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Coral Reef Restoration in the Maldives: an assessment of techniques and challenges

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Abstract

Coral reefs, which are among the most biodiverse ecosystems on the planet, are declining at an alarming rate. To counteract the threats posed by climate change and other anthropogenic impacts, conservation efforts such as active coral reef restoration have increased globally. Ecological restoration aims to assist natural recovery and increase coral reefs resilience in an effort to preserve the many functions and services these iconic ecosystems provide to society. Under current climate scenarios, coastal and island populations are the first to suffer from continued ecosystem degradation. For example, the Maldives' vulnerability to global and local coral reef threats is evident for a nation that lives on shallow reef islands with an economy driven by fisheries and tourism. However, little information is available on suitable, regionally tested coral restoration techniques that could be applied at an ecological meaningful scale in the Maldives. 'Coral gardening', which comprises fragment farming in coral nurseries followed by the transplantation of these corals to a restoration site, appears particularly suitable for remote locations like the Maldives. The method can be applied by local communities or tourism stakeholders to assist local reef recovery, while creating awareness, stewardship and even income opportunities. This research assesses the application of 'coral gardening' for upscaled coral restoration efforts in the Maldives, providing the necessary regional validation and useful insights into the various aspects of this technique for the first time. To evaluate the suitability and performance of this restoration approach across different regions and farming habitats (i.e., lagoon and reef), a total of six mid-water coral rope nurseries were assessed on the local island of Magoodhoo in Faafu Atoll and on Athuruga resort island in Alif Dhaal Atoll. Coral gardening success was examined for three different coral genera, namely *Acropora, Pocillopora* and *Porites,* using a common monitoring protocol. This delivered regional benchmarks for fragment growth over time and at different depths as well as coral survival, which typically exceeded 90% in both farming habitats. In addition, ecological interactions were investigated by

including mutualistic fauna and predator associations in the assessments of farmed and transplanted corals. For example, a positive correlation between *Trapezia* guard crabs and farming stock health was observed, while the corallivorous nudibranch *Phestilla* is newly reported on coral nursery stock. Coral restoration demand and success is further reviewed in the context of natural reef recovery on the restoration site as well as potential ecological implications of restoration activities. Here, coral outplanting was successful and significantly benefitted the degraded reef environment, increasing fish abundance and diversity along with natural coral cover. While the overall study results are encouraging, this research also addresses potential risks to coral restoration success, in particular the negative effects of prolonged monitoring and maintenance disruptions and the impacts of coral disease occurrence. Using a number of real case studies, it is demonstrated how these factors can diminish coral gardening outcomes and project success, if not managed in time. Overall, the findings presented and the practical applications concluded from this work hope to provide a scientific baseline for future restoration efforts that can guides restoration practitioners towards efficient conservation work.

CHAPTER 1

1. Introduction

1.1 Coral Reefs in the Anthropocene

Coral reefs are often referred to as 'rainforests of the sea', illustrating their rich biodiversity as well as their stunning natural beauty. Although coral reef ecosystems cover less than 0.1% of the entire oceans' surface, they host about 25-32% of all known marine life, with more than 800,000 species estimated to still be discovered (Connell, 1978; Spalding *et al.,* 2001; Fisher *et al.,* 2015). Over thousands of years, more than 800 reef-building coral species have produced enormous structures by engaging in a symbiotic relationship with microscopic algae of the genus *Symbiodinium*, also referred to as zooxanthellae, to benefit from their photosynthetic products and to accumulate carbon for calcification and coral growth (Fransolet *et al.,* 2012). Forming the base of a complex and diverse ecosystem, this has allowed various species over millions of years of evolution to find their own niche in an ecosystem that provides shelter, food and reproductive opportunities in a vast ocean (Paulay, 1997).

Likewise, coral reefs provide resources and livelihoods for coastal populations in more than 100 countries the form of provisioning (e.g., food, raw material for construction or trade, genetic resources and pharmaceutical agents), regulatory services (e.g., shore protection, nutrient cycling, water cleaning), supporting services (e.g., sand formation, primary production) and cultural services (e.g., recreation, aesthetic, cultural and educational values) (MEA, 2005). These 'ecosystem services' of coral reef have been valued at US$ 10 trillion/year (Costanza *et al.*, 2014), highlighting their immense economic value as well as potential future financial gains from improving coral reef health (UN Environment *et al.,* 2018).

Nevertheless, coral reefs are considered among the most vulnerable ecosystems to the many local and global threats emerging in the Anthropocene (Carpenter *et al.*, 2008; McCauley *et al.*, 2015; Hughes *et al.*, 2017), which is referred to as the recent time period of significant human impact on the Earth's ecosystems (Waters *et al.*, 2016). Climate change, as a result of rising greenhouse gas concentrations in the atmosphere, has long been recognised as a major threat to coral reefs as it encompasses warming oceans, ocean deoxygenation and acidification, sea level rise and more severe meteorological events (Wellington *et al.*, 2001; Hoegh-Guldberg *et al.*, 2007).

Corals thrive in a limited temperature range, depending largely on their specific photosymbionts (Howells *et al.*, 2012). Continuously increasing global temperatures, coupled with natural temperature fluctuation of the El Niño Southern Oscillations (ENSO) and abnormal changes in weather patterns, can result in rapidly elevated sea surface temperatures (SST), leading to 'coral bleaching' events (Brown, 1997; Lotterhos *et al.,* 2021). The coral appears white as the symbionts are expelled in a stress response, causing the coral to lose its main energy supply. If not reversed in time, mass mortality events, as first described in the 1982/3 can follow (Glynn, 1984). Since then, several large-scale coral bleaching events have severely impacted reefs around the world. For example, the sever 1998 mass bleaching alone killed around 8% of the worlds corals at the time (Souter *et al.*, 2021). As such events increase in frequency and severity, this also reduces the time for corals to recover between disturbances (De'Ath *et al.*, 2012; Hughes *et al.*, 2018).

Tropical shallow waters are also at risk of hypoxia as warm waters and local eutrophication lower oxygen levels, which can lead to mass mortality of marine biota (Hughes *et al.*, 2020). Ocean acidification, the decrease in oceans' pH resulting from increased CO_2 uptake, poses a risk to any calcium carbonite accumulating organism. As coral calcification rates decrease and reef sediments dissolve, net carbonate accretion on coral reefs soon approaches zero (Hoegh-Guldberg *et al.*, 2007; Eyre *et al.*, 2018), meaning that under a continuously high emission scenario almost all reefs are predicted to be eroded by 2050 (IPCC RCP 8.5; Cornwall *et al.*, 2021).

Compromised reef stability is a particular concern as weather and climate extremes are being observed more frequently (IPCC, 2021). Coral reefs act as natural physical barriers, protecting the coastlines against damage from storm waves and tsunamis. Replacement with artificial shore protection is costly and unlikely manageable on a global scale. Without reefs, flood damages is expected to double and costs resulting from frequent storms would approximately triple (Beck *et al.*, 2018). Sea level rise will increase these risks. According to the latest Intergovernmental Panel on Climate Change (IPCC) report annual sea level increase has tripled in the last 100 years and is expected to increase between 0.5 and 1m by 2100 depending on the emission scenario (IPCC, 2021).

In addition to the overarching threat of climate change, coral reefs are facing several other pressures at various scales that can interact synergistically and amplify the negative impacts on reef health and resilience (Ateweberhan *et al.*, 2013). These threats include coastal development (e.g., construction of infrastructure or the creation of new landmasses, sedimentation), water pollution (e.g., eutrophication, solid waste, microplastics, hazardous waste), coral diseases (e.g., increased occurrence of pathogen abundance and virulence), invasive species (e.g. lion fish in the Caribbean), coral predator plagues (e.g., Crown of thorns starfish), fisheries (e.g., destructive fishing methods, overfishing, bycatch and associated pollution) and tourism (e.g., overcrowding, touristic infrastructure, resource overuse; see review in Burke *et al.*, 2011).

Over the last 10 years, coral reefs around the world have seen an unprecedented decline and many reefs are already lost. The Sixth GCRMN (Global Coral Reef Monitoring Network) status report highlights that, although hard coral cover generally recovered to pre-1998 bleaching levels (>30%) in the following decade, between 2009 and 2018 a progressive loss of 14% of the worlds reefs has been witnessed, while algae cover has increased by 20% in the same time (Souter *et al.*, 2021). This loss of live coral cover and reef complexity, followed by a distinct shift in species composition, is mainly attributed to a rapid increase in SST animalities triggering bleaching events as well as sustained high STT over the last years (McWilliam *et al.*, 2020; Souter *et al.*, 2021). The latest global bleaching event (2014-2017) was the longest recorded, giving corals no time to recover, and represents what likely will become the norm in the near future under current climate model projections (van Hooidonk *et al.*, 2020). Even if the ambiguous 1.5°C warming target of the Paris Agreement is met, some changes are already irreversible today and coral reefs threats will continue to intensify in the next decades (IPCC, 2021). However, changes will be considerable faster and implications more severe if current rates of emission continue and global climate policies fail. Therefore, decisions and actions taken in the next years will most likely determine the future of coral reefs. Rebuilding marine life is possible if local threats are addressed and climate change is mitigated (Duarte *et al.*, 2020). Co-dependent strategies outlined to accomplish this are threefold, first, the reduction of global climate threats, second, the improvement of local reef protection and third, investment in active coral reef restoration in order to accelerate recovery and 'buy reefs time' to adapt (Knowlton *et al.*, 2021).

1.2 Coral Reef Restoration

1.2.1 The Development of Restoration Practices

Ecological restoration is defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" by the Society for Ecological Restoration (SER, 2004). Modern-day ecological restoration practices have been applied for several decades, mainly in terrestrial ecosystems in the form of reforestation and revegetation, erosion control, invasive species management and reintroduction of native species among other habitat improvement interventions (Wortley *et al.*, 2013; Novak *et al.*, 2021).

In the marine environment, the creation of artificial reefs with the primary focus of increasing marine life for fisheries dates back centuries (e.g., Japanese artificial reefs, Thierry, 1988).

More recently, underwater structures in the form of scrap material (e.g., Florida's infamous 'Osborne Reef' encompassing 2 Mio tyres, Morley *et al.*, 2008), ships (e.g., the largest one being the aircraft carrier 'USS Oriskany', Johnston *et al.*, 2006), oil rigs (e.g., the 'Rigs to Reefs' program, Fowler *et al.*, 2018) or even art installations (e.g., Cancun Underwater Museum with >500 sculptures, Córdoba Azcárate, 2019) have been sunken around the world with the aim to provide hard substrate for marine biodiversity, protect shores, improve or prevent fishing activities and enhance recreational sites .

The discipline of active coral reef restoration is relatively young, with the majority of research produced in the last two decades (Boström-Einarsson, *et al.*, 2020a). While coral transplantations have been conducted for research purposes since the beginning of the 20th century (e.g., Wood-Jones, 1907), it only began to be considered as a restoration approach from the early 1970s onwards (Maragos, 1974; Birkeland *et al.,* 1979). Coral transplantations remained the dominant method of choice in the few projects reported throughout the 1980's and 1990's (e.g., Plucer-Rosario and Randall, 1987; Oren and Benayahu, 1997), supplemented by the first artificial coral reefs (e.g., car tyres used in the Philippines, Alcala *et al.*, 1981) and substrate stabilization approaches (Edwards and Clark, 1992), typically in response to localized impacts. The need for ecological restoration became more evident in the early 2000s, following the 1998 mass bleaching event and increasing threats posed by natural and anthropogenic stressors (Goreau *et al.*, 2000; Epstein and Rinkevich, 2003). 'Coral gardening', first described in the late 1990's (Bowden-Kerby, 1997; Clark, 1997) has since then become the dominant approach, while an array of new and refined techniques have been developed over the past 20 years (see chapter 1.2.2).

In the last few years, active coral restoration has experienced another activity boost, directing efforts towards project upscaling, efficiency, commercialization, new technologies and interdisciplinary approaches (see chapter 1.2.3). Today, as many coral ecosystems around the world are under imminent threat of disappearing, the target of coral restoration has also shifted away from re-establishing historic baselines or recreating pristine reefs, towards recovering or maintaining crucial ecosystem function and services (Hein *et al.*, 2021).

1.2.2 Coral Restoration Techniques

Restoration methods are commonly classified depending on whether they use asexual or sexual propagation or substrate enhancement methods (e.g. Boström-Einarsson *et al.*, 2020b). Another distinction can be made between approaches conducted in the field (*in situ*) or on land (*ex situ*). However, as projects expand and combine approaches and techniques are being continuedly developed, terminology is indistinct in some cases. A standardised glossary for restoration practices is currently in preparation by the Coral Reef Consortium Management Working Group. Below the most commonly applied techniques are briefly described:

Direct Transplantation

One of the first and most widely applied techniques is direct transplantation, where collected corals are transplanted straight to the restoration site. These corals may originate from healthy 'donor' reefs or could be fragments resulting from colony damage, for example due to hurricanes or ship groundings. This method makes up approximately 20% of all recorded restoration projects, with an average reported survival of 64%, although experimental evidence of the efficacy of this method to enhance reef diversity is often lacking (Boström-Einarsson *et al.*, 2020b). While the early practice of relocating entire colonies from healthy to degraded sites (e.g. Clark and Edwards, 1995) seems an inefficient practice today considering the lack of fragment replication and the risk of translocated colony mortality, it still remains a popular practice for construction mitigation and rescue after local impacts as it is fast and cost-efficient (e.g., Seguin *et al.*, 2008; Rodgers *et al.*, 2017).

Artifical Structures

Artifical reef projects make up about one-fifth of restoration practices (Boström-Einarsson *et al.*, 2020b) and use a wide range of artifical structures and material to enhance substate stability and habitat complexity for marine species diversity and coral growth. Typically, artifical structures are placed on reefs that have previously undergone sever physical damage, for example from dynamite fishing, trawling, coral mining or construction, and are placed in combination with coral transplantations. Structutures range from concrete blocks (e.g. 'Reefballs', Kojansow *et al.*, 2013) and ceramic structures (e.g.,'EcoReefs', Moore and Erdmann, 2002), metal constructions from modular metal frames (e.g.,'Spiders', Williams *et al.*, 2019) or entire wrecks to engeneered structures that enhance coral growth using electricity (e.g.,'Biorock', Goreau and Prong, 2017). 'Green engeneering', structures that mimic natural environments to boost coral settlement and 3D printed structures are the latest addition (e.g., Albalawi *et al.*, 2021). Associated challenges are euqally diverse for these methods, but typically include expensive implementations, lack of scalability or proove of effectiveness (Hein *et al.*, 2021). In addition, unsucessfull projects can add to reef degradation with abandoned artifical objects causing aestetic or even environmental pollution, for example in the case of scrap material such as pollutant leaking tyres (Collins *et al.*, 2002).

Coral Gardening

'Coral Gardening' is currently the most widely applied restoration method as it can be applied at various scales and level of technical expertise, depending on the skills and resources available (Boström-Einarsson *et al.*, 2020b). Common to all projects is an intermediate nursery phase to grow and replicate fragments before outplanting them to the restoration site. Coral nurseries rear fragments under favourable conditions and can be set up either in situ, typically in a sheltered environment such as lagoons, or ex situ in aquaria. To optimise coral yield in the reef environment, several structural designs, such as tables, frames or trees have been tested and improved over the years (Herlan and Lirman, 2008; Johnson *et al.*, 2011; Nedimyer *et al.*, 2011). Among those are mid-water floating nurseries, a useful technique for rearing large numbers of coral fragments (Shaish *et al.*, 2008; Levy *et al.*, 2010). These structures are anchored to the substrate while the coral fragment holding part, typically nets, trays or ropes are situated in mid-water, pulled upwards by air filled containers. The design can reduce sedimentation and predation by demersal corallivores, while ideally increasing water circulation around the growing fragments, and even allowing for temporal adjustments or relocation if environmental conditions become temporary unfavourable (Frias-Torres *et al.*, 2018). While this technique has been applied in restoration projects around the world (e.g., Putchim *et al.*, 2008; Montoya-Maya *et al.*, 2016; Bayraktarov *et al.*, 2020; Ishida-Castañeda *et al.*, 2020), some challenges such as adaptations to local conditions, high manpower for monitoring and maintenance that can be costly, development of ecofriendly material and scalability of projects remain (Hein *et al.*, 2021).

Microfragmentation

Based on the coral gardening concept, this new technique has been developed by the Mote Marine Laboratory as a way to improve restoration of slow growing, massive corals. Donor corals are cut into approximately 1cm² fragments and attached to a substrate, on which fragments of the same genotype fuse during the nursery phase to form a larger colony in a relative short time (Page and Vaughan, 2014; Forsman *et al.*, 2015). The technique has already been applied in a number of projects (e.g. Tortolero-Langarica *et al.*, 2020), although some setbacks such as fish predation have been reporter for in situ appoaches (Koval *et al.*, 2020).

Larval Propagation

This relatively new approch intervenes at the sexual reproduction stage of corals, commonly known as coral spawning. During syncronysed breeding events, millions of coral gametes are released into the water for fertilisation and planktonic development, before a small fraction of larvae eventually settles on the reef. To reduce the high mortality rate at this reproductive stage, coral eggs and sperm are harvested during spawning events, fertalized and reared before either directly applied to the targeted restoration site (e.g. Cruz and Harrison, 2017) or reared ex situ to settle on artifical structures, which are then brought out to the reef. In the later case, a study using concrete tetrapodes with settled coral larvae showed that 'seeding' these structures onto degrades sites could potentially accelerate restoration speed and scale (Chamberland *et al.*, 2017). However, at present this technique still requires a high level of technical know how as well as well timed schedules, while high post-settlement mortality and time required for recruits to grow slow down meaningful ecological outcomes (Hein *et al.*, 2021). Lately, the Reef Restoration Adaptation Program in Australia has trialled a number of interventions including assisted larval movement with vessils and seeding via laval slick translocation to priority sites (RRAP, 2021).

Substate Manipulation

These methods include the practice of restoring and stabilising the physical substrate, for example following ship groundings, to enable coral settlement and prevent mechanical damage to the corals (Lindahl, 2003). This is conducted by the removal of coral rubble or its fixation using, mesh nets, concrete slabs or rock piles for stabilization (e.g., Fox *et al.*, 2005) as continued rubble mobilization on unstable substate has been shown to limit coral recovery (Viehman *et al.*, 2018). Research is now looking into the application of natural and chemical bonding agents such as crustose coralline algae (RRAP, 2021). Currently, this is still a little tested and expensive approach.

Substate enhancement is also conducted through the labour-intensive removal of macroalgae, which clears space for coral recolonization. Since macroalgae fulfil an ecological role in the coral ecosystem positive and negative impacts of this intervention need to be considered (Ceccarelli *et al.*, 2018).

1.2.3 Restoration Goals

The variety of restoration techniques developed to date illustrates that there is not one solution that suits all restoration requirements. Likewise, the rationales for conducting any coral restoration activities vary between projects in terms of desirable outcomes (reviewed in Goergen *et al.*, 2020; Hein *et al.*, 2021). Restoration objectives can be broadly defined as:

(1) Ecological goals: these focus on the concept of ecological restoration by protecting and restoring ecosystem functions and services through accelerated recovery, preservation of endangered species, mitigating population declines and increased reef resilience. The establishment of self-sustaining breeding populations should be considered the central aim (Gann *et al.*, 2019).

(2) Socio-economic goals: these goals may target an increase in community involvement and capacity building through rising education and environmental awareness and new local job opportunities. They may involve enhanced business opportunities, for example by increasing destination attractiveness for tourism or by rebuilding fisheries productivity. Improvement of coastal protection can be another motivation.

(3) Climate change resilience: aims to protect coral reefs against the current and projected adverse effects of climate change by increasing reef resilience.

(4) Event-driven restoration: in response to acute threats such as ship groundings, hurricanes, coral bleaching, disease and corallivory outbreaks or in anticipation of future disturbances, e.g., constructions.

(5) Research: comprises a wide and active field of trialling and evaluating interventions in terms of effectiveness, regional validity, scalability or undesirable effects.

On a project scale, the definition of concrete, measurable goals and associated costs are critical to demonstrate effective restoration progress (Bayraktarov *et al.*, 2019). Likewise, the selected techniques and monitoring parameters should match these goals. Mismatches between stated goals and evaluation metrics are frequently encountered in restoration projects, which bears the risk of losing support for projects or even active restoration as a whole (Boström-Einarsson *et al.*, 2020b). Therefore, it has been suggested to define SMART project goals that are Specific, Measurable, Achievable, Relevant, and Time-bound (Shaver *et al.*, 2020).

1.2.4 Coral Restoration in 21st Century

Over the last few years, the field of coral reef restoration has rapidly developed in many ways. The number of initiatives has steeply increased, ranging from small community led projects to ambiguous, large-scale undertakings. A global review of coral restoration efforts identified more than 360 case studies from 56 countries, most of which were short-term (<18 months) and small-scale (average 100m²) projects, using predominantly fast-growing branching species (Boström-Einarsson *et al.*, 2020b). Similar to restoration efforts in other ecosystems, the field of coral restoration had to face a number of challenges, including a lack of archivable objectives, that are measurable in a standardized manner, leading in some cases to poorly designed projects that did not deliver desired outcomes on a meaningful scale (Bayraktarov *et al.,* 2019; Boström-Einarsson *et al.*, 2020b).

In an effort to upscale restoration and facilitate knowledge sharing and collaboration between scientists, restoration practitioners in the field and international institutions, several organisations have taken on the challenge. For over a decade, the Reef Resilience Network has assisted managers and practitioners with training and resources around the world (RRN, 2021). In the US, the Coral Restoration Foundation has been active since 2007, evolving into one of the largest reef restoration organisations in the world (CRF, 2020). The Coral Reef Consortium, which was founded in 2016, oversees several interdisciplinary working and regional groups, as well as providing knowledge exchange platforms and resources (CRC, 2021). Here, six priorities, namely ‘Restoration Efficiency’, ‘Larval-based Restoration’, ‘Holistic Approaches’, ‘Population Genetics’. ‘Standard Terms and Metrics’ and ‘Capacity Building’ have been identified to lead the field in the next few years (Vardi *et al.*, 2021).

Likewise, the amount of literature on the topic, including peer-reviewed studies, reports from official bodies and grey literature has risen sharply (Boström-Einarsson *et al.*, 2020a). While a handful of manuals and guides, often referring to specific regions, have served restoration practitioners at the beginning of the 21st century (e.g., Precht, 2006; Edwards *et al.*, 2010; Johnson *et al.*, 2011), knowledge gathering and dissimilation has steeply increased, leading to the publication of several freely accessible guides on methods, management and evaluation of coral restoration in 2020 alone (Goergen *et al.*, 2020; Hein *et al.*, 2020; Shaver *et al.*, 2020).

In addition, the International Coral Reef Society (ICRS) released during their last International Coral Reef Symposium 2021 a Science to Policy report on ‘Rebuilding Coral Reefs: A Decadal Grand Challenge’, in which the need for immediate action, latest scientific insights and global decision making guidance are outlined (ICRI, 2021; Knowlton *et al.*, 2021).

The urgent need for coral reef conservation and restoration has also gained more attention and recognition outside the scientific community, as many international organisations have included reef resilience and restoration on their agenda. Among the first partnerships dedicated to preserving coral reefs was the International Coral Reef Initiative (ICRI), which was initiated by 8 founding nations in 1994. To date, ICRI has over 90 members including governments, international and regional organisations as well as partners from the private sector. In 2018, an ad hoc committee on reef restoration has been established in response to the severe and acute threat corals are facing due to increasing temperatures (ICRI, 2021).

Coral restoration is further mentioned in multilateral agreements including the Convention on Biological Diversity and resolutions from the United Nations (UN). As such, the UN have announced the UN Decade on Ecosystem Restoration (2021-2030), which is calling for a global effort to protect and restore vital ecosystem, including coral reefs, to counteract climate change and preserve remaining biodiversity (UNEP, 2022). A new G20 initiative led by Saudi Arabia, the Global Coral Research and Development Accelerator Platform (CORDAP), is also on the way in order to bring together expertise from different perspectives in an effort to scale up coral restoration (CORDAP, 2022).

A range of ambiguous restoration projects have lately been in the centre of attention. In the United States, the National Oceanic and Atmospheric Administration (NOAA) has initiated 'Mission: Iconic Reefs', a collaborative, large-scale restoration effort across seven reef sites comprising more than 80 ha along the Florida Keys (NOAA Fisheries, 2021). In response to an unprecedented outbreak of Stony Coral Tissue Loss Disease (SCTLD), NOAA is currently also coordinating a coral rescue team with the aim to collect approx. 4000 healthy colonies from the wild to take them into land-based care (Shrivanek and Wusinich-Mendez, 2020).

In Australia, the Reef Restoration and Adaptation Program (RRAP) was launched in response to the severe threats faced by the Great Barrier Reef, representing currently one of the largest and most well-funded projects. Approaches range from research on genetic enhanced corals and cryopreservation to large scale aquaculture development and larval slick movement to engineering based solutions on rubble stabilization and cooling/shading mechanisms (RRAP, 2022). Earlier this year, an enormous, 100 ha coral garden project in the Red Sea called 'Shushah Island Coral Reefscape' was announced as a joint venture between the future megacity NEOM and the King Abdullah University of Science and Technology (KAUST) of Saudi Arabia (NEOM, 2021).

Coral restoration has also found its way into the lives of non-professional people in the form of citizen science projects or even as a new, more sustainable source of income. Many projects make use of local knowledge and community groups by employing, for example, local fisherman as restoration practitioners as it is the case in many Latin American countries (Bayraktarov *et al.*, 2020). Active restoration typically requires significant manpower and therefore many initiatives additionally rely on trained volunteers and have established citizen science projects. For example, the Coral Restoration Foundations volunteer and citizen science programs in Florida or ‘Meaningful Diving’ with Corales de Paz in Colombia, just to mention a few ; Corales de Paz, 2020). That citizen scientists can significantly contribute to reef restoration was shown in a study involving 230 participants, where the survival of <1300 corals outplanted by volunteers was comparable to those outplanted by scientists (Hesley *et al.*, 2017). Furthermore, the socio-cultural benefits of involving a wider community, such as increasing awareness and education, creating reef stewardship and the experience of actively contributing to conservation are frequently stated objectives and positive outcomes of restoration projects (Hein *et al.*, 2019).

Finally, funding opportunities have increased and diversified over the last years. A recent report on the global funding landscape for coral restoration revealed that in the last 10-15 years project funds comprised $ 258 million in total, primarily derived from grants provided by government as well as the private sector. Although short-term grants were still the norm, the distribution of projects and funds spread globally across coral reef regions and more new, improved funding opportunities are on the way (Hein and Staub, 2021). For example, the Global Fund for Coral Reefs is a financial instrument seeing to acquire billions of dollars for mobilizing global restoration efforts (GFCR, 2022).

Eventually coral reef restoration also has the capacity to attract financial resources from the private sector as restoration projects may directly benefit, for example, tourism stakeholders such as resorts and diving operations. Furthermore, restoration projects can provide substantial visibility and media exposure for brants, that wish to invest in a ‘green’ and ‘sustainable’ image.

For instance, Mars Inc. has initiated the ‘Mars Assisted Reef Restoration System’, which has successfully installed coral spiders on a large scale in Indonesia (Williams *et al.*, 2019) and is currently expanding the project to other regions (MARS, 2021). Their high-profile campaign ‘Sheba Hope Grows’, a coral garden with 840 spiders spelling out ‘Hope’, gained considerable media attention by reaching 159 Mio media impressions in the first 6 weeks (Sheba, 2021; Van Oostrum, 2021, unpub.data). This is just one example of the potential coral reef restoration projects can have in terms of collaboration from different sectors, public outreach and scalability.

Despite the many promising advances and accelerations, the field of coral reef restoration has seen in the last years, it needs to be considered that also the threats to coral reef ecosystems are accelerating and the window of opportunity for mitigation is closing (see chapter 1.1). Among the first nations to experience the adverse effects of climate change and degraded coral reefs are the Maldives.

1.3 The Maldives

1.3.1 Geography

The Republic of Maldives is located in the central Indian Ocean, stretching for approximately 860 km across the equator from 7° 06' 35” N to 00° 42' 24” S. The archipelago is placed along the central part of the of the Laccadives-Maldives-Chagos submarine ridge, where a double chain reef rim structure developed from prehistoric volcanic activity more than 55 Mio years ago (Lüdmann *et al.*, 2013). Today, the Maldives count 1192 islands across 26 natural atolls. Less than 1% of the Maldivian territory (115,300 km²) is land, which is entirely made of sediments from coral reefs (Perry *et al.*, 2015; Statistical Pocketbook of Maldives, 2021). Coral reef and lagoon habitats (21.373 km²) make up approx. 20% (Naseer and Hatcher, 2004). The

Maldives are among the top ten countries in terms of global reef cover, accounting for about 2% of the reefs worldwide (Burke *et al.*, 2011).

The tropical climate is characterised by two monsoon seasons, which dictate wind directions, temperatures, precipitation, currents and wave, and continuously re-shape the natural shorelines of Maldivian islands. The dry-season's northeast monsoon 'Iruvai' from January to March is followed by the wet-season's southwest monsoon 'Hulhangu' from May to November and average temperatures range from 25°C to 32°C (MMS, 2022).

The Maldivian coral reef ecosystem is home to approximately 250 species of scleractinian corals (Pichon and Benzoni, 2007) and over 1000 reef fish species (Anderson *et al.*, 1998) along with many iconic species such as cetaceans (23 species, Anderson *et al.*, 2012), marine turtles (5 species, Frazier, 1980) and sharks (>36 species, De Maddalena, 2017). New species are continuously being discovered (Vonk and Jaume, 2014; Maggioni *et al.*, 2017; Voigt *et al.*, 2018) as scientists have just began to explore Maldivian coral reef biodiversity and complexity. This rich marine environment has provided food, construction material, tradable goods and protection for people (Brown and Dunne, 1988; Lister, 2016), from the first settlers in the 5th century BCE to the modern Maldivian population, which is currently predicted to exceed half a million people (Statistical Pocketbook of Maldives, 2021). The capital Malé is among the most densely populated cities in the world, while the majority of the population is considered rural and lives on the scattered 187 inhabited islands across the archipelago. The rapidly growing economy has been driven by tourism since its introduction in the 1970's, which is today a major contributor (approx. 25%) to the gross domestic product (GDP), surpassing the traditional fishing industry (Statistical Yearbook of Maldives, 2021).

1.3.2 Environmental Threats

The many anthropogenic and natural threats reefs are facing around the world are also of concern for Maldivian coral reefs.

Coastal Development

With building materials being rare, corals have been mined and used in construction for a long time. Realising the exponential growth in demand and the destruction caused by the loss of reef complexity, this practice was banned in the 1990's, although inflicted damage remains visible for decades (Brown and Dunne, 1988; Jaleel, 2013). More recently, severe local reef degradation has resulted from construction work and land reclamations for infrastructure projects such as harbours and airports, the increase and elevation of island terrain and building new touristic facilities (Rashfa, 2014; Duvat, 2020). These activities impact reef, seagrass and mangrove habitats directly through physical destruction or indirectly through dredging operations that increase turbidity and sedimentation in the proximity, thereby reducing reef health and resilience (Zubair *et al.*, 2011; Pancrazi *et al.*, 2020).

Pollution

Adequate waste management remains a major issue in the Maldives, with few advanced waste technologies available (Mohee *et al.*, 2015). Solid waste typically either goes to landfills like Thilafushi 'rubbish island', is dumped and burned on local islands or ends up at sea. This includes any form of waste from non-biodegradable plastics, electronical waste, construction debris and even hazardous wate like batteries and oily waste from the many maritime vessels (Jaleel, 2013). A recent study found one of the highest microplastic concentrations on a Maldivian island (Patti *et al.*, 2020). Yet, the effect on corals has only been looked at in in a few studies (Saliu *et al.*, 2019).

Coral Diseases and Predation

Linked to increasing pollution, among other stressors, is the risk posed by coral diseases. In particular the Northern Maldives were identified as a high risk area for coral disease susceptibility and pathogen exposure (Maynard *et al.*, 2015). First described in 2012, various coral diseases have been reported from several locations (Montano *et al.*, 2012, 2015). More research is required here to evaluate the current and future effects of coral diseases to reef degradation, and the collective impact with other stressors such as pollution, temperature or coral predation. Outbreaks of the corallivorous 'Crown of thorns' seastar *Acathaster planci* have caused severe destruction to reefs in the Maldives (Pisapia *et al.*, 2016; Saponari *et al.*, 2018). The role of other corallivores such as the seastar *Culcita* spp. or the *Drupella* spp. snail in delaying reef recovery is also under investigation, following recent degradations (Bruckner *et al.*, 2017; 2018; Montalbetti *et al.*, 2019; Saponari *et al.*, 2021).

Overfishing

Human overuse, resulting from a fast-growing population and tourism industry, are also adding pressure to natural reef resources. The offshore tuna fishery has a long tradition in the Maldives, where per capita fish consumption is among the highest in the world and fish is the main export product (FAO, 2022). While the 'pole and line' method used to catch tuna is considered fairly sustainable (Miller *et al.*, 2017), the fishery heavily relies on reef caught bait fish, for which there is insufficient stock management (Gillet *et al.*, 2013). Increased domestic demands along with an insatiable export markets, led to a peak catch of almost 186 000 MT in 2005 followed by considerable decline, highlighting the risk of overfishing (Stevens and Froman, 2019; FAO, 2022). Other fishery targets, such as sea cucumbers, giant clamps or aquarium fish have already been overexploited in much shorter timespans (Adam, *et al.,* 1997; Naseer, 1997). Reef fisheries, in particular grouper fisheries, have also increased significantly over the past 20 years, driven by a high export demand of life fish, catches directly and undocumented sold to tourist resorts and a perceived shift in local preferences towards reef fish (Sattar *et al.*, 2014; Yadav *et al.*, 2021).

Tourism Overuse

Tourism continues to grow in the Maldives, peaking at 1,7 Mio annual arrivals in 2019 and recovered to 1.3 Mio in 2021, following a pandemic-induced drop in 2020. About 70% of guest are accommodated in the 159 resorts, with the rest distributed across almost 160 safari vessels and 800 guest houses (MoT, 2021). The negative effects include direct physical reef damage as a result careless behaviour (e.g., reef trampling, anchor damage, collection of reef 'souvenirs', animal feeding, overcrowding etc., Allison, 1996; Brooks, 2010), damage resulting from tourism related constructions and operations (e.g., new resort islands, water bungalows, airports etc., Cowburn *et al.*, 2018) and the increase in resource utilization required for luxury tourism (e.g., demand for imported food and local fish, water and electricity consumption, sewage and waste etc., Kundur and Murthy, 2013). On the other side, an eco-friendlier, growth controlled tourism approach can yield benefits in the form of a premium tourism market as well as overall economic and environmental benefits (Kapmeier and Gonçalves, 2018). It also allows to create environmental awareness among guest through wildlife encounters, educational talks and activities, for which many resorts employ marine biologists.

Climate Change

The Maldives, in many ways, can be considered a prime example nation when it comes to raising awareness on climate change. Sea level rise is a very real threat to the lowest lying nations in the world (MEE, 2015). Coral bleaching events, through the combined force of warming oceans coupled with El Nino occurrence, have already conspicuously reshaped Maldivian reefs. In 1998, the region was particularly hard hit by a severe mass coral bleaching, that led to a considerable loss of coral cover in the Indian Ocean (McClanahan *et al.*, 2007). On

Maldivian reefs a reduction from 60-40% to approx. 2% coral cover was observed (Zahir, 2000; Morri *et al.*, 2015) along with a subsequent shift in species composition and recruitment patterns as branching genera were most severely affected (McClanahan, 2000; Zahir *et al.*, 2002; Schuhmacher *et al.*, 2005). Further regional bleaching episodes occurred in the following decade, along with a Tsunami in 2004, which had comparatively little impact (Morri *et al.*, 2015). Regional recovery was recorded at least for some species (Lasagna *et al.*, 2010; Tkachenko, 2015). By 2014, coral reefs had recovered to pre-bleaching live coral cover (Morri *et al.*, 2015), but changes in colony size structure and key genera abundances following more recent disturbances indicated a reduced resilience and recovery potential (Pisapia *et al.*, 2016). In 2016, another severe mass bleaching event led to the estimated loss of up to 75% of shallow water corals (Ibrahim *et al.*, 2017; Perry and Morgan, 2017). Again, the reef habitat shaping *Acropora* taxa were most severely affected, but changes in population structures were recorded across genera (Pisapia *et al.*, 2019). Considering the projected increase in severe bleaching events (every 9 years for the Maldives, Van Hooidonk *et al.*, 2016) among other disturbances and the limited number of species that can adapt to these conditions, there is considerable doubt if Maldivian coral reefs will be able to recover in time the future (Perry and Morgan, 2017; Pisapia *et al.*, 2019).

