Coral and Fish Community Development on Artificial Reefs of Different Ages in Bali: Expectations from Ecological Theory.

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i. Abstract

Many severely degraded coral reefs around the world show no signs of natural recovery, even decades after the disturbances were eliminated. In these degraded reefs the lack of suitable substrate and high post-settlement mortality inhibits coral recolonisation and recovery. In reef sites where the physical structure is lost, restoration efforts aim to provide a fixed substrate, either for natural coral settlement or for the transplantation of coral fragments. Artificial reefs have been designed and developed to be used as a coral reef conservation tool for habitat restoration in disturbed coral reefs. Here, the extent to which an artificial reef can provide a habitat for reef species and support coral recruitment was assessed using a model system of artificial reefs in Bali deployed over six-month intervals for up to 3.5 years. A generally positive trend of coral community development was recorded, including increased coral size, density, cover, and richness on artificial reefs with increasing time since deployment. This change over time can be explained by the facilitation model of ecological theory while metacommunity theory can be applied to explain differences between artificial and natural reef communities. However, fish densities in the artificial reef were significantly lower than in the natural reef, were not significantly different to the adjacent sand sites, and did not change over time. Despite significant differences in coral and fish populations between the artificial reefs and adjacent natural reefs, the trajectory of corals at this stage is encouraging. Previous studies on artificial reefs have estimated it may take between 10-20 years for an artificial reef to re-establish the structure and function of a natural reef. Currently there are no published records describing reef restoration outcomes over such timeframes, making the establishment of this baseline and future long-term monitoring of the artificial reef important contributions to the field.

ii. Declarations

I hereby declare that this work is original in its entirety and has never before been submitted for any form of assessment. The practical work, data analysis, presentation and written work presented are all my own unless otherwise stated. The work of others included here has been referenced appropriately.

I grant the Lancaster University institutional repository permission with respect to online access of this work.

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I would also like to thank my local supervisors, Dr I Gusti Ngurah Agung Suryaputra and Dr Rahmadi Prasetyo for their help in allowing me to conduct research in Indonesia.

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1. General Introduction

Coral reefs are among the most biodiverse and productive ecosystems on earth (Burke *et al.,* 2011). While the value of coral reefs is intrinsic for many, there are also tangible physical and economic benefits especially for coastal communities including subsistence fisheries production, coastal protection, and tourism revenues (Burke *et al.,* 2011). The East Asia Seas region identified by the Global Coral Reef Monitoring Network (2021) accounts for over 30% (78,272 km^2) of the world's total coral reef area with nearly 600 coral species and encompasses the Coral Triangle, the global hotspot for reef building corals. Despite their value, it is estimated that 95% of coral reefs in South-East Asia are threatened by anthropogenic impacts with the largest proportions of threatened reefs located in Indonesia and the Philippines (Burke *et al*., 2011). Coral reef systems in many areas are in decline (GCRMN, 2021) and due to their ecological and economic value, considering the threats to reef building corals that have been recognised for decades, these systems have accordingly become a top conservation priority.

Coral Reef Impacts

The greatest threats to coral reefs are the indirect impacts of elevated global atmospheric CO_2 caused by climate change (Burke *et al.,* 2011). Rising global temperatures and more frequent extreme temperature events caused by anthropogenic climate change are leading to more frequent and severe bleaching events in coral reefs globally, forcing regime shifts to macroalgae dominated habitats in some cases (Shaver *et al.,* 2020). Additionally, it is thought that the historic mass extinctions of coral communities were caused by ocean acidification as a result of increased atmospheric CO_2, foreshadowing the fate of present-day reefs in which ocean acidification represents an extinction level threat with the potential to trigger the next mass extinction (Veron, 2008). The IPCC predicts a global atmospheric CO_2 stabilisation level of 500ppm by 2050 which is expected to severely reduce coral growth to an extent where coral reefs as they are known today would be extremely rare (Hoegh-Guldberg *et al.,* 2007).

In some areas coral reefs are threatened to an even greater extent by the direct, local impacts often associated with unsustainable development in coastal communities. These anthropogenic impacts come from a range of damaging activities including physical damage from ships, unsustainable fishing practices, coral mining, blast fishing, pollution, and sedimentation (Lazuardi *et al.,* 2012; Frey and Berkes, 2014; Williams *et al.,* 2019). In most cases reefs suffer more than one of these threats and where one single threat can leave a coral reef vulnerable, the addition of other threats can lead to catastrophic ecosystem collapse (Burke *et al.,* 2011). Further, the wide range of threats to coral reefs corresponds to an equally wide range of impacts on coral reef communities.

Disturbances in coral reef systems generally involve a loss of live coral tissue as well as the physical loss of the coral skeleton which both result in a considerable loss in habitat complexity and can cause profound changes in the entire reef community structure in the long-term (Spieler *et al.,* 2001). Habitat complexity is key to the understanding of community ecology and in terrestrial systems the relationships between components of habitat complexity and species diversity have been thoroughly investigated. In these classical studies, habitats with lower complexity were found to support less biodiverse communities of birds (MacArthur and MacArthur, 1961; Roth, 1976), lizards (Pianka, 1967), rodents (Rozensweig and Winakur, 1969) and insects (Murdoch *et al.,* 1972). This relationship is also found in coral reef ecosystems where structural complexity has a strong positive effect on fish density and biomass as well as wider positive effects on ecosystem services (Holbrook *et al.,* 2002; Graham and Nash, 2013). A loss of habitat complexity results in losses to reef fish diversity and is thought to be caused by an increase in predation pressure and competition (Lingo and Szedlmayer, 2006; Wilson *et al.,* 2006).

In the most extreme cases of habitat loss in coral reefs the entire reef substrate can be lost. Coral mining and destructive fishing techniques can remove whole sections of reef and when coupled with the associated high sedimentation any leftover substrate is often totally covered by loose sand (Caras and Pasternak, 2009). The resulting barren, desert-like habitat offers zero habitat complexity and has almost no chance of natural recovery. As would be predicted given the loss of habitat complexity and live coral tissue, the diversity and abundance of reef fish can be markedly reduced as a result of destructive fishing and coral mining activities (Brown and Dunne, 1988; Caras and Pasternak, 2009). Regardless of the level of recruitment, any coral larvae settling in this degraded habitat will likely be smothered by the chronic disturbance of loose sand sediment (Brown and Dunne, 1988 & Fox, 2004). For example, a mined site in Hoga Island, Wakatobi National Park, Indonesia showed no recovery 20 years post mining (Caras and Pasternak, 2009) while a survey of mined reefs in the Maldives showed virtually no coral recovery even after 25 years (Clark and Edwards, 1999). Likewise, a coral reef impacted by a single blast from destructive fishing techniques can take between 5-10 years to recover but where extensive blast fishing creates mobile rubble fields recovery is estimated to take decades (Fox and Caldwell, 2006).

Even after a non-destructive disturbance, the loss of live coral tissue following a mass coral bleaching event could have a considerable impact on habitat complexity and associated fish populations over longer timescales (Wilson *et al.,* 2006). The growth of corals can resist the slow, constant erosion in reef environments but where reefs experience a bleaching event the lack of live coral tissue leaves the bleached coral skeleton exposed to increased rates of erosion (Sheppard *et al.,* 2002). The erosion of the bleached coral skeleton and reef substrate reduces habitat complexity and this lack of refugia can lead to greater predation pressure. In the years following a bleaching event in the Seychelles where up to 90% of the corals had bleached, the associated reef fish community experienced a decline in small bodied or juvenile individuals which were likely the fish most reliant on the living reef matrix to avoid predation (Graham *et al.,* 2007). While these threats can cause degraded reefs to undergo a regime shift towards a macroalgae dominated habitat, this outcome can be avoided where corals are able to naturally recover (Graham *et al.,* 2015).

