complexity and multiple trophic links (McClanahan et al., 2011; Bruno et al., 2019). Also, protection of highly mobile top predators in often small protected areas seems to be inadequate as these species often travel hundreds of kilometres (Cinner et al., 2018). Lastly, the long-standing fisheries debate whether ARs (and restored reefs) will simply attract or actually contribute to the production of reef organisms (Bohnsack, 1989) is less relevant when restoration is integrated with conservation (Hylkema et al., 2021), as long as restored reefs do not undermine the functioning of nearby natural reefs. Marine protection clearly is not a silver bullet, but neither are climate action or restoration: a combination of efforts at connected spatial scales is foreseen as the most effective approach to safeguard coral reefs.

In addition to the three-tiered coral reef conservation approach of local management, active restoration and climate action, there are emerging techniques that attempt to increase coral resilience against contemporary and expected stressors. These techniques have the potential to improve restoration efforts even when some stressors persist and include assisted evolution, assisted migration and microbiome manipulations (NASEM, 2018). Current implementation of these techniques would be premature and pose the risk of numerous known and unknown negative side effects, yet investments to understand both the potential and perils of these techniques are now timely as development may still take many years (Anthony et al., 2020; Hein et al., 2020b). The techniques might become pivotal to support future restoration success, yet can also result in immediate trade-off induced deficiencies in coral physiology or reduced resilience against other stressors. For example, corals with *Durusdinium* symbionts have higher temperature resilience during heat stress, but are also associated with lower growth during cooler periods and may therefore become outcompeted (Jones and Berkelmans, 2010). Other emerging approaches include environmental manipulations that influence regional temperatures or ocean chemistry (NASEM, 2018). The unknown side effects of these techniques could be immense and, moreover, such interventions reduce the adaptation capacity of corals and therefore require long-term sustained efforts (NASEM, 2018). In contrast to such engineering attempts, the above described physiological and genetic techniques are designed to speed up adaptation to future conditions and are therefore preferred. These techniques require successful mariculture of corals and establishment onto natural reefs (van Oppen et al., 2017) and are therefore also dependent on continued efforts to improve the scale and cost-effectiveness of more basic restoration techniques such as coral gardening.

Half of the live coral cover has already been lost from reefs worldwide and while restoration projects have increased coral cover locally, support of reef functioning and ecosystem services of even a local reef remains undemonstrated. Clearly, upscaling is needed to evaluate and manifest the potential positive impacts of reef restoration (Mumby and Steneck, 2008; Boström-Einarsson et al., 2020). Ecological facilitation to speed up succession and recovery as described in this thesis could enable part of this upscaling. Community involvement could allow for a substantial part of upscaling as well, especially in the numerous countries where such livelihood opportunities can substantially improve human wellbeing. Given the immense economic value of coral reefs (Costanza et al., 2014), a prodigious rise in their conservation spending is not just necessary but also justified (ICRI, 2018). Using these resources to actively involve reef users in the protection of their local reefs, the restoration of degraded areas and the monitoring of associated ecosystem services will all positively influence their environmental awareness and stewardship (Hein et al., 2019). These and additional alternative sustainable livelihoods can further reduce local pressures on coral reefs (Woodhead et al., 2019). Coastal societies can become part of a transformation away from boundless natural exploitation towards maintaining and restoring the natural capital upon which we all ultimately depend.

Conclusion & perspectives

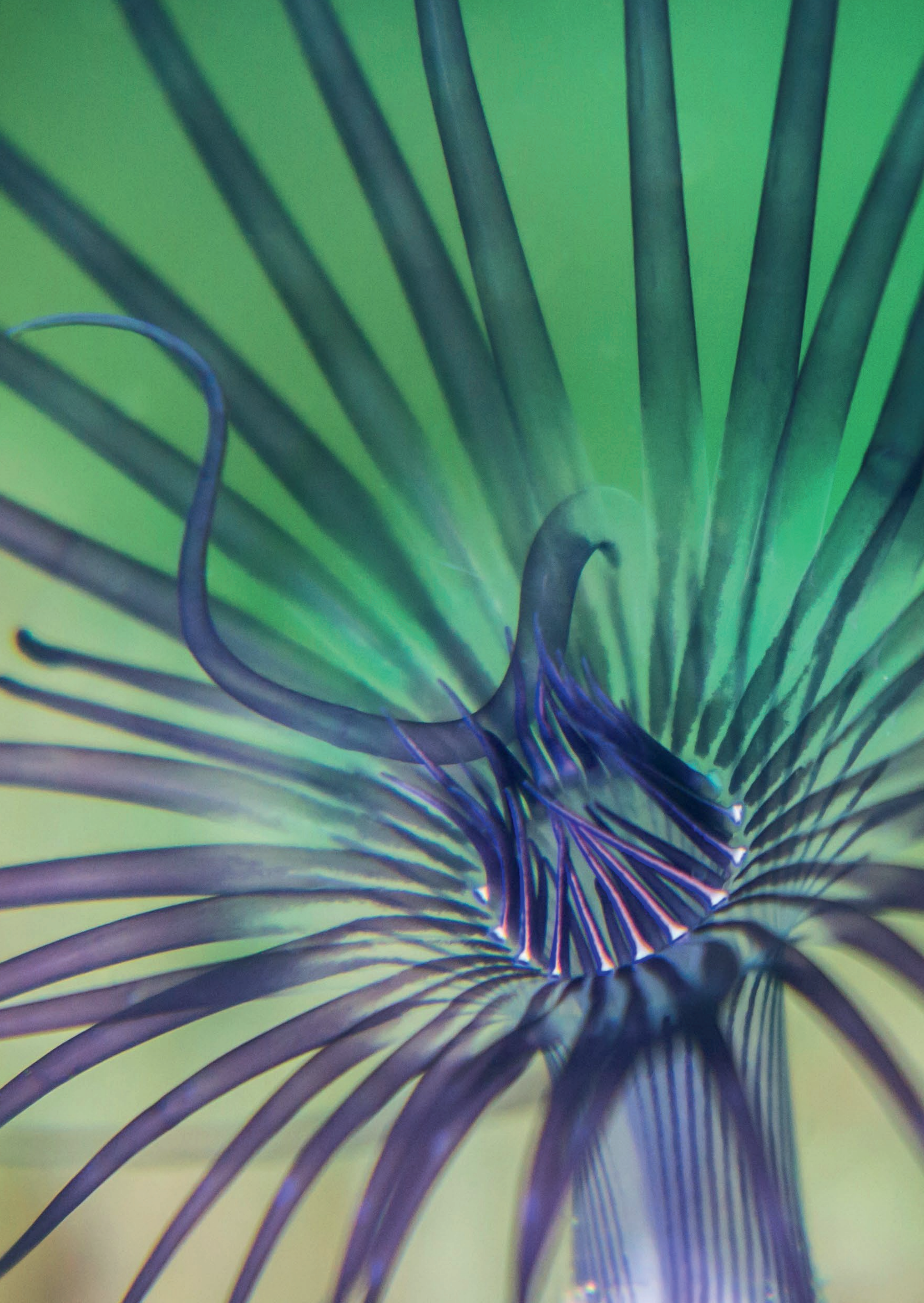
It is clear that the beautiful and economically important coral reefs are disappearing on our watch. Long-term success of traditional reef management is dependent on urgent climate action and could further benefit from well-applied restoration. The emerging field of reef restoration has thus far primarily focused on improving culturing methods for corals and this has resulted in effective coral nurseries, though cleaning maintenance costs are still substantial. Outplanting of corals onto degraded reefs or ARs is still often hampered by predation and competition. This thesis shows how a better understanding and integration of ecological key processes such as facilitating herbivores and discouraging corallivores has the potential to improve the cost-effectiveness of both coral nurseries and outplanting of corals. These insights contribute to developing scalable and effective restoration methods, which can be further combined with research into newer techniques that increase the diversity of corals and adaptive capacity of restored reefs to climate change. The development of such scientifically-validated methods can promote upscaling of restoration efforts to re-establish functional and resilient reefs and associated ecosystem services, especially when organized together with coastal communities. For coral reef managers, restoration practitioners and the supporting scientific community, this thesis concludes with some key practical considerations and research recommendations.