Environmental Protection

The Republic of Maldives actively engages in a range of international treaties, programmes and organizations, dedicated to environmental protection and sustainable development (e.g., UN Sustainable Development Goals, Convention on Biological Diversity, CITES, Paris Agreement). Environmental policies are mainly regulated under the Environmental Protection and Preservation Act and overseen by the Ministry of Environment, Climate Change and Technology. The ministry currently lists several planned undertakings in regards to waste management, clean energy and climate change adaptations along with a presidential decree to ban most single use plastics by mid-2022 (MECT, 2022).

National fishery legislation has banned all destructive fishing practices (dynamite, chemicals etc.) as well as the catch and export of iconic species (e.g. Cetaceans, turtles, rays, Napoleon wrasse, black coral, triton shell, Naseer, 1997). A shark fishing ban was introduced in 2009, given their economic value for tourism (Cagua *et al.*, 2014; Zimmerhackel *et al.*, 2019). 42 Marine Protected Areas and one biosphere reserve have been designated, although they only cover 0.5% and management is overall insufficient (Stevens and Froman, 2019).

While there is a substantial body of regulations, implementation and enforcement is lacking in many cases (Techera and Cannell-Lunn, 2019). For example, Environmental Impact Assessments have been deemed insufficient and engagement and participation of the public is lacking (Zubair *et al.*, 2011).

A considerable number of national and international institutions and non-governmental organisations are also pursuing conservation and education goals in the Maldives, often in collaboration with the tourism sector (e.g., Manta Trust, Maldives Whale Shark Research Program, Marine Savers, Blue Marine Foundation, Blue Prosperity Coalition, the University of Milano-Bicocca's MaRHE Center). One area of active conservation that is currently still lacking in scale in the Maldives is coral restoration.

1.3.3 Coral Restoration in the Maldives

The scientific literature published on coral reef restoration in the Maldives is scarce and mostly dates back to the 1990's. Back then, a single project has been described that comprised a combination of substrate stabilization with artificial reef structures and direct transplantation in response to reef damage from coral mining (Clark and Edwards, 1994, 1995, 1999). On a study site close to Male, different types of artificial concrete structures (total of 360 t) were places on a 4 ha large reef flat, that had shown little natural recovery 20 years after coral mining operations. Artificial structures were found to be rapidly colonized by fish, algae and invertebrates. After one year, fish abundance and species richness had significantly increased, although found markedly dissimilar from a undisturbed reference site (Clark and Edwards, 1994). The transplantation of whole coral colonies to the concrete mats resulted in mixed success, with about half the colonies surviving through the first two years (Clark and Edwards, 1995). Natural recruitment was more successful, in particular on the larger, more complex concrete structures, indicating that reef was not recruitment-limited but recovery was inhibited by the lack of stable settlement substrate. Therefore, it was concluded after 3.5 years of observations that restoration success was proportional to the costs and complexity of different structures, but rather unsuitable on a large scale due to the high costs and effort involved (Clark and Edwards, 1999). While this project was certainly advanced and provided new insight at the time, coral restoration practices have developed considerably since then. In particular the transplantation of whole colonies by denuding an entire reef area is no longer an acceptable practice. Already at the time, it was considered a "costly and time-consuming activity of doubtful efficacy", given the high natural recruitment and damage to the donor site (Clark and Edwards, 1999).

Following this project, a range of techniques and small-scale projects have been conducted in the Maldives, in particular on resort islands, but rigorous methodical evaluation on project effectiveness is typically not widely available and information is scattered across reports, posters, newspaper articles, websites and social media (see Siena, 2018 for details).

From 1996 onwards three Biorock electric reefs were constructed and operated on two resort islands in North Male Atoll. According to the initiators survival of corals grown using the Biorock technology distinctly exceeded their natural counterparts during the 1998 bleaching and the 2004 Tsunami. Nevertheless, active project operations were discontinued shortly after (Goreau and Hilbertz, 2004). Following the first severe mass bleaching in the Maldives, coral restoration became a more pressing issue, especially among luxury resorts Another resort chain implemented the Reefball^{TM} technique in 2001 (Reefball, 2003) but soon switched to the more practical and cost-efficient method of coral frames in 2005, following consultation with a local agency (Reefscapers, 2022). Documentation of this project, comprising three resort islands and 1250 m² of frame area is available in form of a case study (Edwards *et al.*, 2010). It was found that especially the frames with open dome structures reduced predation, sedimentation and good coral growth with more 90% survival after the first year. The socio-ecological perspective of this approach was further evaluated as part of a wider review, finding that in the Maldives guest involvement was a major benefit and also resulted in higher economic revenues while ecological problems, in part, due to the 2016 bleaching event were a major limitations (Hein *et al.*, 2019). Given the low costs, aesthetic appearance and ability of resort guest engagement, coral frames became the most popular restoration technique in resorts across the Maldives, with the main consultancy firm stating to have put alone 8500 frames in the water to date (Reefscapers, 2022). An informal online survey recently found, that the vast majority of coral restoration projects are currently conducted on resort islands in the Maldives, applying a mix of artificial reef s and nursery structures (Siena, 2018). Demand for coral restoration activities is also likely to increase in the future, given the current reef conditions in the Maldives and the future projections, both in terms of increasing local and global threats and growing tourism. A recent study on reef user's satisfaction on two resort islands found that people were not satisfied with coral reef appearance, which were rated as highly important, and high prioritization and support was expressed for coral restoration efforts (Fiore *et al.*, 2020).

Sound project planning and evaluation are key, in order to not risk project failures that waste limited conservation resources, public support and the little time left to save remaining coral reefs (Hein *et al.*, 2021). Yet, compared to other regions, coral restoration is still at an early stage in the Maldives and baseline studies and regional validation of methodologies are needed. Currently, information available to project managers and restoration practitioners in the

Maldives is scattered, dated, and not always following rigorous scientific assessment (i.e., no peer-reviewed publications) and therefore not sufficient for informed decision making.

1.4 Research Objectives

The continuous threat to Maldivian coral reefs, an ecosystem on which the entire nation's economy and eventually existence depends, needs to be addressed urgently, using the full set of conservation tools available. This includes active and upscaled coral restoration efforts across the many local and touristic islands in the most ecological and socio-economic effective way. This research aims to contribute to this challenging undertaking by providing new insights into contemporary restoration approaches that will hopefully be useful for restoration practitioners in resorts and local islands across the Maldives.

Currently, larger coral restoration projects applying the 'gardening concept' of an intermediate nursery phase followed by a transplantation phase (Rinkevich 1995, 2000; Epstein et al. 2001) are relatively uncommon and undocumented in the Maldives. An important step towards advancing coral restoration in the area was made in 2017, when the first edition of the Coral Reef Restoration Workshop was held by MaRHE Center on Magoodhoo. Here, restoration practitioners from various backgrounds were trained in different restoration techniques and four mid-water rope nurseries were installed in the local lagoon. Building on the progress made during the workshop, this work sets out to explore, assess and validate restoration approaches suitable for the Maldives, given local environmental conditions and resources available. Furthermore, potential limitations and pitfalls to restoration success are investigated. Thus, the objectives of this research are:

(1) Testing mid-water rope nurseries for farming corals in the Maldives by assessing their performance across regions and different farming habitats (Chapters 2 & 3);

(2) Providing regional benchmark results for survival and growth of coral genera suitable for the coral gardening technique along with examining key ecological interactions such as mutualism and predation (Chapters 2, 3 and 6);

(3) Investigating potential risks to successful coral restoration outcomes with a particular emphasis on the current Covid-19 pandemic and the projected increasing occurrence of coral diseases (Chapters 4 & 5):

(4) Assessing transplantation success of farmed corals and the ecological implications for the restoration site (Chapter 6);

(5) Understanding efficient 'best practices' for coral restoration projects in the Maldives (Chapters 2 - 6):

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CHAPTER 2

2.1 Exploring the performance of mid-water lagoon nurseries for coral restoration in the Maldives

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2.2 Abstract

Small island nations like the Maldives are highly dependent on healthy coral reefs and the ecosystem services they provide. Lately, Maldivian reefs have experienced considerable degradation as a result of severe mass bleaching events and accumulating threats posed by pollution, human development, coral diseases and outbreaks of corallivores. Coral restoration can be a useful mitigation tool in assisting natural recovery, especially when economically important reef areas such as resort reefs are in poor health with slow natural recovery. This study assesses the performance efficiency of lagoon mid-water rope nurseries for coral gardening in two different atolls in the Maldives for the first time. Three different coral genera, namely *Acropora*, *Pocillopora* and *Porites* were assessed applying a common monitoring protocol. Fragment survival was generally very high, exceeding 90% survivorship for the genus *Acropora* and *Pocillopora,* while nursing success for *Porites* was significantly lower (66%). We further report benchmark growth rates for these genera in mid-water rope nurseries in the Maldives. The study also identifies potential threats to coral nursing success, namely disease occurrence and predation, as we report the corallivorous nudibranch *Phestilla* on in situ nursing stock for the first time. Overall, our results suggest that the use of mid-water rope nurseries in lagoons is an efficient and widely applicable technique for rearing corals in the Maldives. We aim to provide useful insight into best practices for applying this coral gardening technique on a wider scale in the archipelago and highlight future research requirements.

2.3 Implications for Practice

- This study validates and encourages the utilization of mid-water rope nurseries in Maldivian lagoons to upscale coral restoration efforts, for example on resort and local islands
- Our benchmark results for growth and survival of *Acropora* and *Pocillopora* fragments demonstrate their suitability for this method, while alternative techniques for rearing *Porites* fragments should be tested
- We recommend to select lagoons for coral nursing based on their environmental characteristics, in particular sufficient water circulation (slight to moderate current), water volume (lagoon depth of 10m or more) and water quality (reduced exposure to human activities).

2.4 Introduction

Tropical coral reefs, once known as rich and diverse ecosystems, have lately experienced an unpreceded decline in health, biodiversity and services they provide to human kind (Burke et al. 2011; Hughes et al. 2017). As coastal communities are facing the consequences of degraded reef ecosystems, active coral reef restoration has become an increasingly popular mitigation tool and has lately sparked a large number of projects, research and management protocols (Boström-Einarsson et al. 2020). While restoration efforts are globally accelerating, the need to test and validate techniques regionally remains crucial to ensure efficient resource allocation and the long-term success of local restoration projects as part of a wider reef conservation strategy (Hein et al 2021). On a community scale, active coral reef restoration projects are frequently practiced as an in situ approach, applying the 'gardening concept' (Rinkevich 1995; Epstein et al. 2001). In this 2-step process, coral fragments derived from donor colonies or collected by opportunity are grown in a range of artificial nursing structures under optimal growing conditions until they reach a suitable size for transplantation to the degraded site (Rinkevich 2005; Levy et al. 2010). Mid-water floating nurseries and in particular rope nurseries, are a promising technique for rearing large numbers of coral fragments (Shaish et al. 2008; Levy et al. 2010) and are typically placed inside protecting lagoons. They have been successfully tested in the Red Sea (Shafir et al. 2006) and applied in coral restoration projects in various locations such as the Philippines (Shaish et al. 2008), the Seychelles (Frias-Torres et al. 2015) or Latin America (Bayraktarov et al. 2020). However, regional testing is required before upscaling can be considered (Shaish et al. 2008).

Maldivian coral reefs, which are vital to the national economy, have experienced a series of bleaching events, including the latest severe mass bleaching in 2016, followed by the degradation of many valuable recreational reef sites (Pisapia et al. 2016; Ibrahim et al. 2017). Additional stressors including pollution, constructional development, outbreaks of corallivores and coral diseases are further threatening coral reef health (Jaleel 2013; Montano et al. 2015; Saponari et al. 2018). Yet, coral restoration in the Maldives is a less commonly applied practice than one would expect, given the economic importance of healthy reefs and the many challenges corals currently face. Current small-scale restoration activities, typically applying coral frames for educational purposes, are usually initiated by the many luxury resorts (e.g. Hein et al. 2020). Hence, the need for an upscaled restoration approach, applying locally tested methodologies and economically viable project designs, is evident.

Here we assess the performance of lagoon mid-water rope nurseries in the Maldives for the first time, providing an essential pilot study and regional validation of this technique. We monitored coral nursing success of three genera in two different atolls, providing benchmark results for fragment survival and growth for *Acropora*, *Pocillopora* and *Porites* genera in the Maldives.

Based on our observations, we suggest some logistic and location-specific considerations to improve coral gardening success and upscale restoration efforts.

2.5 Methods

2.5.1 Study Design

The study was conducted on Magoodhoo island in Faafu atoll and Athuruga island in Alif Dhaal atoll, in the Republic of Maldives (Fig. 1) between November 2017 and February 2019.
At both locations, mid-water rope nurseries, measuring 3 x 10-m at the coral nursing level, were constructed, four nurseries on the East-side of Magoodhoo's lagoon and one in Athuruga's lagoon.

Magoodhoo's nurseries were stocked in December 2017 with a total of 754 fragments, which were collected from the same lagoon as corals of opportunity between 5 and 10 m depth and deployed in the nurseries between 6.7 and 9.3m depth. The majority of the fragments collected were identified as *Acropora muricata*, an abundant arborescent branching species in Magoodhoo lagoon. The remaining *Acropora* sp. fragments were characterized by irregular, arborescent growth, but finer straight branches. For data analysis fragments were divided into four groups: *Acropora muricata* (Am: N=501), *Acropora* sp. (Asp: N=141), *Pocillopora verrucosa* (Poc: N=13), and *Porites rus* (Pr: N=99). Data collection and nursery cleaning was conducted on a monthly basis until April 2018, resulting in four surveys (S1-S4).

Athuruga nursery was stocked with 400 coral fragments between 5.0 and 6.0 m depth in July 2018. Corals of opportunity from nearby Thudufushi, one of the few reefs with high coral cover in the area (Saponari et al., 2018; 2021), were collected from a depth of up to 4 m and immediately transported to the nursery site. The same three genera (arborescent *Acropora*, *Pocillopora* and *Porites)* and groupings as for Magoodhoo were used (Am: N=100; Asp: N=100; Poc: N=100; Pr: N=100). Four data collection and maintenance sessions (S1-S4) were conducted on a bi-monthly basis until March 2019.

2.5.2 Data Collection and Analysis

The total survey period comprised 154 days since stocking on Magoodhoo and 234 days on Athuruga. For each of the four surveys the following parameters were assessed: 'Survival' was measured as a binary condition (i.e., 'alive' and 'dead'). Fragment 'Health Condition' was classified into the categories '100% alive' (H3)', 'more than 50% alive' (H2), 'less than 50% alive' (H1) and 'pale or partially bleached' (P). 'Growth' was measured as 'Ecological volume' (EV). Three measurements to the nearest mm were taken using a Vernier caliper to calculate:

$$EV = \pi r^2 h, \text{ where } r = (w+l)/4$$

and 'h' representing the longest linear extension of the three perpendicular measurements (h, w, l). Fragment size was measured for a randomly selected, fixed subset on Magoodhoo and for all fragments on Athuruga. Dead fragments were excluded. Environmental and biological data including water temperature, visibility, signs of predation or diseases were also documented. On diseased fragments the affected branch was removed 1 cm below the visibly infected tissue after taking growth measurements.

Statistical analysis was performed using SPSS ver. 26 (IBM, New York) and non-parametric tests were selected where normality assumptions were violated. Survival was compared using a chi-square test of independence. Changes in mean EV between S1 and S4 was compared for each fragment group using the Wilcoxon signed rank test and used to calculate daily growth rates, which were compared using the independent Mann-Whitney test. All data is represented as arithmetic means ± standard error.

2.6 Results

Survival

Overall, fragment survival (Table 1) was high on Magoodhoo (93.4%) and on Athuruga (93.5%), with no significant difference between sites ($\chi^2(1, N=1154)=0.01$, $p=0.932$). On Magoodhoo, fragment mortality was highest at the beginning (4.2% in 48 days), before dropping to 2.4% in the following three months. Survival rates differed between coral genera, with high survival for *Acropora* fragments (Am 100% and Asp 98.6%) as well as for *Pocillopora verrucosa* (100%), although these represented only 2% of the stock. *Porites rus* had a significantly lower survival of 68.7% after 48 days which further decline to 51.5% after 154 days ($\chi^2(9, N=754)=512.26$, $p<0.001$). On Athuruga, the mortality rate was also highest at the start (3.7% after 78 days) and decreased to 2.8% in the 141 days to follow. Again, survival was high for *A. muricata* (98%), *Acropora* sp. (97%) and *P. verrucosa* (99%) after 234 days in the nursery, but significantly lower for *P. rus* (80%; $\chi^2(12, N=400)=208{,}018$, $p<0.001$).

Health

On Magoodhoo, the majority of fragments remained fully healthy throughout the study (88.5 ± 1.1%), while only few fragments had suffered from partial mortality or initial bleaching (Fig.2a). *Acropora* and *Pocillopora* were in good health at all times, (>90%), while only 14% of *P. rus* remained 100% healthy (Fig. 2c). 14 predation events were recorded on Magoodhoo. The corallivorous nudibranch resembling *Phestilla lugubris* (Mollusca, Gastropoda, Nudibranchia) was found on three *P. rus* fragments, of which two died (Fig 3). On the majority of *P. verrucosa* fragments (77%, N=10) fish scars were recorded, although fragments recovered. No diseases were documented throughout the study.

On Athuruga, fragment health was more variable (Fig. 2b). Only 14% of corals were 100% healthy at the first survey, while the majority (69%) were classified as pale or partially bleached. Over time the percentage of healthy corals increased to 42.4 ± 9.7% while pale fragments, found in all species groups, gradually declined to 11% at the end of the study. Partial mortality was also slightly higher and most noticeable in the *P. rus* group (Fig. 2d). The majority of predation events (N=11) on Athuruga were cases of *P. lugubris* on *P. rus* fragments, resulting in partial tissue loss for the fragments. In addition, fish scars on three *A. muricata* fragments were documented. Signs of White Syndrome (WS) were first recorded in the second survey (N=2 at S2 and N=1 at S3) and increased rapidly to 26 cases in the fourth survey. Diseased tissue was found on 21 *A. muricata* fragments and five *Acropora* sp..

Growth

Comparison of fragment growth, represented as increase in 'Ecological volume' (EV) between S1 and S4, showed that all fragments on Athuruga (N=374) and all *Acropora* fragments on Magoodhoo (N=96) gained significantly in size over time, while sample size for *Porites* and *Pocillopora* on Magoodhoo was too small to analyze (see Table 1, Fig. 4). Of all tested species *A. muricata* on Magoodhoo grew the most, with a significant increase of 6,368 ± 1541% (Z=-7.77, p<0.001) in 98 days. On Athuruga, *A. muricata* also increased significantly by 7,180 ± 1196% (Z=-8.595, p<0.001) in 198 days. Similarly, EV of *Acropora* sp. showed a significant 567 ± 87% increase (Z=-3.464, p=0.001) on Magoodhoo and an 800 ± 159% increase (Z=-8.508, p<0.001) on Athuruga. *P. verrucosa* growth could not be analyzed on Magoodhoo as the only surviving fragment was subject to predation. On Athuruga, *P. verrucosa* increased steadily by 544 ± 38% (Z=-8.638, p<0.001). Finally, *P. rus* grew slowly on Magoodhoo with a marginal significant increase of 118 ± 56% (Z=-1.859, p=0.063) as well as on Athuruga, where EV increased significantly by 222 ± 31% (Z=-7.693, p<0.001). Daily growth rates analysis (Table 1) shows that Magoodhoo's *A. muricata* also exhibited the fastest growth rate (0.650 ± 0.16), which was significantly higher than the daily growth rate on Athuruga (0.366 ± 0.06; T=3064, p=0.01). Likewise, *Acropora* sp. daily growth rate was significantly higher on Magoodhoo (0.058 ± 0.01) than on Athuruga (0.041 ± 0.01; T=421, p<0.01).

Environment

While no significant difference was observed in water temperature (Mag: $\bar{x}$ =28.71 ± 0.14°C; Ath: $\bar{x}$=28.63 ± 0.12°C), horizontal visibility varied considerably on Magoodhoo (9.0 to 25.0 m) and was on average significantly higher (16.67 ± 0.64 m) than on Athuruga (7.17 ± 0.34 m; T=23.5, p<0.001).

2.7 Discussion

We assessed the performance of lagoon mid-water rope nurseries in two different atolls to validate their efficiency for coral restoration in the Maldives. By including fragment survival, health, growth, diseases and predation tracking for three coral genera in our monitoring protocol, this study provides useful baseline information for restoration practitioners as similar research has not been reported from the Maldives until now. Overall, our results suggest that lagoon mid-water rope nurseries are a feasible and promising technique for large-scale rearing of corals in the Maldives. Both lagoons provided good nursing conditions and sufficient shelter as structures lasted through-out the study period. Yet, direct comparison revealed that Magoodhoo had better survival, health and growth rates in most cases. Factors influencing nursing success could include stocking procedures and growing depth. On Athuruga, the slightly shallower growing fragments were exposed to more stress during stocking, resulting in more fragments becoming pale or partially bleached at the start of the nursing phase. Nevertheless, fragment survival was generally very high in both locations, exceeding the suggested benchmark of >80% survivorship for the Caribbean (Schopmeyer et al. 2017). Coral fragments of branching genera also grew significantly in size over time, providing benchmark results for the Maldives.

Out of the four species tested, *Acropora muricata*, a rapidly growing lagoon coral, appears to be a very promising candidate for the coral gardening approach. On Magoodhoo, all fragments survived and exhibiting the fastest growth of all assessed groups. On Athuruga, *A. muricata* survival was also high (98%), although health and growth rates were slightly poorer.-The other *Acropora* species in our study followed the patterns observed in *A. muricata* closely, although more *Acropora* species with different growth forms remain to be tested. Easy fragmentation, fast wound healing and high survival rates make branching *Acropora* popular candidates for coral gardening (Lirman et al. 2010). Likewise, their fast and complex growth means they are critically important for reef structural complexity, habitat formation and coastal buffering (Harris et al. 2018), underlining their suitability for restoration projects in the Maldives.

Pocillopora verrucosa, a common and compact growing species, also survived well (99%) and grew slower but steadily in Athuruga lagoon. No signs of disease were recorded in this species and although some fragments initially bleached or showed signs of fish predation, recovery was high. Therefore, *P. verrucosa* proved to be a robust coral, suitable for rearing in mid-water rope nurseries, especially when environmental conditions are not optimal. Whether the slightly slower growth rate due to more compact growth requires a longer nursing period in comparison with *Acropora* species remains to be tested.

Porites rus turned out to be the least suitable species for this restoration technique. In comparison, fragment survival, health and growth were significantly poorer in both locations and the massive growth form makes restocking difficult. These findings are in line with other studies, where *P. rus* performed poorly in suspended nurseries (Shaish et al. 2008). Hence, alternative techniques such as microfragmentation, have been suggested to include these ecological valuable but slow growing corals to the restoration portfolio (Forsman et al. 2015). One particular obstacle encountered with rearing *P. rus* was predation. The corallivorous nudibranch resembling *Phestilla lugubris* (Bergh, 1870) and its predation marks were exclusively found on *Porites* fragments in both locations and were directly linked to a decline in fragment health. This is the first report of *Phestilla* predation on coral nursing stock in the Maldives. The cryptically colored nudibranch is known to have previously infested ex situ coral nursing experiments (Forsman et al. 2006) and hence, may also represent a challenge to the in situ propagation of *Porites*, which should be investigated further.

Direct comparison between the two lagoons of a local and a resort island revealed that site specific characteristics can also contribute to coral nursing success and should therefore be considered during the project planning and site selection process. The overall better performance of Magoodhoo's nurseries may, in part, be attributed to the conducive environmental conditions in the lagoon, in particular water circulation. Magoodhoo`s up to 15 m deep lagoon is located on the atoll rim and connects via two channels to the inner and outer Atoll Sea. This allows for increased water circulation around the nurseries and the growing fragments, which was also reflected in slight to moderate currents and the higher and more variable visibility experienced here. In contrast, Athuruga's bigger and fully enclosed lagoon is characterized by more turbid water and no current at coral nursing depth. Similar water temperatures were observed as both lagoons are relatively large and deep, which protects them against rapid water temperature increases during the dry season.

Water quality may also play a role, especially since Athuruga is located in the center of the second busiest resort atoll (Statistical Yearbook of Maldives 2019). It is worth pointing out that white syndrome (WS) disease incidents were only recorded on Athuruga, which could be indicative of human induced water pollution. WS is a widespread disease in the Maldives, but disease dynamics and potential causes, which could include pollution or temperature stress, remain largely unstudied (Montano et al. 2015). Further research on disease mitigation in a coral gardening context is required, considering the potential economic loss associated with high stock mortality. On Athuruga, the disease spread despite the timely removal of diseased tissue, which has also been observed in other studies (Miller et al. 2014). Since diseases emerge as an increasing threat to coral restoration, a monitoring framework has lately been suggested and a new tool for treating coral injuries from fragmentation has been tested in the Maldives (Contardi et al. 2000; Moriarty et al. 2020).

Although conclusions derived from our study are limited by the number of species tested, variations in survey intervals and the limited duration of the coral nursing period, these are encouraging results in light of local restoration baseline requirements and provide the necessary validation of this technique in the Maldives. Considering the archipelago's high economic dependence on healthy reefs, the many small-scale restoration projects initiated by the tourism industry urgently require scientifically tested approaches and upscaling to an ecological meaningful level. We prioritized testing the fast growing key genera *Acropora* and *Pocillopora*, which were previously severely affected by the 2015/16 corallivorous outbreak and bleaching event (Pisapia et al. 2017; Saponari et al. 2018). However, to increase species diversity and reef resilience additional species and restoration techniques, including the outplanting phase of coral gardening, require further rigorous testing to guide restoration practitioners in the Maldives. In the case of lagoon mid-water rope nurseries, future studies could look into the rearing of mixed species and age classes, which could be advantageous to attract and sustain communities of mutualistic damselfish or *Trapezia* crabs, that can have positive impacts on coral health and resilience (Chase et al. 2018; Stier et al. 2012). Furthermore, not all Maldivian islands have access to sheltered lagoons of suitable depth, so adjustments in structure design and locations should be tested.

We conclude that the performance of our mid-water rope nurseries in two lagoons in the Maldives validates the technique's efficiency for large-scale coral gardening in the Maldives, despite some study limitations. Regional variations also suggest that gardening sites should be carefully selected based on logistic and environmental criteria. Our study represents the first regional assessment of this technique and with our results we hope to encourage restoration practitioners in the Maldives to apply this method to upscale restoration efforts.

2.8 Acknowledgements

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2.10 Illustrations

Table 1: Survival of different fragment groups and their relative proportion of the nursing stock and average daily growth rates with count of analyzed fragments for Magoodhoo (after 154 days) and Athuruga (after 234 days). Significance levels for survival comparison between fragment groups and growth rate comparison for each species between sites are indicated as *** < 0.001, ** < 0.01 and *< 0.05.

	Magoodhoo		**Athuruga**	
Survival		**Stock %**		**Stock %**
All fragments	93.4 %	100%	93.5 %	100%
Acropora muricata	100 %	66%	98 %	25%
Acropora sp.	98.6 %	19%	97 %	25%
Pocillopora verrucosa	100 %	2%	99 %	25%
Porites rus	51.5 %***	13%	80 %***	25%
Daily growth rate		**Count**		**Count**
Acropora muricata	.650 ± .16*	80	.366 ± .06	98
Acropora sp.	.058 ± .01**	16	.041 ± .01	97
Pocillopora verrucosa	N/A	1	.028 ± .002	99
Porites rus	N/A	7	.011 ± .002	80

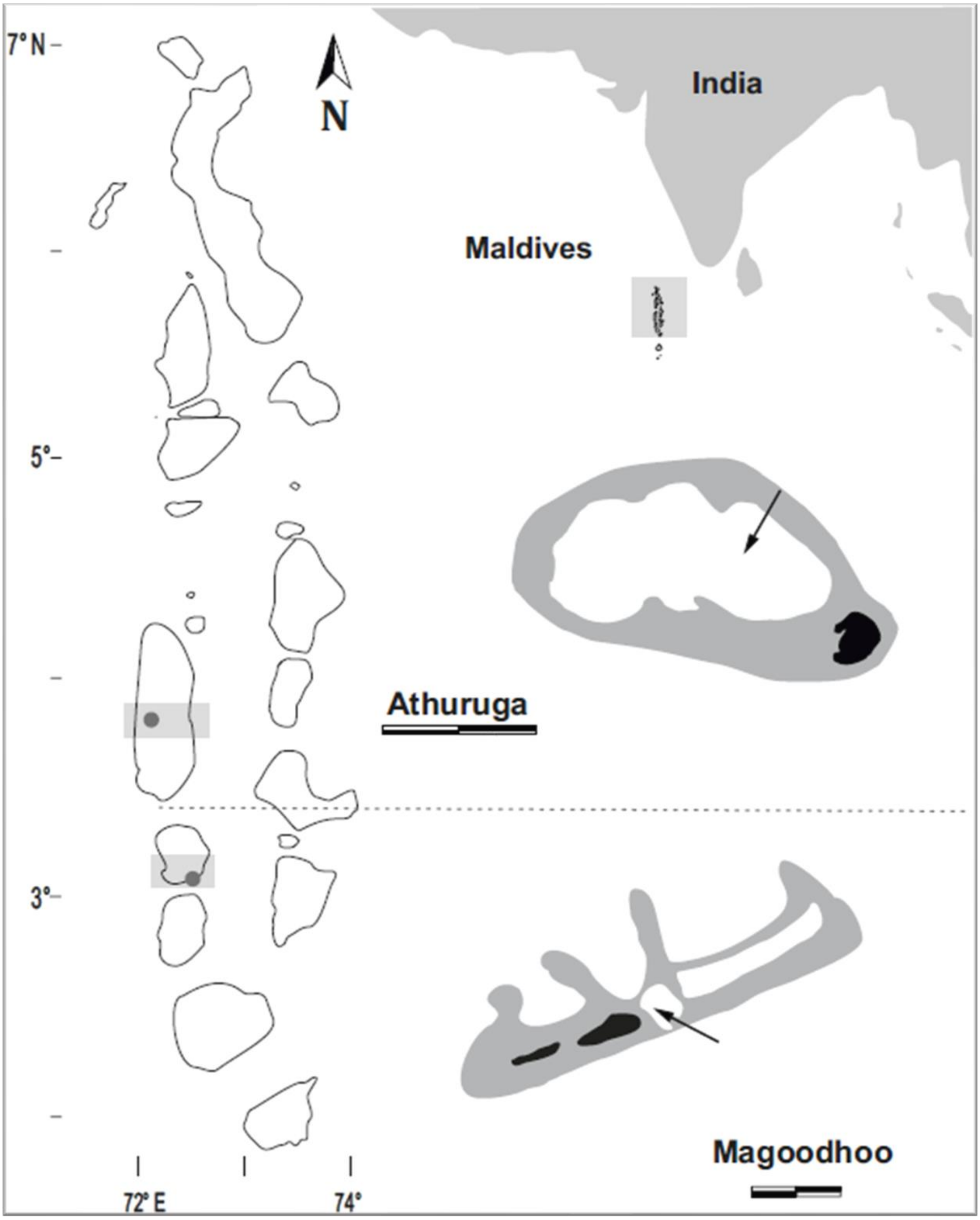

Figure 1: Map of the Maldives showing the study locations, Magoodhoo local island in Faafu atoll (3°04'45''N, 72°57'53''E) and Athuruga resort island in Alif Dhaal atoll (3°53'14''N, 72°48'59''E). Arrows indicate the nursery locations in the lagoons and 1 km scale bars are shown.

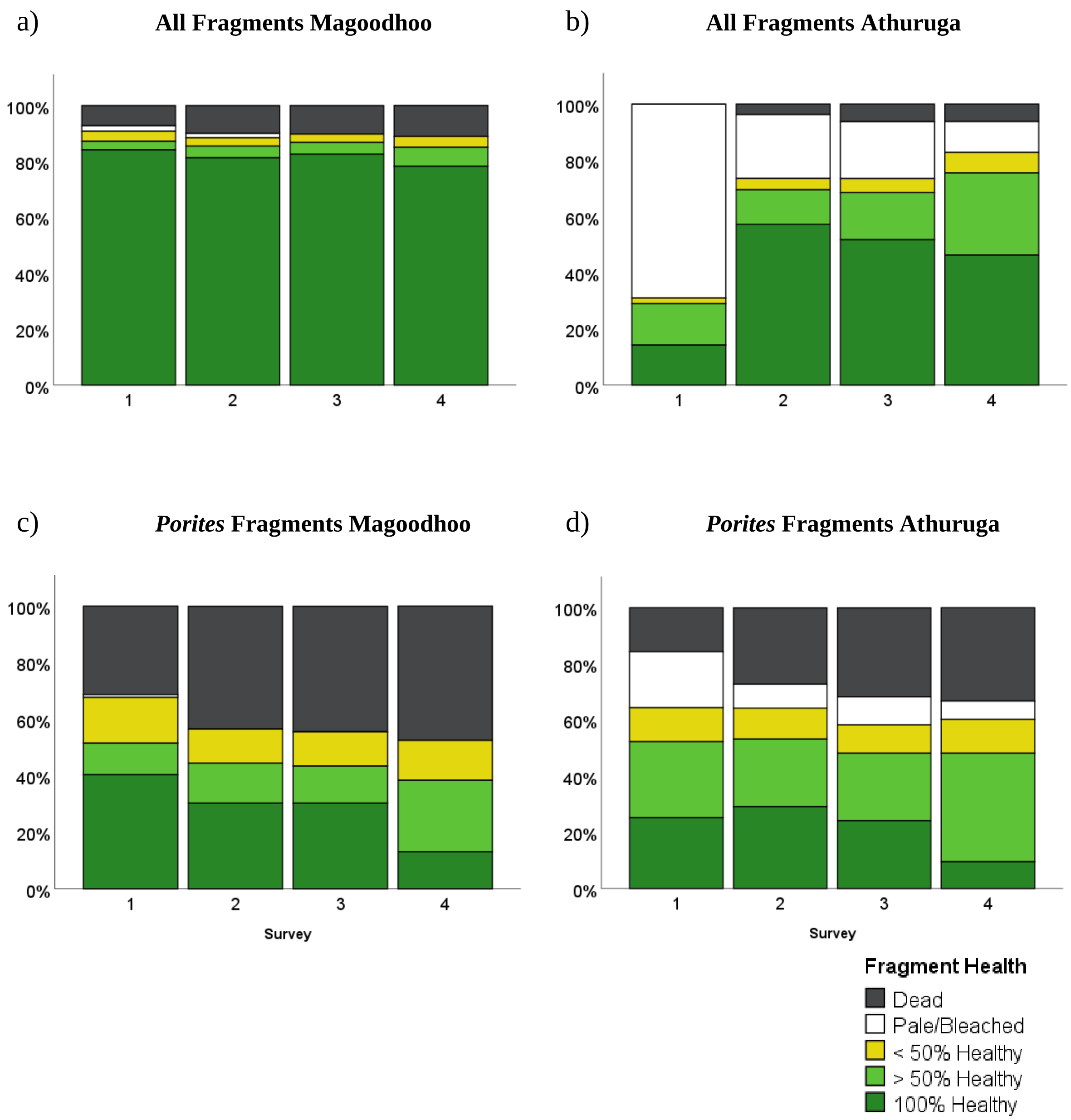

Figure 2: Bar charts of coral health condition on the nurseries over four surveys for a) all fragment groups combined on Magoodhoo (N=754) with low average partial mortality (H2: 3.6 ± 0.6% and H1: 2.2 ± 0.2%) and 4 bleached fragments at S1; b) all fragment groups combined on Athuruga (N=400) with higher average partial mortality (H2: 18.3 ± 3.8% and H3: 4.6 ± 1.1%) and more pale/partially bleached fragments (Am: 12.1 ± 10.1%; Asp: 13.4 ± 10.5%; Poc: 26.9 ± 9.6%; Pr: 11.3 ± 4.9%); c) *Porites rus* on Magoodhoo (N=99); d) *Porites rus* on Athuruga (N=100).