Coral Reef Formation

Coral reef recovery dynamics are underpinned by the same processes which caused their original formation and developing an understanding of these processes can provide valuable insight into coral recovery potential. Coral reefs have existed over periods of hundreds of millions of years by utilising their far-reaching dispersal ability to colonise new substrates provided by the active shifting of tectonic plates (Pandolfi, 2011). Tectonic and volcanic activity have long been recognised as the primary geological processes that provide hard rock substrates which support the climax coral communities that exist in tropical shallows today (Darwin, 1842). More recently, tectonic plate boundaries have been found to have a concordance with the faunal breaks between coral reef provinces, suggesting that the biogeographical structure and composition of coral reefs present today have been continuously influenced by these long-term geological processes (Keith *et al*., 2013).

Coral reefs as they are known today have developed over decades to reach their climax community state and unfortunately the rarity of natural reef substrate formation means that there have been few opportunities to study the primary succession of corals. Estimates from coral communities developing on submerged lava flows in Hawaii suggest it may take up to 50 years for a climax coral community to naturally develop (Grigg and Maragos, 1974). The 1988 volcanic eruption of Gunung Api in Indonesia allowed for a unique opportunity to study the primary succession of the coral community developing on the submerged lava flow compared to the natural recovery of corals in adjacent reefs (Tomascik *et al.,* 1996). Where lava flows become submerged, they can physically smother coral reefs as well as bleach and kill corals in adjacent reefs through an elevated sea temperature. The secondary succession and natural recovery of corals onto the bleached coral skeleton of the adjacent reefs was monitored and compared to the primary succession of corals onto the lava flow (Tomascik *et al.,* 1996). Interestingly, successional processes produced higher average coral diversity, coral abundance, and cover on the new volcanic rock substrate than on the adjacent carbonate reef (Tomascik *et al.,* 1996).

In general ecological theory, succession is the process of community development towards a stabilised climax state. The main models of ecological succession include “facilitation”, “tolerance” and “inhibition” models (Connell and Slayter, 1977). These successional processes have been extensively studied over long time-scales in terrestrial ecosystems (Buma *et al.,* 2017). The *facilitation* model of succession is the gradual turnover of species within a community over time whereby the colonisation of new species is allowed by the presence of the existing community. Alternatively, the *tolerance* model posits that the late-stage colonisers are better adapted to withstand the lower resources available over time. Meanwhile, the *inhibition* model of succession suggests that the successful colonisers limit the ability of future colonisers and only when these competitors are removed, can new individuals inhabit the area. These models of ecological succession are less well studied in coral reef ecosystems but still offer some insight into early coral colonisation processes.

A cross-section of dead reef can reveal the successional processes that underlie the original formation of a coral reef. Through this posthumous cross-section technique Piller and Riegl (2003) found that the volcanic cobble-like substrate in Tulamben, Bali was first colonised by a variety of encrusting corals which grew laterally to bind and stabilise the loose rocks. Perhaps facilitated by this new stability, branching coral grew vertically which created a thicket that enveloped the stabilised rocks until they were totally covered, forming the coral reef (Piller and Riegl, 2003). Interestingly, the lateral-growth basal coral assemblage and the coral assemblage found between the shore and the reef are the same and represent a pioneer coral assemblage composed of species which persist despite perpetual wave action (Piller and Riegl, 2003). While the coral thicket had become stressed and bleached during a warming event in 1998, the skeleton was recolonised by lateral growth form, encrusting species, providing evidence of successful recruitment and recovery after reef wide disturbance (Piller and Riegl, 2003). In this way, developing an understanding of coral recruitment and the complexities of coral reef succession is key to understanding recovery on disturbed reef systems (Pearson, 1981).

More recently on Reunion island, the coral community succession on lava flows of different ages was compared to natural reef sites and evaluated in terms of coral community diversity, structure and demography (Jouval *et al.*, 2020). On these lava flows, the lack of early successional pioneer species suggests the successional processes that formed the coral communities on the lava flows do not follow the ‘facilitation’ model (Jouval *et al.,* 2020). Here, the other theories of succession could better explain the turnover of species over time. The dominance of early successional species (*Pocillopora* spp.) on older stage lava flows suggests that the tolerance and/or inhibition models of ecological succession are influencing coral community composition. An understanding of what drives these different successional processes is key for coral reef conservation and restoration efforts as they can provide a valuable insight into the recovery dynamics of a coral reef following disturbances.

Coral-Fish Community Dynamics

Reef fish and coral communities are two components of the coral reef ecosystem that are strongly associated, and both are pivotal in the ecological feedback mechanisms which define coral reef population dynamics (Fig. 1). Mumby and Steneck (2008) outlined these feedback mechanisms whereby the recruitment of corals is facilitated by the grazing pressure from reef fish and the recruitment of reef fish is dependent on refugia provided by corals (Graham *et al.,* 2007). Conversely, where reef fish are locally absent, coral recruitment is suppressed by algal growth while reef fish recruitment is limited by the lack of habitat complexity, thus reducing future grazing intensity and reinforcing the feedback (Mumby and Steneck, 2008). Results from exclusion experiments in coral reefs support these ecological feedback mechanisms as herbivorous fish have been shown to facilitate the recruitment of coral through the suppression of algae (Smith *et al.,* 2010; Doropoulos *et al.,* 2016; Holbrook *et al.,* 2016).

Fish in other trophic levels have also been found to influence this coral-fish population dynamic, especially predatory fish which help to suppress corallivore populations (Shaver and Silliman, 2017). More generally, by simply sheltering within a coral structure reef fish can enhance the growth of the coral through the provision of nutrients. Holbrook *et al.,* (2008) found significantly higher levels of ammonium in the water surrounding corals occupied by fish and recorded that these inhabited corals grew significantly more than those that lacked fish. The abundance of reef fish is closely linked to the health of the coral reef whereby complex reef habitats shelter fish recruits and reduce predator efficiency (Mumby and Steneck, 2008). Additionally, chemical cues on coral reefs have been shown to positively influence the recruitment of pelagic reef fish juveniles (Lecchini *et al.,* 2013) and coral larvae (Weber *et al.,* 2019). Through these established ecological feedback mechanisms, both reef fish and corals are equally influential components of the coral reef community as a whole.

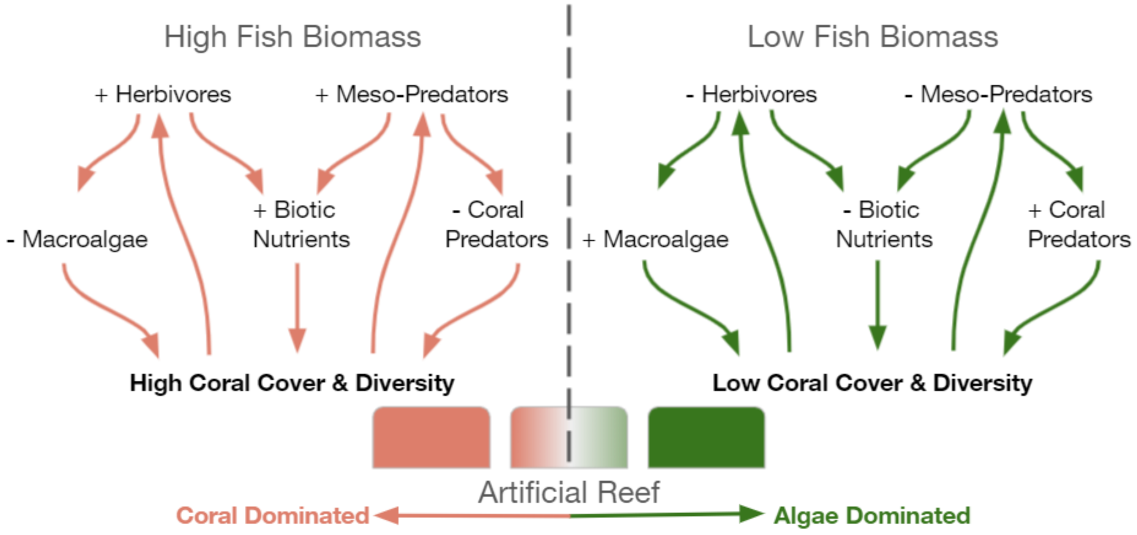

Figure 1. Coral community dynamics and feedback loops between corals and reef fish on an artificial reef. (Shaver and Silliman, 2017)

Dispersal and Settlement

Within this feedback system the recruitment of coral and fish larvae during their pelagic stage can influence reef recovery. The recruitment of these pelagic larvae is dictated by their dispersal ability, and the stochastic supply of larvae from surrounding and distant reefs (Planes *et al.,* 2009). After disturbance events and habitat loss the potential for the natural recovery and secondary succession of a reef strongly depends on the dispersal ability of reef building coral species in terms of self-recruitment within the reef, local recruitment from adjacent reefs as well as stochastic rescue inputs from further away broodstocks within the metacommunity (Planes *et al.,* 2009). Where smaller isolated disturbances can be relatively quick to recover via locally sourced recruits, extensive reef-wide disturbances depend on the recruitment of coral larvae from the further away surviving reefs to replenish depleted coral communities (Fox and Caldwell, 2006).