The following practical considerations are suggested to improve the cost-effectiveness and success of coral reef restoration efforts:

- Placement of mid-water coral nurseries nearby natural reefs to allow free bio-assisted fouling control and improve coral performance
- Use of elevated AR designs for coral outplanting in areas where predation pressure of invertebrate corallivores such as *Acanthaster* spp. sea stars or *Drupella* spp. snails is high
- Use of concrete AR structures to restore rubble fields in areas with high natural coral recruitment
- Establishment of sufficiently large no-take zones to safeguard development of healthy and diverse fish communities
- Use of pilot studies across several reefs and protection zones to determine which local coral reef community is most supportive of restoration efforts
- Formulate clear and widely-supported project goals and monitor at the appropriate socio-ecological scales and timespan to evaluate progress and allow for adaptive management

The following research topics are recommended to build upon this thesis and further improve the cost-effectiveness of reef restoration:

- Study the impact of marine protection on restoration success over several years, with a special focus on the influence of herbivory, corallivory and nutrient cycling on outplanted corals
- Determine how species selection, AR spatial layout, outplant density and outplant size influence predation pressure on outplanted corals
- A cost-benefit analysis of outplanting a pioneer coral assemblage vs. a diverse coral assemblage including massive corals
- A cost-benefit of restoring rubble fields by substrate stabilisation without coral gardening vs. coral outplanting vs. AR implementation
- Determine to which extent attraction from surrounding reefs and local production contribute to the fish and invertebrate communities associated with restored reefs
- Continue research that may increase the adaptability of corals to climate change by assisted evolution