Figure 3: The corallivorous nudibranch resembling *Phestilla lugubris* was recorded on in situ nursing stock for the first time. The coral skeleton of this *Porites* fragment is completely obliterated where the animal laid its egg ribbons (Photo by L. Saponari).

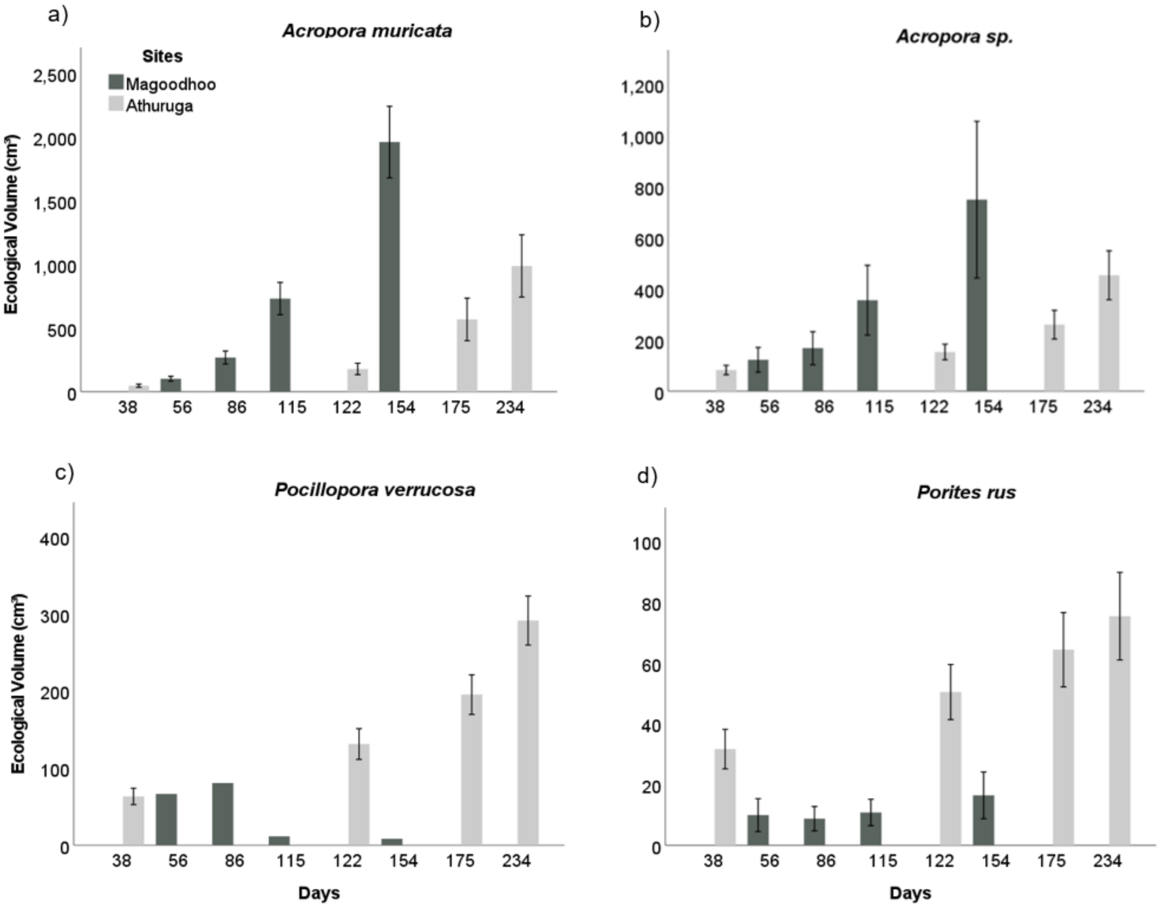

Figure 4: Comparison of fragment mean 'Ecological volume' increase on Magoodhoo (dark bars) and Athuruga (light bars) during the study period for a) *Acropora muricata* increasing from 101.56 ± 9.8 cm³ to 1,961.41 ± 140.4 cm³ on Magoodhoo and from 47.22 ± 6.1 cm³ to 987.55 ± 122.1 cm³ on Athuruga; b) *Acropora* sp.; increasing from 122.36 ± 24.0 cm³ to 748.41 ± 153.1 cm³ on Magoodhoo and from 82.61 ± 9.2 cm³ to 452.73 ± 47.8 cm³ on Athuruga; c) *Pocillopora verrucosa* was subject to predation on Magoodhoo and grew on Athuruga from 63.15 ± 5.3 cm³ to 291.12 ± 15.9 cm³; d) *Porites rus.* increasing from 9.93 ± 2.7 cm³ to 16.43 ± 3.8 cm³ on Magoodhoo and from 31.66 ± 3.3 cm³ to 75.40 ± 7.2 cm³ on Athuruga. Error bars indicate ± 2 SE.

CHAPTER 3

3.1 Comparing different farming habitats for mid-water rope nurseries to advance coral restoration efforts in the Maldives

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3.2 Abstract

The need for comprehensive and effective coral restoration projects, as part of a broader conservation management strategy, is accelerating in the face of coral reef ecosystem decline. This study aims to expand the currently limited knowledge base for restoration techniques in the Maldives by testing the performance of mid-water rope nurseries in a lagoon and a reef habitat. We examined if different coral farming habitats impacted fragment survival, health and growth of two coral genera and how the occurrence of mutualistic fauna, predation and disease influenced coral rearing success. Therefore, two nurseries were stocked with a total of 448 *Pocillopora verrucosa* and 96 *Acropora* spp. fragments, divided into different groups (four *Pocillopora* groups: lagoon nursery at 5m; reef nursery at 5, 10 and 15m; two *Acropora* groups: lagoon nursery at 5m and reef nursery at 5m). Eight fragment replicates from the same donor colony (*Pocillopora* genets: N=14, *Acropora* genets N=6) were used in each group and monitored for one year.

Our results show that fragment survival was high in both farming habitats (>90%), with *P. verrucosa* surviving significantly better in the lagoon and *Acropora* spp. surviving and growing significantly faster in the reef nursery. *P. verrucosa* growth rates were similar between reef and lagoon habitat. Different rearing depths in the reef nursery had no impact on the survival of *P. verrucosa* but coral growth decreased considerably with depth, reducing fragments' ecological volume augmentation and growth rates by almost half from 5 to 15m depth. Further, higher fish predation rates on fragments were recorded on the reef, which did not impact overall nursery performance. Mutualistic fauna, which correlated positively with fragment survival, was more frequently observed in the lagoon nursery. The occurrence of disease was noted in both habitats, even though implications for fragment health were more severe in the lagoon.

Overall, our study demonstrates that lagoon and reef nurseries are suitable for rearing large numbers of coral fragments for transplantation. Nevertheless, we recommend to consider the

specific environmental conditions of the farming habitat, in particular water quality and year-round accessibility, in each case and to adjust the coral farming strategy accordingly. We hope that this novel research encourages the increased application of mid-water rope nurseries for ‘coral gardening’ to advance coral reef recovery and climate resilience in the Maldives.

3.3 Introduction

Coral reef restoration has become an increasingly applied tool and internationally adapted approach to counteract the worldwide degradation of coral reefs (United Nations Environment Assembly 2019; Boström-Einarsson et al., 2020). While sometimes criticized for not tackling the underlaying problem and therefore using limited conservation resources inefficiently (Bellwood et al., 2019; Morrison et al., 2020), supporters argue that, in concert with other environmental measures, rigorously managed local restoration projects can improve social, economic and ecological resilience, and therefore increase the odds for reef survival and recovery (Hein et al., 2019, 2021; Duarte et al., 2020). Such projects may also prove valuable in the face of global threats that are often beyond the level of local or even national control.

The low-lying archipelago of the Maldives, a country that owes its existence to the 26 natural coral atolls, is on the forefront of experiencing the adverse effects of climate change. Over the next decades, the nation’s mere existence will depend on its ability to protect its population, infrastructure, economy and coral reef ecosystem from the risks posed by warming oceans, sea level rise and severe weather events (Sovacool, 2012; Storlazzi et al., 2018). Maldivian coral reefs are essential for the country’s economy, that heavily relies on tourism and fisheries (Statistical Yearbook of Maldives, 2020). Nevertheless, Maldivian reefs have already seen considerable degradation following several mass bleaching events (Tkachenko, 2015; Perry & Morgan, 2017) along with other threats such as pollution, corallivores and disease outbreaks (Jaleel, 2013; Montano et al., 2015; Saponari et al., 2018; Montalbetti et al., 2019). Monitoring data from the most recent mass-bleaching in 2016 reported that 73% of shallow water corals were bleached across the Maldives (Ibrahim et al., 2016). Subsequent changes in Maldivian coral community structure included the disproportionately high mortality of reef-building *Acropora* species as well as an observed shift from mature populations towards small and medium sized colonies (Pisapia et al., 2019). Preserving and restoring the resilience of Maldivian coral reefs, through environmental protection and active restoration should therefore be of immediate priority to brace the archipelago against climate change. After all, healthy and structurally complex reefs can, for example, provide protection against coastal erosion (Harris et al., 2018) and may even help islands to grow upwards in response to sea level rise (Masselink et al., 2020).

In the past, restoration projects in other locations have demonstrated the ability to mitigate the continued degradation of coral reefs. For example, large scale, long-term reef restoration was successfully conducted in Indonesia, following physical reef degradation from blast fishing and other human activities. Coral cover increased significantly following rehabilitation treatment to stabilize substrate in Komodo National Park (Fox et al., 2019) and the deployment of artificial structures with attached coral fragments increased not only live coral cover by more than 50%, but also demonstrated minimal subsequent bleaching impacts despite warm waters and continued disturbances (Williams et al., 2019).

Surprisingly, coral reef restoration activities are not widely applied in the Maldives. Peer-reviewed studies of direct transplantation and concrete blocks as artificial reef structures date back to the 1990s (Clark & Edwards, 1994, 1995). Currently, the dominant form of restoration appears to be the application of metal frames, also known as spiders, as artificial reefs, a practice that can be easily applied in a resort setting and also serves as an educational tool (Edwards et al., 2010; Hein et al., 2019). However, larger active restoration projects applying the 'gardening concept' of a farming and an outplanting phase (Rinkevich 1995, 2000; Epstein et al. 2001) are relatively uncommon and undocumented, especially in community or resort-based projects.

Mid-water floating nurseries and in particular rope nurseries, allow small, fragmented corals to grow fast under optimal conditions due to increased light and water flux, reduced sedimentation and overgrowth as well as protection from demersal predators (Shafir et al., 2006; Levy et al., 2010). They have proven an effective tool in gardening projects around the world in order to increase fragment survival and growth while continuously building a bigger re-sourcing and farming stock (Shafir & Rinkevich, 2010; Frias-Torres et al., 2018; Bayraktarov et al., 2020). When deciding on the in-situ nursery location, it is recommended to consider water quality, depth, shelter and accessibility while also aiming for similar environmental conditions of the targeted transplantation site (Frias-Torres et al., 2018). Therefore, nurseries are often placed in shallow lagoons, where the growing fragments are protected from the forces of currents and weather as well as corallivorous reef predators (Levy et al., 2010). The nurseries soon turn into floating ecosystems by attracting fish assemblages which can reduce cleaning requirements and costs as they consume biofouling (Shafir et al., 2006; Shafir & Rinkevich, 2010). However, reef environments typically already host diverse fish communities that could provide cleaning services or even pose a predation risk (Frias-Torres et al., 2015; Seraphim et al., 2020). On the reef, environmental conditions are also more likely to resemble the future transplantation site, while nursey structures are more exposed to natural forces and likely more difficult to construct. Selecting a suitable rearing environment is therefore a crucial factor for the success of any coral gardening project and requires careful, knowledge-based assessment. In the Maldives, coral reefs and their lagoon habitats cover approximatively 20% of the county's Territorial Sea (Naseer & Hatcher, 2004). Yet potential nursery sites may vary considerably in their characteristics and decision driving evidence remains to be verified for this part of the Indian Ocean.

This study provides an in-depth comparison of the performance of mid-water rope nurseries in a lagoon and reef habitat in the Maldives over a one-year monitoring period for the first time. We assessed the survival, health and growth of the same genotypes of *Pocillopora verrucosa* and *Acropora* spp. fragments to better understand the positive and negative implications of these farming environments and their specific challenges. With our findings we hope contribute to the informed decision making in active restoration projects and encourage the wider application of this technique in the Maldives, particularly in tourist resort settings.

3.4 Materials & Methods

3.4.1 Study Design

This study assessed coral nursery farming performance in two habitats, an inner atoll reef and a sheltered lagoon environment, on Athuruga Resort Island (3°53'14"N 72°48'59"E) in Alif Dhaal atoll, in the Republic of Maldives (Fig. 1a). Two mid-water rope nurseries, one in each location, were simultaneously stocked in February 2020 and fragment development was monitored for one year. The lagoon nursery (LN) was situated away from daily resort activities, about 500m from the main island, anchored at 10m depth and comprised horizontally suspended 10m long coral ropes attached to PVC pipes at 5 m depth (Fig. 1b). Athuruga's large lagoon, measuring approximately 1200m from West to East and 650m from North to South, is surrounded by a reef rim and only connects via a narrow artificial channel to the inner Atoll Sea. No currents are experienced here and visibility is typically low. The lagoon floor is characterized by a sandy bottom with an abundant echinoderm fauna, in particular various sea cucumber species and large seastars such as the corallivorous *Culcita* sp.. The isolated reef patches that, following the 2016 mass bleaching, mainly comprise of dead corals and some living *Porites* colonies concentrate the limited fish life. The reef nursery (RN) was placed parallel to the island's southern house reef, that exhibits a steep slope in this area. Here, the once abundant and diverse live coral cover has also been severely reduced to less than 5%, following the latest bleaching and an outbreak of the corallivorous seastar *Acanthaster planci* (Saponari et al., 2018, 2021), with some larger massive coral colonies and a comparably abundant reef fish community remaining. The RN was anchored at 20 m depth, about 5-10 m away from the reef slope and a more streamlined design (no PVC pipes) was chosen to account for the increased exposure to slight to moderate currents on the reef. Horizontally suspended, 14 m long coral ropes were directly attached to the vertical anchoring ropes at three different depths (5, 10 and 15 m) (Fig. 1c).

For the purpose of this study, the two nurseries were stocked with a total of 544 experimental fragments from two coral genera, namely *Pocillopora* and *Acropora*.
Pocillopora verrucosa fragments derived from 14 donor colonies (12-18cm diameter) that were previously reared in the two mid-water rope nurseries on Athuruga (hereafter referred to as lagoon or reef 'donor farming habitat' of experimental fragments). These donors were originally collected in 2018 from two natal sites with similar conditions to Athuruga's farming habitats. *Pocillopora* donors growing in the reef nursery originated from artificial substrate on Athuruga reef (i.e., mooring lines) and were reared between 7 and 18m depth. Donors growing in the lagoon nursery at 5m were originally collected from the shallow back reef of Thudufushi. Island (3°47'05"N 72°43'49"E), since Athuruga lagoon did not offer sufficient live corals for nursery stocking. All donor colonies were assumed to be of different genotype as they were initially collected as corals of opportunity spaced more than 10m apart (Edwards & Gomez, 2007; Foster et al., 2007). In order to prevent any bias in nursery comparison resulting from possible habituation to the farming habitat or translocation to a different habitat, seven 'reef donor' and seven 'lagoon donor' colonies were used for the experiment (see supplementary Fig. S1 for experimental design graphic).

To compare coral farming performance between the lagoon and the reef habitat and for different depths in the RN, a total of 448 *P. verrucosa* fragments were stocked, divided into four groups (Poc_LN_5m; Poc_RN_5m; Poc_RN_10m; Poc_RN_15m) according to nursery habitat and rearing depth. Each of the 14 donor colonies were fragmented in 32 similar sized fragments, ranging from 3-10cm in diameter depending on the selected fragmentation size for each donor colony. Then, a subset of 8 fragments was used for each study group, resulting in a total of 112 fragments per group with the same distribution of fragment genotypes and sizes. Fragmentation of *P. verrucosa* donor colonies from the RN and LN and restocking occurred on the nursery site and underwater using SCUBA equipment. To limit handling stress and damage, the stocked ropes were immediately reattached to the nurseries. Fragments that required translocation to a different rearing habitat were continuously submerged in separate containers and transported by divers the same day. Excess fragments were reared on separate ropes in the nurseries and excluded from the study.

Acropora fragments were directly collected as corals of opportunity from a nearby reef (3°48'51''N 72°45'10''E) from less than 5m unshaded depth. Six suitable colonies were selected based on their fragmentable size (15-20 cm in diameter), similar arborescent branching morphology and distance between them (>30m) to increase genetic diversity. As available *Acropora* spp. fragments possibly comprise more than one species, all comparisons are made at the genus level. The donor colonies were kept in shaded and spacious containers filled with fresh seawater and transported to Athuruga within one hour, followed by the same fragmentation and stocking procedure as for *P. verrucosa*. In the nurseries, *Acropora* spp. fragments represented two study groups of 48 fragments each, growing at 5m depth in the LN and the RN (Acr_LN_5m; Acr_RN_5m). Again, subsets of 8 similar sized fragments (3-11cm diameter) per donor colony were used, likely representing six different genotypes.

A monthly monitoring and maintenance protocol was established for a one-year farming period. The protocol was interrupted due to Covid-19 from months three to eight, resulting in a total of seven surveys (T1, T2 and T3-T7 post interruption) and three growth measurements at stocking (T0), post interruption (T3) and after one year (T7) for all fragments. Water temperature was recorded at 5m depth during each dive using a Suunto dive computer.

3.4.2 Data Analysis

The status of nursery-grown experimental fragments was analyzed applying the following parameters suggested by Frias-Torres et at. (2018): ‘Survival’ was determined as a binary condition (‘alive’ and ‘dead’) for each treatment group, habitat and genus and was compared using the chi-square test of independence. Fragment ‘Condition’ (see Fig. 2) was recorded as a categorical variable for each survey, distinguishing between fragments with 100% living tissue (H3), more than 50% of coral tissue is alive (H2), and less than 50% living tissue on the fragment (H1) and is shown in percentage for each category and fragment group. It was further noted, whether fragments showed any signs of bleaching, disease or algae overgrowth. Predation incidents were recorded when fresh bitemarks or predation scars were evident on the fragments. The presence of any sessile corallivores, mutualists or any other visible fauna associated with the coral was also recorded. The percentage of fragments with diseased tissue was calculated for the last survey (T7), while associated fauna and predation rates were calculated as percentage of affected corals per study group for each survey and averaged across the study period. For predation and disease calculations dead fragments were excluded. Differences between habitats and depths as well as associations between mutualistic fauna and fragment survival were analyzed using the chi-squared test, with a post hoc residual analysis for different depth groups with a Bonferroni adjusted alpha level of 0.008 for the predation analysis.

Fragment initial size at stocking and ‘Growth’ was calculated for all fragments as ‘Ecological volume’ (EV) by taking three measurements to the nearest mm using a Vernier caliper, where:
EV = πr2h, where r = (w+l)/4
with ’h’ representing the longest linear colony diameter of the three perpendicular measurements (h=height, w=width, l=length; see Shafir et al., 2006). The difference in EV at

the start (T0) and the end (T7) of the study was compared using the Wilcoxon signed rank test and used to compute 'Size augmentation' and 'Daily growth rates' for all living fragments in each group. Growth rate data was natural log transformed to meet the homogeneity of variance assumption and analyzed using an ANOVA with Turkey's post hoc test.

In addition, the relationship between fragments' initial size (EV at T0) and the subsequent growth rate for *P. verrucosa* fragments was investigated using a Pearson correlation to obtain a better understanding of optimal stocking size for this species.

The experimental design further allowed to test for any differences between *P. verrucosa* fragments originating from 'reef reared' and 'lagoon reared' donors (i.e., whether fragments from lagoon or reef reared donor colonies grew significantly different in the RN and the LN farming habitat). Therefore, mean differences in growth rates between fragments originating from reef and lagoon farming habitats were compared within each study group using the Mann-Whitney test.

All statistical analysis was performed using SPSS ver. 27 (IBM, New York) and all data is represented as arithmetic means ± standard error. Non-parametric test statistics were used when the normality assumption was violated.

3.5 Results

Survival

Overall, the survival of the experimental stock (N=544) was high (91%) after one year (T7) with differences between *Pocillopora verrucosa* (94%; N=448) and *Acropora* spp. (89%; N=98) fragment survival being marginally non-significant ($\chi^2(1, N=544)=3.59$, $p=0.058$). For *P. verrucosa* the survival rate was above 90% for all four groups with the highest survival recorded in the LN (99%), which was significantly different from the RN survival (χ^2(1, N=448)=6.95, p=0.008). Here, the average survival rate for all depths was 92% and rearing depth had no significant effect on survival (χ^2(2, N=336)=1.334, p=0.513; see Table 1). In contrast, the survival of *Acropora* spp. fragments, all growing at 5m depth, was significantly higher in the RN (96%) than in the LN (81%; see Table 2) (χ^2(1, N=96)=5.031, p=0.025).

Condition

Similarly, the majority of *P. verrucosa* fragments (RN: 88%; LN: 96%) were fully alive (H3) after one year (T7) with only a few partially alive corals (H2 and H1) found in each RN group (N=4 at 5m; N=6 at 10m and N=2 at 15m; see Fig. 3). In the LN only 3 fragments had suffered partial mortality (H2). No signs of disease were observed in *P. verrucosa* stock in the LN, while 3.6% of RN fragments were diseased with a rapid tissue loss syndrome (see Moriarty et al., 2020) at the last survey (N=3 at 5m, N=6 at 10m and N=2 at 15m; Table 1).

For *Acropora* spp. fragment health was more variable. In the RN 63% of the fragments were fully alive, while 33% had suffered partial mortality (H2=23%; H1=10%) due to algae overgrowth. In the LN, the spread of 'White Syndrome' disease (see Montano et al. 2012) had considerably impacted fragment condition (H2: 46%; H1: 35%; see Fig. 3) with no fully alive fragments remaining after one year and 18% of the living stock showing diseased tissue at T7, which was also the main cause of death in this group (Table 2).

On *P. verrucosa* fragments the average predation rate was significantly lower in the LN (37 ± 18%) than in the RN (47 ± 14%) (χ^2(1, N=3481)=13.504, p<0.001), where predation decreased significantly from 5m (423 predation incidents in total) to 15m depth (245 predation incidents; see Table 1) (χ^2(2, N=2592)=90.483, p<0.001). In the RN, predation events were also more consistent throughout the study period (in 6 out of 7 surveys), while in the LN predation on fragments was only recorded in three surveys. Predation on *Acropora* spp. was only recorded once on two fragments in the RN. Corals only showed fish predation marks in both habitats, which never made up more than 5% of the fragment's surface and visibly healed between surveys.

Of the fragment inhabiting fauna, guard crabs of the genus *Trapezia* were most frequently observed (90%; N=475), while other small crabs, shrimps and fish made up the remaining 10%. Coral associated fauna was significantly higher in the LN ($\chi^2(1, N=3584)=193.24$, $p<0.001$). Specifically, associated fauna was on average most frequently observed on *P. verrucosa* fragments in the LN (26 ± 7%), while only found in 7 ± 2% of RN fragments. Similarly, 23 ± 5% of *Acropora* spp. fragments in the LN were associated with fauna while in the RN it was only 4 ± 2%. A significant positive relationship between *P. verrucosa* survival and *Trapezia* crabs occurrence was found ($\chi^2(1, N=3584)=9.674$, $p=0.002$).

Temperature or stress induced bleaching was not an issue during the rearing period and water temperatures never exceeded 30 °C at 5m depth in either habitat. Temporary bleaching of the upper fragment tissue was only observed in 3 fragments (1 Poc at LN ;1 Poc and 1 Acr in RN) during the study. Brown algae (*Sargrassum* sp.) overgrowth was most noticeable on *Acropora* fragments in the RN, where 10 fragments had suffered partial tissue damage at T3 due to the interrupted maintenance schedule. In contrast, blue-green algae, identified in the field as mainly *Schizothrix calcicola* were prevalent on the LN structure, but did not overgrow living fragments.

Growth

Fragment size was calculated as Ecological Volume, which increased significantly for all groups during the one-year survey period (Fig. 4). The largest EV size increase (2195 %) was observed in *P. verrucosa* fragments in the LN, which grew significantly from 41 ± 2 cm^3 to 905 ± 31 cm^3 in 371 days ($Z(N=111)=-9.15$, $p<0.001$; Fig.4a). This was closely followed by fragments growing also at 5m on the RN, which increased by 1957 % (from 40 ± 3 cm^3 to 780 ± 31 cm^3; $Z(N=101)=-8.72$, $p<0.001$). On the RN fragment size augmentation (Table 1) decreased with depth. At 10m depth fragment increase was 1364% (43 ± 3 cm^3 to 580 ± 22 cm^3; $Z(N=102)=-8.77$, $p<0.001$) while at 15m the EV increase was reduced to a 1127% increase (38 ± 4 cm to 390 ± 40 cm^3; $Z(N=106)=-8.94$, $p<0.001$).

Therefore, daily growth rates for *P. verrucosa* varied significantly between fragment groups ($F(3, 416)=36.284$, $p<0.001$). Post hoc testing revealed that there was no significant difference in daily growth rates between the lagoon (M=0.08 ± .005) and the reef (M=0.07 ± .004) at 5m ($p=0.848$). However, on the RN daily growth rates (see Table 1) varied significantly between the three rearing depths, with shallower depths showing faster growth rate ($p\leq0.001$).

EV also increased for both *Acropora* spp. groups (Fig.4b) during the one-year (353 days) farming period, in the LN by 738% (from 40 ± 5 cm^3 to 295 ± 38 cm^3; $Z(N=38)=-5.37$, $p<0.001$) and in the RN by 1098% (from 36 ± 4 cm^3 to 390 ± 40 cm^3; $Z(N=46)=-5.91$, $p<0.001$). Size augmentation and daily growth rates (Table 2) varied significantly between the LN and the RN at 5 m ($Z(N=84)=579$, $p=0.008$), with fragments growing much faster on the reef.

Initial size

Average initial size at stocking for all *P. verrucosa* fragments was 5.22 ± 1.1 cm in diameter (h), ranged from 2.7 to 10.0 cm. A significant negative correlation between initial size EV and subsequent growth rate was found, with smaller fragments showing a faster growth rate ($r(418)=-0.56$; $p<0.001$). This pattern was even more evident when analyzing treatment groups separately to account for the effect of depth (LN_5m: $r(109)=-0.65$; RN_5m: $r(99)=-0.65$; RN_10m: $r(100)=-0.63$; RN_15m: $r(104)=-0.68$; all $p<0.001$; see Fig. 5).

Donor farming habitat

To investigate possible impacts of different donor farming habitats on fragments' growth rates in the two nurseries, the observed effect of initial size had to be controlled for first. Therefore, fragments from two reef farmed donor colonies with the two smallest mean stocking sizes as well as fragments from two lagoon farmed donor colonies with the largest stocking means were removed from the analysis. The remaining 141 fragments from 'reef farmed donors' and 156 fragments from 'lagoon farmed donors' were non-significantly different in stocking size at T0 (Z(N=320)=12419.5, p=0.646) .

Growth rate comparison for these fragments at T7 revealed that *P. verrucosa* fragments that derived from reef donor colonies (M_{Reef} =0.0597 ± .003) grew significantly faster than fragments from lagoon farmed donor colonies (M_{Lag}=0.0478 ± .003) (Z(N=297)=8322, p<0.001). This was also the case when comparing daily growth rates for each study group separately (Fig. 6). In all but the RN_5m group fragments of reef farmed donors grew significantly faster than fragments that derived from lagoon donors, including the lagoon group (Poc_LN_5m), where fragments originating from reef farmed donors grew faster in the new habitat than fragments derived from lagoon farmed donor colonies (Z(N=79)=577, p=0.047).

3.6 Discussion

This study conducted a direct comparison and comprehensive assessment of mid-water rope nursery performance in a lagoon and a reef habitat in the Maldives for the first time. Our evaluations are based on fragment survival and growth as well as the occurrence of predation, disease and mutualistic fauna.

In both coral farming habitats, fragment survival was very high (81-99%) throughout the one-year study period. Similar survival rates have been reported, for example, from the Caribbean (85-96% for *Acropora cervicornis* after 12 months in in-situ nurseries; Schopmeyer et al. 2017) or the Philippines (96.4 ± 2.2% for *Pocillopora damicornis* after 10 months in a rope nursery; Levy et al., 2010). High fragment survival is critical for the success of the labor-intensive rearing phase of the coral gardening approach, so sufficient healthy colonies are available for the subsequent transplantation phase (Edwards & Gomez, 2007; Frias-Torres et al., 2018). However, direct comparison revealed that *Pocillopora* fragments' survival was significantly higher in the LN, while *Acropora* fragments survived better in the RN. Closer inspection revealed that fragment survival and condition of both genera were affected differently by the spread of disease, which appeared to be coral genus and habitat specific, as only *Pocillopora* was affected on the reef while only *Acropora* was affected in the lagoon. For *Acropora* fragments, the negative effect of disease was also clearly noticeable when comparing growth, which was twice as fast in the disease-free RN stock. These findings highlight the need to investigate coral diseases in coral restoration further, in particular possible transmission routes, time and density dependences in nurseries and mitigation measures. In this context, water quality and human induced pollution, in particular when operating in a resort setting, also require further attention. Disease outbreaks can significantly impact coral farming success and there is an additional danger of introducing disease to transplantation sites (Moriarty et al., 2020).

Coral predation is another factor that can hinder coral restoration success (Miller et al., 2014; Koval et al., 2020). Our study confirms that mid-water rope nurseries are very effective in keeping corals safe from known Maldivian corallivores such as the snail *Drupella* sp. or the starfish *Culcita* sp., which are regularly encountered in both habitats (Montalbetti et al., 2019; Saponari et al., 2021). All recorded predation incidents were from fish and hence they were more commonly observed on the reef, as one would expect. Nevertheless, predation scars were small and healed between survey intervals, therefore not directly impacting fragment condition. It should further be tested, if predatory fish occurrence could be reduced on the reef by placing the nursery structure further away from the safety of the reef slope (here only 5-10m between structure and reef), if seafloor topography allows it.

We also investigated the occurrence of mutualistic fauna in the nurseries, in particular guard crabs, which can have positive impacts on coral health (Glynn, 1987; Stewart et al., 2006). The many benefits of hosting mutualistic fauna such as damselfish, decapods and hydrozoans have been widely studied, showing that it can reduce corallivory, sedimentation, predation, disease and even coral bleaching (McKeon & Moore, 2014; Montano et al., 2017; Chase et al., 2018, 2020). In line with these findings, our results suggest a positive correlation between guard crab presence and fragment survival. *Trapezia* sp. was first recorded in the coral stock after 8 months (T3), when fragments had reached a suitable size and branch complexity to host guard crabs. The percentage of fauna hosting corals was significantly higher in the lagoon, for both *Acropora* and *Pocillopora* fragments. There could be two, not mutually exclusive explanations for this observation. First, *Trapezia* sp. predators such as small reef inhabiting wrasses were never encountered during the surveys in the lagoon, while they have been regularly observed on the RN during maintenance work, which could indicate a higher predator abundance on the reef. In fact, increased predation pressure has previously been linked to reduced abundance of mutualistic decapods in *Pocillopora* colonies (Stier & Leray, 2014). Second, the LN hosted additional, older *Pocillopora* stock that was already populated by *Trapezia* crabs and hence population of the new fragments could have been facilitated. Movement of guard crabs between coral hosts to increase their reproductive success has been well documented (Castro, 1978) and deserves further attention. For instance, rearing fragments of mixed-age could be used to increase the abundance of mutualistic fauna and improve coral health in farming stocks.

Apart from coral survival, growth can be considered an important indicator of coral-farming success as it determines rearing time in the nurseries and therefore influences cost effectiveness and eventually restoration outcome (Edwards et al., 2010). Corals can reduce mortality risk by growing to a certain size (Connell, 1973; Highsmith, 1982), hence several studies have looked at fragment size and depth as variables in coral nurseries (Forsman et al., 2006; Soong & Chen, 2003). Direct comparison between the LN and the RN showed that at shallow depth, *P. verrucosa* fragments grew at a similar rate indicating no apparent difference in farming environments. The insignificantly slower growth rate at 5m in the RN is likely a result of the longer coral ropes that were pulled downwards (up to 7m depth at the lowest point) as coral weight increased over time, even if this was counteracted with additional buoyancy devices. Although rearing depth had no effect on survival, *P. verrucosa* growth rates decreased by 27% from 5 to 10 and another 21% from 10 to 15m on the reef as light levels decrease. Light availability is an important environmental parameter determining coral growth and typically reflected in the abundance of fast-growing corals in shallow depths (Gladfelder et al., 1978; Grigg 2006) and the increased calcification rate in shallow waters (Huston 1985), for which several mechanisms have been described (Allemand et al., 2011). The marked reduction in growth rate can be considered the main disadvantage over shallow farming locations such as lagoons. However, as it was the case in our study, the use of additional rearing levels at depth increased stocking capacity per nursery structure and could be an option to improve coral farming capacities and fragment output. Furthermore, the performance of outplanted colonies reared at different depths remains to be investigated.

To advance coral rearing success, fragment initial size should also be considered, although optimal size is likely species, method and location specific (Edwards & Gomez, 2007; Edwards et al., 2010). Our results for *P. verrucosa* in the Maldives indicate that smaller fragments grew significantly faster. We used an average stocking size of about 5 cm, with fragments ranging from 2.7 to 10 cm in maximum linear extension. In comparison, *P. damicornis* reared in rope nurseries in the Eastern Tropical Pacific exhibited a higher survival for fragments bigger than 2 cm but no significant difference in growth rate was found between size classes (Ishida-Castañeda et al., 2020).

Another interesting observation was that fragment genotypes deriving from ‘reef-reared’ donor colonies grew significantly faster in the RN as well as in the LN. One may expect that corals habituated to a particular environment may exhibit less stress after fragmentation if environmental conditions remain similar. Yet, we found that corals previously collected and farmed in the reef habitat generally outperformed fragments previously cultured in the lagoon, even after controlling for initial size. One noteworthy difference between donor colonies was initial rearing depth, which was generally deeper for ‘reef-reared’ donor colonies. *Pocillopora* is known to exhibit considerable environmental plasticity to adapt to variable conditions such as depth and water flow (Soto et al., 2019), but whether this could be a possible explanation for our observation and to what extent it is relevant to restoration practices remains to be further studied.

Finally, we observed some noteworthy points about nursery structure maintenance in our comparison of farming habitats. The removal of biofouling and sessile invertebrates typically constitutes a considerable workload and therefore cost factor in coral gardening (Precht, 2006). Algae were observed growing over the nursery structures in both habitats, especially at shallow depths. In the RN, overgrowth decreased noticeably with coral growing depth, likely as a result of reduced light, which reduces maintenance requirements. It has also been proposed that reef environments, home to a diverse community of herbivores and invertivores fish, can reduce nursery maintenance by providing a natural cleaning service and removing predators (Gochfeld & Aeby, 1997; Frias-Torres et al., 2015; Frias-Torres & van de Geer, 2015). While this study did not intend to investigate the contribution of natural cleaning services, the five-month forced maintenance pause provided some useful insight. No significant damage or overgrowth of the fragments occurred in either habitat, except for some *Acropora* spp. fragments growing at 5m on the RN, that were in part overgrown by brown algae.

It is also worth noting that the LN was placed further away from the island and daily resort activities, which impeded accessibility but did not prevent, for example, disease occurrence. In contrast, the RN was located along a popular diving and snorkeling route on the easily accessible house reef, therefore benefitting from increased public awareness and support for the project.

We limited our study to branching and fast growing *Acropora* and *Pocillopora* species, which are suitable and commonly used genera for this restoration method (Levy et al., 2010; Mbije et al., 2010). They are also promising candidates for restoring habitat complexity, considering that these key genera have been disproportionally affected by the previous mass-bleaching events (Pisapia et al., 2017). However, additional species should be included in the future to increase species diversity and therefore resilience of restoration sites.
Although our study site represents a typical resort island, situated in one of the most popular Maldivian atolls (Statistical Yearbook of Maldives 2020), it should be considered that our findings are limited to a single location. Likewise, here we only assessed the first although important step of the coral gardening approach with research on the transplantation success of lagoon and reef reared corals to be conducted in the future. For instance, possible application advantages of reef rope nurseries for the transplantation phase could include more similar environmental conditions and shorter transportation to restoration sites.