Hubbell (1997) suggested that one of the most important features of reef-building coral species is their very high vagility due to the potential of pelagic larvae to disperse over long distances. In this way, countless coral larvae have the potential to colonise a myriad of distant reefs and in turn can dynamically couple these communities into a larger metacommunity, stabilising reef community composition regionally (Hubbell, 1997). Within a biodiverse reef locality, the coral species that make up the complex benthic community generally employ one of two dispersal techniques when it comes time to spawn, these species are either broadcast spawners or brood spawners. These two techniques could help to avoid interspecific competition since broadcast spawning coral species allow for metacommunity-wide dispersal on the scale of tens of kilometres and brood spawning coral species have a smaller, within reef, dispersal range (Jones *et al.,* 2009). While, in the aftermath of a disturbance in a reef, the self-recruitment ability of brooding corals is important, it is thought to be supplemented by the stochastic longer distance dispersal by broadcast spawning corals since no examples of 100% self-recruitment have been documented (Jones *et al.,* 2009).

While the supply of larvae on reefs is governed by stochastic processes often at large spatial scales, the settlement and survival of coral larvae can be limited by local processes. Post-disturbance, reefs in both Komodo National Park (blast fishing) and the Seychelles (coral bleaching) did not show evidence of natural recovery despite ample supply of coral settlers, suggesting the recovery was limited by high post-settlement mortality for coral recruits (Fox, 2004; Chong-Seng *et al.,* 2014). The unstable rubble substrates left behind following destructive disturbance effects have been shown to cause high recruit mortality through the smothering of settled larvae (Johns *et al.,* 2018; Ceccarelli *et al.,* 2020). Many rubble fields in the Philippines show virtually no recovery of hard coral even 20–30 years post-blasting (Raymundo *et al.,* 2007).

Additionally, some bleaching impacted reefs in the Seychelles had undergone a regime shift to macroalgal-dominance and yet despite retaining their substrate and attracting sufficient coral settlers, no juvenile corals were found in these sites (Chong-Seng *et al.,* 2014). This phase-shift can induce considerable changes in the microbial community and the biofilms that were once beneficial for coral recruitment can be lost (Weber *et al.,* 2019). Over time, the remaining coral skeleton is eroded and the resulting losses to habitat complexity can increase predation pressure on existing fish communities and limit fish recruitment (Sheppard *et al.,* 2002; Graham *et al.,* 2007). In this way, substrates that are either unstable or macroalgae laden can act as a demographic bottleneck and inhibit coral and fish community recovery (Chong-Seng *et al.,* 2014). In areas where post-settlement survival is low, the natural recovery of the reef can be slow and, in some cases, impossible.

Metacommunity Theory

The extensive dispersal ability of corals allows for relatively distant individual reefs to influence each other through the import and export of juveniles, forming a highly complex, dynamic metacommunity. In many areas around the world coral reefs are in decline (GCRMN, 2021) and so developing an understanding of the metacommunity wide demographic processes that sustain the traditionally high biodiversity found in these systems (Burke *et al.,* 2011) becomes crucial for conservation practices moving forward. The metacommunity concept allows for conservation and restoration efforts to be adapted to consider their effect on the metacommunity as a whole. While traditional community composition frameworks focus on the species interactions and processes within a local environment, metacommunity theory posits that this composition is also influenced by the dispersal of individuals within a metacommunity and other regional scale processes (Leibold *et al.,* 2004).

When investigating a network of habitats through the metacommunity theory framework there are different paradigms which vary in their analysis of species composition. The four main paradigms of metacommunity theory include the species sorting, mass effects, patch, and neutral paradigms. These paradigms explain the potential mechanisms behind species composition and coexistence within a metacommunity to allow ecologists to develop an understanding of the spatial biodiversity patterns of these complex ecosystems. While it is unlikely that any one of the paradigms identified below will be solely responsible for the species composition within a metacommunity, it is more likely that each of these sets of processes will play interactive roles in structuring a metacommunity (Liebold *et al.,* 2004).

Within a metacommunity where habitat patches are heterogeneous the *species sorting paradigm* can help to explain the composition of species. In an environment with unlimited dispersal and equal access, environmental conditions at a patch can predict the species found in that habitat (Logue *et al.,* 2011). Within this paradigm there exists a strong correlation between the local species composition and the environmental conditions within a patch, resulting in the development of unique communities supported by heterogeneous habitats within a metacommunity (Leibold *et al.,* 2004). For example, fish species that are highly coral associated (or reliant) would thrive in a healthy coral reef but may struggle in an area with little live coral tissue due to a lack of suitable shelter (Boström-Einarsson *et al.,* 2018). Other reef fish species that are not reliant on live coral for shelter or food can survive in degraded reef habitats with little live coral tissue. This relationship allows for the prediction of the community present within an area based on the environmental characteristics of the patch itself.

The *mass effects paradigm* is an extension of the species sorting paradigm in which the community dynamics within a metacommunity of heterogeneous habitats are influenced by dispersal driven mass effects, resulting in source-sink relationships between populations in different patches (Liebold *et al.,* 2004). Environmental conditions can allow certain species to dominate, causing population dynamics which are generally positive as a result of the birth rate being higher than the death rate. This net gain of individuals can allow for greater dispersal and emigration to other patches within the metacommunity. Where these individuals are not supported by the new habitat, their population dynamics tend to be generally negative due to greater competition. Nevertheless, dominant populations from the original patch can become a source of individuals to other patches, helping to supplement the potentially negative population dynamics (Logue *et al.,* 2011). In this way, despite their lesser competitive ability, smaller populations can exist within a patch where other species are dominant.

Alternatively, the *patch paradigm* suggests that the patterns of species distribution, abundance and interactions in a metacommunity of homogenous habitats are driven by a colonisation-competition trade-off (Logue *et al.,* 2011). This trade-off is represented by a spectrum with poorer competitors at one end which are generally outcompeted but also have a greater dispersal ability to colonise new habitats and avoid competition (superior colonisers) while at the other end strong competitors will often outcompete other species but will have a lesser dispersal ability (superior competitors) (Yu and Wilson, 2001). New habitats are rarely created in a natural climax community and so superior competitors dominate while superior colonisers are rare. However, disturbance effects which lead to habitat loss (e.g., strong wave action, storm weather, unsustainable fishing practices, etc.) can lead to the deterministic removal of superior competitors due to their limited dispersal ability (Nee and May, 1992). The resulting lower quality habitat (e.g., coral rubble or sand sediment) remaining after a disturbance event can be rapidly colonised by the superior colonisers with their greater dispersal ability. In this way, the superior colonisers can exist within the metacommunity by avoiding direct competition and instead colonising areas where the superior competitors have recently gone extinct (Levins and Culver, 1971). Similarly, biodiversity can be maximised where a reef system suffers chronic small scale disturbances that inhibit successional development and allow for both superior colonisers and competitors to co-exist (Connell, 1978). Grigg and Maragos (1974) found that over time the biodiversity on a developing coral reef rose to a maximum, then declined before the climax stage was reached, supporting the intermediate disturbance hypothesis (Connell, 1978).