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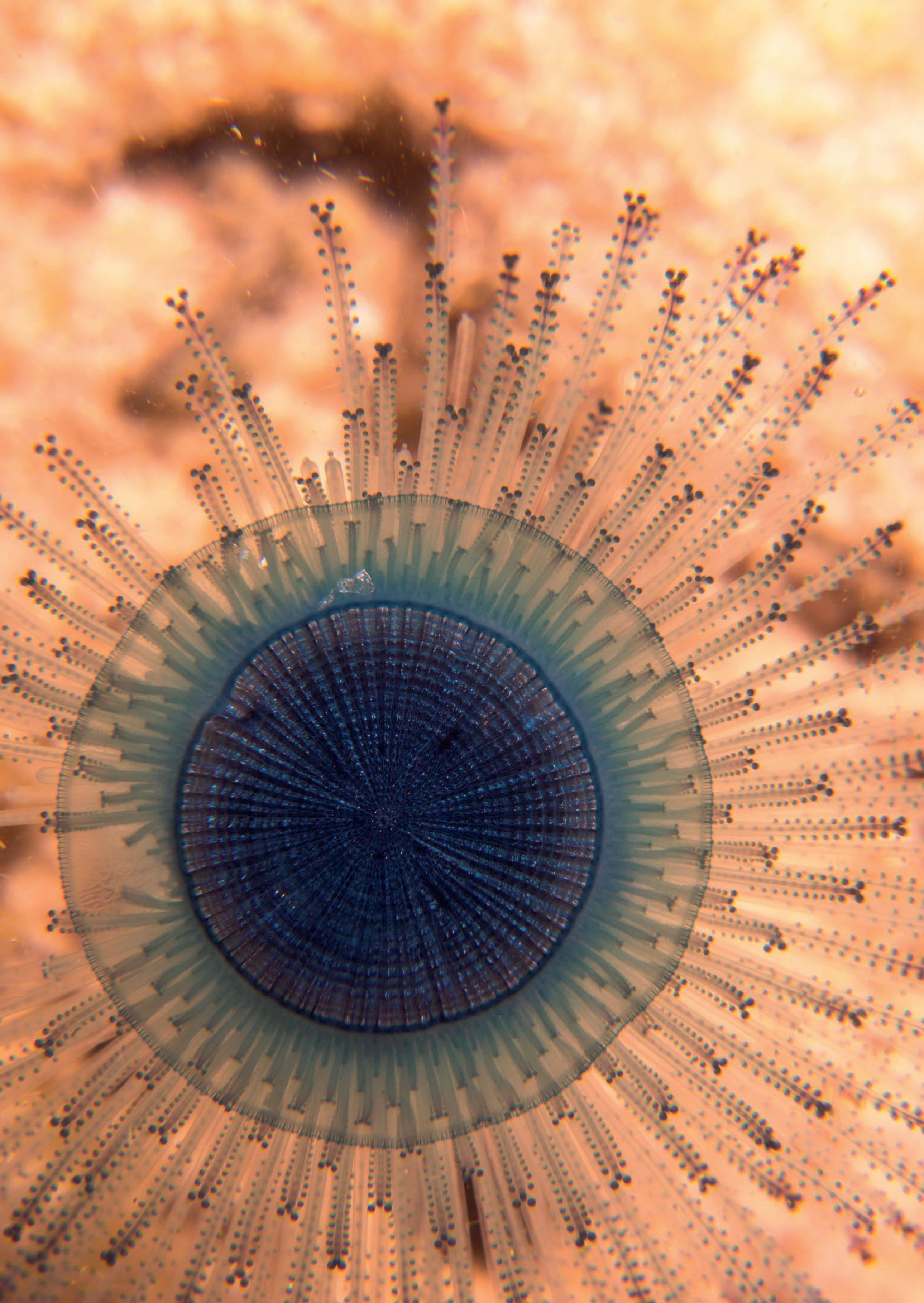
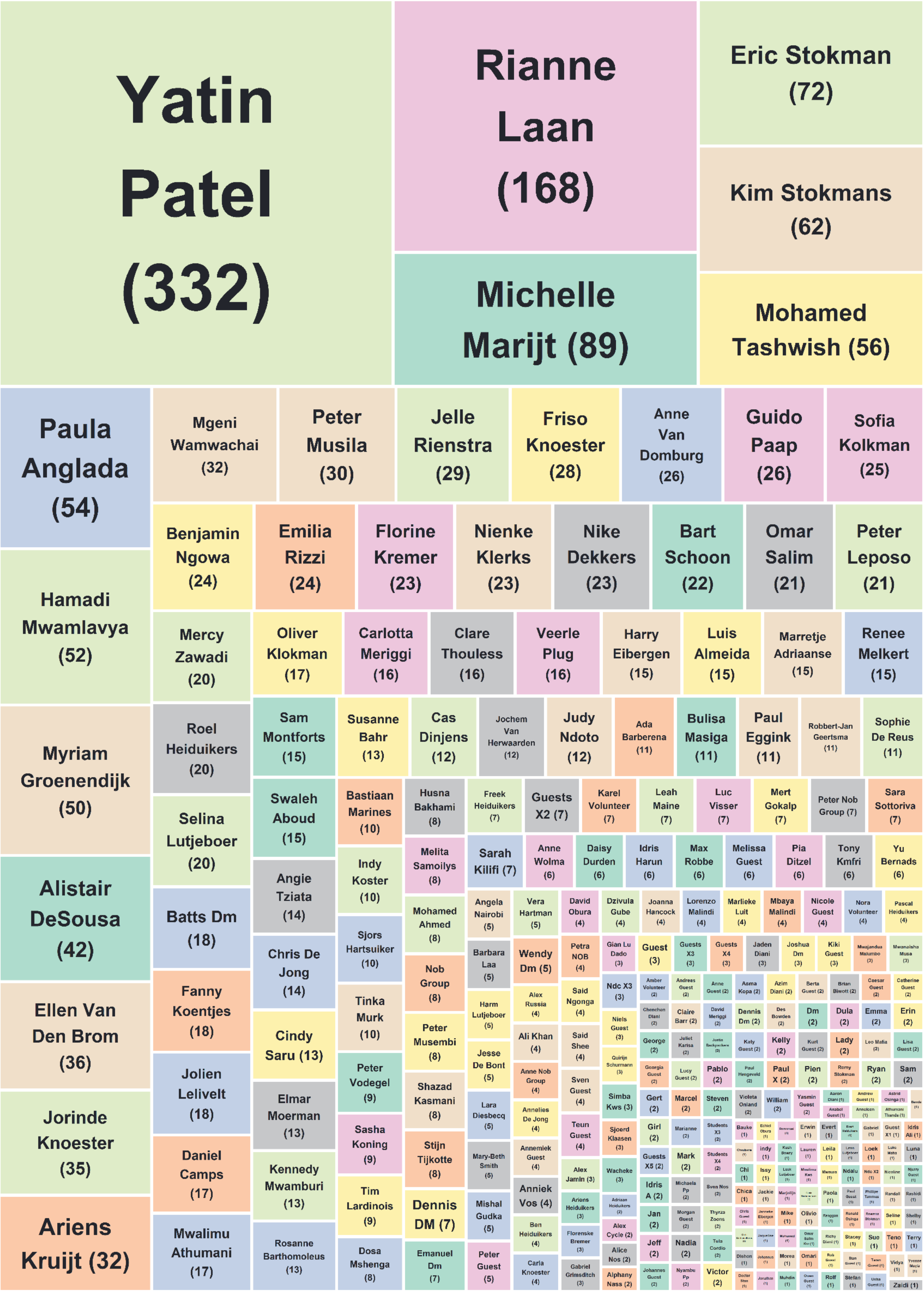


Total buddies: 289 (total dives: 1613)



Acknowledgements

Despite the common perception that I live an underwater life among fish and other strange creatures, I have been interacting (and sometimes even communicating) with humans as well throughout this study. Some of these interactions have been particularly important and/or pleasant, and therefore I'd like to extend my gratitude to the following people in particular.

I am grateful to Tinka for allowing me to stick around at MAE from the start, first as intern, then as master thesis student and of course as PhD (did someone say Postdoc?). You have given me the freedom to design and pursue research largely independently, and I hope you are as happy with the outcome as I am. I want to thank Ronald for his guidance throughout, always supportive with kind words of wit and wisdom. To the remainder of the MAE crew: thank you for believing in my existence even though I rarely made a live appearance. Though some notable exceptions are good times with Diede's abzu games, Mert's documentary trip and, of course, Joshua's PhD journey: thank you all for showing me there's life above water as well.