Nevertheless, we hope to provide some new insight for restoration projects in the Maldives as such pilot studies are recommended to refine location and methods application (Shaver et al., 2020). In that way our study hopes to contribute by providing a sound assessment of mid-water rope nursery performance over a one-year study period in the Maldives and offers direct comparison of coral farming performance in a lagoon and reef habitat, which has not been conducted until now. As both nursery designs and habitats have been tested successfully, we suggest that Maldivian tourist resorts as well as local islands are suitable places for coral gardening projects, by the current standards of such endeavors and in a broader environmental management context (see Hein et al., 2021). Not only do they offer an opportunity to educate tourists and local on the immediate threat this ecosystem is facing, they also offer a 'hands-on' approach in the face of seemingly overwhelming climate change threats. In parallel, such projects can help to draw attention to local disturbances, for example tourism overuse or pollution, which are more likely to get addressed in the context of a local awareness and restoration project.

3.7 Conclusions

We conclude that reef and lagoon environments can provide suitable coral-farming habitats for mid-water rope nurseries in the Maldives, as our study demonstrated high survival and growth rates for *Pocillopora* and *Acropora* fragments over a one-year rearing period.

This provides a good starting point for the application of the coral gardening approach, although increased species diversity should be included as a restoration goal. We also found some habitat and genus-specific differences, that are worth considering in future restoration projects. In direct comparison, the robust *Pocillopora* fragments performed better in a lagoon habitat and were less impacted by disease, while *Acropora* rearing success was better in the reef habitat. Smaller initial size (<5cm) at stocking increases growth rates for *Pocillopora* in both habitats, while increased rearing depth decreases fragment growth. We suggest that mutualistic fauna, here more abundant in the lagoon, could be increased by stocking fragments together with older colonies to facilitate transmission. Furthermore, apart from fish predation, our mid-water rope nurseries provided good protection from corallivory in the lagoon and reef habitat. How different farming habitats and rearing depths translate into outplanting success of coral gardening remains to be tested.

Finally, we consider reef mid-water rope nurseries a useful addition to the coral restoration tool kit in the Maldives, especially when lagoon farming habitats are not available, not easily accessible or conditions are unsuitable. Our streamlined rope nursery design withstood the high currents and fish abundance in the reef environment, while providing additional rearing space at depth. Therefore, we hope that this novel research provides some valuable insights for restoration practitioners and a step towards expanding restoration efforts in the Maldives.

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3.10 Illustrations

Table 1: Coral nursery performance of *Pocillopora verrucosa*. The table shows fragment survival, disease incidents, predation and associated fauna rate (average rate of affected fragments per survey), Ecological volume (EV) size augmentation and daily growth rates after a one-year farming period (T7=371 days) for the different study groups reared in mid-water rope nurseries in a lagoon (LN) and reef (RN) habitat at different depths.

Group	**Nursery Habitat**	**Depth** (m)	**No. of Fragments**	**Stocking Period** (days at T7)	**Survival** (% at T7)	**Disease** (% at T7)	**Predation Rate** (mean% ± SE)	**Fauna Occurrence** (mean% ± SE)	**EV Size Augmentation** (cm^3 at T7 ± SE)	**Daily Growth Rate** (at T7 ± SE)
Poc_LN_5m	Lagoon	5	112	371	99.11**	0	37.19 ± 18.14	25.64 ± 6.83***	863.60 ± 29.99	0.08 ± .005
Poc_RN_5m	Reef	5	112	371	90.18	2.97	58.64 ± 15.56***	11.48 ± 3.10	739.74 ± 5.17	0.07 ± .004
Poc_RN_10m	Reef	10	112	371	91.07	5.88	48.66 ± 13.78	4.46 ± 1.28	539.14 ± 20.55	0.05 ± .003***
Poc_RN_15m	Reef	15	112	371	94.64	1.89	39.75 ± 15.45***	5.23 ± 1.51	386.31 ± 13.56	0.04 ± .002**
Poc_RN_total	Reef	all	336	371	91.96	3.56	47.32 ± 13.50***	7.06 ± 1.89	552.28 ± 14.24	0.05 ± .001
Poc_all	all	all	448	371	93.75	2.62	52.63 ± 15.45	11.70 ± 3.10	634.56 ± 14.73	0.06 ± .002

Significance levels: *** < 0.001, ** < 0.01 and *< 0.05

Table 2: Coral nursery performance of *Acropora* spp.. The table shows fragment survival, disease incidents, predation and associated fauna rate (average rate of affected fragments per survey), Ecological volume (EV) size augmentation and daily growth rates after a one-year farming period (T7=353 days) for the different study groups reared in mid-water rope nurseries in a lagoon (LN) and reef (RN) habitat.

Group	Nursery Habitat	Depth (m)	No. of Fragments	Stocking Period (days at T7)	Survival (% at T7)	Disease (% at T7)	Predation (mean% ± SE)	Fauna (mean% ± SE)	EV Size Augmentation (cm³ at T7 ± SE)	Daily Growth Rate (at T7 ± SE)
Acr_LN_5m	Lagoon	5	48	353	81.25*	17.95	0	22.62 ± 5.40	254.50 ± 35,23	0.02 ± .002**
Acr_RN_5m	Reef	5	48	353	95.83*	0	0.62 ± 0.67	3.87 ± 2.36	353.84 ± 38.23	0.04 ± .006**
Acr_total	all	5	96	353	88.54	8.24	0.32 ± 0.35	13.24 ± 3.61	308.90 ± 26.72	0.03 ± .003

Significance levels: *** < 0.001, ** < 0.01 and *< 0.05

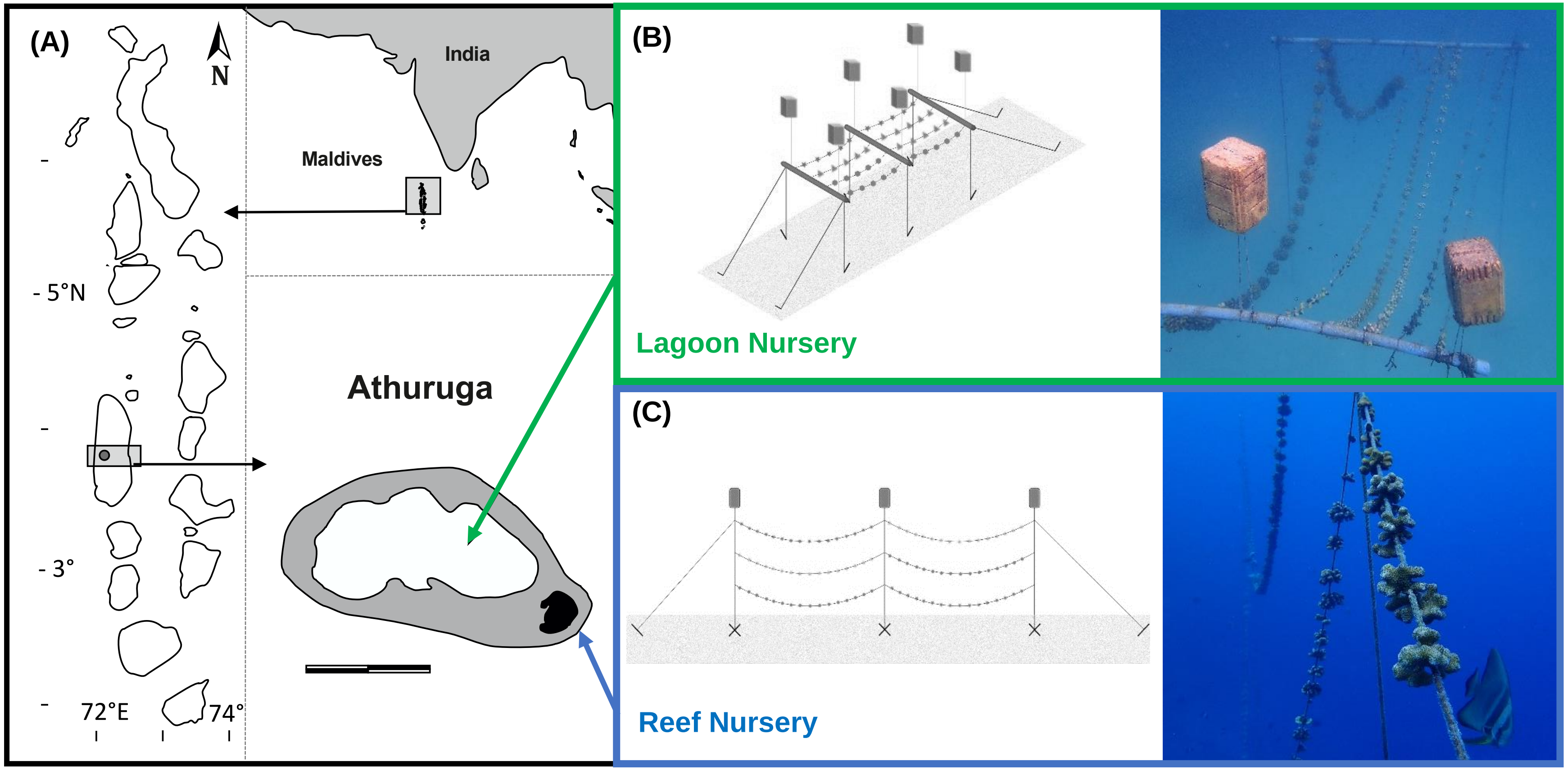

Figure 1: Study location and mid-water rope nursery design. (A) Map showing the Republic of Maldives, where Athuruga Resort Island (3°53'14"N 72°48'59"E) is located in the center of Alif Dhaal atoll (scale bar: 1km; island in black, reef in grey, water in white). (B) Lagoon mid-water rope nursery (LN) adjusted from Levy et al. (2010) measuring 3m in width and 10m in length at coral rearing level at 5m water depth. The main structure consists of 3 PVC pipes, connected with 10mm rope to the anchoring iron bars and air-filled buoyancy containers pulling the structure upwards. (C) Reef mid-water rope nursery (RN) with adjusted streamline design, build parallel to the reef and anchored at 20m depth. Coral ropes are attached at 3 different depth levels (5, 10 and 15m).

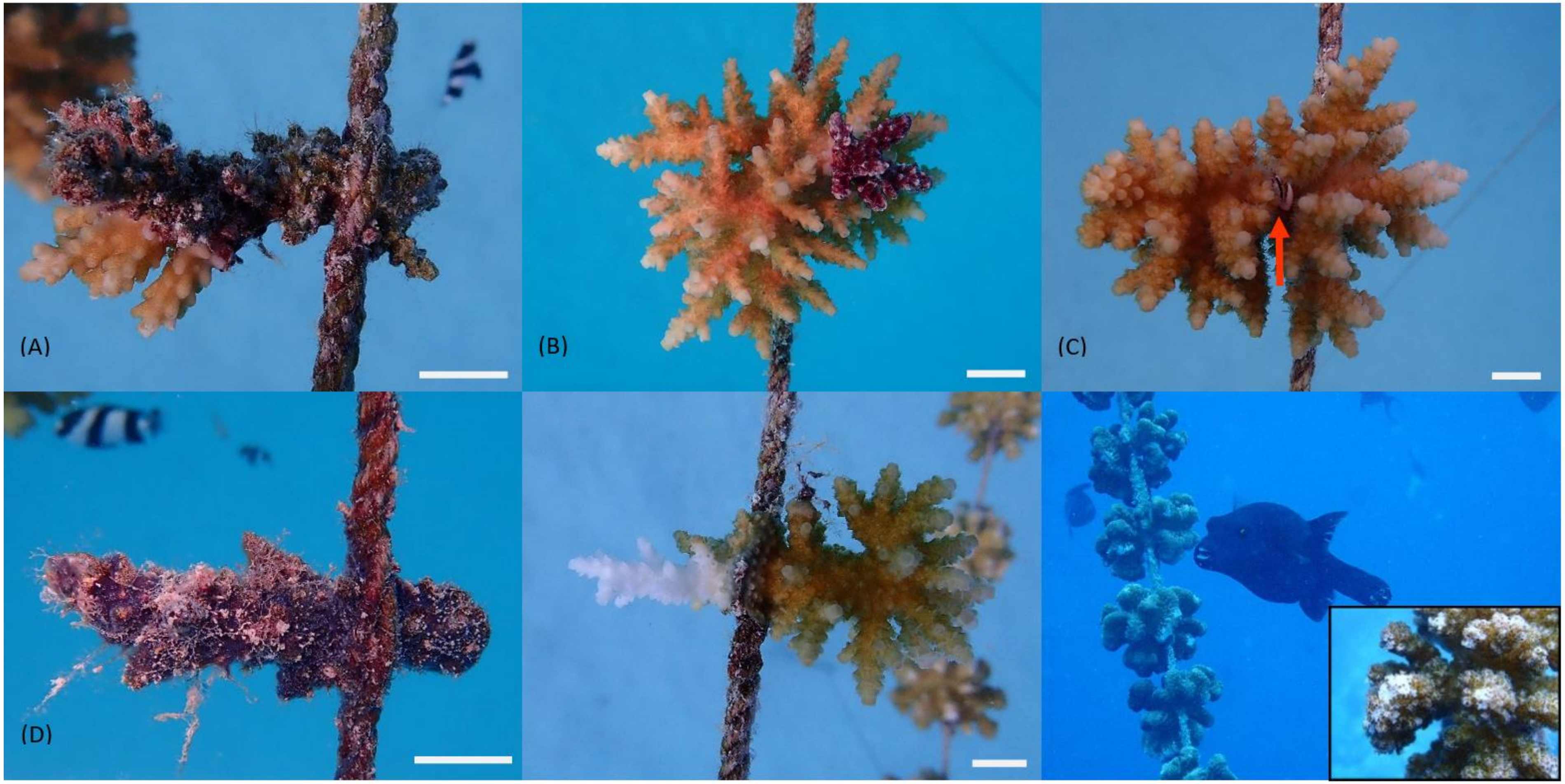

Figure 2: Categories for coral fragment assessment. (A) H1: less than 50% tissue alive. (B) H2: more than 50% tissue alive. (C) H3: 100% tissue alive; arrow indicates a guard crab *Trapezia* sp. (D) 100% mortality. (E) 'White syndrome' diseased fragment. (F) fish predation and fresh predation marks. 1cm white scale bars

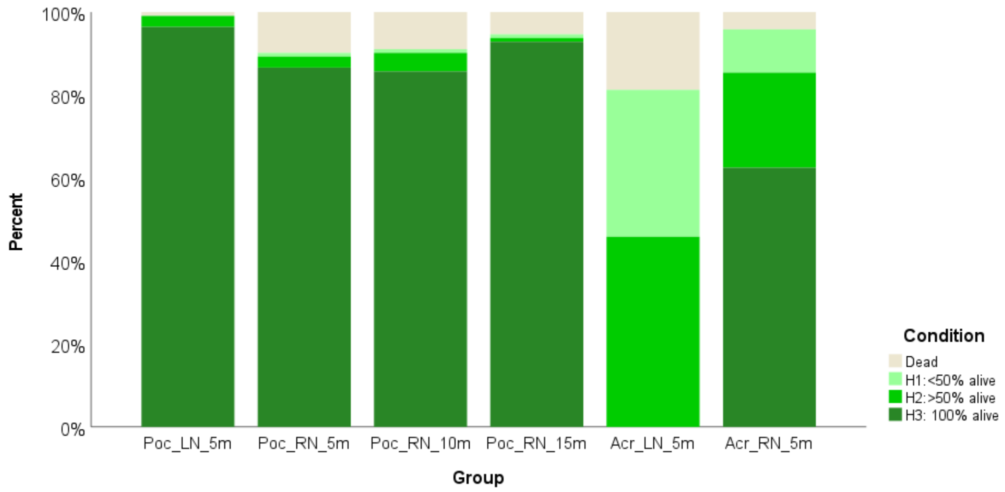

Figure 3: Condition of coral fragments after one year. The figure shows four groups of *Pocillopora verrucosa* (Poc) and two groups of *Acropora* spp. (Acr) growing in a lagoon (LN) and a reef (RN) mid-water rope nursery at different depths for one year (T7).

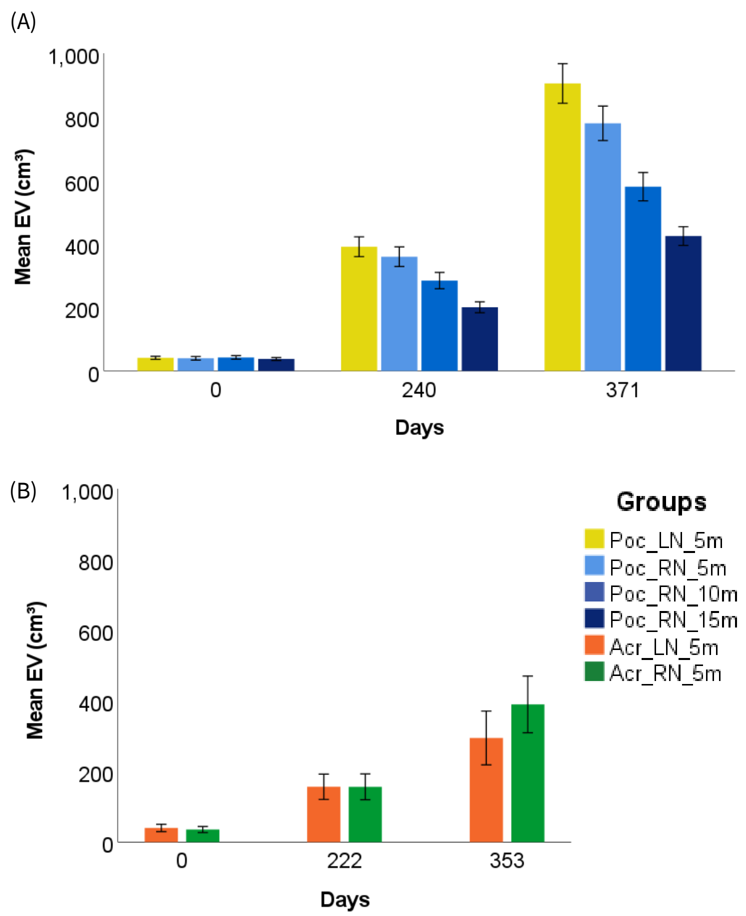

Figure 4: Coral Ecological Volume increase over one year. The graphs show mean Ecological Volume (EV) at three different times (T0, T3, T7) during the one-year study period in a reef (RN) and a lagoon (LN) mid-water rope nursery for (A) *P. verrucosa* (Poc) fragments at different depths and (B) *Acropora* spp. (Acr) fragments at 5m depth. Error Bars: +/- 2 SE.

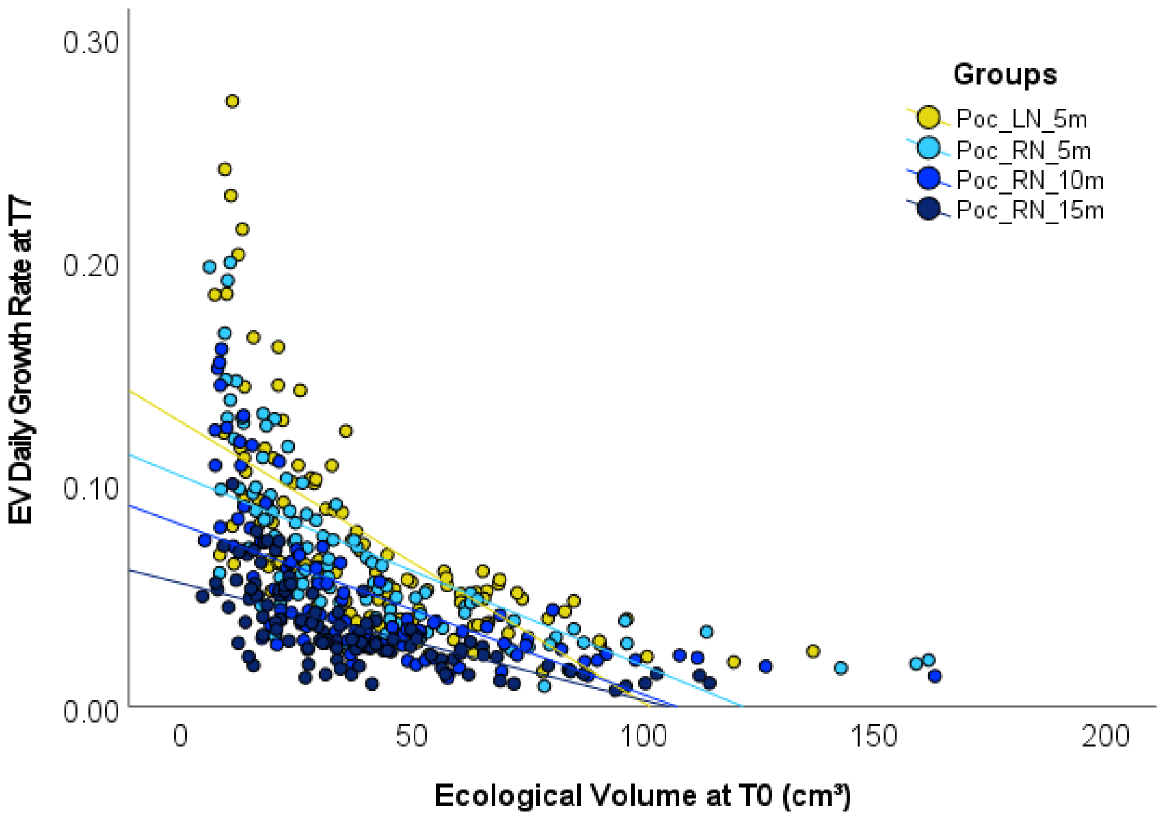

Figure 5: Correlation between *Pocillopora verrucosa* fragment stocking size and growth. The scatterplot shows a significant negative correlation between fragment Ecological Volume (EV) at T0 and the EV daily growth rate at T7 ($r(418)=-0.56$; $p<0.001$). A linear regression line was fitted for each group (LN_5m: $R^2_{Linear}=0.42$; RN_5m: $R^2_{Linear}=0.42$; RN_10m: $R^2_{Linear}=0.40$; RN_15m: $R^2_{Linear}=0.46$).

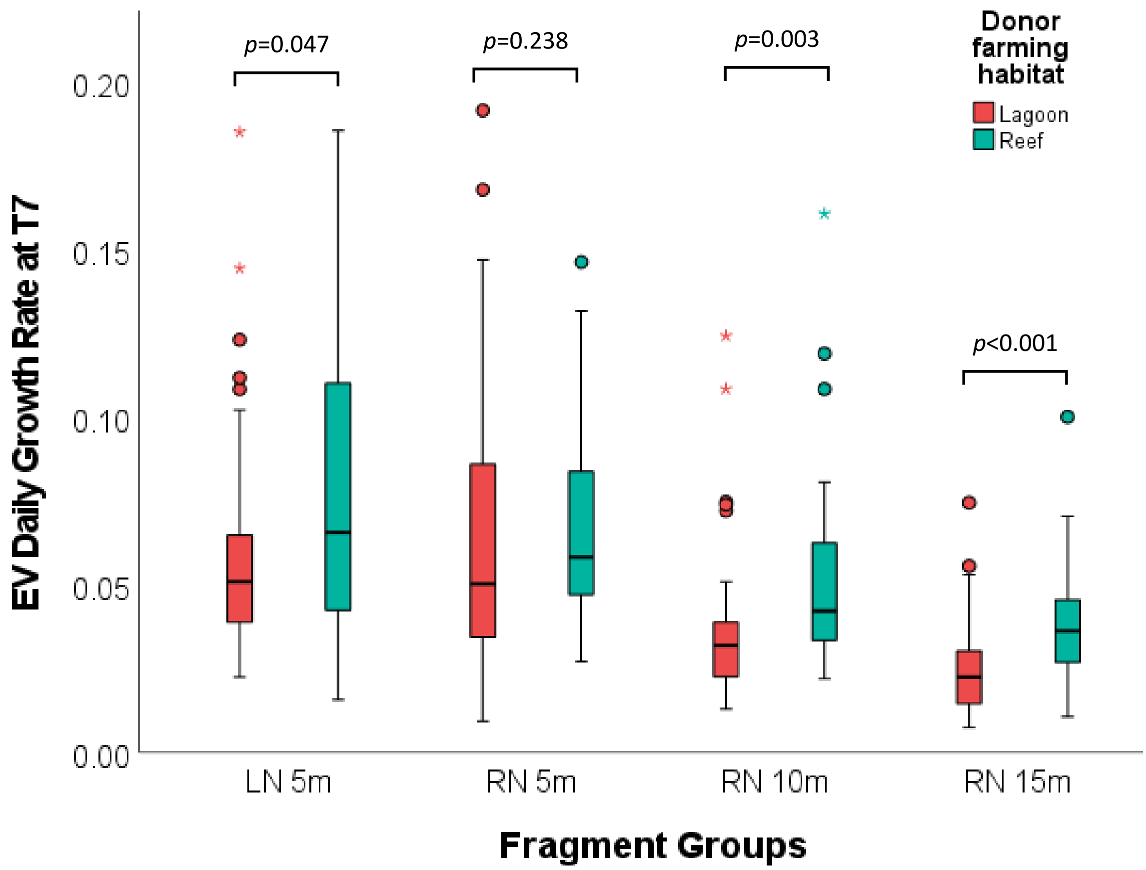

Figure 6: Growth rate comparison of *Pocillopora verrucosa* fragments from different donor farming habitats for each study group. The boxplots show the comparison fragments within each study group (LN 5, RN5, RN10 and RN15), originating from different donors that were previously grown in either the 'lagoon' or the 'reef' farming habitat. Fragments derived from reef nursery reared donor colonies grew significantly faster in the lagoon nursery and at 10 and 15m depth in the reef nursery.

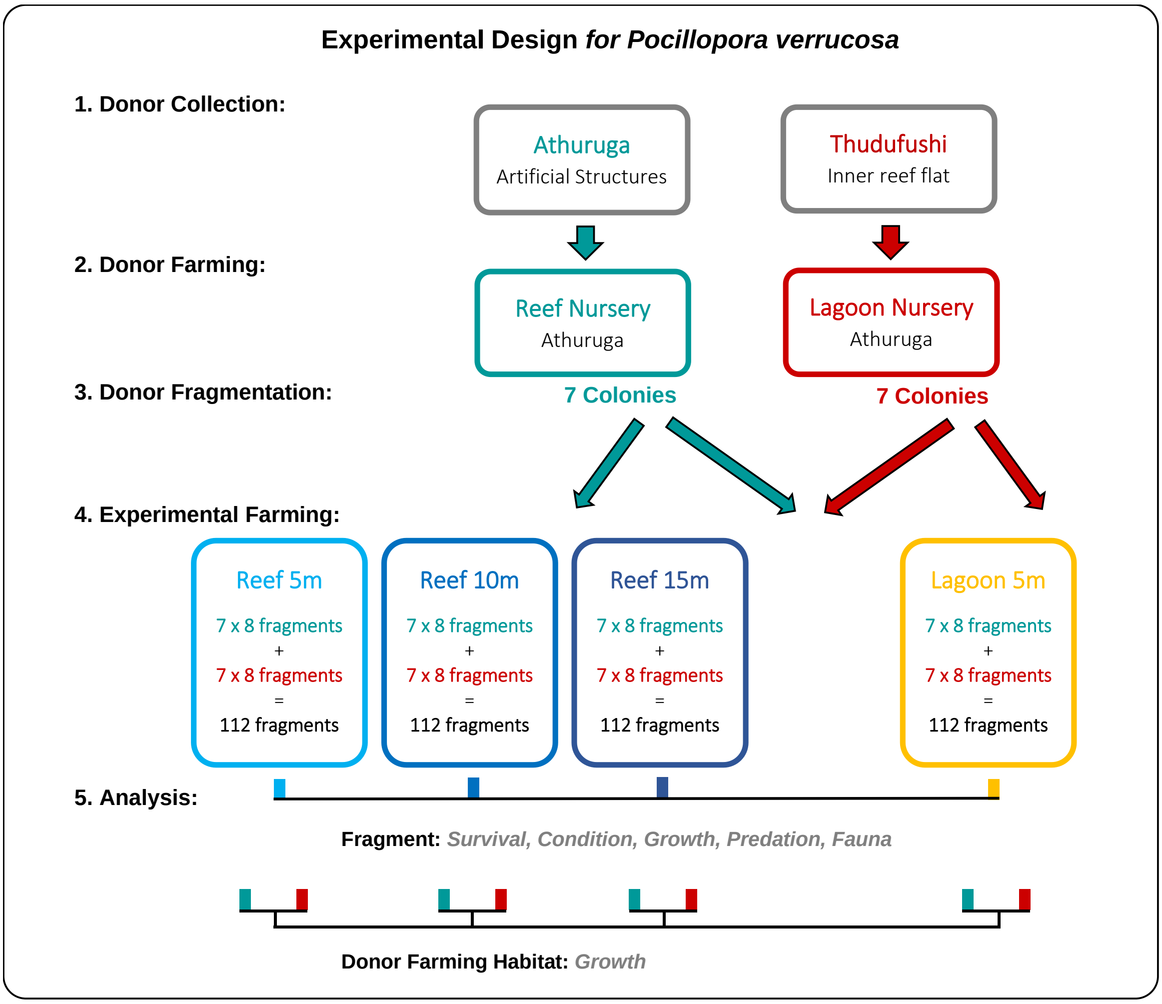

Figure S1: Experimental design used for *Pocillopora verrucosa* fragments. Donor colonies were collected as fragments of opportunity in 2018 and reared in two different nursery habitats on Athuruga. Colonies were fragmented and reciprocally stocked in 2020 in the lagoon and reef nursery at different depths. After a one-year monitoring period differences in fragment parameters such as survival, condition, growth and interactions with mutualists or predators were analysed.

CHAPTER 4

4.1 Effects of the COVID-19 lockdowns on the management of coral restoration projects

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4.2 Abstract

Coral restoration initiatives are gaining significant momentum in a global effort to enhance the recovery of degraded coral reefs. However, the implementation and upkeep of coral nurseries are particularly demanding, so that unforeseen breaks in maintenance operations might jeopardize well established projects. In the last two years, the COVID-19 pandemic has resulted in a temporary yet prolonged abandonment of several coral gardening infrastructures worldwide, including remote localities. Here we provide a first assessment of the potential impacts of monitoring and maintenance breakdown in a suite of coral restoration projects (based on floating rope nurseries) in Colombia, Seychelles and Maldives. Our study comprises nine nurseries from six locations, hosting a total of 3554 fragments belonging to three coral genera, that were left unsupervised for a period spanning from 29 to 61 weeks. Floating nursery structures experienced various levels of damage, and total fragment survival spanned from 40% to 95% among projects, with *Pocillopora* showing the highest survival rate in all locations present. Overall, our study shows that, under certain conditions, abandoned coral nurseries can remain functional for several months without suffering critical failure from biofouling and hydrodynamism. Still, even where gardening infrastructures were only marginally affected, the unavoidable interruptions in data collection have slowed down ongoing project progress, diminishing previous investments and reducing future funding opportunities. These results highlight the need to increase the resilience and self-sufficiency of coral restoration projects, so that the next global lockdown will not further shrink the increasing efforts to prevent coral reefs from disappearing.

Key words:

Coral Reef, Pandemic, floating rope nursery, Indian Ocean, Caribbean, *Acropora*, *Pocillopora*

4.3 Implications for Practice

- Regular, ideally monthly, monitoring and maintenance are key components of ‘coral gardening’, and necessary resources (e.g., emergency funds, additional or local workforce and redundancy in fundamental structural components) should be allocated to prepare against unexpected events.
- Ensuring sufficient/redundant buoyancy for floating rope nurseries and a long-lasting life span of structures and materials are key factors to ensure coral survival over several months in the absence of maintenance.
- Coral restoration managers should account for frequent, unforeseen schedule breakdowns in their planning. The timely adoption of effective contingency plans ensuring a rapid and effective response to critical situations is a necessary step towards the development of more effective restoration projects less vulnerable to failure and hence capable to attract more funds.

4.4 Introduction

Besides their fundamental contribution to biodiversity (Fischer et al. 2015; Strona et al. 2021), coral reefs provide countless ecosystem services (Spalding et al. 2017), supplying hundreds of millions of people with food, income and natural resources, as well as contributing significantly to exports and tourism revenues (Costanza et al. 2014). However, coral ecosystems are now experiencing an unprecedented decline due to climate change and other anthropogenic stressors (Hoegh-Guldberg et al. 2017; Hughes et al. 2017a, 2017b), with current coral reefs covering only 50% of their historic extent (De’ath et al. 2012; IPBES 2019). In an attempt to alleviate this critical situation, coral restoration initiatives, based on the general concept of “assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (SER 2004), are flourishing worldwide (Boström-Einarsson et al. 2020).

The exploration of coral restoration strategies dates to the 70s, when the first artificial reefs were established, and self-contained experiments (e.g., transplantation by Maragos, 1974) were performed. Today, the field can count on numerous, advanced techniques (e.g., asexual propagation, sexual propagation and substrate enhancement methods; see Boström-Einarsson et al. 2020) that permit to plan coral restoration actions at the local, regional or global scale (Omori 2019, Boström-Einarsson et al. 2020). The goals of coral restoration projects might extend far beyond the intended ecological scope of increasing coral cover and include socio-economic objectives such as creating environmental awareness and job opportunities for communities (SMART objectives, see Shaver et al. 2020). The project goals determine the technical expertise required for the practical implementation (which might go from the simple use of opportunistic or asexually propagated fragments to that of selective breeding of enhanced corals), as well as the monitoring and maintenance strategies which also depend on the underlying scientific objectives. In turn, these aspects define the cost effectiveness and scalability of a project (Hein et al. 2021).

Currently, about half of all restoration projects use the cost-effective, two-step 'coral gardening approach' (Bayraktarov et al. 2019; Bostrom-Einarsson et al. 2020). In coral gardening, coral fragments are typically first reared under favorable growing conditions (i.e., an optimal combination of exposure to light, sedimentation, water flow, temperature etc.) in artificial in-situ or ex-situ structures before they are transplanted to the target (degraded) restoration site (Epstein et al., 2001; Rinkevich, 1995, 2000). Among the different potential *in-situ* nursery structures apt to the task, which include, amongst the others, tables, frames or trees, mid-water floating nurseries have proven very efficient, permitting to rear thousands of asexually produced fragments at low costs (Shaish et al., 2008; Levy et al., 2010). For this, they are commonly used in a large number of projects and localities such as in the Red Sea (Shafir et al., 2006), Philippines (Shaish et al., 2008), Tanzania (Mbije et al. 2010), Seychelles (Frias-

Torres et al., 2015), the Arabian Gulf (Nithyanandan et al., 2018) and Latin America (Bayraktarov et al. 2019).

Regular monitoring and structure maintenance during the coral nursery phase (typically monthly) play a critical role for a project's success (Shafir et al. 2006, Frias-Torres et al., 2018). Monitoring consists of data collection on stock rearing performance, primarily represented by growth rate and survivorship, and structure inspections. Maintenance includes repairs, manual cleaning of the nurseries to protect growing corals from biofouling, competition and corallivorous organisms (e.g., Levy et al. 2010; Shafir et al. 2010, Frias-Torres et al. 2018). These tasks, and particularly the need for continuous maintenance, can be very labor-intensive, with the effort varying from hundreds to thousands of person-hours, depending on nursery type, project scale and objectives (e.g., Shaish et al. 2008; Mbije et al. 2010). Hence, the availability of supporting workforce has been identified as the main challenge for the coral gardening method (Hein et al. 2021), with many successful projects relying on volunteering or citizen science initiatives, or on the collaboration with tourism entities (Hesley et al. 2017).

Unpredictable and unexpected global events can generate additional challenges and even trigger critical failures in otherwise solid and effective restoration projects. The novel SARS-COV-2 (the disease caused by Severe Acute Respiratory Syndrome Coronavirus 2 and labelled COVID-19), originally reported in 2019, was declared a pandemic by the World Health Organization in early 2020. The pandemic has impacted almost every aspect of human society (El Keshky et al. 2020), including the field of research and conservation management, for example by reducing the availability of educational and research opportunities (Rashid & Yadav 2020; Pokhrel & Chhetri 2021), delaying supply chains (Guan et al. 2020), reducing planning security and restricting movement. In an attempt to control rising infection rates, governments enforced border closures, travel restrictions and strict lockdowns in all major countries, a needed measure with numerous side effects. For example, conservation activities that rely on tourism flow and public engagement were severely affected, as documented for US national parks (Miller-Rushing et al. 2021).