Uniquely, the *neutral paradigm* assumes that ecologically similar species within a community are demographically identical. These trophically similar species are thought to have the same dispersal ability, birth, and death rates, and even the same probability of speciation over historic timescales (Bell, 2001). Within the neutral theory there exists a stable and universal 'diversity parameter' identified as a linear function of the average speciation rate across the entire metacommunity and the sum of the population sizes of all species within the metacommunity (Hubbell, 2005). This function is very slightly less than unity when the distribution of the metacommunity is in a steady state, meaning that at equilibrium diversity there is a slight excess of deaths over births which is exactly balanced by the slow rate of introduction of new species into the metacommunity (Hubbell, 2005). Unlike other paradigms, the neutral paradigm suggests that coral reef community assembly depends entirely on demographic stochasticity (Logue *et al.,* 2011) through the random dispersal of individuals rather than patch heterogeneity or differences in dispersal ability.

Coral Reef Restoration

Conservation practices in many threatened areas around the world prioritise ‘restoration’ through active intervention with the aim to assist the recovery of reef structure, function and key reef species to combat environmental and anthropogenic pressures (Hein *et al.,* 2020). A key part of this restoration is the enhancement of resilience within the restored habitat to ensure recovery after future disturbances. This improved resilience could become invaluable in the future where increased anthropogenic carbon emissions are predicted to increase the frequency of disturbances within coral reefs (Burke *et al.,* 2011; Montefalcone *et al.,* 2018). These impending climate related disturbances are difficult to prevent on a local level and so community conservation efforts can take positive steps to resolve the local, direct anthropogenic pressures that currently impact coral reefs. The management and mitigation of these local pressures in an effort to improve resilience represents a crucial step in the integration of a restoration process and will be critical in preventing the future degradation of coral reefs (Burke *et al.,* 2011; Gilmour *et al.,* 2013).

In the aftermath of a disturbance, the environmental and community conditions pre-disturbance can influence the potential for a habitat to recover naturally. High structural complexity, coral recruitment and herbivore biomass have all been shown to increase the likelihood of natural recovery in coral reef systems and reduce the risk of a regime shift towards macroalgal dominance post disturbance (Graham *et al.,* 2015). The preservation or enhancement of these key factors should be a priority for conservation practices to enhance the resilience of a reef. In degraded sites where these crucial aspects of reef health are inadequate, or where there is insufficient time for recovery between disturbance events, direct restoration becomes crucial (Boström-Einarsson *et al.*, 2020). To halt and reverse coral loss the original threats to coral reefs need to be mitigated and actions across a range of scale are required including local active restoration and passive conservation of reefs, regional land use changes to reduce sedimentation and pollution, as well as global policy reform to reduce anthropogenic ocean warming and acidification (Bruno and Selig, 2007).

Artificial Reef Structures

The need for direct restorative intervention becomes clear in degraded sites where a loss of habitat and structural complexity is preventing natural coral recolonisation due to high post settlement mortality as a result of blast fishing (Fox, 2004) or coral mining (Clark and Edwards, 1994; Caras and Pasternak, 2009). In reef sites where the physical structure is lost, restoration efforts aim to provide a fixed substrate, either for natural coral settlement or for the transplantation of coral fragments, to restore the structural complexity of the reef (Spieler et al., 2001). The deployment of an artificial reef can immediately restore the structural complexity lost after severe disturbance events and has been shown to effectively support complex reef fish communities (Clark and Edwards, 1994; Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006; Perkol-Finkel *et al.,* 2006; Hylkema *et al.,* 2020).

However, the construction and deployment of an artificial reef can incur significant environmental impacts and these should be considered when developing a restoration program. Concrete structures are the most common type of artificial reefs (Baine, 2001; Razak *et al.,* 2022) and the use of widely available Portland cement is convenient but does carry a substantial environmental impact (Boström-Einarsson *et al.,* 2020). The production of Portland cement is incredibly energy intensive and releases large amounts of CO_2 into the atmosphere through the burning of fossil fuels (Bilodeau and Malhotra, 2000). The aggregates added to cement to constitute concrete, including sand, gravel and crushed rock, also have their own environmental costs associated with the extraction and processing of these raw natural materials (Sreebha and Padmalal, 2011; De Brito and Saikia, 2013). Moreover, the high pH of concrete substrate has been shown to limit the recruitment of marine benthos within the first 6 months of deployment (Gilbeau *et al.,* 2003). Recent developments have been made to avoid these impacts including the utilisation of low pH cement (Xu *et al.,* 2019) or recycling inert materials (Carral *et al.,* 2018) for use in artificial reefs. Alternatively, in sites where the loose dead coral fragments create a mobile rubble field large quarried rocks and weighted nets have been deployed to stabilise the loose substrate and allow for the rubble to consolidate and coral to recruit effectively (Fox *et al.,* 2005; Fox *et al.,* 2019).

Artificial reefs were defined by the United Nations Environment Programme (2009) as “submerged structure[s] deliberately constructed or placed on the seabed to emulate some functions of a natural reef, such as protecting, regenerating, concentrating, and/or enhancing populations of living marine resources.” The recorded history of artificial reefs began in Japan in the 1600’s where the rubble and debris from demolished buildings was submerged in coastal waters to aggregate fish and grow kelp (Stone *et al.,* 1991). Since then, artificial reefs have traditionally been used for fisheries enhancement and coastal protection from small scale tyre reefs made by independent fishers to larger scale government-led artificial reef programs (McGurrin *et al.,* 1989). More recently, artificial reef structure designs have been adapted and developed to be used as a coral reef conservation tool for habitat restoration and recovery in disturbed coral reefs (Paxton *et al.,* 2020). For restoration purposes, the ultimate goal of an artificial reef is to ensure the long term survival and proliferation of coral and fish communities into a self-sustaining functioning ecosystem (Razak *et al.,* 2022).

Analogous to natural reef recovery (Grigg and Maragos, 1974; Tomascik *et al.,* 1996), the temporal variability of the benthic community on artificial reefs is driven by successional processes initiated by the recruitment of epibenthic species (Becker *et al*., 2018). Within the first month a pioneer algal complex is established on artificial surfaces (Higgins *et al.,* 2019). Within this pioneer community, the growth of crustose coralline algae is associated with the production of coral settlement cues and has been shown to significantly increase coral recruitment (Dixson *et al.,* 2014). While the presence of this pioneer algal matrix does limit the space available for coral settlement, it provides an important food source for herbivore communities and can lead to increased grazing pressure within an artificial reef (Pratchett *et al.,* 2008). High grazing pressure can remove algal competitors, making space for corals to settle (Smith *et al.,* 2010; Doropoulos *et al.,* 2016; Holbrook *et al.,* 2016).

Herbivorous reef species supported by an artificial reef play a crucial role in suppressing the initial pioneer algae and facilitating the succession of corals, as recorded in the natural benthic succession of submerged lava flows (Grigg, 1983). In degraded reefs where coral recolonisation is limited by a lack of hard substrate, the successful coral growth and recovery recorded on submerged lava flows (Tomascik *et al.,* 1996) could also be achieved by artificial substrates. An investigation into the early successional processes on artificial substrates found that a diverse algal community had developed in two months, while the first coral colony, brooding corals that planulate monthly (*Pocillopora*), was observed after six months, followed by branching corals (*Acropora*) and massive growth form corals (*Porites*) which were first recorded ten months post deployment (Clark and Edwards, 1994). As such, after one year of successional processes driving species composition, the beginnings of a biodiverse benthic community with an assortment of coral colonies of varied growth morphology and reproductive method should have developed on the artificial reef. In the long-term, it is estimated that the development of a climax community from a bare substrate could take up to 50 years (Grigg and Maragos, 1974).