A massive thanks to Eric for all his ideas and enthusiasm, which led to the spark that ignited REEFolution. To past & present board members, Yvonne, Guido and all volunteers: your devotion is what kept the project and, occasionally, me running. A big thanks to Harm, Selina & Pilli Pipa crew, whose logistical support has been crucial. To the members of Mkwiro BMU and especially Moha: thank you for believing in this project from the start!

To all students (and co-authors): thank you for actually listening to me during the sporadic moments that I had something to say. And of course thanks for all the data collection, ideas & entertainment: I will never forget what I remember now. Karibu tena: Carlotta, Jolien, Oliver, Mathilde, Paula, Anne (Tassie), Niké, Robbert-Jan, Kim, Sam, Emilia, Sophie, Stijn, Violeta, Ellen, Fanny, Marlieke, Jochem, Brian, Asma, Omar, Myriam, Susan, Nienke, Sofia, Angie, Veerle, Thyrza, Cas, Peter, Sjors, Jip, Florenske, Renée, Florine, Luís, Chris, Rosanne, Sasha, Susanne, Daisy, Anne, Quirijn, Bart, Nieki, Tim, Laura, Evelien, Kristina, Richard, Kyra, Marretje, Jelle, Miguel, Gian Lu, Luc, Anniek, Indy, Vera & Sara! Thanks also to all the volunteers and friends who visited and showed an interest in the project!

A sincere thank you to all the Reef Rangers that have grown alongside with REEFolution over the years. Your presence has given the project a steady and yet most spirited foundation. Asante sana: Dosa, Mwalimu, Cindy, Mercy, Peter, Mgeni, Idrisu, Husna, Idrisa, Said, Sadam, Judy, Mwanaisha, Bulisa, Omar & Dzivula! My appreciation to you all is much greater than my Swahili currently can express.

A diverse assortment of other people has enlightened and supported me in various ways. I fondly remember the dives and shared underwater passion with Rianne, I look up to Hamadi (because he always climbs higher trees than I do), I treasure the creativity sprees with Ada and I am looking forward to more hikes and dances with Alistair. A big thanks also to all dive buddies for all the dives made in and around Kenya (opposite page, dives in brackets): you are like fish to me.

Lastly, I cherish my family. I thank my parents for their unabating support to follow my own path, even when that path has led me to the bottom of the ocean, some 7000 km away. My brother, for all the active adventures and, critically, introducing me to diving. My sister, for sharing and showing me how to live life off the beaten track. Yu & Kobus for happy times back home. Mercy, for all the love and warmth given (despite me spending most time with fish). And yes, lastly, Yatin, for creating a second home for me in Shimoni, as well as a third home underwater together with our rummy frogfish friends.

Appendix A: Authorship statement

PhD candidate's name : Ewout Knoester
First promotor : Tinka Murk
Title of PhD thesis : Facilitating the facilitators: Advancing coral reef restoration by considering ecological keystone species
Date of public defence: 26-05-2023 13:30

Chapter 1 General introduction. The general research aim, specific research questions and its general scientific and social perspective were proposed by me. I wrote a draft and received feedback from my promotor and co-promotor and finalized the text.

Chapter 2. I formulated the research aim together with my promotor and co-promotor. The research questions and methodology were established together with master student VE Plug, who performed data collection under my guidance. Preliminary data analysis was performed by VE Plug and this was used for the final data analysis and graphing performed by me. I wrote a draft of the manuscript and all co-authors provided feedback in two rounds. See for more details the author statement in the manuscript.

Chapter 3. I formulated the research aim together with my promotor and co-promotor. The research questions and details on methodology were established together with master students N Klerks and SB Vroege-Kolkman, who performed the data collection under my guidance. Preliminary data analysis was performed by N Klerks and this was used as basis for the final data analysis and graphing performed by me. I wrote a draft of the manuscript using parts of the thesis of N Klerks and all co-authors provided feedback in two rounds. See for more details the author statement in the manuscript.

Chapter 4. I formulated the research aim together with my promotor and co-promotor. The research questions and details on methodology were established by me, and I performed the data collection, data analysis and graphing. I wrote a draft of the manuscript and my promotor and co-promotor provided feedback in two rounds.

Chapter 5. I formulated the research aim together with my promotor and co-promotor. The research questions and methodology were established together with master student E Rizzi, who performed the data collection under my guidance. Data analysis and graphing was performed by me. I wrote a first draft of the manuscript to which the last co-author provided feedback and I used that to write a final draft to which all co-authors commented. See for more details the author statement in the manuscript.

Chapter 6. I formulated the research aim together with my promotor and co-promotor. The research questions and details on methodology were established together with master students JJ Rienstra, QJF Schürmann and AE Wolma, who assisted me in data collection. Data analysis and graphing was performed by me, with some assistance of JJ Rienstra. I wrote a first draft of the manuscript to which the last co-author and students provided feedback and I used that to write a final draft to which all co-authors provided feedback. See for more details the author statement in the manuscript.

Chapter 7 General discussion. I wrote the first draft and revised the text once using the feedback of my promotor and co-promotor.