Although the discipline of coral restoration has witnessed some setbacks in its young history, often related to natural events such has tsunami and hurricanes (Symons et al. 2006; Hernández-Delgado et al. 2014), the current practical challenges are unprecedented. The pandemic has affected efforts and activities around the globe, often impacting funding, interrupting supplies, and immobilizing workforce. Recent research in the Tropical Western Atlantic showed, that the disruptions to coral restoration practitioners caused by the COVID-19 pandemic on were related to financial uncertainty, lack of reliable workforce, and inability to access field sites, due to government lockdowns and travel/boating restrictions that impeded even local workers to perform regular work (Cheek 2020). This resulted in the abrupt suspension of monitoring and maintenance activities and offers an example of how the pandemic-related containment measures might have substantially impacted coral restoration projects. Two years into the pandemic, it is unclear to what extent COVID-19 will impact restoration efforts worldwide. Shedding light on their current situation emerges as critical to improve restoration projects' resilience and improve preparedness against any future unexpected scenarios.

To this end, here we explore how the COVID-19 pandemic has impacted a representative suite of coral restoration projects (using mid-water rope nurseries for coral gardening) in the Caribbean Sea (Colombia) and in the Indian Ocean (Seychelles and Maldives). In our study areas coral reef ecosystems are not only important from an ecological and biodiversity perspective, they also provide vital support to the local economies, especially through tourism. The Caribbean and Indo-Pacific are already facing multiple natural and anthropogenic threats such as bleaching events (Pisapia et al. 2019; Cramer et al. 2021), corallivores outbreaks

(Saponari et al. 2018) and diseases (Montano et al. 2012; 2015; Estrada-Saltivar et al. 2020) that have caused repeated mass mortality events and an extensive loss of coral cover, and therefore require active intervention, including coral restoration as a potential effective form of mitigation.

In Colombia, a collaboration between the provincial environmental authority and regional NGOs resulted in the adoption of the large-scale mid-water floating rope nursery system developed in Seychelles to substantially upscale Colombia´s restoration efforts (Bayraktarov et al. 2020). In the Seychelles, coral restoration efforts started already in 2010, after various mass bleaching events and tsunamis had negatively impacted coral reefs. Between 2012 and 2014, the Reef Rescuers Project of Nature Seychelles successfully employed mid-water rope nurseries to grow over 45000 corals (Montoya-Maya et al. 2016). To upscale restoration practices in the Maldives, mid-water nurseries have been successfully installed over the last few years in several resorts, including Athuruga island, as well as on the local island of Magoodhoo (Dehnert et al. 2021). Here, we report and discuss qualitative and quantitative data assessing the effects of lack of monitoring & management in four coral restoration projects in Colombia, Seychelles and Maldives following COVID-19 related travel restrictions, and countrywide multiple lockdowns leading to the absence of available workforce in all cases. In doing that, we discuss various general aspects related to the broader implications of the monitoring & managing break down, and we propose potential practical solutions and recommendations to reduce the potential impact of similar events in the future.

4.5 Material and Methods

We assessed the impacts of a mandatory and abrupt halt in maintenance and monitoring on four coral restoration projects located in Colombia (one project with two nurseries), Seychelles (one project with one nursery) and Maldives (two projects with two and four nurseries) (Fig 1). We collected data from a total of nine floating rope nurseries of one to five years old, ongoing restoration projects (Table 1). Although these nurseries slightly differ in dimensions and holding capacities, they all follow the design by Levy et al. (2010) and Edwards (2010). Briefly, the floating rope nursery consist of 3 to 5 high-pressure PVC pipes (HP PVC) placed approximately 5 m apart, each with 10 to 20 m-long coral holding ropes (4 to 5mm braided nylon) perpendicularly attached with anti-slip knots (Frias-Torres et al., 2018). The nurseries are attached to the deep sandy seabed by anchor lines (10mm braided nylon) tied to 1.5 to 1.6m long angle bars hammered halfway into the seabed and maintained at a depth of 4-6 m below the sea surface by using recycled 18-liter plastic jerrycans or buoys (Frias-Torres et al., 2018).

In Colombia (Fig 1a) data were collected from two floating rope nurseries that were installed in 2018: one nursery with a total of 1500 5-cm fragments of *Acropora palmata* and one nursery with approximately 200 10-cm fragments of *A. cervicornis*. Both structures are part of the same nursery site, which is located southeast of Providencia Island inside the reef lagoon, about 200 meters from the coast, each nursery running parallel to the coastline and separated by 5 meters of open sand. In contrast to nurseries in the Maldives and the Seychelles, both jerrycans and 20-cm polystyrene buoys were used to float the nursery. Monitoring and maintenance comprised monthly data collection on fragment health, removal of algae and biofouling with toothbrushes from coral ropes and PVC pipes, buoyancy adjustments (i.e., addition and replacement of jerry cans or polystyrene buoys), and anchoring reinforcing (i.e., hammering of angle bars). Anchor ropes were replaced annually, with last change conducted in October 2019. Monitoring and maintenance were conducted by park rangers and local fisher folks previously trained in coral gardening and supervised by research staff from project organizations. Both nurseries experienced a no-attendance period of 30 weeks (210 days) after the last monthly monitoring session in February 2020. No last-minute preparations were conducted prior to the start of the pandemic lockdown in March 2020.

In the Seychelles (Fig 1b) data relate to a single floating rope nursery (fully refurbished in 2018) stocked with 192 fragments of the genus *Pocillopora*. Monthly monitoring and maintenance, including cleaning of ropes, PVC, jerrycans and anchors was performed by the staff employed at Nature Seychelles. The lockdown and COVID-19 related restrictions caused the limitation in the workforce and no actions could be taken prior the no-monitoring and maintenance period. The nursery was left unattended for a total of 46 weeks (325 days) after the last monthly monitoring session in May 2020.

In the Maldives, data from two locations (Athuruga and Magoodhoo island) in two different atolls were collected (Fig.1c). On Athuruga Resort Island in South Ari Atoll, two floating rope nurseries constructed in the lagoon (in 2018) and in the house reef (in 2020) were filled with 346 fragments (83 *Acropora*, 190 *Pocillopora* and 73 *Porites*) and 770 fragments (301 *Acropora* and 469 *Pocillopora*), respectively. In the reef nursery, 214 of these fragments (198 *Acropora* and 16 *Pocillopora*) were stocked just one month before shutdown, still showing healing fragment wounds, hereafter referred to as ‘new stock’, while all other, ‘older stock’ were at least farmed for two months. Monthly monitoring, including data collection on fragment health and growth, and structure cleaning and repairs as described above, were conducted by the resort’s marine biologists until the nurseries had to be abandoned on short notice in April 2020 for a period of about 29 weeks (200 days). Just before the resort closure, some last-minute preparations, including cleaning coral ropes, cleaning and topping up air filled jerrycans, and adding redundant jerrycans for additional structure support, were conducted in the house reef nursery, while no actions could be taken to prepare the lagoon nursery to a period of non-monitoring and maintenance.

On the second Maldivian study site in Faafu Atoll, four mid-water rope nurseries were constructed in the lagoon of Magoodhoo Island in 2017 (Fig 1c), where the MaRHE center marine field station is located, hosting 846 fragments (84. % *Acropora*, 13.5% *Pocillopora* and

2% *Porites*). They were monitored monthly following the same monitoring protocol applied on Athuruga by the center's research staff till February 2020 and then abandoned without further preparations for 61 weeks (425 days) due to travel restrictions.

On return to study sites in Colombia, Seychelles and the Maldives, a qualitative assessment of the general state and quality of structures was performed. In addition, a quantitative assessment of fragment condition (categorical: 'alive', 'partially alive' or 'dead') was conducted using direct counts where possible or estimated when nursery conditions did not allow for accurate counts.

4.6 Results

After a 29-61 week period of unplanned no-maintenance, eight of the nine assessed nurseries were partially or fully collapsed, with fragment survivorship ranging from 40% to more than 90% (Table 1).

In Colombia, the two nurseries were found partially (i.e., some structure elements retaining positive buoyancy) and fully (i.e., all elements on the seafloor) collapsed after 30 weeks. We recorded a survival rate of approximately 60% for the gardened colonies of *A. palmata* in the partially collapsed nursery and 40% for those of *A. cervicornis* in the fully collapsed nursery. Since no sign of diseases or predation were observed, the mortality was mainly attributed to macroalgae overgrowth and sand abrasion, as a result of the nursery structures sinking to the bottom. The collapse was partially due to the lack of buoyant force from lost or punctured jerry-cans or collapsed buoys (4 out of 10) combined with the increased weight of coral fragments. Most of the ropes got entangled with each other and adjacent corals fused, complicating the assessment and rescue of healthy coral colonies (Fig. 2). The growth of additional corals, in this case hydrocorals of the genus *Millepora*, was extensively observed on the PVC pipes of both nurseries. Although both nurseries were structurally repaired, complete removal of hydrocorals was nearly impossible. While ropes with surviving *A. palmata* colonies were placed back in the nursery, all surviving *A. cervicornis* colonies were outplanted to a nearby reef.

In the Seychelles, the nursery abandoned for 46 weeks also partially collapsed. Although six of the 12 jerrycans were punctured, we found that structural damages were mainly attributed to the corals' increased weight that caused the partial collapse of the structure. This resulted in the loss of those colonies that remained on the sandy bottom for a long period of time (see Table 1). Overall, the structure experienced significant damage with approximately 25% of the fragments showed signs of suspected diseases and were removed.

In the Maldives, on the island of Athuruga, the two nurseries were abandoned for 29 weeks during the wet South-West monsoon season, characterized by enduring storms and rough sea conditions. On return, the reef nursery was found in a good condition. All anchors were still in place and none of the ropes were damaged or entangled. Although two out of the 12 jerrycans were found punctured and another one was missing, the structure's buoyancy was still granted by the additional jerrycans. The recorded overall fragment survival was high (80.4%), even though fragments from the new stock, that had been farmed for only one month before the forced abandonment, suffered a much higher mortality (54.2%, all *Acropora* fragments) than the older stock (6.3%, 31 *Acropora* and 8 *Pocillopora* fragments). Most *Acropora* fragments from the new stock died due to biofouling.

In contrast, Athuruga's lagoon nursery suffered a partial structure collapse (Table S1). Of the eight jerrycans attached to the PVC frame (tree per outer pipes and two on middle pipe), the two supporting the middle part of the nursery frame deflated. Two of the six coral ropes and two of the four tension lines tore in several places (all two-years old 5mm nylon) (Fig. S1). Despite the partial collapse, fragment survival was high (94.5%; dead fragments: 15 *Acropora*, 1 *Pocillopora*, 3 *Porites*) as most coral ropes were supported by the outer frame structure and did not reach the bottom. Only 20 fragments that sank to the sandy lagoon floor at 15m suffered partial mortality (5.8%; 5 *Pocillopora* and 15 *Porites* fragments). The survival of *Pocillopora* fragments (99.5%, n=190) was higher than the *Acropora* fragments (81.9%, n=83), which were impacted by algae overgrowth and possibly disease. Following the assessment, all necessary structural repairs were conducted, damaged fragments were removed or restocked and monitoring was continued.

Compared to Athuruga, more damage was observed on the four mid-water rope nurseries located in Magoodhoo. All of them were found fully collapsed, with structural elements twisted and entangled, after over a year (61 weeks) of unplanned non-monitoring and maintenance. While we identified in the punctured and deflated jerrycans (Fig 3a) the main cause of nurseries' structural collapse, it is reasonable to assume that, at least in some cases, the weight of older fragments might have played a significant role (Fig 3b, Fig 4a-c).

Following the nurseries' collapse, approximately 20% of coral colonies spent a considerable time lying on the bottom, and some of the colonies were completely covered by sand. As a result, ~5% of fragments suffered partial mortality, while ~15% suffered total mortality (Fig 4d-f). Conversely, approximately 80% of colonies survived as entanglement and overlapping of colonies prevented direct contact with the seafloor. As observed in Colombia, most of the ropes were entangled with other ropes, coral colonies, PVC pipes and jerrycans, in some cases indicating a twist of the entire structure. Consequently, some coral colonies grew over adjacent ropes, or fused with fragments of the same genotype on neighboring ropes, limiting the precise counts of survival. Mortality was almost exclusively due to suffocation by sediment, while we detected no signs of algal overgrowth, bleaching, predation and diseases. Additionally, many jerrycans and PVC pipes were found to be fully covered by *Pocillopora* colonies of an average size of over 15 cm in diameters (Fig 5). Extensive repairs and ad-hoc outplanting of larger colonies followed the damage assessment.

4.7 Discussion

Here we explored the question of whether and to what extent the interruption of monitoring and maintenance activities due to global mobility restrictions as a result of the Covid-19 pandemic has impacted ongoing coral restoration projects. The pandemic has affected conservation activities, including coral restoration projects, in various ways, by halting practical operational activities, reducing available workforce, and delaying management planning (Cheek 2020; Corlett et al. 2020; Miller-Rishing et al. 2021). In this context, we found that COVID19-related restrictions on maintenance to coral nursery infrastructure resulted in significant loss of farmed corals with further negative implications for project progress. Therefore, this unfortunate situation forces us to consider the possibility that similar scenarios might materialize again in the future and hence calls to improve our preparedness. Identifying critical vulnerabilities and developing protocols to prevent future, unexpected maintenance breakdowns or, at least, mitigate the resulting impacts emerges as a novel priority in coral restoration.

In this study, we have made the first steps in this important direction, by assessing how multiple coral reef restoration projects that were initiated before the onset of the COVID-19 pandemic have responded to prolonged abandonment enforced by global mobility restrictions. As the pandemic was almost instantaneous, the research had not been planned beforehand. Consequently, we had to take the most information possible from the available data, and our resulting assessment is a quali-quantitative one. We have focused on different aspects quantifying the resilience of coral nurseries to abandonment, namely structural performance and coral survivorship, paired to considerations on the effects of restrictions on project management. The considered projects are informative in that: (1) they are representative of different environmental settings being located in three distinct biogeographic provinces in two oceans (see Spalding et al. 2007) but are still comparable as: (2) they make use of a consisted restoration approach, ‘coral gardening’ through floating rope nurseries; (3) they have similar size in terms of number of reared colonies; and (4) they make use of one common coral growth form (i. e. branching) and at least one common genera (i. e. *Acropora*). Moreover, the coral gardening approach, because cost-effective, is also currently one of the most applied techniques practiced by coral restoration projects around the world (Bayraktarov et al. 2020; Bostrom-Einarsson et al. 2020), which makes our conclusions widely applicable and of interest to a wide audience.

Our observations from Colombia, Seychelles and Maldives highlight that buoyancy and material life span are fundamental in ensuring structural longevity for floating rope nurseries since, at all three locations, most of damages to the coral nurseries were due to the consequences of the loss of buoyancy. Specifically, the buoyancy of the nurseries was compromised not only by failures in the materials (e.g., loss of floating devices), but also as a consequence of excessive weight of the reared coral colonies. This emphasizes the importance of preemptively setting up redundant floating devices as both a backup and an enhancement to the necessary ones, as also proven by the case of Athuruga house reef nursery, where the effects of abandonment were mitigated and minimized due to the timely adoption of similar preemptive measures. Some of the failures detected in our study case are likely due to the common adoption of relatively cheap and/or recycled materials in the construction of nurseries. Although it can increase cost, a starting investment in more robust flotation devices with a longer life span and requiring less maintenance, such as “plastic” nautical buoys, could be rewarding in the long term. More in general, investing in the targeted development of reliable and efficient (and possibly plastic-free) flotation devices, as well as of new materials for tension ropes and the other nurseries' structural components could not only benefit coral restoration, but also lead to technological innovations applicable to other fields.

As this study is limited to floating rope nurseries, the key inferences and recommendations may not be the same for the whole set of methodologies utilized for coral gardening including trees, tables, spiders etc. and do not fully represent the operational modifications that these programs will make in the future. Therefore, an analysis of impacts on other techniques and programs worldwide would be required to identify key risks and recommendations across the whole spectrum of coral restoration approaches.

Our assessment indicates that coral restoration projects might suffer substantial damages after less than one year with no-maintenance. In our study, different coral genera responded differently to the abandonment, with *Pocillopora* fragments (especially those stocked at least one month before the suspension of maintenance) having the better rate of survivorship on Athuruga (Maldives), where direct comparison was possible. When Acroporid corals suffered substantial mortality (e.g., Colombia), most of it was due to a combination of sedimentation caused by the collapse of the rope nurseries onto sandy bottoms and algal overgrowth. While impacts from the algal overgrowth stress the need for cleaning efforts in nurseries (Levy et al. 2010; Shafir et al. 2010, Frias-Torres et al. 2018), direct comparison between the Maldivian projects suggests that the degree of cleaning effort needed could vary on a per-case basis. For instance, the low presence of algae observed in Magoodhoo 61 weeks after the last maintenance activity highlights how the choice of an optimal site (in ecological and environmental terms) can significantly reduce the need for active maintenance.

Furthermore, the colonization of jerrycans and PVC pipes by new coral recruits of different species observed in Magoodhoo and Colombia, with some of the colonizers being unexpected and locally rare to Magoodhoo, emphasizes the idea that coral nurseries might act as floating ecosystems (Shafir & Rinkevich, 2010) offering further arguments supporting the importance of restoration actions (Hein et al. 2021).

Whilst colony mortality and nursery structure failures can be mitigated and minimized during periods of forced site absence, monitoring of projects involving data collection, analysis, and evaluation of nursery and outplant sites cannot continue without the necessary in-situ workforce. As the projects discussed here demonstrate, the global work force immobility made it often impossible for organizations, including NGOs, universities, and touristic resorts, to retain international workers or volunteers on site. Continuity in monitoring and data collection activities is a critical element in restoration project, possibly reducing the likelihood for success even during "normal" circumstances (Hein et al. 2019; Bostrom-Einarsson et al. 2020; Shaver et al. 2020). Such criticality has now been made apparent by the COVID-19 pandemic. Interruptions in data collection and analysis, as experienced by all three case studies, can also undermine the confidence of stakeholders and funders in restoration actions, generating a dangerous loop where the cost of securing projects against failure cannot be covered, and the subsequent failures compromise further funding acquisition.

In conclusion this study provides evidence that floating nursery structures, in the investigated areas, can endure several months of abandonment with little preparation, if necessary, as long as sufficient buoyancy is ensured. However, disruption of monitoring and data collection can cause a cascade of events, resulting in potential financial and planning uncertainty, which can ultimately jeopardize overall longevity, performance, and success of these projects. Management strategies should start with the preparation of contingency plans focusing also on workforce sources. In particular, project budgets should prioritize the involvement of local workforce to minimize the potential impact of restrictions in mobility. This might be a win-win strategy bringing also substantial benefit to local economies. The current pandemic not only continuously forces researchers and conservationists to adapt their *modus operandi*, but also highlights our society’s fragility and dependence on resilient and healthy ecosystems, for which coral restoration projects around the world make every effort.

4.8 Acknowledgments

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4.10 Illustrations

Table 1: Comparison of floating rope nursery projects in Colombia, Seychelles and the Maldives and the impact of forced monitoring and maintenance interruption resulting from the Covid-19 pandemic.

Location	No of Nurseries (build in)	Coral nursing environment	Monitoring and Maintenance	Interruption time	No. of fragments	Genera/Species	Fragment Survival	Nursery condition	Main issues	Project implication
Colombia - Providencia	1 (2018)	6m deep lagoon; sandy bottom; current: slight; temp. range: 28-30°C	Monthly; 1 research staff, 1 technician and 4 trained fisher folks; ca.20 person-hours/month	30 weeks	1500	*Acropora palmata*	60%	Partially collapsed	Lack of buoyancy, macroalgae overgrowth	Considerable coral loss, structure repair
Colombia - Providencia	1 (2018)	6m deep lagoon; sandy bottom; current: mild; temp. range: 28-30°C	Monthly; 1 research staff, 1 technician and 4 trained fisher folks; ca.20 person-hours/month	30 weeks	200	*Acropora cervicornis*	40%	Fully collapsed	Lack of buoyancy, macroalgae overgrowth	Major coral loss, difficult repair
Seychelles	1 (2018)	sandy bottom at 17m, exposed to NW wind trade;	Monthly; 3 technical staff; 2 to 4	46 weeks	192	*Pocillopora spp.*	75%	Partially collapsed	Lack of buoyancy;	Minor coral loss after

		current medium during SE wind trade; temp. range: 26 – 31°C	volunteers; ca. 10 person-hours/month						weight of fragments	structure repair
Maldives – Athuruga Resort Island - Lagoon	1 (2018)	15m deep lagoon; sandy bottom; current: no; temp. range: 28-30°C;	Monthly; 2 resort staff; ca.10 person-hours/month	29 weeks	346	83 *Acropora*, 190 *Pocillopora*, 73 *Porites*	94.5%	Partially collapsed	Lack of buoyancy; macroalgae overgrowth, disease	Minor coral loss after structure repair
Maldives – Athuruga Resort Island – Reef	1 (2020)	20m deep inshore reef; rubble & sandy bottom; current: intermediate; temp. range: 28-30°C;	Monthly; 2 resort staff; ca. 16 person-hours/month	29 weeks	770	301 *Acropora*, 469 *Pocillopora*	80.4% (46% new stock; 94% older stock)	Fully functioning	Macroalgae overgrowth	Minor (partial loss of young fragments)
Maldives – Magodhoo Local Island	4 (2017)	15m deep lagoon; sandy bottom; current: slight; temp. range: 28-30°C;	Monthly; 2 research staff; ca.20 person-hours/month	61 weeks	846	715 *Acropora*, 114 *Pocillopora*, 17 *Porites*	~80%	Fully collapsed	Lack of buoyancy; weight of fragments	Considerable loss of data, corals and difficult repair

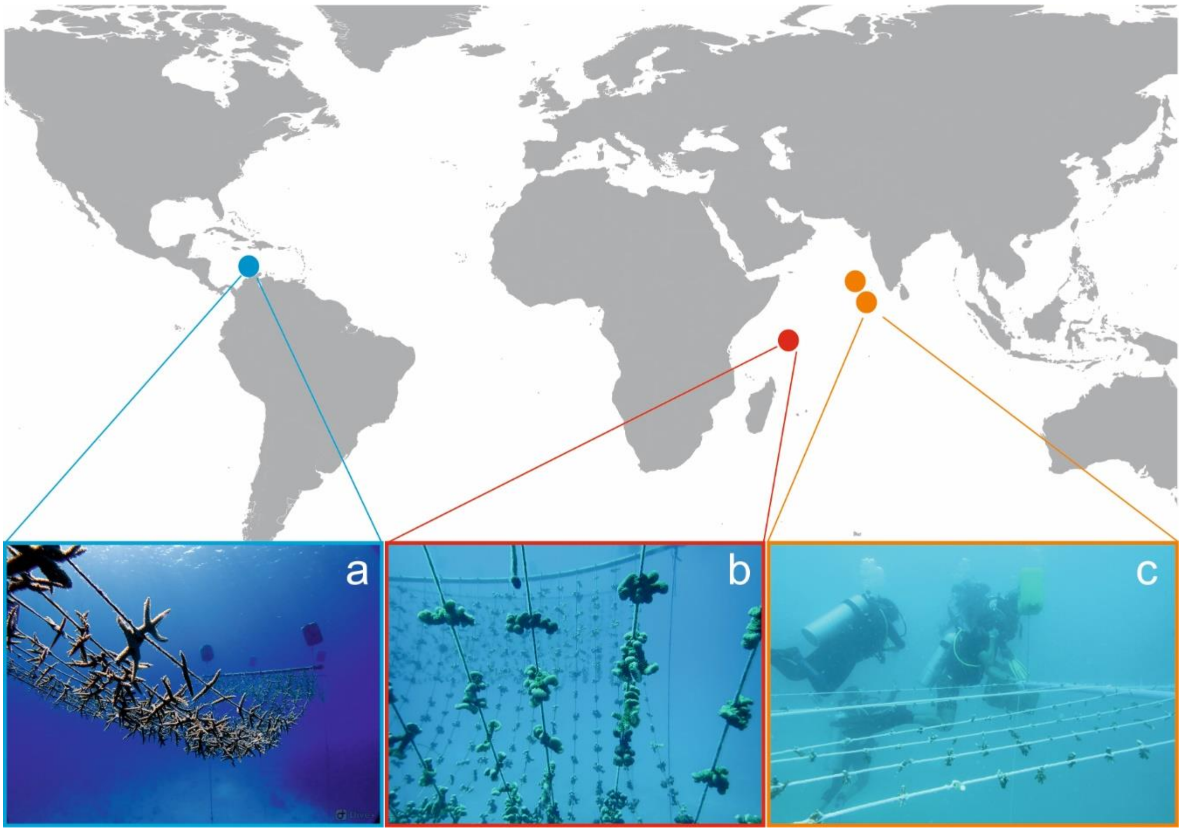

Figure 1: Map of the study area where the projects are located; a) Providencia Island in Colombia; b) Seychelles; c) Maldives. In Colombia, the two nurseries were installed in the same nursery site, 200 meters from the coastline of Providencia Island, inside the reef lagoon (13°20'3.20"N 81°21'28.09"W). In the Seychelles, the nursery was placed ca. 600m offshore, NW from Cousin Island (4°19'34"S 55°39'26.1"E). In the Maldives, on Athuruga resort island (3°53'14"N 72°48'59"E) one nursery was placed in the lagoon, about 350m away from the shore and one on the house reef, 50m from the shore. On Magoodhoo local island (3°04'45"N 72°57'53"E) four nurseries were placed in the lagoon, approximately 200m away from the shore.

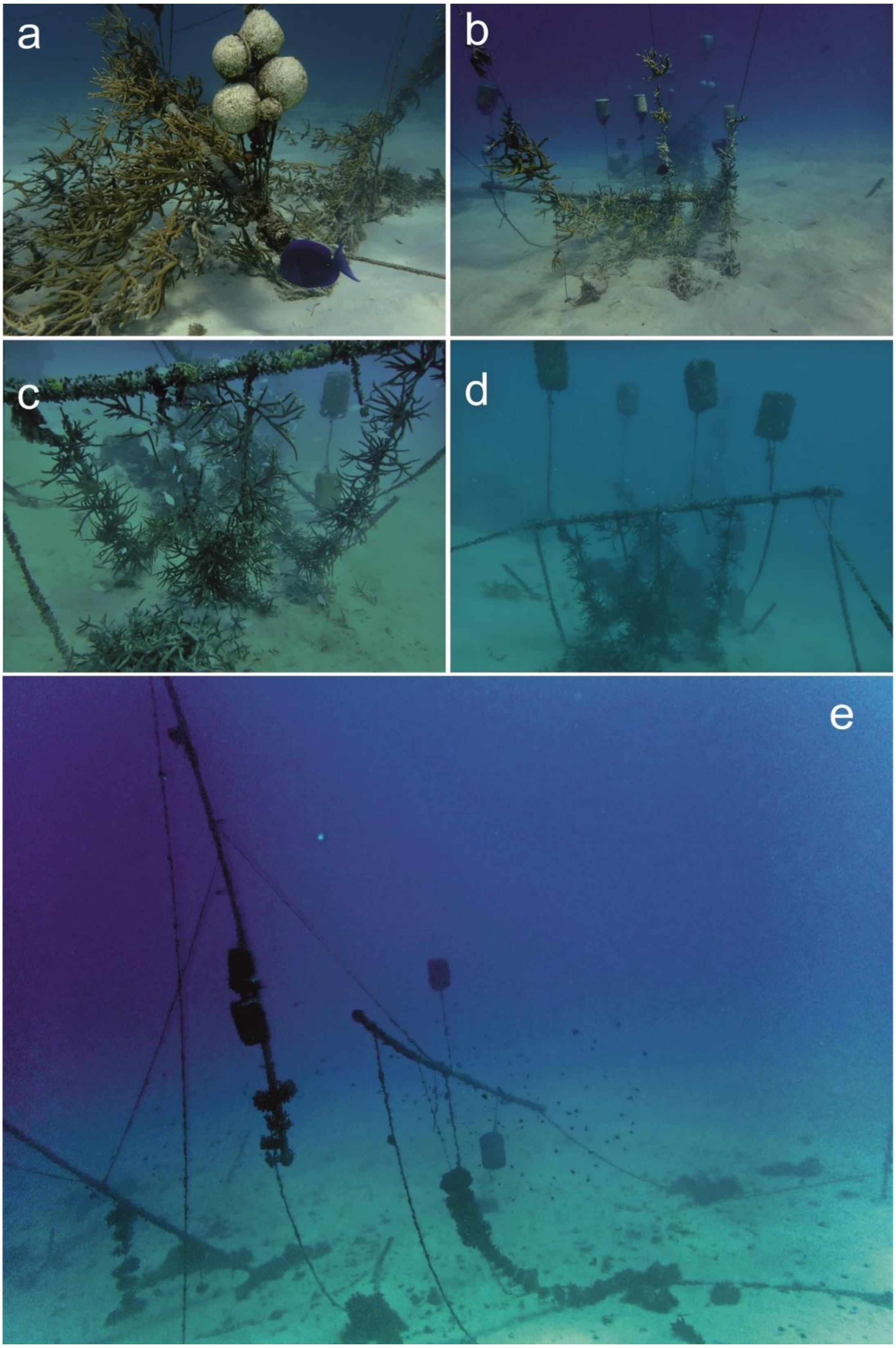

Figure 2: Panel showing similar collapsing patterns between the three different locations; a-b) Providencia Island, Colombia; c-d) Magoodhoo Island, Maldives; e) Seychelles

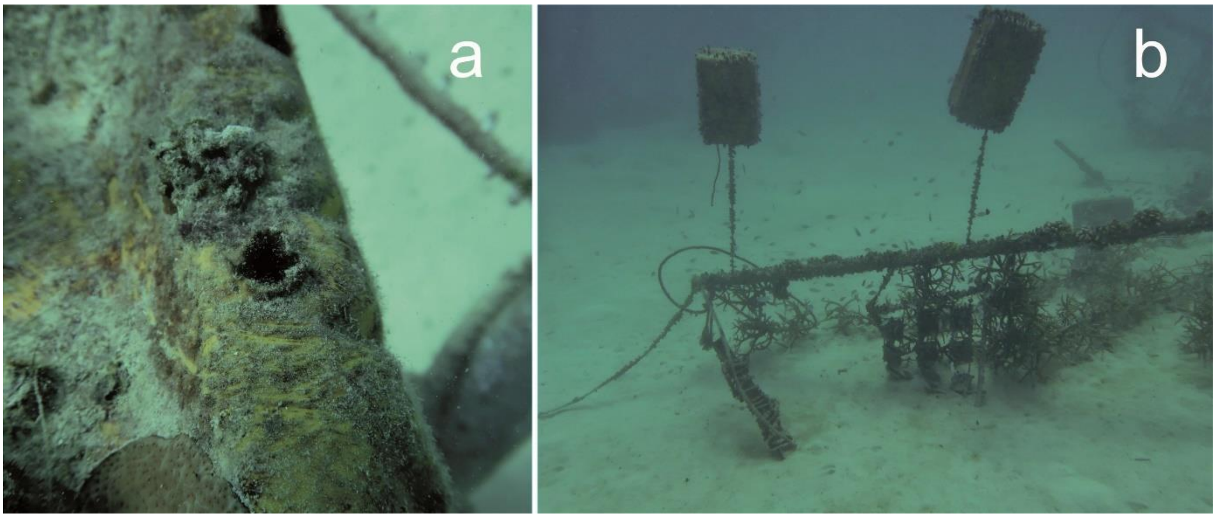

Figure 3: a) Close-up of a punctured jerry can. b) A collapsed floating rope nursery located in Magoodhoo Island (Maldives)

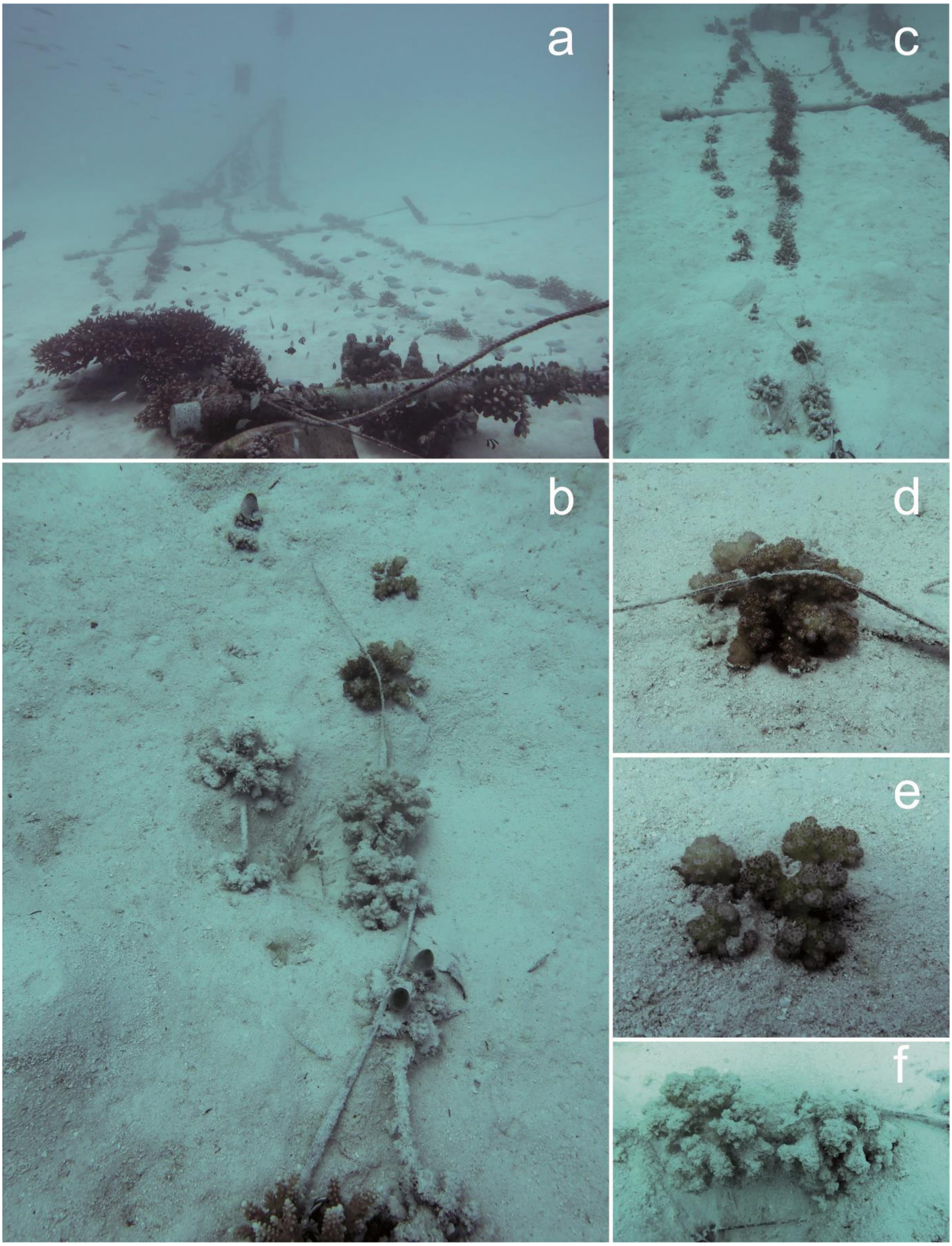

Figure 4: a-c) Overview of a collapsed floating rope nursery in Magoodhoo Island with ropes and colonies laid on the bottom; d-e) Fragments of *Pocillopora* partially covered by sand; f) Recently dead colonies of *Pocillopora*

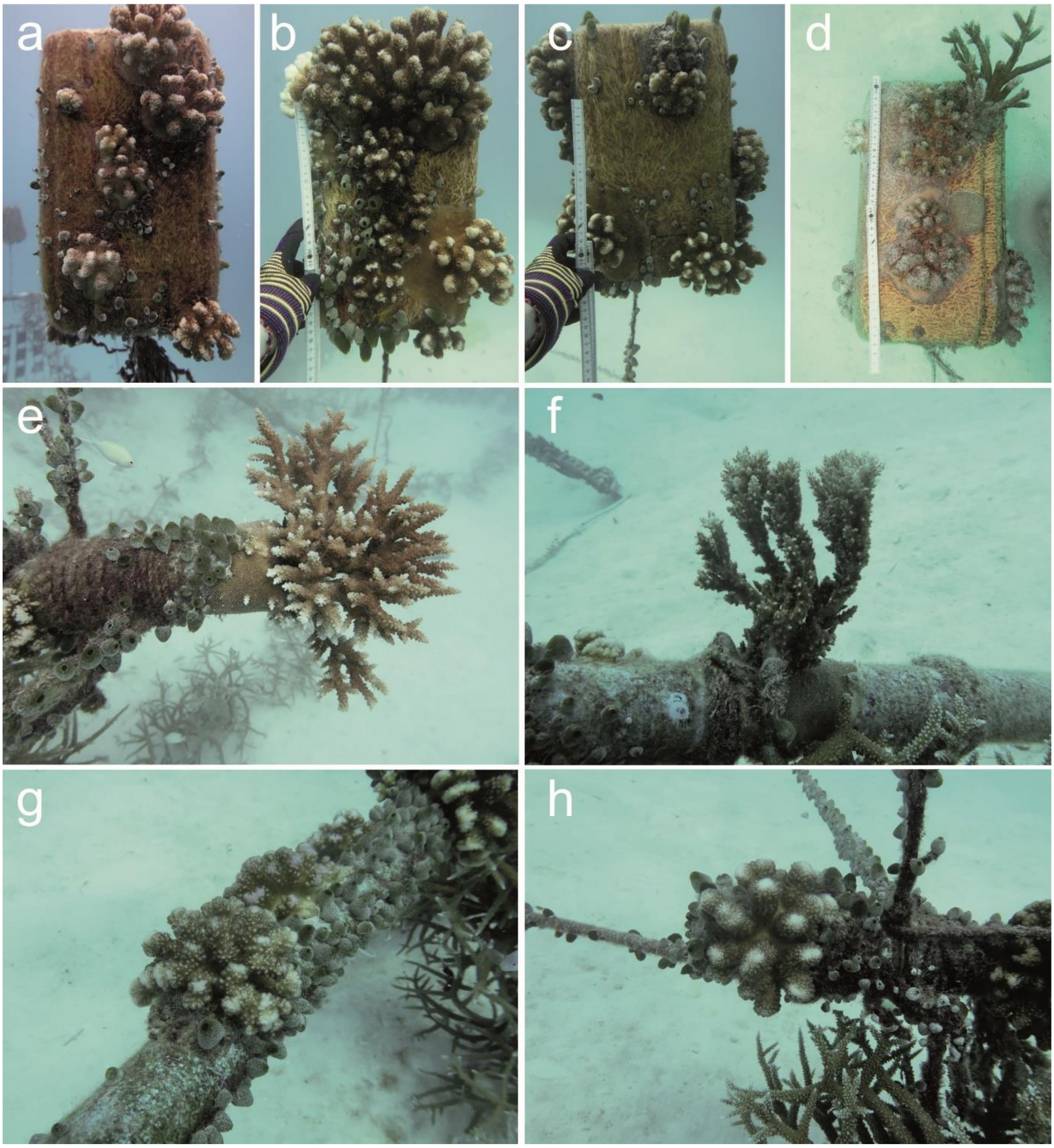

Figure 5: Images showing coral colonies overgrowing PVC pipes and jerry cans in Magoodhoo Island; a-d) Jerrycans fully covered by *Pocillopora* colonies over 15 cm in diameter; e-f) *Acropora* spp. colonies unexpectedly overgrowing PVC pipes; g-h) Examples of *Pocillopora* colonies growing on PVC pipe and entangled ropes, respectively.