Bali

The Bali Marine Rapid Assessment Programme conducted in 2011 recorded a remarkably diverse fish community, indicating that Bali is one of Indonesia's richest marine areas and globally important with regards to conservation significance (Allen and Erdmann, 2012). Coral and rocky reefs were by far the richest habitat in terms of fish biodiversity while areas dominated by sand, silt, or rubble substrates were comparatively poor (Allen and Erdmann, 2012). Bali hosts a diverse reef coral community, with a confirmed total of 406 reef-building coral species found during the surveys. These results for site and overall richness are similar to those from Bunaken National Park and Wakatobi (392 and 396 spp. respectively), and higher than the Komodo and Banda Islands (342 and 301 spp.) (Turak and Devantier, 2012). Reefs of high conservation value were widespread along the East and North coasts of Bali and as such this island has strong potential for the development of a network of MPAs if given sufficient logistic resources and long-term support (Turak and Devantier, 2012). Coral reefs in Bali also have a considerable potential economic value and represent a large proportion of the US$3 billion annual tourism value calculated from Indonesian reefs (Spalding *et al.,* 2017). Classical threats to coral reefs including destructive fishing, coral mining, sedimentation, urban pollution and waste, coral bleaching, and unsustainable tourism were all found to be currently present in Bali (Lazuardi *et al*., 2012). These conclusions show that the coral reefs in Bali have global conservation significance and the anthropogenic pressures threatening these biodiversity hotspots makes Balinese coral reefs a top conservation priority.

At any given coral reef, the different local threats and pressures can provide unique challenges and so conservation efforts require different considerations when it comes to designing restoration practices. The Indonesian island of Bali is a perfect example of this variation where tens of thousands of artificial reef structures with different shapes and sizes have been deployed in degraded reefs around the island (Wicaksana, 2020). Among these are the 'Biorock' structures deployed in Pemuteran which produce a weak electrical current, promoting the growth of transplanted corals (Hilbertz and Goreau, 1996). Alternatively, 'Reef

Ball' units are also popular and have been deployed in damaged reefs all over the world due to their heavy, domed concrete structure which provides valuable coastal protection as well as an excellent habitat for reef species (Barber and Barber, 1996). Similarly, more affordable hand-made concrete structures known as 'Hexadomes' were deployed in Les village to alleviate ornamental fishing pressures on natural reefs (Yunaldi *et al.,* 2011). More simply, resin-sand-coated steel 'reef stars' (previously known as reef spiders) have been deployed at rubble sites in Nusa Dua to transplant coral fragments and stabilise the rubble substrate (Ampou *et al.,* 2019; Williams *et al.,* 2019; Wicaksana, 2020). Deployed more recently in Buleleng, 'Bioreeftek' is an innovative design which uses coconut shells to provide structure in damaged reefs (Ampou *et al.*, 2020). Even on the same island, different reefs are subject to a variety of local threats and pressures, leading to the innovation of many artificial reef structure designs to help solve these unique site-specific challenges. This is highlighted by the Indonesian Coral Reef Garden initiative in which 95,768 artificial reef structures of various designs were deployed in five areas around Bali in late 2020 (Suriyani, 2021). While some structures may perform better than others in a given site, each design has its own benefits and it is unlikely that one design is perfect for all situations (Paxton *et al.,* 2020), especially taking socio-economic considerations into account.

Previous studies on artificial reefs have estimated it may take decades for an artificial reef to re-establish the structure and function of a natural reef (Clark and Edwards, 1999; Ampou *et al.,* 2019). Currently there are no records describing reef restoration outcomes over such timeframes, making this baseline study and future plans for long-term monitoring important contributions to the field. The overarching aim of this study is to evaluate the effectiveness of an artificial reef as a conservation tool for habitat restoration in a severely degraded coral reef ecosystem. This aim was examined by comparing successional performance indicators including reef fish abundance & diversity, and coral recruitment & cover between artificial reefs of different ages and adjacent natural reef & sand sites. The changes in artificial reef communities over time have been explored in terms of expectations from ecological theory.

2. Coral and Fish Community Development on Artificial Reefs of Different Ages in Bali.

2.1. Abstract

Many severely degraded coral reefs around the world show no signs of natural recovery, even decades after the disturbances were eliminated. In these degraded reefs the lack of suitable substrate inhibits coral recolonisation and recovery. In reef sites where the physical structure is lost, restoration efforts aim to provide a fixed substrate, either for natural coral settlement or for the transplantation of coral fragments. Artificial reefs have been designed and developed to be used as a coral reef conservation tool for habitat restoration and recovery in disturbed coral reefs. Here, the extent to which an artificial reef can provide a habitat for reef species and support coral recruitment was assessed using a model system of artificial reefs in Bali deployed over six-month intervals for up to 3.5 years. When compared to adjacent natural reef communities, the generally smaller size of corals in the artificial reef resulted in a lower coral cover despite the higher coral density. A generally positive trend was recorded in coral communities, including increased coral size, density, cover, and richness on artificial reefs with increasing time since deployment. However, fish densities in the artificial reef were significantly lower than in the natural reef, were not significantly different to the adjacent sand sites, and did not change over time. Despite significant differences between coral and fish community compositions between the artificial reefs and adjacent natural reefs, the trajectory of corals at this relatively early stage is encouraging. Previous studies on artificial reefs have estimated it may take between 10-20 years for an artificial reef to re-establish the structure and function of a natural reef. Currently there are no published records describing reef restoration outcomes over such timeframes, making the establishment of this baseline and future long-term monitoring of the artificial reef important contributions to the field.

2.2. Introduction

Coral reefs are among the most diverse ecosystems on earth and while the value of these precious ecosystems is intrinsic for many, there are also tangible physical and economic benefits (Burke *et al.,* 2011). Despite their value, it is estimated that 95% of coral reefs in Southeast Asia are threatened by anthropogenic impacts with Indonesia and the Philippines representing the largest proportions of threatened reefs (Burke *et al*., 2011). The greatest threats to coral reefs are the indirect impacts of elevated atmospheric CO_2 caused by anthropogenic climate change, namely mass bleaching and ocean acidification (Burke *et al.,* 2011). The IPCC predicts that an increase to 1.5°C above pre-industrial levels would lead to a decline in coral reefs by 70-90% and under the current global warming predictions this 1.5°C increase is likely between 2030 and 2052 (IPCC, 2018). Concurrently, the direct anthropogenic impacts that cause disturbances in coral reef systems come from a range of harmful activities including physical damage from ships, unsustainable fishing practices, coral mining, blast fishing, pollution, and sedimentation (Lazuardi *et al.,* 2012; Frey and Berkes, 2014; Williams *et al.,* 2019). To halt and reverse coral loss the original threats to coral reefs need to be mitigated and actions across a range of scales are required including local active restoration and passive conservation of reefs, regional land use changes to reduce sedimentation and pollution, as well as global policy reform to reduce anthropogenic ocean warming and acidification (Bruno and Selig, 2007).

The seemingly perpetual impacts of traditional coral mining are widespread in Balinese reefs (Lazuardi *et al.,* 2012; Sudiarta, 2018) where whole sections of reef were removed followed by high sedimentation which totally covered any leftover substrate in loose sand (Caras and Pasternak, 2009). Dramatic decreases in coral cover, richness and abundance were reported in mined reefs, followed by significant beach erosion even years after the ban on coral mining was introduced, and subsequent monitoring found very little recovery of mined reefs throughout Bali (Caras and Pasternak, 2009). A mined reef in Wakatobi National Park, Indonesia showed no recovery 20 years post mining (Caras and Pasternak,

2009) while a survey of mined reefs in the Maldives showed virtually no coral recovery after 25 years (Clark and Edwards, 1999).

Coral reef recovery dynamics are underpinned by the same processes which caused their original formation and developing an understanding of these processes can provide valuable insight into coral recovery potential (Pearson, 1981). Coral reefs as they are known today have developed over decades to reach their climax community state and unfortunately the rarity of natural substrate formation means that there have been few opportunities to study the primary succession of corals. Predictions from coral communities developing on successive submerged lava flows in Hawaii suggest that a climax coral community may take up to 50 years to develop naturally (Grigg and Maragos, 1974).

After disturbance events and habitat loss, the potential for the natural recovery and secondary succession of a reef could depend on the community conditions pre-disturbance. High structural complexity, herbivore biomass and coral recruitment can all increase the likelihood of natural recovery and avoid the risk of a regime shift towards macroalgal dominance post disturbance (Graham et al., 2015). In this way, coral recovery is heavily reliant on the dispersal ability of reef building coral species in terms of self-recruitment within the reef, local recruitment from adjacent reefs as well as stochastic rescue inputs from further away broodstocks within the metacommunity (Planes *et al.,* 2009).