2023-01-23
Signature PhD candidate

Signature promotor for agreement

Appendix B: Training and Supervision Plan

Training and Supervision Plan (TSP)

GENERAL INFORMATION

Name PhD candidate	Ewout Knoester	
Project title	Facilitating the facilitators: Advancing coral reef restoration by considering ecological keystone species	
Group	Marine Animal Ecology	
Co-promotor	Ronald Osinga	
Promotor	Tinka Murk	
Project term	from 11-2017	until 11-2022

A. The Basic Package	year	credits☑
WIAS Introduction Day	2021	0.3
WGS Course on Scientific Integrity & Ethics in Animal Sciences	2019	1.5
WIAS Course on Essential Skills	2019	1.2
Subtotal Basic Package		**3.0**

B. Disciplinary Competences	year	credits
Write PhD research proposal	2019	6.0
WIAS Course Statistics for the Life Sciences	2019	2.0
MSc course in Data Analysis in Ecology: Statistics for Ecologists & Field Biologists	2020	5.0
Indo-Pacific Coral Identification Workshop, Natural History Oxford	2017	0.5
Subtotal Disciplinary Competences		**13.5**

C. Professional Competences	year	credits
WGS Course on Research Data Management part 1 - 3	2019	0.45
WGS Course on Supervising BSc and MSc thesis students	2019	0.6
WGS Course on Reviewing a Scientific Paper	2019	0.1
Write grant proposal to Ecology Fund of KNAW (Koninklijke Nederlandse Akademie van Wetenschappen)	2017	0.5
Write grant proposal to GEF Small Grants Programme for the REEFolution Foundation	2018	0.5
Review proposals Research Master Cluster	2020	0.5
Subtotal Professional Competences		**3**

D. Societal Relevance *(recommended)*	year	credits
Promote REEFolution to lay public at World Environment Day (KY) & Duikvaker Fair (NL)	2018-2019	0.2
Interview for a Wageningen University & Research short documentary	2018	0.1
Co-author magazine article on reef restoration research for the WIAS magazine	2022	0.5
Present progress of restoration project to park rangers at Kenya Wildlife Service (yearly)	2017 - 2020	0.4
Subtotal Professional Competences		**1**

E. Presentation Skills *(maximum 4 credits)*	year	credits
11th symposium Western Indian Ocean Marine Science Association Mauritius (poster presentation)	2019	1.0
14th International Coral Reef Symposium Online (oral presentation)	2021	1.0
15th International Coral Reef Symposium Bremen (oral presentation)	2022	1.0
Presentation & exhibition: Impulse Buliding, WUR	2022	1.0
Subtotal presentations		**4**

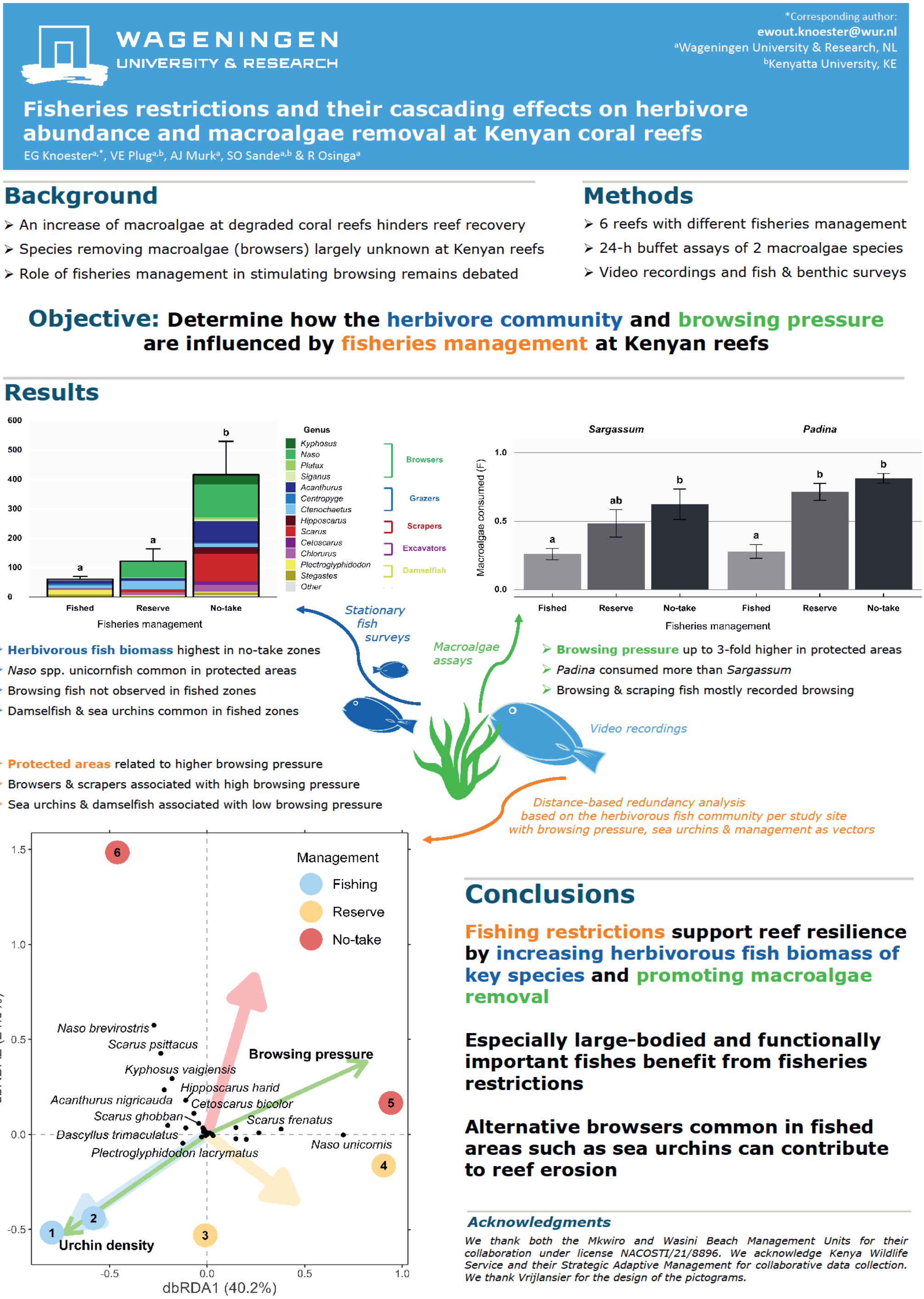
F. Teaching competences *(max 6 credits)*	year	credits
Guest lecture Technical University of Mombasa	2019	1.0
Supervising 9 MSc theses	2017 - 2022	3.0
Supervising 6 MSc internships	2017 - 2022	2.0
Subtotal Teaching competences		**6**