Table S1: Mid-water floating nurseries structure assessment on Athuruga, Maldives after 29 weeks of non-maintenance. A categorical scale was used to discern information on structural conditions. The categories were scaled as follows: 1 – Excellent (very good condition and full functionality); 2 – Good (good condition with no reduction in functionality); 3 – Moderate (showing signs of damages, but maintaining close to full functionality); 4 – Poor (presence of evident damages resulting in reduced functionality); 5 – Very poor (presence of major damages compromising functionality). The total time the material had been in use is also indicated.

	Anchor		**Vertical ropes**		**Coral ropes**		**Buoyancy device**		**Tension Lines**		**PVC Pipes**	
Material	Iron L bars		10mm twisted nylon rope		5 mm twisted nylon rope		Jerry cans (for oil)		5 mm twisted nylon rope		3m long PVC pipes	
	Time in the water	Condition	Time in the water	Condition	Time in the water	Condition	Time in the water	Condition	Time in the water	Condition	Time in the water	Condition
Lagoon Nursery	28 months	Good	28 months	Good	9 & 28 months	Good - Moderate	9-18 months	Moderate-Poor	28 months	Poor	28 months	Good
Reef Nursery	21 months	Excellent	9 months	Good	9 months	Good	6-9 months	Good-Moderate	9 months	Good	NA	NA

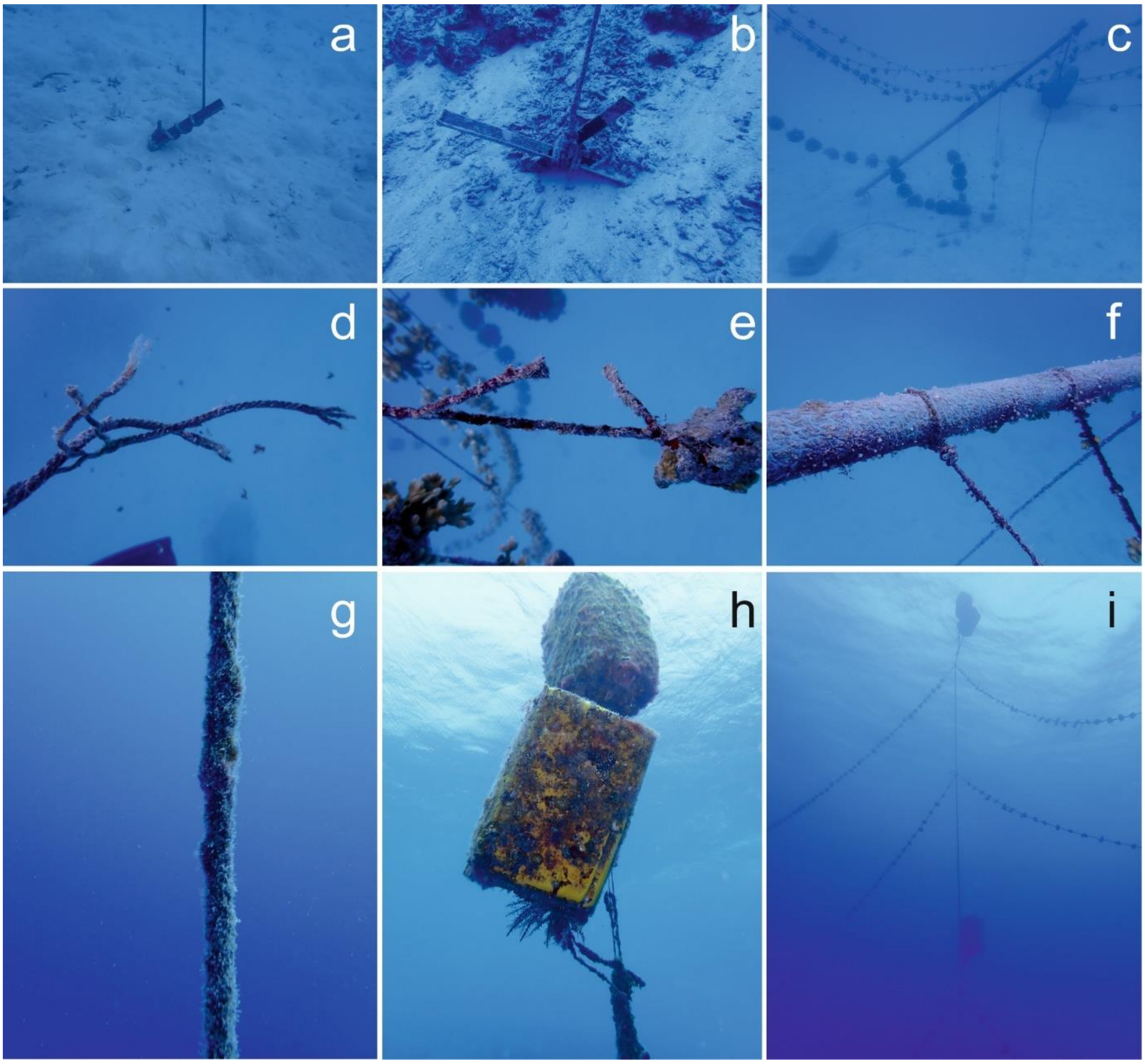

Figure S1: Condition of nursery material on Athuruga, Maldives; a)-b) anchors; c) partially collapsed lagoon nursery; d)-e) coral ropes; f) PVC pipe; g) vertical rope; h) jerrycans; i) reef nursery

CHAPTER 5

5.1 Disease assessment in 'coral gardening' nurseries and implications for coral restoration success

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Keywords: white syndrome, prevalence, incidence, Acropora, Pocillopora, mid-water nursery

This section is inserted as submitted to Biodiversity and Conservation

5.2 Abstract

Coral diseases are a threat to continuously degrading coral reefs and their abundance and virulence is expected to increase in the future. Active conservation, specifically coral restoration projects are increasingly implemented worldwide. Yet, little is known about the implications of disease occurrence in a coral restoration context. This study describes white syndrome disease pathogenesis in two coral genera, farmed in mid-water rope nurseries in a Maldivian reef and lagoon habitat. Over a 112-day monitoring period, disease metrics were obtained from 448 *Pocillopora* and 96 *Acropora* fragments, to assess the impacts of unmitigated disease progression. Infected, reef-farmed *Pocillopora* had a low prevalence (2.2%) and incidence (0.007), but survival (91%) was significantly reduced in comparison with the healthy lagoon-farmed stock (99%). Vice versa, the lagoon-farmed *Acropora* had a high disease prevalence (78.5%), incidence (0.064) and a lower survival (79%), in comparison with the disease-unaffected *Acropora* reef stock (98%). This had contrasting implications for coral gardening success. While *Pocillopora* was considered suitable for outplanting, especially since subsequent mitigation interventions were successful, the diseased, lagoon-reared *Acropora* stock posed a potential risk to the restoration site and was not transplantable, following one year of farming effort. Our findings demonstrate that unmitigated diseases can cause major setbacks to restoration success. Coral gardening projects are likely to be particularly at risk, especially if 'risky practices' are employed. Since there is currently a lack of available diagnostic and mitigative tools, this study hopes to provide some original insight for restoration practitioners.

5.3 Introduction

Coral reef ecosystems are under increasing threat from multiple stressors, including the spread of diseases (Harvell et al. 2007; Hughes et al. 2017). Diseases are also of concern when it comes to the active conservation of coral reefs in the form of coral restoration (Zimmer 2006; Forrester et al. 2012; Moriarty et al. 2020). While the discipline of coral restoration has gained much momentum in terms of scientific advancements as well as its increasingly widespread and upscaled practical application (Omori 2019; Hein et al. 2021), the systematic assessments of disease occurrence, transmission and mitigation in a coral restoration context are lacking. Therefore, the role of coral diseases instigating or amplifying coral mortality are poorly understood (Moriarty et al. 2020). Moreover, coral restoration practitioners may unintentionally apply 'risky practices', that favour disease dissemination.

'Coral gardening', for example, one of the most commonly applied restoration practices (Boström-Einarsson et al. 2020), requires high coral survivorship during the fragment farming phase in coral nurseries as well as the outplanting phase, in order to be ecologically and economically effective (Epstein and Rinkevich 2001; Shaver et al. 2020). It also frequently involves densely stocked, asexually reproduced fragments of low genotype diversity and monospecific nurseries with fast growing branching coral genera, all of which can increase host susceptibility to pathogens (Vollmer and Kline 2008; Mydlarz et al. 2010; Young et al. 2012). Furthermore, the spread of coral diseases could increase mortality of colonies transplanted to the restoration site, particularly when these are suffering from increased handling and adaptational stress. It also poses the risk of introducing infectious diseases to restoration sites and adjacent reefs (Shore and Caldwell 2019; Moriarty et al. 2020). Therefore, a better understanding of the causes and consequences of coral diseases is imperative for project management, along with the investigation of possible mitigation measures to improve restoration effectiveness and active coral reef conservation.

The negative impacts of coral diseases are also likely to increase in the future, in both restoration as well as natural reef environments. Over the last decades, an increasing number of new syndromes and severe disease outbreaks has been described to impact coral reefs worldwide (Aronson and Precht 2001; Willis et al. 2004; Miller et al. 2009; Hobbs et al. 2015; Alvarez-Filip et al. 2019). Disease outbreaks are also expected to intensify, as climate change induced stress along with other anthropogenic activities are likely to accelerate coral susceptibility to disease as well as pathogen abundance and virulence (Harvell et al. 2007; Burge et al. 2014; Maynard et al. 2015). In particular, thermal stress has been identified as a major trigger for disease (Bruno et al. 2007; Randall et al. 2014; Brodnicke et al. 2019). Other disease correlated stressors resulting from human activities include tourism (Lamb et al. 2014), plastic pollution (Lamb et al. 2018), coastal development leading to increased sedimentation (Pollock et al. 2014), nutrient enrichment (Bruno et al. 2003) and sewage input (Sutherland et al. 2010) as well as physical disturbances from fishing (Lamb et al. 2015) or ship groundings (Raymundo et al. 2018).

Coral diseases are often difficult to identify and mitigate in situ for several reasons. Detecting and differentiating diseases from other environmental stressors based on macroscopic inspection requires expertise, which may be a challenge for restoration projects. Disease causes are complex and difficult to establish in an uncontrolled environment, with additional laboratory studies and manipulative experiments required (Mera and Bourne 2018). Also, pathogen identification remains challenging given the complex and still poorly understood host microbiome (Ainsworth et al. 2017), and there is currently a distinct lack of widely available diagnostic tools (Pollock et al. 2011). Similarly, effective mitigation instruments or strategies are still lacking from the coral restoration toolbox. This lack of knowledge is illustrated, for example, by the continued rapid spread of Stony coral tissue loss disease (SCTLD), which was first observed in Florida in 2014 and has since then caused considerable damage to at least 20 stony coral species across Caribbean countries with various interventions being of mixed success (Aeby et al. 2019; Alvarez-Filip et al. 2019; Shilling et al. 2021).

Overall, coral disease research remains a challenge as few pathogens and their transmission routes have been identified (Shore and Caldwell 2019). In addition, there is often confusing regional variation in syndrome nomenclature (Richardson 1998; Bourne et al. 2014). For example, white syndrome (WS) is a collective term for Indo-Pacific scleractinian coral diseases that are characterized by an advancing band of tissue lesions exposing the white skeleton (Willis et al. 2004). While WS with different epidemiologies has been reported from various locations throughout the Indo-Pacific, causative agents are rarely identified and variations in disease manifestation and progression are likely a result of multiple influencing factors and causes (Bourne et al. 2014). WS has also been frequently reported from the Great Barrier Reef, in particular in combination with heat stress events (Willis et al. 2004; Hobbs et al. 2015; Brodnicke et al. 2019).

Our case study was conducted in the Maldives, in the Indian Ocean, where coral reefs are vital to the nation's prosperity and active conservation and restoration is required to increase reef resilience under future climate scenarios (Venton et al. 2010; Van Hooidonk et al. 2016). Indeed, Maldivian coral reef ecosystems have been severely degraded following a series of mass bleaching events (Tkachenko 2015; Pisapia et al. 2016; 2019) along with other threats such as outbreaks of corallivores, water pollution and other anthropogenic pressures (Jaleel 2013; Saponari et al. 2018; Patti et al. 2020). Hence, the northern Maldives were identified as a high risk area for coral disease susceptibility and pathogen exposure due to a combination of climate stress and local activities (Maynard et al. 2015). Coral diseases were first documented in 2010 here, when five syndromes affecting different coral genera were identified (Montano et al. 2012). WS was found to be the most widespread disease, in particular among the genus *Acropora* (Montano et al. 2015), yet causes and dynamics of Maldivian coral disease epidemiology remain largely unstudied. WS was also identified as the main cause of *Acropora* fragment mortality in the first assessment of mid-water coral nursery performance in the Maldives (Dehnert et al. 2021), highlighting the need for further research on the impacts of coral diseases in restoration.

This study systematically assesses disease occurrence and progression in mid-water rope nursers for two commonly used coral genera in order to evaluate the impacts of disease on coral rearing success. We use standard disease metrics commonly applied in coral disease research to put our findings into perspective of what is known about disease progression in the coral reef ecosystems and to extend this important research to the field of coral restoration.

5.4 Methods

5.4.1 Study Design

The study was conducted on Athuruga Resort Island (3°53'14"N 72°48'59"E) in Alif Dhaal atoll, in the Republic of Maldives in 2020/21. The islands' coral restoration project comprises two coral gardening sites (see Dehnert et al. 2021 for location map and details on construction and monitoring). One mid-water rope nursery is situated inside the island's large enclosed lagoon with coral fragments growing at 5m depth (hereafter lagoon nursery) and a second mid-water rope nursery is situated parallel to the island's southern house reef with fragments growing at 5, 10 and 15m depth (hereafter reef nursery).

Both nurseries were stocked with *Pocillopora verrucosa* fragments from 14 different, nursery reared donor colonies, with a subset eight fragments per donor colony used for each coral rope, resulting in three coral ropes with 112 fragments each at 5,10 and 15m depth in the reef nursery and one coral rope with 112 fragments growing at 5m depth in the lagoon nursery.
In addition, six *Acropora spp*. donor colonies of opportunity from a nearby reef (3°48'51"N 72°45'10"E) were used to stock two coral ropes with 48 fragments (eight fragments per donor colony) and placed at 5m depth in the lagoon and the reef nursery.

All *Pocillopora* and *Acropora* donor colonies were assumed to be of different genotype as they were initially collected as corals of opportunity spaced more than 10m apart (Edwards and Gomez 2007; Foster et al. 2007). Each donor colony was fragmented into similar sized fragments, with selected fragmentation sizes for individual colonies ranging from 3-11cm in diameter. Coral fragments were stocked in February 2020 (T0) and following a five months COVID-19 related interruption due to resort closure, monthly monitoring was resumed. A bi-weekly disease monitoring protocol was applied from November 2020 onwards for 112-day (9 surveys: S1-S9) to track the unmitigated occurrence and spread of coral disease in the two mid-water nurseries in different farming habitats. Afterwards, mitigation measures were conducted on the reef nursery, removing all diseased and dead fragments, with reassessment after 10 weeks.

5.4.2 Data Analysis

All diseased fragments were visually assessed in situ, photographed (Olympus TG5) and disease morphology was described using the standardized framework by Work and Aeby (2006) and compared with relevant literature (e.g., Raymundo et al. 2008; Hobbs and Frisch 2010). A disease monitoring protocol was designed, following the monitoring regime for coral restoration projects suggested by Moriarty et al. (2020), which included the following measures: Disease 'prevalence', the percentage of diseased fragments in the healthy nursing stock, and 'incidence', the proportion of new cases per survey was calculated for each genus, nursery habitat and survey. Disease 'percental progression' of infected fragments was tracked as the percentage of live tissue loss between surveys and calculated as daily rate for all affected fragments. Mean disease progression between the infected genera were tested using the non-parametric Mann–Whitney U-test. In order to better understand possible transmission processes, it was further recorded whether any of the adjacent fragments on the same rope were diseased at the time of new fragment infection, or whether infections occurred randomly on the coral ropes. Additionally, coral nursery structures were monitored for any coral predators, that could act as a potential vector and predation scars on the fragments were also recorded.

Lesion extension and progression over time were described by classifying the 'disease pattern' of fragments as either 'apparent' (i.e., acute to subacute progressing freshly diseased tissue and exposed bare 'white skeleton') or 'latent' (i.e., a temporary halt in progression of a previously acute lesion with initial algae colonization of the skeleton but no fresh tissue loss. The lesion then experienced another acute progression during a later survey). Coral restoration farming stock impact of the disease was assessed by estimating the percent 'tissue cover' of healthy, diseased, recently dead and dead tissue for all fragments. To compare farming performance of healthy and diseased stocks, fragment 'survival' was also calculated including all stocked fragments. Survival was compared within stocks at the start and the end of the study (exact McNemar test) as well as between diseased and healthy stocks in different habitats (Chi-squared test). In addition, mortality rates were calculated whereby disease mortality was distinguished from non-disease related mortality where it was evident (e.g., algae overgrowth). Finally, ‘fragment condition’ was assessed for all farming stocks, discriminating between healthy, partially dead, diseased and dead fragments (see Frias-Torres et al. 2018).

Statistical analysis was performed using SPSS ver. 27 (IBM, New York) with all data represented as arithmetic means ± standard deviation. Non-parametric test statistics were used when the normality assumption was violated.

5.5 Results

5.5.1 Disease in *Pocillopora*

Pocillopora stock was only affected by disease in the reef nursery (20 diseased fragments, 6.3 % of the stock, N=320), while no disease incidents were recorded in the lagoon nursery. Disease gross morphological appearance was similar for all fragments on the reef and is referred to as *Pocillopora* white syndrome in the absence of further microbial analysis. Lesions were characterised by rapid tissue loss, revealing a ca. 1 cm wide band of bare, white skeleton with distinct edges and serrated margins on the intact tissue side and green to red coloured, algae overgrown skeleton on the other side. Lesions were first observed at the base, where the fragment was in contact with the nylon rope and progressed in an acute to subacute manner directional across the fragment (Fig. 1a).

Average disease prevalence was 2.2 ± 0.7% and during the study the percentage of infected fragments increased slightly from 1.6% at the start to 2.6% at the end (Fig. 2a). The mean incidence was 0.007 ± .01 cases per survey (Fig. 2b). This translates to an average of about 7 acute diseased fragments in the reef nursery at any survey (Table 1). Disease percental progression on affected fragments was on average 1.28 ± 1.4% of fragment tissue loss per day (Fig. 2c). Once infected, individual fragment health continuously declined and no fragments were observed to recover. The average time from infection to death was 36 ± 28 days (N=12), ranging from minimum14 to maximum 112 days. Disease transmission was direct in most cases, from one fragment to the next on the rope. Of all diseased cases, 18 fragments had a diseased adjacent fragment at the time of infection while only 2 random infections were observed. While an etiologic diagnosis was not reached in the field, no benthic predators (e.g., corallivorous gastropods) were observed in the immediate surrounding of the affected fragments that could have functioned as disease vectors. Fish predation marks were recorded in both habitats (reef: on 59 ± 13% of fragments; lagoon: on 40 ± 49% of fragments).

Looking at the impacts of disease on farming success, the analysis of disease pattern over time revealed that in the diseased reef stock there was only a small number of apparent cases with continuous, visible disease progression throughout the survey period (Fig 3a). Therefore, the impact on farming stock live tissue was also not severe, with decline of less than 10% during the study (Fig 3c). Nevertheless, reef nursery stock survival, which was 95.2 % to begin with, decreased significantly to 91.4 % at the end of the disease-monitoring period (p<0.001), at which point fragments had been farmed for 55 weeks. It was established that disease was the main cause of fragment death during the monitoring period (disease mortality rate 3.75%, see Table 1). In contrast, *Pocillopora* stock survival was significantly higher in the lagoon nursery ($\chi 2$=8.050, p=0.005), which was not affected by disease and remained unchanged at 99.1%. The negative impact of disease is further illustrated by the direct comparison of fragment condition between the diseased reef and the healthy lagoon stock (Fig. 4).

The introduced mitigation measure of removing the diseased fragments stopped the spread along the ropes in 100% of the cases. Of the 14 *Pocillopora* fragments that had a diseased and therefore removed adjacent fragment, none was infected after 10 weeks. Nevertheless, the disease was still present on the reef, as one newly and random infected fragment was recorded during this time. Thus, post-mitigation prevalence for all *Pocillopora* fragments was reduced to 0.36%.

5.5.2 Disease in *Acropora*

The *Acropora* stock was severely affected by disease in the lagoon nursery (37 diseased fragments, 88 % of the stock, N=42), while there was no disease incident recorded in the reef nursery. Comparison of gross lesion characteristics of *Acropora* spp. stock in the lagoon suggest that fragments were suffering from *Acropora* white syndrome, following the description of Work and Aeby (2006) and Montano *et al.* (2012). Lesions were of moderate extend, displaying a 2-3cm large, diffuse area of acute tissue loss affecting polyps and coenosarc and revealing the bare, intact white skeleton. Multiple branches of a fragment were affected either simultaneously or successively, always rapidly expanding from at the apical tip of the branch towards the base, before tissue loss was temporary halted and the exposed, bare skeleton turned red (algae covered). In most cases a subsequent alteration between a latent progression and an acute phase was noted along the same lesion trajectories (Fig. 1b).

Mean prevalence was high with 78.5 ± 12.6% and increased from 52.4% at the start to 89.8% at the end (Fig. 2a). Also, disease incidence was higher (M=0.064 ± .07) and more variable than in *Pocillopora,* as new cases per survey declined over time in the increasingly diseased stock (Fig. 2b). In contrast, disease percental progression was significantly slower for *Acropora*, with an average fragment tissue loss of 0.42 ± 0.8% per day (Fig. 2c). Furthermore, infections did generally not result in total fragment mortality. In fact, only two infected fragments died during the survey, where time from infection to death was 70 and 84 days. Disease transmission pattern was less evident, with 11 random infections and 26 cases, where an adjacent fragment was infected at the time of disease appearance, which was inevitable as the number of diseased fragments in the stock increased over time. Imminent predator presence or predation scars could not be observed in relation with disease occurrence in the lagoon nursery.

On average, the lagoon nursery had 12 apparent and 19 latent diseased fragments per survey (Table 1). A closer investigation of the disease pattern of fragments in the diseased nursery stock revealed that the percentage of healthy fragments continuously declined while apparent and latent diseased fragments made up the majority of the stock (Fig. 3b). Also, the number of apparent cases decreased towards the end while the percentage of latent cases increased. This resulted in a considerable impact on farming stock live tissue. The proportion of dead fragment parts in the diseased lagoon stock increased as a result of gradual disease spread, exceeding the tissue gain generated by natural fragment growth. At the end of the study, about 50% of the farmed fragment tissue area was dead (Fig. 3d). Comparison of the diseased lagoon nursery and the healthy reef nursery showed that *Acropora* survival was significantly lower in the diseased stock ($\chi2=6.095$, $p=0.014$), where it decreased by 8.3% to 79.2 % during the monitoring period, while reef stock survival decreased only by 2.1%, at which point total rearing time was 52 weeks (Table 1). Due to smaller sample size, the decline in survival was not statistically significant (lagoon: $p=0.125$; reef: $p=1$). Disease induced mortality rate in the lagoon was higher (7.1%) than the non-disease related mortality rate in both habitats (lagoon: 2.4%; reef: 2.1%). Finally, *fragment* condition was severely impacted by disease and therefore varied considerably between the reef (64% fully healthy) and the lagoon nursery (0% fully healthy) at the end of the study (Fig. 4).

5.6 Discussion

This research describes the occurrence, progression and different impacts of coral disease in *Pocillopora* and *Acropora* coral gardening stocks, providing initial insight into the potential risks that coral diseases can pose to coral restoration outcomes in a real case scenario. We recorded similar white syndrome disease pathologies with tissue loss in *Pocillopora* and *Acropora*, two branching coral genera commonly used in coral restoration (Boström-Einarsson et al. 2020). In our Maldivian case study, all fragments were reared in mid-water nurseries in a reef and a lagoon habitat. While *Pocillopora* white syndrome was only documented in the reef nursery, *Acropora* white syndrome was only spreading in the lagoon nursery. This circumstance provided a unique opportunity to document the unmitigated disease occurrence in two coral gardening stocks and to assess the impacts on overall coral farming success by comparing the diseased stock of each genus with the performance of the corresponding healthy stock with identical fragment composition (i.e., genotypes, size, rearing time). Our results revealed two distinct patterns of disease progression between the coral genera, with contrasting implications for overall restoration success.

Disease in *Pocillopora* spread gradually, from one fragment to the next. Although, lesions progressed faster in infected fragments and were lethal in most cases, disease prevalence and incidence were much lower than observed for *Acropora* in the lagoon nursery. Therefore, the overall impact on stock farming success in the reef nursery was not severe, with less than 4% disease inferred fragment mortality after 112 days of unmitigated disease progression. However, survival in the healthy *Pocillopora* stock in the lagoon nursery was still higher, demonstrating the notable negative impact of disease occurrence in this farming stock. In direct comparison, WS spreading among *Acropora* stock in the lagoon nursery had much more severe impacts on farming output. Mean disease incidence was approximately 10 times higher than in the *Pocillopora* stock and WS was prevalent in almost 90% of the stock at the end of the survey, although not all infections were lethal. Yet, latent disease progression, and in particular the instant resumption of lesions progression after a period of no advanced visual tissue necrosis, made disease development unpredictable. At the end, approximately half of the farmed tissue biomass was lost and fragment survival was considerably lower in the lagoon than in the healthy reef nursery.

Overall consequences for the restoration project were considerable, as essentially the entire *Acropora* lagoon stock was unsuitable for transplantation after one year of farming effort. In contrast, more than 90% of the disease affected *Pocillopora* reef stock was transplantable, which is on the upper end of nursery farming outputs of coral gardening projects (Shaish et al. 2008; Bayraktarov et al. 2019). It needs to be highlighted that transplanting farmed stocks that have experienced cases of disease poses the risk of introducing coral disease to the restoration site, therefore compromising survival of outplanted and naturally occurring corals (Moriarty et al. 2020). Therefore, careful assessment should precede any transplantation activities. In the case of *Pocillopora*, the risk was considered low as 1) disease prevalence was low after mitigation, 2) apparent and acute to subacute lesion progression made diseased fragments easily detectable and 3) disease occurrence with identical macroscopic characteristics were already present on the nearby restoration site. In contrast, the diseased *Acropora* stock, contained at the end of the survey mainly fragments with latent progression, which may be difficult to detect at first sight and was only identified as a result of constant monitoring. Therefore, the risk of cross-contamination was evaluated as high and the *Acropora* lagoon stock was not used for outplanting.

Although specific disease aetiology (i.e., cause or origin) could not be established in the field, due to a lack of microbiological analysis, our observations allow to draw some conclusions regarding the transmission, which can be useful to select appropriate mitigation measures. First, no common coral predators such as *Drupella*,sp. or *Coralliophila* sp., were found on any fragment throughout the survey as floating rope nurseries make access to fragments difficult for these species (Frias-Torres et al. 2018; Saponari et al. 2021). Some corallivores are thought to facilitate the spread of diseases, either by serving as a vector for pathogens or by creating feeding scars (Nicolet et al. 2018; Shore and Caldwell 2019). Such lesions, especially deeper injuries, have been shown to function as a point of entry for water-borne disease pathogens (Gignoux-Wolfsohn et al. 2012). In our study, fish predation may initially have been a contributing factor in the reef nursery, where most fragments had deep fish predation scars throughout the survey, although no clear correlation with disease occurrence was observed.

Once a *Pocillopora* fragment was infected, the disease spread directional and directly via the rope, from one coral to the next, with tissue lesions typically first observed at the rope-fragment interception. In the *Acropora* stock a more random transmission pattern was observed, with lesions initiating at the apical growing tip, from where tissue necrosis moved towards the centre of the fragment, which could point towards a water-born transmission. In addition, the role of macroalgae, which grew more extensively on the nursery structure in the lagoon, remains to be investigated in this context as, for example, a study from the Caribbean demonstrated that physical contact with algae that could serve as a reservoir for a bacterial pathogen, could trigger white band disease (Nugues et al. 2004).

To date, only a few pathogens have been identified in coral diseases, for example *Vibrio* bacteria responsible for WS in several coral species and locations in the Indo-Pacific (Sussman et al. 2008), but since WS is a collective term for a group of coral diseases, more detailed research is required to establish a species and location specific aetiology. Other studies have also reported the presence of the pathogenic bacterium *Vibrio* spp. in relation to Rapid Tissue Necrosis (RTN) in *Pocillopora damnicornis* from field studies and in aquarium cultures, where this disease was easily transmitted from one coral to another (Ben-Haim and Rosenberg 2002). This, in some way resembles what was observed in the reef *Pocillopora* stock but more research is required to support a microbial origin of the described *Pocillopora* WS pathology. The fact that

Pocillopora and *Acropora* white syndrome showed two distinct and habitat specific disease dynamics, could suggest the possibility of two distinct aetiologies. Alternatively, disease patterns could vary in response to the affected host species or specific environmental conditions, as for example observed for black band disease (BBD) in the Maldives. Here, lesion morphological appearance and progression rates differed considerable between the chronically affected *Goniopora cf. columna* and the acute diseased *Psammocora haimiana* (Montano et al. 2015). However, further histopathological and molecular studies, which are difficult to conduct in the field, would need to validate either hypothesis.

Due to the predominantly direct disease transmission pattern, the selected mitigation of removing segments of rope with diseased *Pocillopora* proved to be a useful technique in order to break the transmission cycle. No mitigation measures were conducted in the lagoon at the end of the monitoring period, as at this point WS had already impacted the majority of fragments. However, WS occurrence on two *Acropora* species and unsuccessful mitigation was already reported from a different coral gardening stock in the same lagoon in 2018. Back then, WS pathogenesis was very similar and infected branches were instantly removed below the visually diseased tissue. Still, disease progression accelerated, with new infections occurring randomly in the stock (Dehnert et al. 2021). In line with these findings, a study on outplanted Acroporids in the Caribbean showed that treatments of diseased corals by either excision of healthy branches or using a band of epoxy around lesions had no significant benefit (Miller et al. 2014). It appears that such treatment techniques so far are only effective for a small number pathogens or hosts, for example the mechanical removal of WS diseased tissue (Dalton et al. 2010), a double band of marine epoxy on colonies with black band disease (Aeby et al. 2015) or amoxicillin treatment for stony coral tissue loss disease (Shilling et al. 2021). A new technique for treating coral injuries by applying an antiseptic bilayer film with injectable antioxidant biopolymer has recently been tested in the Maldives (Contardi et al. 2020), which could be developed into a useful tool for disease treatment in coral restoration.

Coral restoration projects are continuously growing in scale and coral nurseries, similar to the one described here, are being used to grow ten thousands of fragments, for example in the Seychelles (Montoya-Maya et al. 2016), Latin America (Bayraktarov et al. 2020) or in Florida's 'Mission: Iconic Reefs'(NOAA 2021). However, theses may also be particularly vulnerable to uncontrolled disease spreading, as coral gardening involves a range of potentially risky practices that can facilitate infection and progression. Almost 60% of corals used in restoration projects have a branching morphology, for example the genus *Acropora*, which makes up 30% alone (Boström-Einarsson et al. 2020). These fast-growing species are thought to have a naturally lower resistance to diseases than slow growing species (Palmer et al. 2008; Mydlarz et al. 2010). Furthermore, in contrast to natural occurring corals that typically avoid touching, asexually reproduced and therefore often closely related fragments are tightly stocked and connected through the nursery structure (i.e., ropes). To maximize nursery outputs and preserve wild populations, extensive fragmentation of a small number of donor colonies creating monospecific nurseries is often practiced, for example in the Caribbean (Lohr et al. 2015). As restoration targets become more ambiguous, the potential risk to thousands of fragments with little genetic diversity growing in monocultures is obvious, if disease management is not considered. Therefore, disease prevention should already start with a diverse donor sourcing process (Baums et al. 2019). Furthermore, farmed corals that are outplanted to the restoration site have to sustain transportation and adaptation stress, which has been linked to increased bleaching and disease occurrence (Forrester et al. 2012).

On the positive side, coral restoration may offer a new opportunity for large-scale selective breeding of more disease resilient genotypes, but research is just beginning to look into the complex issue of enhancing corals through assisted evolution (Van Oppen et al. 2015).

Currently, very little information on the threat of disease in coral restoration projects is available. While our case study reports the effects of disease occurrence during the first farming step of the gardening process, disease monitoring should also be considered for transplanted corals, especially since there is a risk of introducing undetected diseases to the outplanting site. Further research on coral disease management and mitigation strategies in a coral restoration context is urgently required, in particular applicable diagnostic tools that can direct restoration practitioners towards effective mitigation measures. Additionally, restoration projects should routinely include disease surveillance in their protocols, avoid risky practices that could facilitate the spread of diseases and take a precautionary approach if in doubt. In the absence of reliable diagnostic tools, a rigorous monitoring regime and an adaptive action plan to mitigate disease impacts should be applied (see Moriarty et al. 2020).This is fundamental, considering the potential restoration setbacks and the economic losses associated with high stock mortality, as for example observed in our *Acropora* stock, as well as the ecological risk of accelerated disease spread in an already threatened ecosystem.