Direct restorative intervention becomes necessary in degraded reef sites where a loss of habitat and structural complexity prevents natural coral recolonisation due to high post settlement mortality resulting from blast fishing (Fox, 2004) or coral mining (Clark and Edwards, 1994; Caras and Pasternak, 2009). In reef sites where the physical structure is lost, restoration efforts are aimed at providing a fixed substrate, either for natural coral settlement or for the transplantation of coral fragments, to restore the structural complexity of the reef (Spieler et al., 2001). The deployment of an artificial reef can immediately provide structural complexity and has been shown to effectively support complex coral and fish communities

(Clark and Edwards, 1994; Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006; Perkol-Finkel *et al.,* 2006; Hylkema *et al.,* 2020).

Analogous to the recovery that occurs after volcanic activity (Grigg and Maragos, 1974; Tomascik, 1996) or *Acanthaster planci* predation on natural reefs (Pearson, 1981), the temporal variability of the benthic community on artificial substrates is driven by successional processes, initiated by the recruitment of epibenthic species (Becker *et al*., 2018). The pioneer species which first colonise an artificial reef tend to establish an algal complex within the first 2-4 weeks (Higgins *et al.,* 2019). While the presence of other algal species within the pioneer community limits the space available for coral settlement, this algal community can support herbivore communities and therefore increase grazing pressure within an artificial reef (Pratchett *et al.,* 2008). High grazing pressure drives the patterns of algal succession, facilitating the settlement and recruitment of coral onto an artificial substrate by enhancing coral facilitators and removing algal competitors (Smith *et al.,* 2010; Doropoulos *et al.,* 2016; Holbrook *et al.,* 2016). In the long-term, it is estimated that the development of a climax community from a reef-wide disturbance could take up to 50 years (Grigg and Maragos, 1974). On a medium timescale, the estimated time necessary for an artificial reef to re-establish the structure and function of a natural reef is between 10-20 years (Clark and Edwards, 1999; Ampou *et al.,* 2019).

Artificial reefs can be a useful model system to explore successional processes in reef ecosystems and can lead to a better understanding of recovery dynamics after disturbance in natural reef systems. Despite decades of restoration work, few projects have evaluated this natural recovery onto artificial reefs and there are no records describing reef restoration outcomes over such timeframes, making the establishment of this baseline and future plans for long-term monitoring important contributions to the field. In their review of coral restoration methods, Boström-Einarsson *et al.* (2020), found a lack of appropriate and standardised monitoring with 60% of all reef restoration projects surveyed reporting less than 18 months of restored sites monitoring. This lack of documentation, coordination and sharing of knowledge reduces our ability to learn from the past and increases the risk of repeatedly testing similar methods and hypotheses (Boström-Einarsson *et al.*, 2020). The assessment of past restoration projects including their successes or failures provides a valuable resource for future restoration efforts.

This study used a model system of artificial reefs in Bali deployed over six-month intervals for up to 3.5 years to explore the following questions: 1) to what extent does an artificial reef support the settlement and recruitment of corals?; 2) To what extent does an artificial reef provide a habitat for reef species that reflects nearby natural reef communities?; 3) How do these artificial reef communities change over time? Specifically, successional performance indicators including reef fish abundance & diversity, and coral recruitment & cover were assessed and compared between artificial reefs of different ages as well as adjacent natural reef & sand sites. The assessment of communities developing on artificial reefs of different ages and the evaluation of these primary successional processes provides a valuable insight into colonisation and recovery dynamics in coral reef ecosystems as a whole. Community composition data collected on the artificial reef was also analysed and compared with data collected in adjacent coral reefs to provide important context and establish a long-term goal. Overall, the assessment of this artificial reef can be used to gain insight into the effectiveness of artificial reefs as a conservation tool for habitat restoration and recovery in disturbed coral reef ecosystems.

2.3. Methods

2.3.1. Study Site

The extent to which an artificial reef can provide a habitat for reef species and support coral recruitment was assessed using a model system of artificial reefs in Bali. The shoreline in Tianyar village, Bali (8°12'S, 115°30'E) was likely once skirted by a largely complete, connected natural reef (Fig. 2). However, the development of local infrastructure created anthropogenic pressures on the reefs, of which coral mining was the most devastating, resulting in reef scale habitat loss (Caras and Pasternak, 2009). With the lack of a natural reef substrate any corals recruiting to this mined area would be susceptible to being smothered by the loose sand sediment, resulting in high post-settlement mortality (Brown and Dunne, 1988). In the absence of a natural input of new rock substrate (e.g., lava flow: Grigg and Maragos, 1974; Tomascik *et al.*, 1996) this mined site would likely never recover without intervention (Clark and Edwards, 1999; Caras and Pasternak, 2009), clearly showing the need for an artificial reef (Clark and Edwards, 1994).

This was understood by 'Yowana Bhakti Segara', a fisher community in Tianyar village who were inspired by the conservation efforts in the nearby Les village (Yunaldi *et al.,* 2011) to enforce a no-take zone and began the construction of their own artificial reef in 2017. The deployment of the artificial reef in this site aimed to provide a physical structure which would facilitate the natural recruitment and subsequent growth of coral as well as support a diverse community of reef fish. The presence of the adjacent natural reefs shows that local abiotic conditions are conducive to coral development and suggests that the site is not recruitment limited. These are important factors to consider when planning a restoration programme and so the artificial reef in Tianyar was appropriately deployed along a similar depth contour between the two natural reefs (Fig. 2). Artificial reef structures here are constructed using a mix of 10 parts locally quarried volcanic sand, 2 parts Portland cement and 1 part calcium carbonate powder to create a concrete which is then reinforced using steel bars.

Figure 2. Map of Tianyar coral reef with six sampling locations marked within each of the four sites. Sites from left to right: west natural reef (purple), artificial reef (pink), sand (green), east natural reef (blue). The ages of each of the artificial reef aggregations sampled here are labelled. The location of the artificial reef within Bali and within South East Asia is also labelled. Photo credit: Google ©

Structures of various designs were deployed weekly between 2017-2020, totalling over 7,000 individual structures which make up the artificial reef in Tianyar. Structures deployed at the same time were aggregated (Table 1) and irregularly stacked to provide varied reef heights and surface orientations, simulating the habitat complexity of a natural patch reef (Fig. 3) (Appendix 1). In this way, the artificial reef in Tianyar is made up of a network of smaller artificial reef aggregations, each distinct in their time of deployment. While the physical differences in these aggregations can lead to flaws in experimental design, this heterogeneity is intended as part of the artificial reef design and is representative of most community based restoration efforts.

Table 1. Properties of the sampled artificial reef aggregations of different ages

Artificial reef aggregations				
Age (years)	Depth (m)	Number of structures	Max height (m)	Location (GPS)
1	8.5	80	0.4	-8.19041, 115.49481
1.5	8	90	1	-8.19042, 115.49559
2	5.2	200	1	-8.19061, 115.49444
2.5	7	105	0.5	-8.19055, 115.49514
3	7.5	52	0.6	-8.19053, 115.49487
3.5	9	20	0.2	-8.19041, 115.49537

Figure 3. A group of handmade quadrupedal artificial reef structures 1 year after deployment in Tianyar, Bali, Indonesia. Photo credit: Ketut de Sujana Mahartana.

Individual concrete structures were handmade and designed to incorporate habitat complexity and enhance coral settlement by ensuring artificial reef surfaces were rough since corals preferentially settle within the complex interstices of a substrate (Spieler *et al.* 2001; Whalen *et al.,* 2015). Complexity on a larger scale in the form of protective space was purposefully varied both within and around structures to support diverse reef fish communities (Clark and Edwards, 1994; Lingo and Szedlmayer, 2006) (Fig. 4).