Education and Training Total (minimum 30 credits)*	**30.4**

**One ECTS credit equals a studyload of approximately 28 hours*

Appendix C: Posters

Poster chapter 2



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[b]Kenyatta University, KE

Fisheries restrictions and their cascading effects on herbivore abundance and macroalgae removal at Kenyan coral reefs

EG Knoester[a,*], VE Plug[a,b], AJ Murk[a], SO Sande[a,b] & R Osinga[a]

Background

- An increase of macroalgae at degraded coral reefs hinders reef recovery
- Species removing macroalgae (browsers) largely unknown at Kenyan reefs
- Role of fisheries management in stimulating browsing remains debated

Methods

- 6 reefs with different fisheries management
- 24-h buffet assays of 2 macroalgae species
- Video recordings and fish & benthic surveys

Objective: Determine how the herbivore community and browsing pressure are influenced by fisheries management at Kenyan reefs

Results

- **Herbivorous fish biomass** highest in no-take zones
- *Naso* spp. unicornfish common in protected areas
- Browsing fish not observed in fished zones
- Damselfish & sea urchins common in fished zones

- **Browsing pressure** up to 3-fold higher in protected areas
- *Padina* consumed more than *Sargassum*
- Browsing & scraping fish mostly recorded browsing

Distance-based redundancy analysis based on the herbivorous fish community per study site with browsing pressure, sea urchins & management as vectors

- **Protected areas** related to higher browsing pressure
- Browsers & scrapers associated with high browsing pressure
- Sea urchins & damselfish associated with low browsing pressure

Conclusions

Fishing restrictions support reef resilience by increasing herbivorous fish biomass of key species and promoting macroalgae removal

Especially large-bodied and functionally important fishes benefit from fisheries restrictions

Alternative browsers common in fished areas such as sea urchins can contribute to reef erosion

Acknowledgments

We thank both the Mkwiro and Wasini Beach Management Units for their collaboration under license NACOSTI/21/8896. We acknowledge Kenya Wildlife Service and their Strategic Adaptive Management for collaborative data collection. We thank Vrijlansier for the design of the pictograms.

Poster chapter 3

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[b]Kenyatta University, KE

Coral predation and implications for restoration of Kenyan reefs: the effects of site selection, coral species and fisheries management

EG Knoester[a,*], N Klerks[a,b], SB Vroege-Kolkman[a,b], AJ Murk[a], SO Sande[a,b], R Osinga[a]

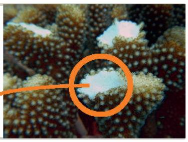
Background

- Coral reef restoration efforts often suffer from coral predation (corallivory)
- Corallivory might relate to low coral cover, vulnerability of coral species or type of fisheries management
- A better understanding on corallivory can be used to improve restoration techniques

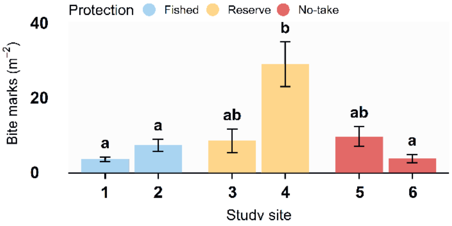
Objective: To determine the effects of coral cover, corallivore communities and fisheries management on coral predation on both natural and outplanted corals

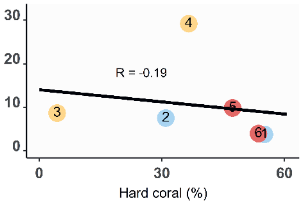
Methods

- 6 reef sites with varying levels of coral cover and three different levels of fisheries management
- Benthic and fish communities characterized through surveys
- Fish bite marks counted on all natural coral colonies and outplanted branching fragments



Results



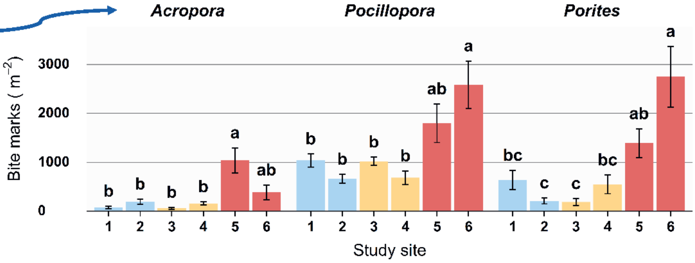


Natural coral colonies

- No correlation between coral cover and bite mark density
- No clear effects of fisheries management
- Highest bite mark densities on branching coral genera

Outplanted coral fragments

- Higher bite mark densities compared to natural coral colonies
- Strong predation inside no-take zones
- High predation resulting in reduced live coral tissue



High **corallivorous snail** densities were associated with low coral diversity

Facultative corallivorous fish were most abundant in no-take zones

Obligate corallivorous fish correlated with coral cover

Conclusions

Reefs with low coral cover (often targeted for restoration) do not necessarily experience greater coral predation

Improved outplanting methods and coral species considerations are needed to address the high predation pressure

Equivocal role of fisheries management requires further study: potential negative effects of facultative corallivorous fish such as parrotfish on reef restoration efforts

Acknowledgments

We thank both Mkwiro and Wasini Beach Management Units for their collaboration under license NACOSTI/21/8896. We acknowledge Kenya Wildlife Service and their Strategic Adaptive Management for collaborative data collection. Thanks to Hamadi Mwamlavya for assisting with the fish surveys. We thank Vrijlansier for the design of pictograms.