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5.9 Illustrations

Table 1 Table showing disease metrics for *Pocillopora* (POC) fragments and *Acropora* (ACR) stock in a reef and a lagoon mid-water rope nursery after 112 monitoring days

Genus	**Nursery Habitat**	**Depth**	**Stock Size**	**Survival Start**	**Survival End**	**Disease Mortality**	**Non-Dis. Mortality**	**Prevalence %**	**Incidence Rate**	**Acute Cases**	**Chronic Cases**	**Random Infections**	**Adjacent Infections**
		(m)	(T0)	%	%	%	%	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Total	Total
POC	Reef	5-15	336	95.2	91.4	3.8	0.3	2.2 ± 0.7	0.007 ± .01	6.9 ± 2.1	0	2	18
POC	Lagoon	5	112	99.1	99.1	0	0	0	0	0	0	0	0
ACR	Reef	5	48	97.9	95.8	0	2.1	0	0	0	0	0	0
ACR	Lagoon	5	48	87.5	79.2	7.1	2.4	78.5 ± 12.6	0.064± .07	12.4 ± 5.6	19.1 ± 9.2	11	26

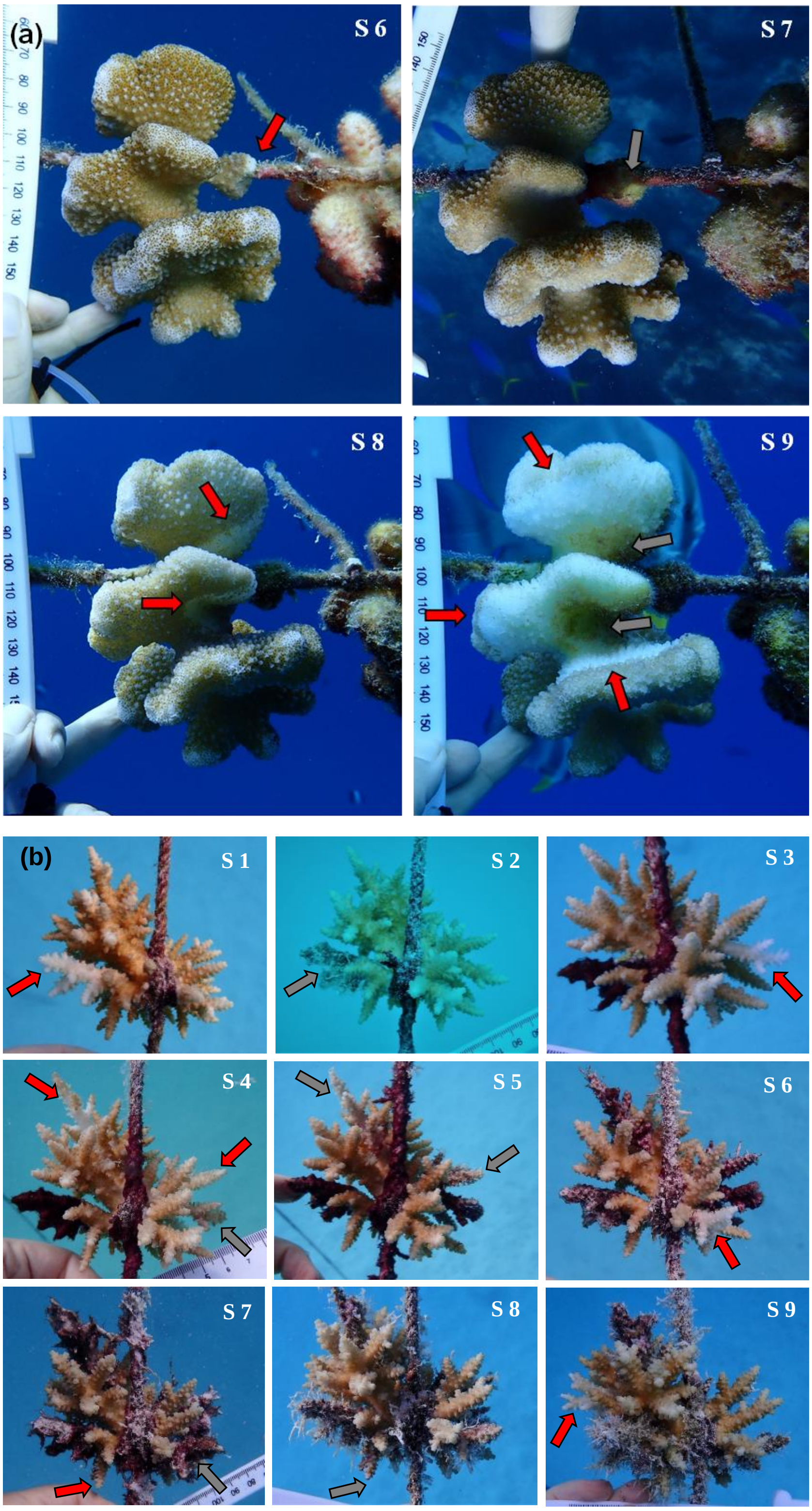

Fig. 1 Disease progression. **a** Progression of *Pocillopora* white syndrome in a fragment in the reef nursery over a period of 56 days. **b** *Acropora* white syndrome lesions occurring on several branches of a fragment in the lagoon nursery over a monitoring period of 112 days. Red arrows indicate fresh lesions while grey arrows indicate dead tissue resulting from diseased tissue identified in the previous survey

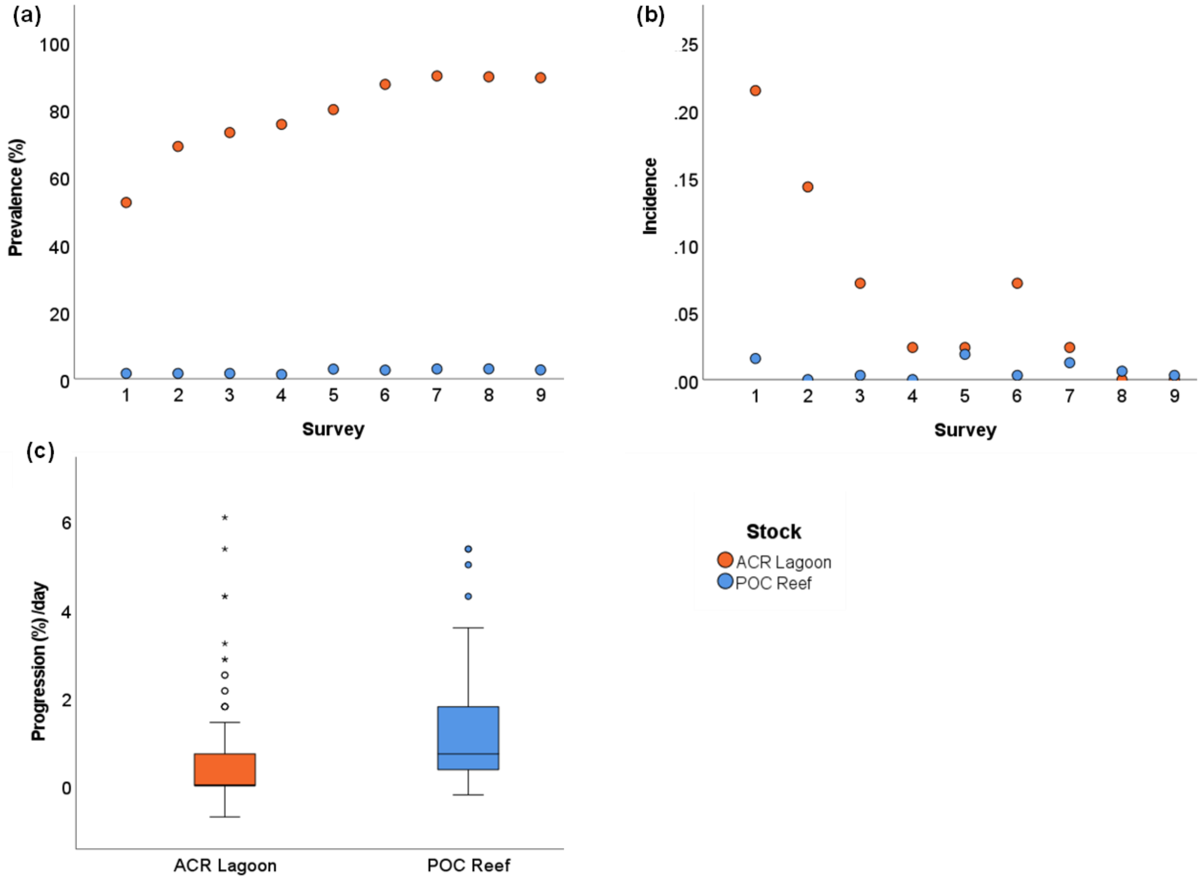

Fig. 2 Disease metrics for infected nursery stocks, *Acropora* in the lagoon nursery (N=47) and *Pocillopora* in the reef nursery (N=320) over 112 days of monitoring: **a** Prevalence, the percentage of infected fragments in relation to available hosts (ACR: M= 78.5 ± 12.6 %; POC: M= 2.2 ± 0.7%); **b** Incidence, the rate of new cases per survey (ACR: M=.064 ± .07; POC: M= .007 ± .01); **c** Mean disease progression in infected fragments as percent of total fragment tissue was significantly higher (Z=-6.507, p<.001) in *Pocillopora* (M=1.28 ± 1.4% per day) than in *Acropora* (0.42 ± 0.8% per day)

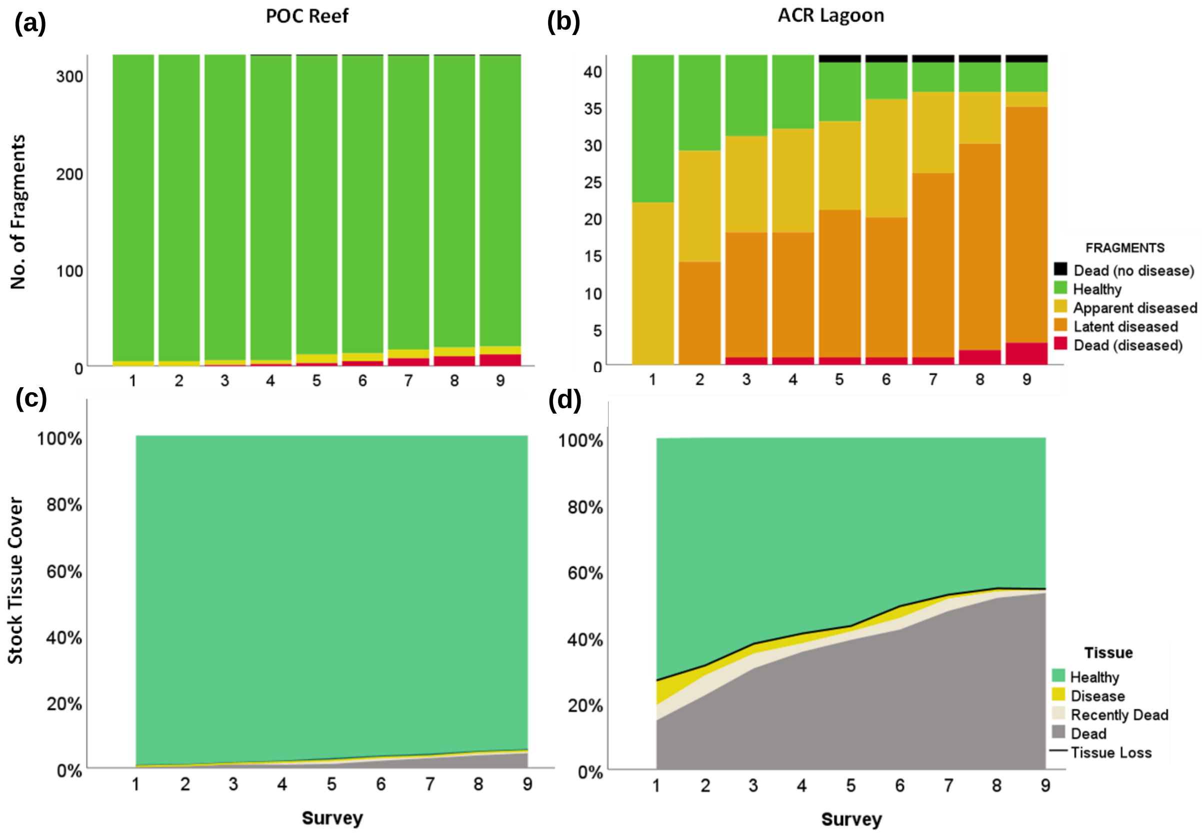

Fig. 3 Graphs showing the different impacts of disease on farming stocks in terms of disease pattern and tissue cover loss during the 112-day long study. **a** Fragment disease pattern of *Pocillopora* stock in the reef nursery with only a few apparent (i.e., acute and visible) disease cases; **b** Fragment disease status of *Acropora* stock in the lagoon nursery with an increase of 'apparent' or 'latent' (i.e., no visible progression) diseased cases over time; **c** Area graph showing the limited (<10%) impact of disease on healthy stock tissue for *Pocillopora* in the reef; **d** Considerable loss of healthy tissue cover (up to 50% - black line) due to the spread of disease in the lagoon *Acropora* stock

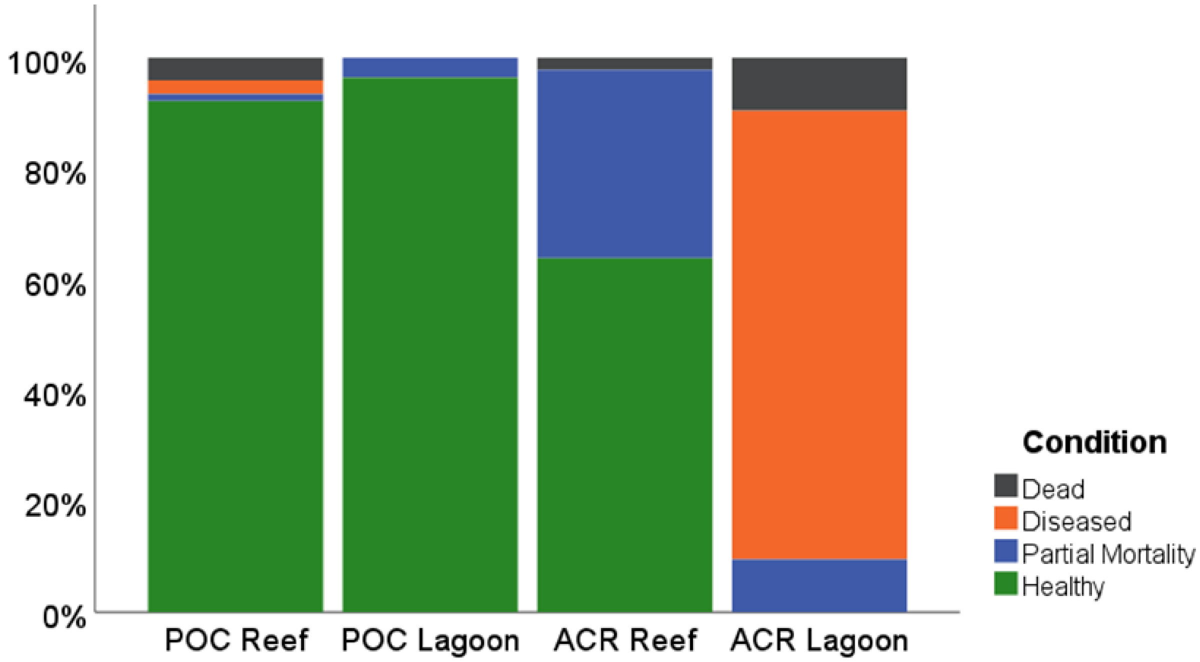

Fig. 4 Bar charts showing fragment condition of the *Pocillopora* and *Acropora* stock in the reef and the lagoon nursery after 112 days of disease monitoring. For *Pocillopora*, the difference in condition between the diseased reef stock (92% fully healthy) and the healthy lagoon stock (96% fully healthy) is relatively small. For *Acropora*, the difference is much more noticeable with 64% of fragments fully healthy in the unaffected reef nursery and no fully healthy fragments and 81% of stock diseased at the end of the survey

CHAPTER 6

6.1 Ecological footprint of coral gardening outplanting in the Maldives

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Keywords: coral restoration, transplantation, ecological restoration, coral nursery, Pocillopora, coral rubble

This section is inserted as submitted to Restoration Ecology

6.2 Abstract

As coral reefs continue to degrade at an alarming rate, coral restoration efforts are increasing worldwide in an attempt to keep up with the global challenge of preserving these iconic ecosystems and the many services they provide. Coral gardening, the farming and outplanting of coral fragments, is a commonly applied practice, however regional validation is required before upscaling can be considered. This study follows up from the successful farming of fragments in mid-water rope nurseries, by reporting on the successive outplanting of these corals. Specifically, 60 *Pocillopora verrucosa* colonies were transplanted to a degraded reef at different depths (1-12 m), applying three transplantation patterns (equal, clustered, random). After one year, 72% were considered successfully transplanted (alive and still attached), with detachment being the main challenge at wave impacted shallow depths, while loose coral rubble caused more partial mortality at depth. Transplantation stress was observed at 1-6 m depth, but had no impact on survival or growth. *Drupella* sp. predation was most common at 3 m and 79% of transplants had mutualistic fauna after one year. Outplanting significantly benefitted the reef environment with a higher fish abundance and diversity along with an increase in natural coral cover (H=2.7; 6.2% increase) in comparison with the control sites. These are promising results, considering that the restoration site has shown little natural recovery in the last few years (coral cover <4%). We hope that our findings provide useful initial insight and help to guide effective restoration practices in the Maldives.

6.3 Implications for practice

- Outplanting large (~15cm), farmed colonies provides prompt detectable benefits for reef communities on degraded reefs.
- Restoration outcomes can be improved by continued monitoring and maintenance following outplanting to reattach colonies, mitigate predation and coral rubble coverage.
- Environmental factors such as seasonal storm exposure in relation to reef orientation and temperature stress during warmer periods should be considered in the restoration site selection, and transplantation depth and technique should be adjusted accordingly. If resources are limited, we suggest to prioritize transplantation to the shallow reef slope over flat and crest.
- Transplantation should focus on locating stable substate and minimal exposure to loose coral rubble instead of specific patterns.

6.4 Introduction

Coral reef ecosystems have experienced accelerated degradation over the last decades (Hughes *et* al. 2017; Souter et al. 2021), resulting in expanding coral restoration efforts and developments around the world (Omori 2019; Boström-Einarsson et al. 2020) in an attempt to safeguard 'high value' reefs and enhance reef resilience in the face of climate change (Rinkevich 2015). 'Coral gardening', which comprises of a nursery phase followed by an outplanting phase, is among the most widely applied techniques (Rinkevich 2014; Boström-Einarsson et al. 2020). Different nursery structures and outplanting techniques have been applied for about 20 years (Rinkevich 2000; Shafir et al. 2006; Bayraktarov et al. 2020), with the principal ecological motivation of assisting natural recovery and re-establish resilient and self-sustaining reefs (Rinkevich 2015; Bayraktarov et al. 2019).

However, restoration success is most commonly evaluated in short-term biological responses (Boström-Einarsson et al. 2020). More than half the transplantation studies have solely used survival and growth as indicators of ecological restoration success, without reporting other ecological or socioeconomic indicators (Hein et al. 2017). Though, a more holistic approach to coral restoration management is required, for example by defining ecological or socio-economic 'SMART' goals and using common parameters for the assessment of goal-based restoration performance (Shaver et al. 2020). For ecological driven restoration targets these include measures of coral population enhancement (e.g., coral cover, health, diversity and reproductive capacity) as well as community and habitat enhancement (e.g., reef fauna, habitat complexity and quality) (Goergen et al. 2020). As coral restoration projects are increasing in scale, complexity and interdisciplinary approaches, it remains clear that there is no 'one solution fits all' strategy to the challenges ahead (Hein et al. 2021). Likewise, prior regional assessment, validation and if necessary, adaptation of restoration practices, and in particular coral outplanting, remains a critical first step to use conservation resources efficiently.

Small island nations like the Maldives have relied throughout their history on healthy coral reefs for food, shore protection and natural resources for building or trade (Jaleel 2013). However, the nation's most valuable asset has lately seen considerable degradation as a result of several coral mass bleaching events (Pisapia et al. 2016; Perry and Morgan 2017) along with the multiple regional pressures (Jaleel 2013; Montano et al. 2015; Saponari et al. 2018). Active interventions, including effective coral restoration to save in particular the 'high value' resort reefs seem urgently required. Especially coral gardening appears a suitable approach here as it is scalable, offers opportunities for local tourism and can intervene prior to disturbances such as constructions and land reclamation (Hein et al. 2021). Nevertheless, validated information on best restoration practices in the Maldives is very limited. While the socio-economic aspects of the few Maldivian coral restoration projects have already been investigated (Hein et al. 2019;

Fiore et al. 2020), the first ecological assessment of mid-water coral nurseries was published only recently (Dehnert et al. 2021).

Our study aims to follow up on this work by providing the first regional insight into the consecutive outplanting of nursery farmed corals to a degraded reef. Therefore, we analysed 1) the effects of transplantation depths and patterns on restoration outcome; 2) interactions of transplanted corals with the reef environment to assess indicators of ecological success; 3) common parameters like coral survival and growth for comparison with other studies. Finally, results are reviewed in the context of the wider reef environment to evaluate the feasibility of upscaling and to guide future restoration practices.

6.5 Methods

6.5.1 Study Design

This study monitored a total of 78 *Pocillopora verrucosa* colonies over a period of one year on Athuruga Resort Island in the Maldives (Fig. 1a). Corals were previously farmed in a nearby lagoon mid-water rope nursery at 5m depth (see Dehnert et al. 2021). In spring 2020, the transplantation of 60 healthy colonies (circa 15 cm) to the degraded housereef was conducted while an additional 18 colonies remained in the lagoon nursery as a control. Colonies were outplanted to three marked reef transplantation plots (TPs) at different depths. Each plot measured 5 x 2-m, with the centre at 3 m on the crest (TP3), 6 m on the shallow reef slope (TP6) and 12 m on the deep reef slope (TP12). All TPs were divided into three subareas for different transplantation patterns using six colonies each: 1) equally spaced, 2) clustered and 3) random (Fig. 1b), totalling in 54 colonies transplanted to the three TPs. Furthermore, three control plots (CP3, CP6, CP12) of the same size and depth, and with similar natural coral cover and reef topography were established about 50m away from the TPs. These control plots did not receive any coral transplants to observe natural recovery.

The remaining six *P. verrucosa* were transplanted randomly on the outer reef flat at 1m depth, to test their survival in presumably harsher conditions. All colonies were cemented using Ordinary Portland Cement with a Sika Fume additive and attachment was controlled after 24 hr and corrected where necessary. No further interventions were made once the monitoring had begun.

6.5.2 Data Collection and Analysis

Data was collected 1-2 weeks after transplantation (T1), after six months (T2) and after one year (T3). Coral 'survival' (binary: alive; dead) and 'condition' (categorical: fully healthy; partial mortality; pale/partially bleached) of each located colony was assessed. Colony 'attachment' was categorised as either 1) attached in original position; 2) loose or detached in position; 3) detached and displaced; 4) attached but displaced with underlaying substate; 5) lost. 'Transplantation success' was considered as colonies that were alive and attached. Coral 'growth' was measured at T1 and T3 using three perpendicular measurements (h, w, l) to calculate 'Ecological Volume' as EV = πr2h, where r = (w+l)/4 (see Shafir et al. 2006; Dehnert et al. 2021).

Colonies' ecological interactions were recorded as closely associated macro-fauna (e.g., mutualistic crustacean, juvenile fish, etc.) as well as observed corallivores and predation scars. Fish counts were conducted for all TPs and CPs (10 min stationary plus 5 min inside each plot and simultaneously for each depth). Fish habitat use of the plot was recorded as 'resident' (i.e., remaining inside), 'in & out' (i.e., movement across the plot with repeated entries/exits) and 'transient' (i.e., crossing only once). Species abundance, richness and the Shannon Diversity

Index *H* were calculated to compare mean values between TPs and CPs (M_{TP} and M_{CP}). 'Coral cover' inside all plots was calculated at T1 and T3 using image analysis Coral Point Count (CPCe) software. Substate cover of the surrounding restoration site, was assessed at T1 and T3, using nine 10-m long Line-Intercept-Transects (LIT) per depth (1m, 3m, 6m and 12m), totalling in 36 LITs per survey.

Statistical analysis was conducted in SPSS version 27 (IBM, New York, NY, U.S.A.), representing all data as arithmetic mean ± standard deviation. Transplantation success was assessed across depths and patterns using a chi-square test. Mean EV at T3 was compared between groups using a one-way ANOVA and Tukey's post hoc test with Levene's test significance set to .001. Change in coral cover was compared between all TPs and CPs combined using an independent t-test.

6.6 Results

6.6.1 Survival and growth

After one year, transplantation success was 72% for all 60 outplanted *P. verrucosa*. While coral survival was even higher (85%), transplantation success was mainly affected by detachment (25%) of which 13% were lost after one year (Table 1). Coral condition varied between TPs (Fig. 2), especially at T1, where transplantation stress was observed at TP3 (72%) and TP6 (34%), however colonies generally recovered. Partial mortality increased in all plot over the year, either due to predation or due to coral rubble coverage. At T3, rubble was a particular problem at TP12, where 47% of colonies had rubble trapped between branches as opposed to the shallower plots TP6 (13%) and TP3 (8%). All control corals in the lagoon survived, with two colonies displaying partial mortality at T3.

Transplantation success noticeably increased with depth. At T3 only 11 out of 18 colonies were still alive and attached at TP3, while for TP6 and TP12 it was 15 and 16 colonies respectively (Table 1), although, given the small sample size, not statistically significant (χ^2(2, N=54)=4500, *p*=0.105). Transplantation of additional colonies to the reef flat was unsuccessful, with a single coral still attached and alive at T3, following severe wave action during the stormy summer monsoon season. TP transplantation density was 1.8 colonies/m² using three different patterns. At T3, 13 colonies with equal or cluster patterns were still 'alive and attached, while for the randomly placed group it was 16, although again not significant (χ^2(2, N=54)=1.929, *p*=0.381).

While mean EV of colonies was similar for all corals at T1 (Fig. 3a), a significant difference in growth was found between the three transplantation plots as well as the control group at T3 (F(3, 67)=8.055, p>0.001). Post hoc testing revealed that colonies from TP3 and the lagoon were significantly bigger than colonies growing in the deeper TP6 and TP12 plots (Fig. 3b).

6.6.2 Associated fauna

Closely associated fauna decrease slightly after transplantation (M_{T1}=33.3%; M_{T2}=28.8%), but steeply increased again after one year (M_{T3}=79.4%). TP6 had the highest percentage associated fauna throughout the study (Table 1). While mutualistic guard crabs *Trapezia* sp. and hermit crabs, were dominant at T3, small, juvenile fish were more common at TP6.

Coral predation was found highest directly after transplantation, with 22% of colonies affected exclusively by parrotfish predation, which caused 5-60% tissue loss in targeted colonies. At T2 and T3, predation decreased and occurred exclusively by *Drupella* sp. snails, which were found on colonies at 3m (N=14) and 6m (N=7) only (Table 1).

Fish counts comprised a total of 1432 individuals from 95 species over three surveys (Table S1). Overall species abundance (M_{Tran}=93 ± 32; M_{Con}=66 ± 15), richness (M_{Tran}=25 ± 7;

M_{Con}=18 ± 5) and diversity (M_{Trans}=2.7 ± 0.4; M_{Con}=2.3 ± 0.4) were higher in the transplantation plots than at the control plots (Table 2). Furthermore, habitat use in the TPs was more often 'resident' (36%) or 'in & out' (46%) than in the CPs while 'transient' behaviour was more frequently observed in the CPs (28%).

6.6.3 Coral cover

Natural coral cover inside the TPs increased from 4.3% at T1 to 10.5% at T3. This was a significantly different to CP coral cover (T(4, 6)=3.592, p=.023), with percentage increases being higher for all transplantation sites (TP3 234% vs. CP3 203%; TP6 253% vs. CP6 152%; TP12 229% vs. CP12 141%; Table 2). Overall, Athuruga reef was dominated by dead coral, coral rubble and sand at all depths in both years (Fig. 4a). Hard coral cover was low at T1 (0.6-1.1%), in particular on the reef flat, where algae cover was most abundant (29%). At T3, hard coral cover had slightly increased at all depths (1.3-5.2%) and *Pocillopora* and *Porites* were the dominating coral genera (Fig. 4b).

6.7 Discussion

Our study describes the generally successful outplanting of nursery farmed corals to a degraded reef in the Maldives. Survival of outplanted colonies was high (85%), considering the average reported survival rate of 65% after one year in coral gardening transplantation studies (Bayraktarov et al. 2019). To increase the number of indicators for successful ecological transplantation beyond survival and growth, which is a common criticism of transplantation studies (Hein et al., 2017), we also monitored coral condition and detachment rates, associations with macrofauna and predation as well as natural coral cover increase and substrate composition across the restoration site.

In general, it is worth considering that our transplanted *P. verrucosa* colonies were substantially larger in diameter than in other outplanting studies that typically use smaller fragments (<10cm) and shorter farming times (≤1 year) (e.g., Shafir et al. 2006; Shaish et al. 2008). Yet, increased nursery time of Pocilloporidae also increases arborescent morphology, which provides clear post-transplantation advantages (Ishida-Castañeda et al. 2020). Transplanting large colonies may have also amplified the observed ecological interactions which, given the limitations of a small single species sample and a one year monitoring duration, may have been less clear otherwise.

Overall, restoration challenges and outcomes varied notably between different transplantation depths while transplantation patterns had little effect. Transplantation success was mainly impacted by detachment of colonies as a result of increased wave actions and storm damage during the southwest monsoon season. Hence, detachment was more frequently observed at shallow, more exposed depths. As the study design mandated no interventions post outplanting, detached but relocated colonies were not reattached and often lost over time. This highlights the importance for coral gardening projects to include a post-outplanting monitoring and maintenance phase for the restoration site in their project planning as prompt reattachment could have enhanced restoration outcome.

Apart from detachment, instable substrate and coral rubble was a major challenge, especially at 12 m depth. Here, loose rubble released from the shallower reef areas during adverse weather, was caught in the branches, covering life coral tissue and increasing partial mortality. Unconsolidated substrate, which limits coral recruitment, is a major barrier to natural recovery

(Ceccarelli et al. 2020; Hein et al. 2021). Our observations indicate, that loose rubble is also a potential risk for outplanting efforts on a reef slope. Again, active site management, including removing rubble from outplanted colonies, would have likely reduced observed tissue loss, although this would constitute a constant effort. It therefore highlights the importance of ongoing research on substrate stabilization as part of the restoration toolkit (Ceccarelli et al. 2020). Considering that coral rubble will persist and increase on degraded reefs long after acute bleaching events or other temporary threats, this may also drive a community shift away from common coral reef species towards reef organisms benefiting from rubble microhabitats (Wolfe et al. 2021).

Transplantation stress in the form of pale or partially bleached tissue was observed in colonies transplanted to the same or shallower outplanting depth than their original farming depth, but colonies generally recovered. Since transplantation had to be conducted during the hottest time of the year for logistical reasons, it may indicate the robustness of *P. verrucosa.* ‘Transplant shock’ has been shown to negatively affect transplantation success in other species (e.g., Forrester et al. 2012), especially under changing environmental conditions. In this context, the importance of alterations in the coral microbiome during coral gardening steps has recently been investigated, indicating that, *P. verrucosa* bacterial community structure remained stable while *A. millepora* displayed a greater variations in response to environmental changes (Strudwick et al. 2022). Since our transplantation study was limited to a single species, this remains to be investigated further.

Fish predation was highest directly after colonies were introduced to the reef, which required ‘rescue-cementing’ the following day. However once firmly attached, fish predation was no longer impacting these relatively large colonies. In contrast, fish predation can threaten outplanting success if fragments are smaller (e.g., microfragmentation, Koval et al. 2020). At

TP3, one third of the colonies suffered from partial mortality, which was largely inflicted by *Drupella* sp.. This is a common predator on Athuruga and in the Maldives, with a preference for branching coral and the potential to delay reef recovery (Saponari et al. 2021).

Overall, our results suggest a positive interaction of the outplanted colonies with the environment as shown by the higher fish abundance, richness and diversity as well as the more intense habitat use in comparison with the control plots. Natural coral cover increase was also found to be significantly higher in the transplantation plots. This is in line with studies arguing for more attention towards ecological processes and interactions in coral restoration (e.g. Shaver and Silliman 2017) and the application of additional ecological metrics to assess restoration success. For example, a large scale coral restoration project in the Seychelles demonstrated a positive correlation between the presence of coral recruits and juveniles and areas with transplanted corals (Montoya-Maya et al. 2016).

Athuruga reef has been severely impacted by an outbreak of *Acanthaster planci* in 2015 and the subsequent mass bleaching, reducing coral cover to approximately 2% (Saponari et al. 2018; 2021). Our substrate cover analysis confirms this and restoration is required for this reef area of high touristic value. Moreover, natural coral cover, on average still below 4% in 2021 and with slow recovery, followed the same patterns as observed in our transplantation plots with harsh conditions and low coral cover on the flat and crest, while steadily improving at 6 and 12m depth. From these observations and our transplantation results it could be argued that, when resources are limited, restoration efforts should be focused on the shallow slope in this case, in order to achieve the greatest output. At TP6, conditions were found most balanced and favourable. Here, the high transplantation success resulted from a combination of moderate exposure to wave action, coral rubble and predation while associated fauna and light availability for coral growth was high. On the contrary, the reef flat provided the most challenging environment due to high exposure to tidal and wave action, sunlight and elevated water temperatures. These made the transplantation procedure already challenging, hence only 6 colonies were outplanted, of which only one survived as it was firmly wedged into a dead coral block. Considering the rich coral cover of the reef flat less than 10 years ago, this clearly highlights the limitations of current outplanting practices under future climate scenarios (van Hooidonk et al. 2020), where frequent heat stress events and more severe meteorological events exacerbate reef structure erosion. Such constrains on recovery are also indicated by the substate assessment across the restoration site, which shows that coral cover was particularly low on the reef flat and dominated by dead coral and algae cover. Therefore, in this case further restoration efforts in this reef zone would probably require additional structural support (e.g., artificial reef structures or substrate stabilization) and selection of the most heat-stress resistant corals in a long-term restoration project.

Nevertheless, our study indicates that the outplanting of nursery farmed corals to degraded reefs can have rapid ecological benefits for reef communities and habitat quality. Since no comparable research is available for the Maldives, we hope to provide some useful new insights for large-scale applications of the coral gardening approach.

6.8 Acknowledgements

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6.10 Illustrations

Table 1: Transplantation success and interactions with reef fauna of outplanted *Pocillopora verrucosa* colonies. The table shows the number of healthy and attached/surviving/detached/lost colonies over a period of one year (T1: after transplantation; T2: after 6 months; T3: after 12 months). Further, the percentage of colonies which hosted macro-fauna in the form of small fish or crustaceans and the percentage of corals affected by predation are shown.

Location	Depth	Colonies	Alive & Attached			Survival			Detached			Lost			Coral Associated Fauna			Coral Predation		
			T1	*T2*	*T3*	*T1*	*T2*	*T3*	*T1*	*T2*	*T3*	*T1*	*T2*	*T3*	*T1*	*T2*	*T3*	*T1*	*T2*	*T3*
	(m)	(N)													%	%	%	%	%	%
Flat	1	6	5	2	1	6	2	1	1	0	0	0	4	4						
Crest (TP3)	3	18	17	16	11	18	18	16	1	2	5	0	0	2	38.9	33.3	56.3	16.7	27.8	6.3
Slope (TP6)	6	18	18	15	15	18	17	17	0	2	2	0	1	1	44.4	35.3	93.8	0.0	0.1	5.9
Slope (TP12)	12	18	18	16	16	18	17	17	0	1	0	0	0	1	16.7	17.6	88.2	50.0	0.0	0.0
	Total %	**100**	**96.7**	**81.7**	**71.7**	**100**	**90**	**85**	**3.3**	**8.3**	**11.7**	**0**	**8.3**	**13.3**						
	Mean %														**33.3**	**28.8**	**79.4**	**22.2**	**9.3**	**4.0**
	SD														14.7	9.7	20.2	25.5	16.0	3.5

Table 2: Results from fish and coral counts for each transplantation plot (TP) and Control plot (CP) over one year (T1: after transplantation; T2: after 6 months; T3: after 12 months). The table shows species abundance and richness as well as the Shannon Diversity Index *H* for each plot as well as the average for all transplantation or control sites. How fish used the reef plots is indicated as percentages. Further, the percentage of live hard coral cover for each plot is shown.