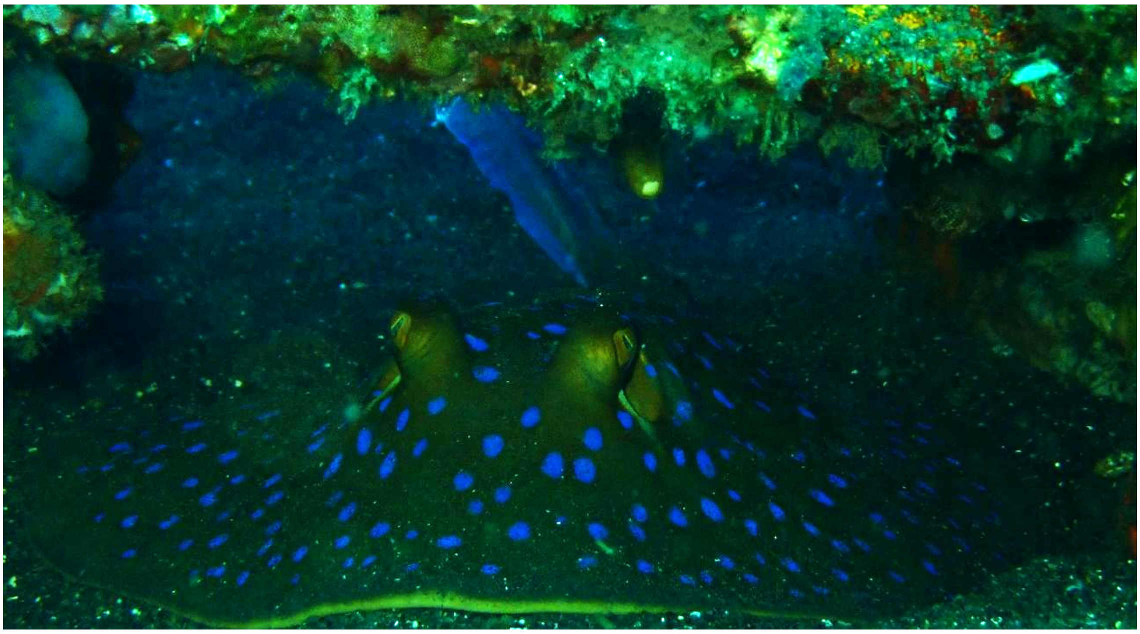

Figure 4. A bluespotted ribbontail ray (*Taeniura lymma*) utilising the protective space under an artificial reef structure. Photo credit: I Ketut de Sujana Mahartana.

2.3.2. Study Design

This restoration program is a community-led project and the artificial reef was not intended as an experimental study. As such, this study design was superimposed onto the existing artificial reef to meet the objectives of this study.

Artificial Reefs

The Tianyar artificial reef network encompasses over 20 groups of artificial reefs; only six of these artificial reef aggregations were identified for this study, distinct in their time of deployment (Fig. 2). Each aggregation was made up of at least 20 structures deployed at the same time between 4-9 m depth within the no-take zone in Tianyar, Bali. These aggregations of artificial reef structures are not uniformly distributed and do vary in some physical properties (Table 1.) The first aggregation contained the oldest structures from the first deployment in October 2017, with subsequent aggregations deployed at consecutive six-month intervals to represent a linear time series. These six aggregations of structures deployed from October 2017 to April 2020 provide a range of artificial reefs between 1 - 3.5 years since deployment (referred to as age in years). Here, the artificial reef represents a model system to explore how reef communities change over time, and how these communities compare to those in adjacent sites.

Natural Reef (East and West)

Six sampling locations were haphazardly selected between 4-9 m depth within both adjacent natural reef sites (to the east and west of the artificial reef). The distance between the artificial reef and the east and west natural reefs was ~50 and ~100 m respectively. Community assessments in these reefs are crucial when investigating the extent to which the artificial reef provides a habitat for reef species that reflects nearby natural reef communities.

Sand

Each of the six artificial reef aggregations were paired with an adjacent sand area between 4-9 m depth. The assessment of sand sites provides an important context for assessing the effectiveness of an artificial reef in that these sand communities are likely similar to those found pre-deployment.

2.3.3. Benthic Community Assessment

Photoquadrat

The benthic community composition, density and cover was assessed using a square PVC quadrat which was held just above the substrate and photographed from above (Fig. 5). Ten quadrat replicates were haphazardly chosen within each of the six sampling locations at the four sites. The dimensions of the quadrat were calculated based on the size of the artificial reef structures and the resolutions required for the identification of benthic organisms from the photograph (Bianchi *et al.,* 2004). Given the relatively small size of an individual artificial reef structure and the resolution required to identify coral juveniles, a 40 x 40 cm quadrat ($0.16m^2$) was used. Only the benthic community found within the confines of the quadrat was sampled.

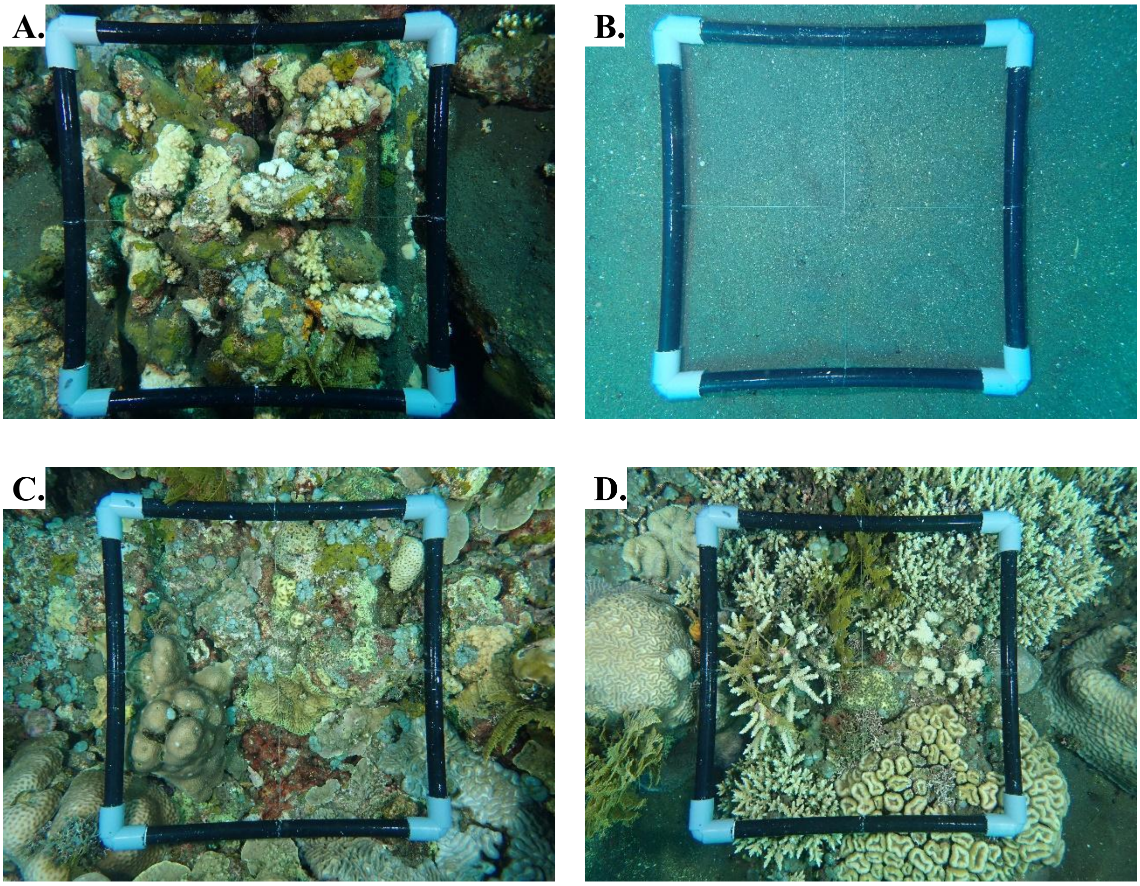

Figure 5. Photoquadrat (40 x 40 cm) benthic community survey method at four different sites. **A.** Artificial reef structure 3 years post deployment. **B.** Sand substrate adjacent to the artificial reef. **C.** Natural reef east of the artificial reef. **D.** Natural reef west of the artificial reef. Photo credit: I Gede Sudarma.