Poster chapter 4

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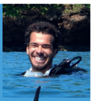
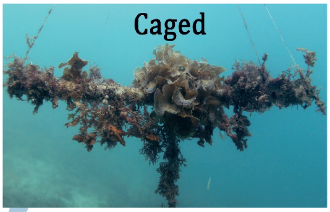
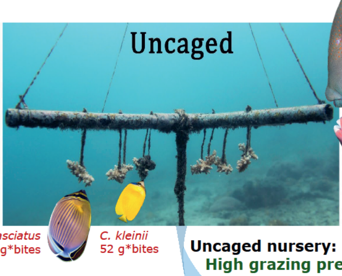
2019 Feb 14;611:143-55

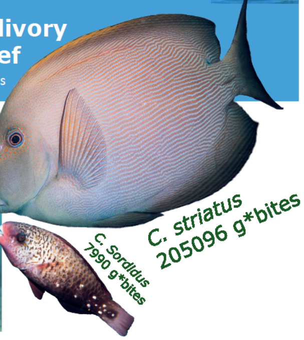


Benefits of herbivorous fish outweigh costs of corallivory in coral nurseries placed close to a Kenyan patch reef

E.G. Knoester*, A.J. Murk, R. Osinga; Marine Animal Ecology Group, Wageningen University, the Netherlands

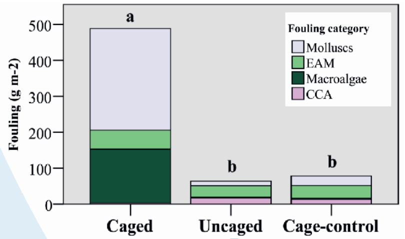




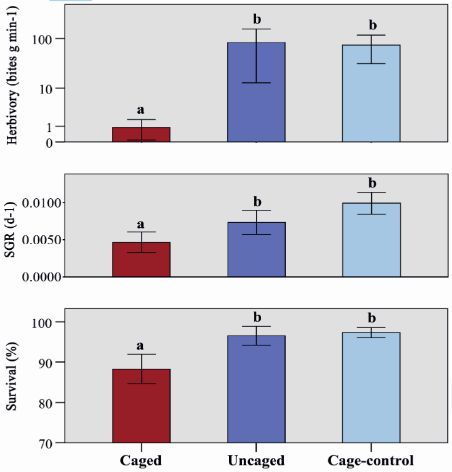


Caged nursery:
100-fold increase macroalgae

Uncaged nursery:
High grazing pressure
Limited coral predation



***Mean fouling (g m^{-2}) per treatment** at end of 100-d experiment. N = 15. Differing letters note differences ($p < 0.05$) between sum of fouling*



Herbivory (n = 30), coral growth (n = 15) and survival (n = 15). Herbivory expressed as fish bites scaled to body mass and divided by duration of video. SGR = specific growth rate. Bars are ±2 *se*

Uncaged nursery:
Better growth
Higher survival

Objective

To determine the net effect of herbivory and corallivory by fish on the growth and survival of coral in mariculture

Background

- Coral nurseries plagued by fouling
- Manual fouling removal is expensive
- Natural reef has free cleaning by grazers
- Natural reef hosts coral-predating fish

Conclusion

Benefits of fouling control by herbivorous fish outweigh costs of incidental corallivory

Recommended to place coral nurseries near natural reef

Acknowledgments

REEFolution FOUNDATION

*We are much indebted to **Pilli Pipa** for their logistic support, **Yatin Patel & Rianne Laan** for their fieldwork assistance and we applaud the **REEFolution Foundation** for their commitment to restore Kenya's coral reefs*

Methods

- Caged, uncaged and cage-control nurseries (n = 15)
- Each nursery: 10 *Acropora verweyi* fragments
- Coral monitored on growth, survival and bite marks
- Fouling collected and weighed at end of experiment
- Remote video recording rates of herbivory and corallivory (n = 30)

Poster chapter 5

WAGENINGEN
UNIVERSITY & RESEARCH

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Biomass of key grazing herbivorous fish species is an important determinant of fouling control and coral growth in coral nurseries

EG Knoester[a,*], E Rizzi[a,b], AJ Murk[a], R Osinga[a]

Background

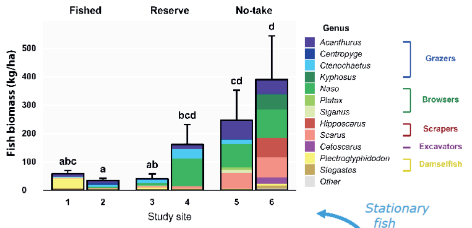
- ➢ Concerns about high costs and small scale of coral reef restoration
- ➢ Grazing herbivores can reduce nursery cleaning costs
- ➢ Quantitative link between herbivorous fish and cleaning benefits unknown

Methods

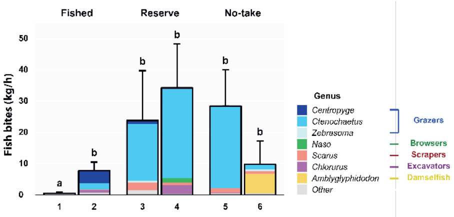
- ➢ 4-month study at 6 Kenyan reef sites
- ➢ 3 types of fisheries management
- ➢ 7 replicate coral nurseries per site

Objective: **To determine quantitative links between herbivorous fish communities, grazing pressure, fouling density & nursery coral growth**

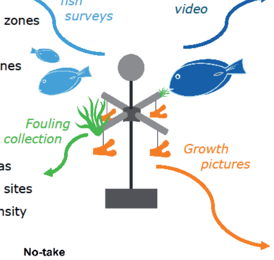
Results



- ➢ **Herbivorous fish biomass** highest in no-take zones
- ➢ Grazers relatively common at most sites
- ➢ Browsers & scrapers only present in no-take zones

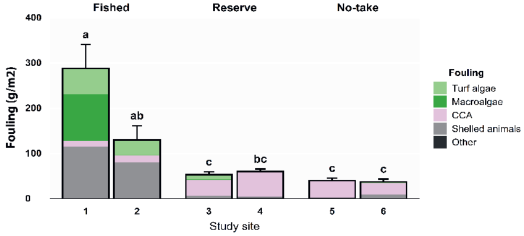


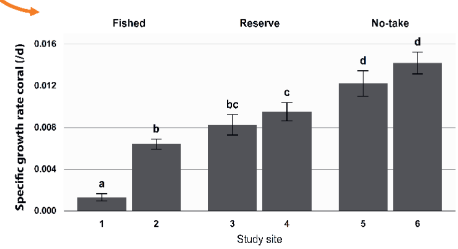
- ➢ **Grazing pressure** 6-fold higher in protected areas
- ➢ No correlation total herbivorous fish biomass and grazing
- ➢ Correlation key species *Ctenochaetus* biomass and grazing



- ➢ **Fouling density** 4-fold lower in protected areas
- ➢ Establishment of turf and macroalgae in fished sites
- ➢ No correlation grazing pressure and fouling density

- ➢ **Coral growth** higher in protected areas
- ➢ Especially high coral growth in no-take zones
- ➢ Negative correlation coral growth and fouling





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We thank both the Mkwiro and Wasini Beach Management Units for their collaboration under license NACOSTI/21/8896. We acknowledge Kenya Wildlife Service and their Strategic Adaptive Management for collaborative data collection. A special thanks to Cindy Chorongo, Bulisa Masiga, Judy Nduta and Mercy Zawadi for counting countless fish bites. We thank Vrijlansier for the design of all pictograms.