	3m						**6m**						**12m**							**All Transplants**		**All Controls**	
	T1		*T2*		*T3*		*T1*		*T2*		*T3*		*T1*		*T2*		*T3*						
	TP	CP	TP	CP	TP	CP	TP	CP	TP	CP	TP	CP	TP	CP	TP	CP	TP	CP		Mean	SD	Mean	SD
<u>*Fish Species:*</u>																							
Abundance	79	43	102	61	91	53	95	86	119	91	159	74	61	59	54	67	77	61		**93**	32	**66**	15
Richness	25	19	28	28	29	18	29	24	35	18	32	16	20	12	16	13	15	15		**25**	7	**18**	5
Diversity (*H*)	2.8	2.6	2.8	2.6	3.0	3.0	3.0	2.6	2.9	1.9	2.8	2.1	2.7	2.1	1.9	1.7	2.2	2.1		**2.7**	0.4	**2.3**	0.4
<u>*Habitat use:*</u>																							
In & out %	43	51	41	33	46	53	55	49	45	30	26	14	46	36	65	58	44	46		**46**	10	**41**	14
Resident %	24	33	16	23	35	32	36	31	36	8	68	43	34	49	22	12	48	48		**35**	15	**31**	15
Transient %	33	16	20	44	19	15	9	20	19	63	6	43	20	15	13	30	8	7		**16**	8	**28**	18
<u>*Coral Cover:*</u>																							
Plot Cover %	4.9	7.2			11.5	14.6	7.0	6.5			17.8	9.8	1.0	3.7			2.3	5.2	***T1***	**4.3**	3	**5.8**	1.8
																			T3	**10.5**	7.8	**9.9**	4.7

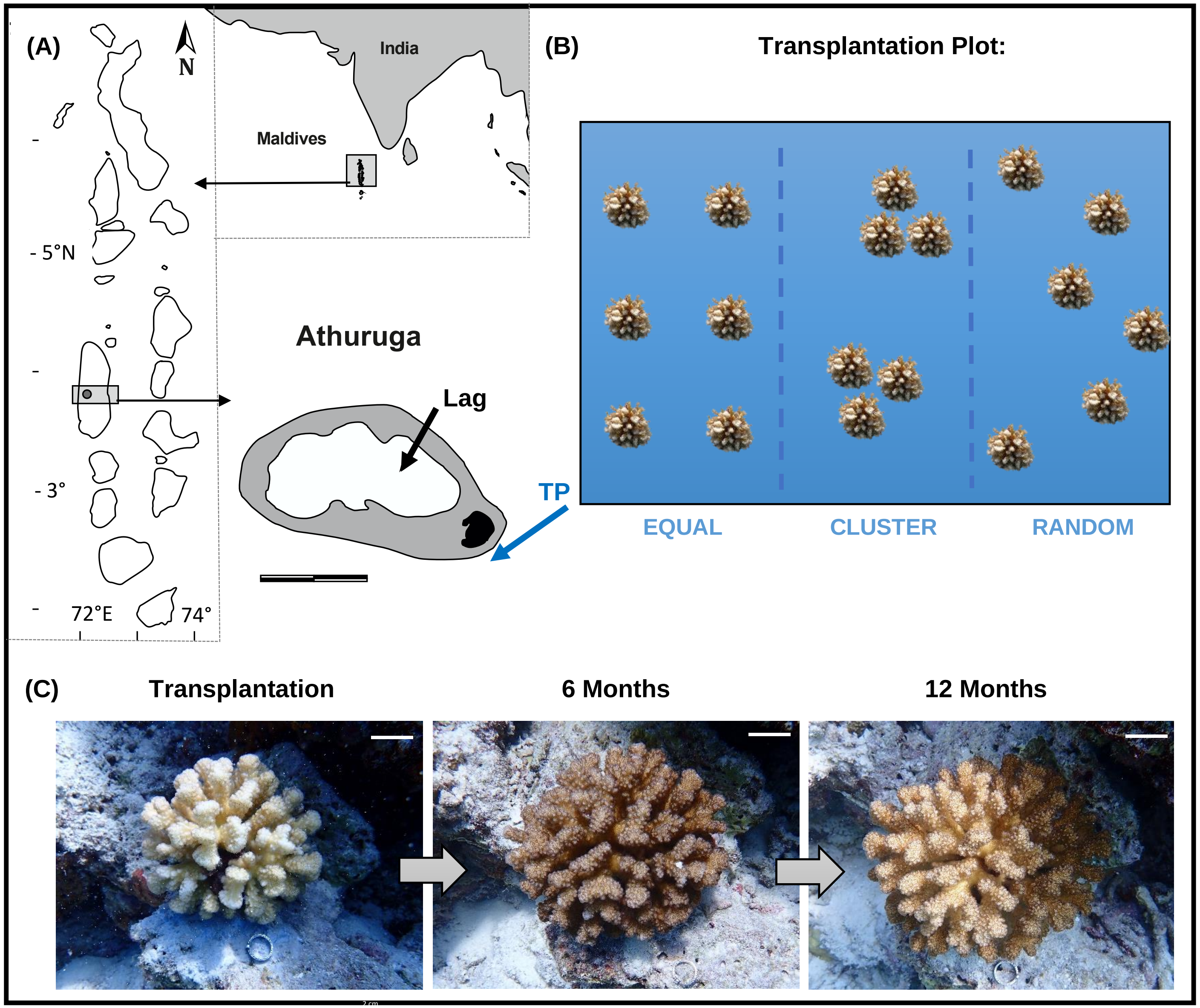
(A)
N
India
Maldives
5°N
3°
72°E
74°
Athuruga
Lag
TP
(B)
Transplantation Plot:
EQUAL
CLUSTER
RANDOM
(C)
Transplantation
6 Months
12 Months

Figure 1: Study location and design. (A) The Rebublic of Maldives in the Indian Ocean and Athuruga Resort Island (3°53'14"N 72°48'59"E) in Alif Dhaal atoll (black: island, grey: reef, scale bar 1km). The restoration site is located in the southern house reef with arrows indicating the three transplantation plots at 3, 6 and 12m (TP) and the lagoon nursery location. (B) Example transplantation plot measuring 5m horizontally by 2m vertically with three different outplanting patterns; (C) Colony after transplantation (T1), after 6 months (T2) and after one year (T3), scale bar 4cm.

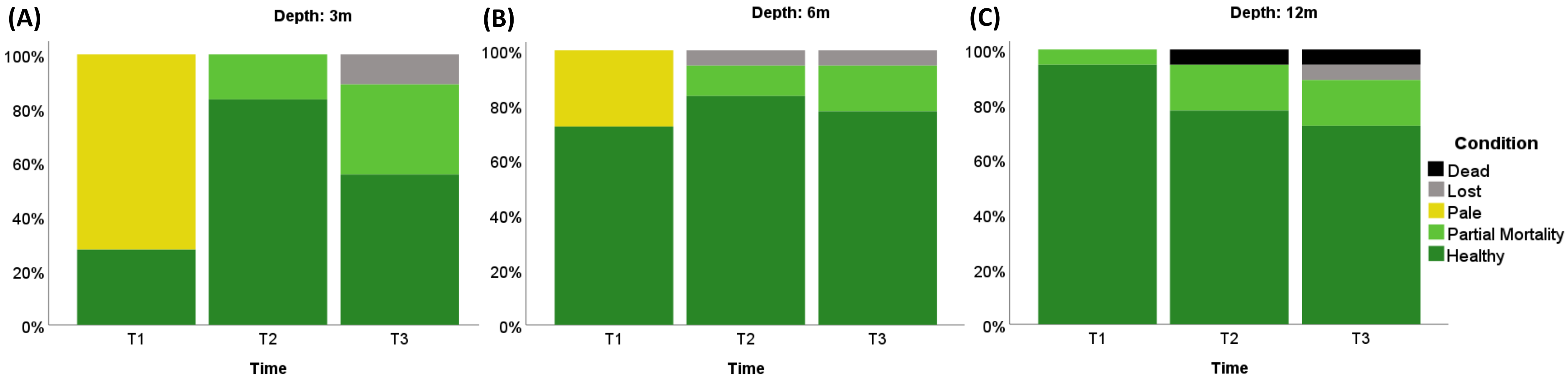

Figure 2: Condition of *Pocillopora verrucosa* colonies (N=18 per depth) at different transplantation plots after transplantation (T1), after 6 months (T2) and after 12 months (T3). (A) At TP3 on the reef crest most colonies were found pale or partially bleached (73%) after transplantation but 83% had fully recovered at T2. At T3 56% remained fully healthy while partial colony mortality was found in 34% of colonies. (B) At TP6 on the shallow reef slope 28% of transplanted corals experienced slight bleaching at T1 with 83% of all colonies being fully healthy at T2 and 6% lost. At T3 partial mortality increased (17%). At TP12 on the deeper reef slope 94% of colonies were fully healthy at T1, which decreased over time (78% at T2 and 72% at T3). Partial mortality increased to 17% at T2 and T3) and remaining colonies were either lost (6%) or dead (6%).

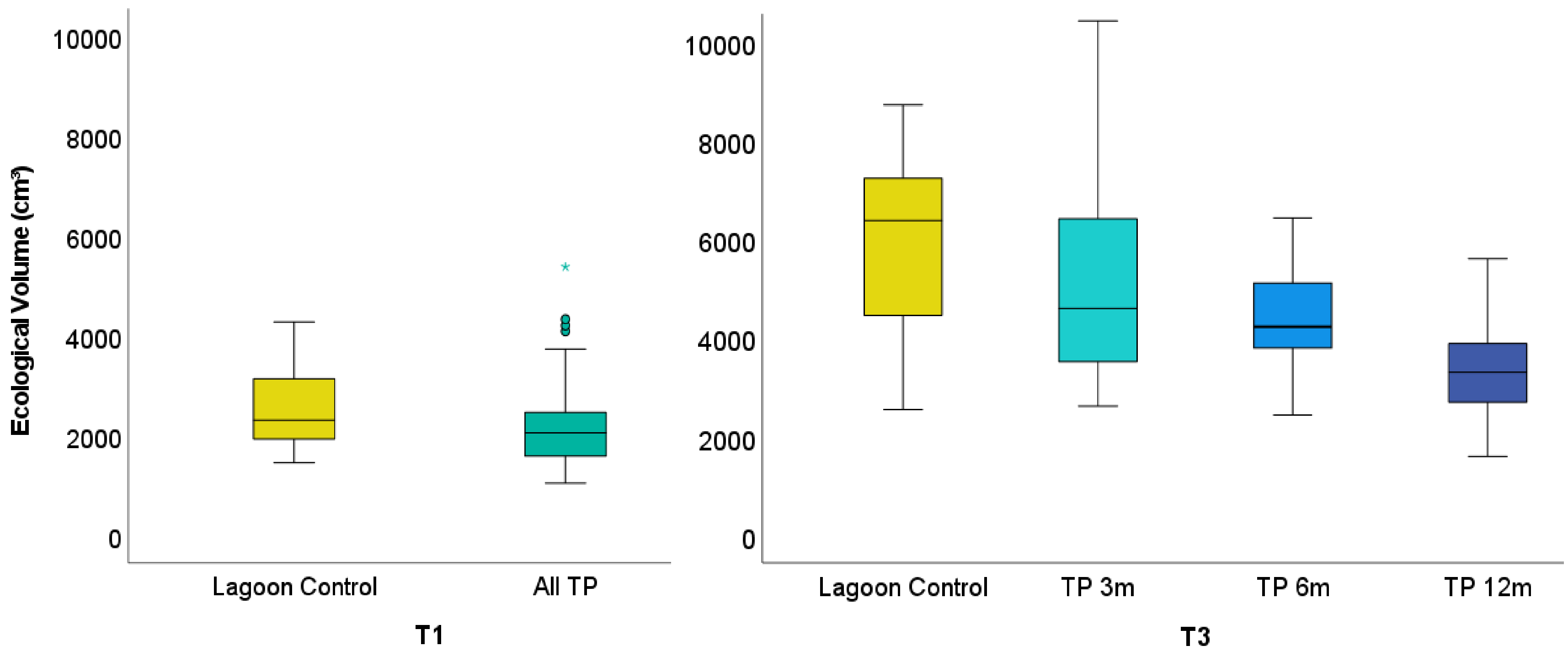

Figure 3: Comparison of mean colony size measures (EV) for *Pocillopora verrucosa* at the begin of the study (T1) and after one year (T3). (A) Lagoon control group that remained in the lagoon nursery at 5m (T1: M_{Lag}=2497 ± 818 cm^3; N=18) was not significantly different from all colonies transplanted to the reef (TP at T1: M_{Reef}=2180 ± 887 cm^3; N=54); (B) Lagoon control after 1 year (T3:M_{LAG}=5852 ± 1870 cm^3), TP 3m: colonies at the 3m transplantation plot on the crest (M_{TP3}=5187 ± 2078 cm^3); TP 6m: colonies at the 6m transplantation plot on the reef (M_{TP6}= 4395 ± 1067 cm^3) and TP12m with colonies growing at the deeper reef slope at12m (M_{TP12}= 3299 ± 1021 cm^3). A significant difference between corals growing at TP 3m and Lag 5m and the corals growing at 6m and 12m on the reef was found (F(3, 67)=8.055, p>0.001).

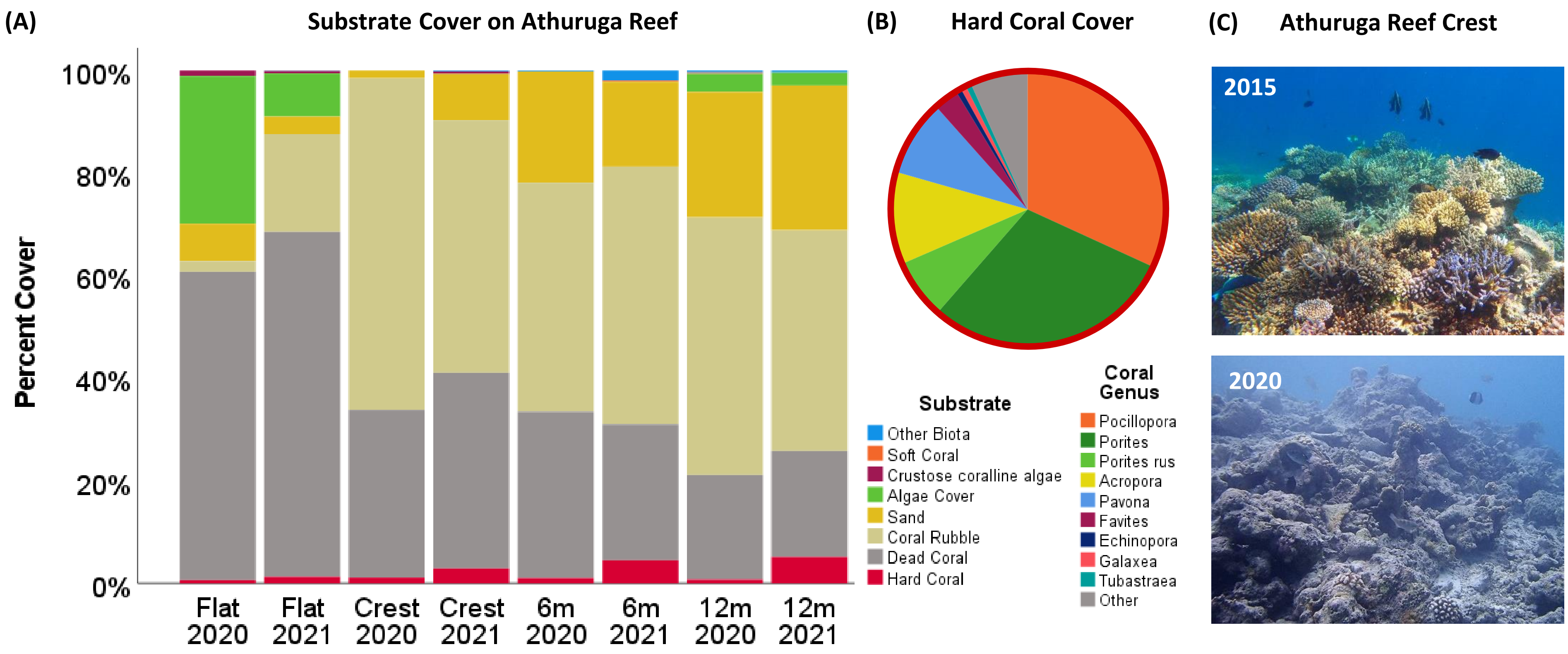

Figure 4: Substate cover from the restoration site, Athuruga reef, calculated from a total of 72 10m LITs. (A) The percentage cover at different depths (flat at ~1m; crest at 2-3m and reef slope at 6m and 12m) is shown for surveys conducted in April 2020 and April 2021. Coral cover increased slightly (flat: 0.6 to 1.3%; crest: 1.1 to 2.9%; 6m slope: 1.0 to 4.5% and 12m slope 0.7 to 5.2%). (B) Distribution of recorded coral genera during all surveys. (C) Crest of Athuruga house reef in March 2015 and April 2020 (photo credit: I. Dehnert).

Table S1: Species list from fish counts.

Family	Species	Individuals Observed
Acanthuride	*Acanthurus tennentii*	1
Acanthuride	*Naso brevirostris*	1
Acanthuride	*Naso unicornis*	1
Acanthuride	*Naso fageni*	2
Acanthuride	*Naso hexacanthus*	2
Acanthuride	*Naso sp.*	2
Acanthuride	*Acanthurus lineatus*	3
Acanthuride	*Zebrasoma sp*	3
Acanthuride	*Acanthurus nigricauda*	4
Acanthuride	*Naso elegans*	5
Acanthuride	*Zebrasoma scopas*	7
Acanthuride	*Acanthurus thompsoni*	12
Acanthuride	*Acanthurus leucosternon*	22
Acanthuride	*Ctenochaetus striatus*	120
Balistidae	*Balistuides viridescens*	1
Balistidae	*Balistapus undulatus*	29
Balistidae	*Odonus niger*	96
Belonidae	*Platybelone argalus*	21
Blenniidae	*Ecsenius minutus*	4
Caesionidae	*Caesio teres*	17
Caesionidae	*Caesio varilineata*	49
Carangidae	*Caranx melampygus*	2
Chaetodontidae	*Chaetodon meyeri*	1
Chaetodontidae	*Chaetodon xanthochepalus*	1
Chaetodontidae	*Chaetodon kleinii*	2
Chaetodontidae	*Chaetodon trifasciatus*	2
Chaetodontidae	*Forcipiger flavissimus*	2
Chaetodontidae	*Heniochus pleurotaenia*	3
Chaetodontidae	*Chaetodon guttatissimus*	4
Chaetodontidae	*Forcipiger longirostris*	5
Chaetodontidae	*Heniochus diphreutes*	12
Chaetodontidae	*Hemitaurichthys zoster*	64
Fistulariidae	*Fistularia commersonii*	10
Holocentridae	*Sargocentron caudimaculatum*	4
Kyphosidae	*Kyphosus cinerascens*	4
Labridae	*Cheilinus trilobatus*	1
Labridae	*Hemicoris batuensis*	1
Labridae	*Bodianus axillaris*	2
Labridae	*Hemicoris batuensis*	2
Labridae	*Hemigymnus fasciatus*	3
Labridae	*Hemigymnus melapterus*	6
Labridae	*Cheilinus fasciatus*	7
Labridae	*Hemitautoga hortulanus*	8
Labridae	*Gomphosus caeruleus*	10
Labridae	*Epibulus insidiator*	11
Labridae	*Stethojulis albovittata*	20

Labridae	*Labroides dimidiatus*	21
Labridae	*Pseudocheilinus hexataenia*	31
Labridae	*Thasassoma amblycehalum*	39
Labridae	*Thasassoma hardwicke*	81
Labridae	*Thalassoma lunare*	124
Lethrinidae	*Lethirinus sp.*	6
Lutjanidae	*Macolor niger*	1
Monacanthidae	*Paraluteres prionurus*	3
Mullidae	*Parupeneus macronema*	6
Nemipteridae	*Scolopsis bilineata*	1
Ortaciidae	*Ostracion cubicus*	1
Pomacanthidae	*Pomacanthus imperator*	1
Pomacentridae	*Pomacentrus pavo*	1
Pomacentridae	*Chromis lepidolepis*	2
Pomacentridae	*Dascyllus carneus*	2
Pomacentridae	*Dascyllus trimaculatus*	2
Pomacentridae	*Pomacentrus caeruleus*	3
Pomacentridae	*Dascyllus aruanus*	8
Pomacentridae	*Pomacentrus nagasakiensis*	14
Pomacentridae	*Chromis dimidiata*	17
Pomacentridae	*Abudefduf vaigiensis*	18
Pomacentridae	*Pomacentrus chrysurus*	25
Pomacentridae	*Pomacentrus indicus*	30
Pomacentridae	*Chromis atripectoralis*	35
Pomacentridae	*Centropyge multispinis*	44
Pomacentridae	*Pomacentrus philippinus*	121
Scaridae	*Hipposcarus harid*	2
Scaridae	*Scarus quoyi*	2
Scaridae	*Chlorurus strongylocephalus*	6
Scaridae	*Scarus frenatus*	16
Scaridae	*Scarus scaber*	23
Scaridae	*Scarus niger*	24
Scaridae	*Chlorurus sordidus*	57
Serranidae	*Epinephelus spolotoceps*	1
Serranidae	*Variola louti*	1
Serranidae	*Cephalopholis miniata*	2
Serranidae	*Cephalopholis sp.*	2
Serranidae	*Aethaloperca rogaa*	3
Serranidae	*Cephalopholis sexmaculata*	6
Serranidae	*Cephalopholis lepardus*	7
Serranidae	*Cephalopholis argus*	12
Serranidae	*Pseudanthias squamipinnis*	20
Siganidae	*Siganus corallinus*	6
Synodontidae	*Synodus sp.*	2
Tetraodontidae	*Arothon mappa*	1
Tetraodontidae	*Canthigaster valentini*	5
Zanclidae	*Zanclus cornutus*	8
Total	**95**	**1432**

CHAPTER 7

7.1 Conclusions

Coral reefs worldwide have recently seen unprecedented decline in what is now referred to as the Anthropocene (Hughes *et al.*, 2018). Since the first severe mass bleaching event in 1998, coral ecosystems have experienced an increasing frequency and severity of heatwaves, leaving little time for natural recovery. The latest global bleaching event (2014-2017) was the longest ever recorded (Eakin *et al.*, 2019), in which the Great Barrier Reef alone has lost half its corals (Hughes *et al.*, 2019). Thermal stress coupled with an array of other anthropogenic stressors has killed approximately 14% of the world's corals in less than a decade (Souter *et al.*, 2021). This poses an imminent threat, not only to the rich biodiversity that is supported by coral reefs, but also to the approximately 400 million people that depend on coral reefs for food, protection, income and other services (Costanza *et al.*, 2014; Spalding *et al.*, 2017).

In an effort to maintain critical reef ecosystem services and to 'buy time' for reefs to recover and increase in resilience, coral reef restoration efforts have intensified, applying time-tested as well as novel techniques at various scales. Considering the enormous conservation task ahead, restoration projects will increasingly require the engagement of local communities and other stakeholders, that depend on scientifically validated and regionally tested 'best practices' to conduct active restoration efforts safely and efficiently.

The Republic of Maldives is an excellent example in this regard. Coral reefs are the primary asset of this Small Island Developing State, which is therefore extremely vulnerable to climate change and other anthropogenic driven threats (Becken *et al.*, 2011; Van Hooidonk *et al.*, 2016). Coral restoration, as part of a wider conservation and adaptation strategy, may offer a chance to save in particular some of the 'high value' reefs on which the tourism industry relies on. Coral gardening could be a particular suitable approach here as this technique provides realisable, scalable and proactive opportunities for projects on a touristic resort or local island level (Hein *et al.*, 2021). Such community driven projects can also facilitate the reduction local stressors while enhancing education and stewardship for the reef, or even providing new income opportunities if well managed (Hein *et al.*, 2017). However, there is also a real risk of failure if restoration aims are unrealistic or not accomplished due to poor planning and management (Shaver *et al.*, 2020). In order to prevent the waste of precious conservation initiative and resources, such approaches require rigorous scientific assessment and regional validation before upscaling can be considered. For the Maldives, research on coral restoration is very limited and the coral gardening approach had not been applied at scale until now.

This research set out to address these knowledge gaps by examining various aspects of the coral gardening technique. Previous research indicated that for rearing large number of coral fragments under favourable conditions, mid-water coral nurseries can be a suitable choice (Shafir *et al.*, 2006; Levy *et al.*, 2010). In chapter one the first assessment of this technique in the Maldives is provided, describing the performance of five lagoon mid-water coral rope nurseries of identical design, located on a local island in Faafu Atoll as well as on a resort island in Alif Dhaal Atoll. A common monitoring protocol was applied to evaluate performance criteria such as survival and growth among others for three different coral genera farmed in the nurseries. This work provided the first regional restoration benchmarks for coral gardening in the Maldives. Given the high survival and fast growth rates of the branching genera, it was concluded, that this farming technique is suitable for upscaling regional restoration efforts to an ecological meaningful level. In particular, it provides a useful and immediately applicable alternative or addition to the currently used ‘coral frame’ method, which is still the most commonly applied technique, especially on a small-scale on resort islands (Reefscapers, 2022). The study also identified the need for further investigation of the specific environmental conditions of a coral farming habitat, as significant differences in nursery performances between sites were observed.

Chapter two describes the systematic comparison of different farming habitats for mid-water nursery to provide specific recommendations for optimising coral farming output. Nurseries are typically placed inside protective lagoons at shallow depth, yet such nursery habitats may not always be locally available. To assess the suitability of inner atoll reefs as an alternative farming habitat to lagoons, the simultaneous rearing performance of two coral farming stocks, identical in species composition, fragment size and genotype distribution, were compared over one year. The study was able to demonstrate that mid-water nurseries with adjusted design to the more current exposed reef environment can achieve equally successful farming outputs to lagoon habitats, while providing additional rearing capacities at depth. This comprehensive experiment further revealed significant, species-specific rearing advantages of different farming habitats, while also assessing the relative implications of fragment predation and mutualistic fauna associations in each habitat. The study also resulted in a number of practical suggestions for restoration practices, for example the farming of mixed age groups to facilitate the exchange of mutualistic organisms.

With the onset of the global Covid-19 pandemic, it soon became clear that such unanticipated events not only disrupt almost every aspect of human life, but can also pose a considerable risk to coral restoration efforts worldwide. Such implications and suggested future mitigation strategies are described in chapter three. Here, the specific impacts of an abrupt suspensions in coral gardening monitoring and maintenance procedures and the abandonment of mid-water coral nurseries are reported from different projects located in Colombia, Seychelles and Maldives. The study showed that, while floating nurseries can sustain several months without maintenance (i.e. cleaning and structure repairs) when sufficiently prepared in advance, structure collapse due to insufficient buoyancy and prolonged absence of maintenance for more than one year is to be expected. The consequences of such structural failures can reach beyond apparent stock mortality as it may also imply significant backs in research aims and critical project goals, jeopardizing future project support. Therefore, the need to increase the resilience and self-sufficiency of coral restoration projects, by preparing emergency plans and securing local resources and workforce, are highlighted.

Coral disease, another major risk to coral gardening success was assessed in chapter four. The occurrence of coral disease was already noticed in one of the nurseries during the first nursery assessment, demanding further research into the potential impacts and available mitigation measures. The dedicated study in this chapter documents the unmitigated disease progression in coral nurseries for the first time, providing several comparable disease assessment metrics. Furthermore, the specific disease inflicted impacts on coral farming stock survival and direct implications for project success are described. Coral diseases are expected to increase in occurrence and virulence in the future (Harvell *et al.*, 2007), posing a potential threat to restoration efforts, and in particular to coral gardening projects that commonly use disease facilitating practices. The findings in this chapter provide important new insight into the disease associated risks to coral restoration, which have received little attention until now. It further highlights the need for advanced disease diagnostics and mitigation tools, accessible to restoration practitioners.

The last chapter completes the assessment of the coral gardening technique, by evaluating the transplantation success of nursery farmed corals to a degraded Maldivian reef from the ecological perspective. Survival and growth of outplanted colonies in relation to transplantation depth and pattern were monitored over a one-year period, while other ecological indicators such as associated macro-fauna, predation and other mortality risks were also assessed. It is worth noting that corallivorous species including *Acanthaster planci*, *Culcita* sp. and *Drupella* sp. can play a critical part in prolonging reef recovery and their role on Maldivian reefs was assessed alongside this research (Saponari *et al.*, 2018, 2021; Montalbetti *et al.*, 2019; see Appendix).

Finally, transplantation success was reviewed in perspective to the wider restoration reef environment by assessing natural recovery of coral cover and fish community structure and habitat use. The observed ecological benefits for the degraded and only slowly recovering restoration site are promising first outcomes for future restoration efforts. This study constitutes the first report of coral gardening outplanting in the Maldives and the only scientific record of coral transplantation in the archipelago since the 1990s (Clark and Edwards, 1995), hoping to provide contemporary guidance for regional restoration projects.

In summary, this research was able to explore and validate both phases of the coral gardening technique, which is considered a suitable approach for restoration in the Maldives. Benchmark results for coral genera commonly used in restoration are provided and the environmental interactions affecting coral gardening success are investigated. Furthermore, factors that could cause a significant risk to coral restoration projects worldwide are addressed. The discipline of coral restoration is constantly evolving, and other techniques for restoring a wide range of diverse and resilient coral species will require testing in the future to enhance restoration efforts. However, as little research has been conducted on coral restoration practices in the Maldives, these new insights hopefully provide useful guidance and encouragement for restoration practitioners across the archipelago to upscale coral restoration in this still beautiful but fragile coral reef ecosystem.

Looking forward it is clear that, despite the many recent advances made in the discipline of coral restoration, they are still exceeded by the current and projected rates of coral ecosystem degradation. Therefore, it is important to acknowledge the benefits but also the limitations of coral reef restoration, which should be seen as one of many approaches needed in a wider coral conservation management strategy. Given the latest Intergovernmental Panel on Climate Change projections (IPCC, 2021) and the slow progress made during the latest COP26 climate conference in 2021, the window for ‘averting the climate catastrophe’ as UN Secretary-General António Guterres has described it, is closing (UN, 2021). Coral reefs will be largely lost, if carbon emissions are not drastically reduced in the next ten years and the target of limiting global warming to 1.5°C is exceeded (IPCC, 2018). However, recovery of marine life is possible if challenges are met with dedicated actions (Duarte *et al.*, 2020). As coral restoration initiatives, networks and collaborations are growing worldwide, it may give coral reefs a ‘fighting chance’. Human dependence on a healthy coral reef ecosystem is evident, not only for small island nations like the Maldives. Therefore, inaction would be wantonly negligent.

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APPENDIX

Abstracts of articles produced during the PhD programme, which are not related to the topic of coral reef restoration are listed below.

I. New insights into the ecology and corallivory of *Culcita* sp. (Echinodermata: Asteroidea) in the Republic of Maldives

Montalbetti E, Saponari L, Montano S, Maggioni D, Dehnert I, Galli P, Seveso D

Hydrobiologia (2019), DOI 10.1007/s10750-018-3786-6

Although corallivory is recognized as a threat affecting the structure and integrity of coral reef habitats, ecological data on most species of coral consumers remain limited, slowing down the development of conservation and restoration strategies of the reef ecosystems. In this study, the population distribution and corallivorous behaviour of the cushion sea star *Culcita* sp. were investigated in the south region of Faafu Atoll, Maldives. Most sea stars were found on reef slopes within 0–10 m depth and in areas characterized by low live coral cover. Several coral genera were preyed on by the sea star. Although most of the consumed corals belong to the genus *Acropora*, a feeding preference for the genera *Pocillopora* and *Pavona* and a consistent avoidance of the genus *Porites* were observed. Furthermore, the majority of the prey corals were small colonies (\10 cm diameter), even though *Culcita* sp. appeared to be capable of partially consuming larger colonies. Dietary preferences for specific coral colonies or genera have the potential to generate local shifts in coral community composition and structure and may affect reef recovery following natural and anthropogenic disturbance in an already impacted environment such as the Maldivian reefs.

II. Assessing population collapse of *Drupella* spp. (Mollusca: Gastropoda) 2 years after a coral bleaching event in the Republic of Maldives

Saponari L, Dehnert I, Galli, P, Montano S.

Hydrobiologia (2021), DOI: 10.1007/s10750-021-04546-5

Corallivory causes considerable damage to coral reefs and can exacerbate other disturbances. Among coral predators, *Drupella* spp. are considered as delayer of coral recovery in the Republic of Maldives, although little information is available on their ecology. Thus, we aimed to assess their population structure, feeding behaviour and spatial distribution around 2 years after a coral bleaching event in 2016. Biological and environmental data were collected using belt and line intercept transects in six shallow reefs in Maldives. The snails occurred in aggregations with a maximum of 62 individuals and exhibited a preference for branching corals. Yet, the gastropods showed a high plasticity in adapting feeding preferences to prey availability. *Drupella* spp. were homogenously distributed in the study area with an average of 9.04 ± 19.72 ind/200 m². However, their occurrence was significantly different at the reef scale with the highest densities found in locations with higher coral cover. The impact of *Drupella* spp. appeared to be minimal with the population suffering from the loss of coral cover. We suggest that monitoring programs collect temporal- and spatial- scale data on non-outbreaking populations or non- aggregating populations to understand the dynamics of predation related to the co-occurrence of anthropogenic and natural impacts.

III. Shaping coral traits: plasticity more than filtering

Brambilla V, Barbosa M, Dehnert I, Madin J, Maggioni D, Peddie C, Dornelas M

Submitted to MEPS on 02.09.2021

Physical ecosystem engineers are organisms that create and modify habitats via their own physical structures, thereby influencing all the taxa associated with those habitats. Understanding whether plasticity or environmental filtering determine the variation in ecosystem engineer physical structure is necessary to understand their role in ecosystem dynamics. Here, we explored coral survival and the plasticity of morphological traits that are critical for habitat provision in coral reefs. We conducted a reciprocal clonal transplant experiment in which branching corals from the genus Porites and Acropora were moved to and from a deep and a shallow site within a lagoon in the Maldives. Survival and trait analyses showed that transplant destination consistently induced the strongest changes, particularly among Acropora spp. The origin of the corals only marginally affected some of the traits. We also detected variation in the way individuals from the same species and site were differentiating their shape, showing that traits linked to habitat provision are phenotypically plastic. The results suggest coral phenotypic plasticity, rather than filtering, plays a significant role in determining zonation of coral morphologies, and consequently the habitats they provide for other taxa.

IV. Coral niche construction: coral recruitment increases along a coral-built structural complexity gradient

Brambilla V, Baird AH, Barbosa M, Dehnert I, Madin JT, Peddie C, Dornelas MA

bioRxiv preprint posted on 15.10. 2021, DOI: 10.1101/2021.10.14.464352

Niche construction is the process through which organisms modify environmental states in ways favourable to their own fitness. Here, we test experimentally whether scleractinian corals can be considered niche constructors. In particular, we demonstrate a positive feedback involved in corals building structures which facilitate recruitment. Coral larval recruitment is a key process for coral reef persistence. Larvae require low flow conditions to settle from the plankton, and hence the presence of colony structures that can break the flow is expected to facilitate coral recruitment. Here, we show an increase in settler presence on artificial tiles deployed in the field along a gradient of coral-built structural complexity. Structural complexity had a positive effect on settlement, with an increase of 15,71% of settler presence probability along the range of structural complexity considered. This result provides evidence that coral built structural complexity creates conditions that facilitate coral settlement, while demonstrating that corals meet the criteria for ecological niche construction.

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