Conclusions

- ➢ **High coral growth in protected areas partially linked to grazing pressure**
- ➢ **Additional growth benefits unexplained, possibly nutrient cycling by fish**
- ➢ **Grazing pressure dependent on both fish biomass and species composition**
- ➢ **Cost-effectiveness coral nurseries increased by healthy fish communities**

Poster chapter 6

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Community-managed coral reef restoration in southern Kenya: does artificial reef (AR) design influence ecosystem recovery?

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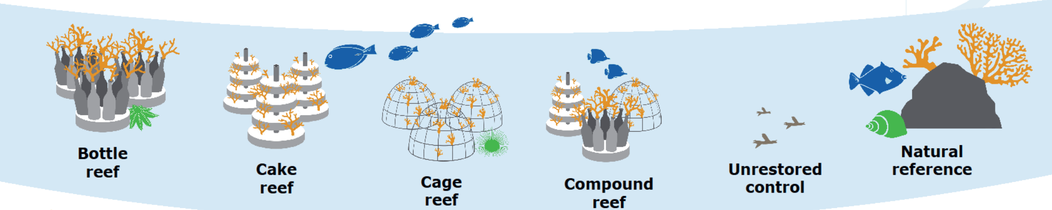
Background

- Restoration and use of ARs common in reef conservation
- Monitoring often limited to coral survival only
- Ecosystem monitoring needed to evaluate success

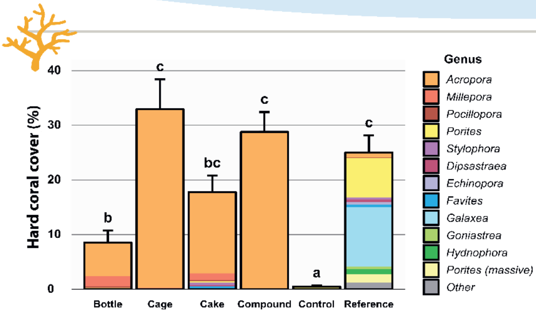
Methods

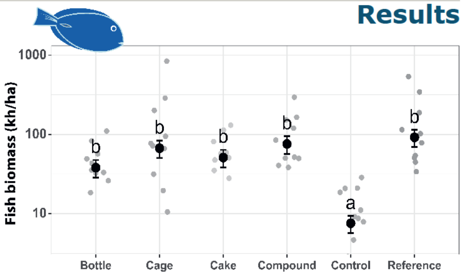
- 18 coral species outplanted, mainly *Acropora* spp.
- 2-year monitoring on corals, fish and invertebrates
- 4 AR designs (16 m^2), control and reference (n = 10)

Objective: **To determine the effect of AR design on coral performance, fish community & key invertebrates**



Results





- Average 60% fragment survival, resulting in good coral cover
- Highest cover on Cages, by preventing *Acanthaster* predation
- ARs *Acropora* dominated, highest diversity on Cakes
- 32 coral genera recruited on ARs, highest density on Cakes

- Fish biomass 5-12x higher on ARs & Reference than Control
- No differences in fish biomass between AR designs
- Strong positive correlation fish biomass and coral cover
- Above patterns comparable for fish abundance & richness

Invertebrates:

Corallivorous snails & sea urchins most abundant on Reference reefs

Sea stars & sea cucumbers were rare

Gastropods common at ARs, but more diverse at Reference reefs

Acknowledgments

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Conclusions

Reef restoration with ARs positively influenced all ecological parameters for recovery

Recommended to combine AR designs and consider different strengths and weaknesses:

- **Cages shows good coral survival by preventing predation by invertebrates**
- **Concrete ARs promote coral diversity through natural recruitment**
- **Coral cover more important than AR design for fish community**
- **All AR designs could be improved to accommodate key invertebrates**

Photo specifications

Cover page: A close-up of a triggerfish (*Balistapus undulatus)* in the Wasini Channel, Kenya

Quote page: Hard and soft corals at Pink Reef, Mpunguti Reserve, Kenya

Contents page: A close-up of the meandering hard coral *Platygyra* near Wasini village, Kenya

Summary page: A collection of soft corals at Pilli Pipa Restaurant, Shimoni, Kenya

Page 6: Areal view of corals and sea urchins in Kilifi Creek, Kenya

Page 16: Convict surgeonfish (*Acanthurus triostegus*) in Kisite Marine Park, Kenya

Page 40: A close-up of the coral-eating crown-of-thorns sea star (*Acanthaster* sp.) with commensal shrimp at Dolphin Point, Mpunguti Reserve, Kenya

Page 64: A coral nursery tree at Mkwiro Community Managed Area, Kenya

Page 84: A school of blue-striped snappers (*Lutjanus kasmira*) in Kisite Marine Park, Kenya

Page 108: An artificial reef as home for various fish in Mkwiro Community Managed Area, Kenya

Page 142: A hard coral dominated reef at Dolphin Point, Mpunguti Reserve, Kenya

Page 154: A close-up of an anemone at Firefly House Reef, Shimoni, Kenya

Page 167: A close-up of a blue button hydroids (*Porpita porpita*) in Shimoni, Kenya

Page 178: A fisherman heading out at sunrise, Jambiani, Zanzibar

Back page: A colony of the soft coral *Tubipora musica* during a night dive at Sin City, Shimoni, Kenya

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