All visible coral colonies were identified to genus level where possible and the area of each colony was measured using FIJI digital image processing software (Schindelin *et al.,* 2012). In this way, the number of individual corals, their respective size (cm^2) and the genus to which they belong were all recorded. Where the quadrat overlapped a coral, only the coral area within the quadrat was measured. The density of corals was standardised to 1 m^{-2} by multiplying the total number of coral colonies within a quadrat by 6.25. The size of all corals within the quadrat was summed and then divided by the total area of the quadrat (1600 cm^2) and multiplied by 100 to find the coral cover (%). Additionally, the photographs were analysed using the Coral Point Count (CPC) software which randomised 100 points within the quadrat and the benthic organisms found under each point were identified to the lowest possible taxon to calculate their percentage cover (Kohler and Gill, 2006). These organisms include corals (28 different genera), algae (the Epilithic Algal Matrix (EAM), crustose coralline algae, and macroalgae), hydroids, sponges, and tunicates. Where no benthic organism was present, the substrate was identified as either sand, rubble or bare rock.

2.3.4. Fish Community Assessment

Underwater Visual Census (UVC) Stationary Point Count (SPC)

The density and community composition of reef fish were assessed using the UVC SPC method (Bohnsack and Bannerot, 1986 via Hylkema et al., 2020). For each of the six sampling locations, two independent UVC surveys were performed. The divers approached the area horizontally to record the fish species present (Fig. 6). All fish within a virtual cylindrical column, with a radius of 2 m, were recorded. The observer stopped outside the 2 m radius and started the stationary count timer, first recording all schools and then recording all other fish for five minutes (Bohnsack and Bannerot, 1986). Subsequently, the survey area was thoroughly searched for a further five minutes to record all cryptic fish residing within the refuge of the substrate. All fish assemblage surveys were carried out by the same observer.

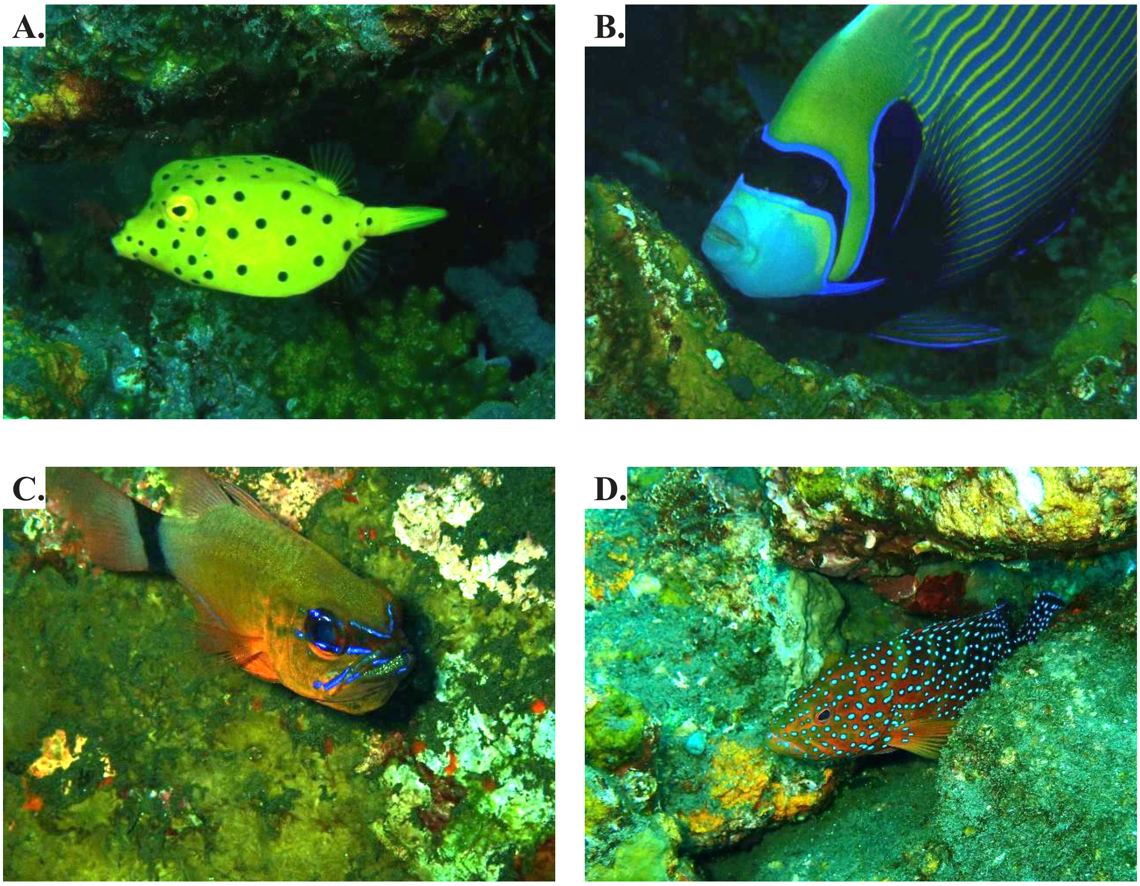

Figure 6. Fish species sampled in the artificial reef. **A**. Yellow boxfish juvenile (*Ostracion cubicus*) – Invertivore. **B**. Emperor angelfish (*Pomacanthus imperator*) – Invertivore. **C**. Ring-tailed cardinalfish (*Apogon aureus*) – Invertivore. **D**. Coral grouper (*Cephalopholis miniata*) – Piscivore. Photo credits: I Gede Sudarma

All fish were identified to species level and counted in terms of the maximum group size visible at any point during the survey. In this way, the number of individual fish and the species to which they belong were recorded. All species identified were categorised into their respective feeding guilds using the available feeding behaviour data on Fishbase (www.fishbase.org). Where a species was recorded feeding on multiple trophic levels, it was categorised based on the food item of the highest trophic level. Fish densities (m^{-2}) were calculated per survey by dividing the number of individual fish present in the survey by the area of the survey circle (12.57 m^2).

2.3.5. Data Analyses

Statistical analyses were performed in R version 4.0.5. (R Core Team, 2021) using R studio version 1.4.1106. One-way ANOVA tests were conducted using the aov function to detect significant differences in coral size, coral density, coral percentage cover, EAM percentage cover, and fish density both between sites and within the artificial reef. Coral percentage cover data were square root transformed while coral size and fish density data were log transformed to satisfy the assumption of normal data distribution.

Tukey's post-hoc tests were conducted to examine the significance of site or artificial reef age using the estimated marginal means function from the package "emmeans" (Lenth and Herve, 2019). The "emmeans" function allowed for the pairwise comparison of either the different sites or artificial reef ages to test for significant differences.

The "vegan" package was used to test for differences in community composition (Oksanen *et al.,* 2020). The Shannon-Wiener biodiversity indices (BDI) of both coral and fish communities for each site as well as each artificial reef age group were calculated using the "diversity" function. Coral community composition was analysed at genus level, while the fish community composition was analysed to species level. The "vegdist" function was used to calculate the Bray-Curtis dissimilarity metrics of the multivariate fish and coral count data. The "metaMDS" function was used to perform nonmetric multidimensional scaling based on the dissimilarity metrics. The "adonis" function was used to test whether the dissimilarity metrics between sites were significantly different. The "pairwiseadonis" package and function were used to test the pairwise differences in the dissimilarity metrics between sites (Arbizu, 2017).

2.4. Results

2.4.1. Benthic Community at Different Sites

In total, 2,469 corals representing 28 coral genera were counted and measured using the quadrat survey method across all four sites (Appendix 5). The corals in the East Natural Reef (ENR) and West Natural Reef (WNR) sites were significantly larger than corals in the Artificial Reef (AR) and Sand (S) (AR: 5.5 ± 0.2 SEM cm^2 ; S: 4.6 ± 1.6 cm^2 ; ENR: 80.3 ± 7.7 cm^2 and WNR: 63.1 ± 4.5 cm^2, one-way ANOVA, F(1, 3) = 555.9, $p < 0.05$) (Fig. 7) (Fig. 8A).

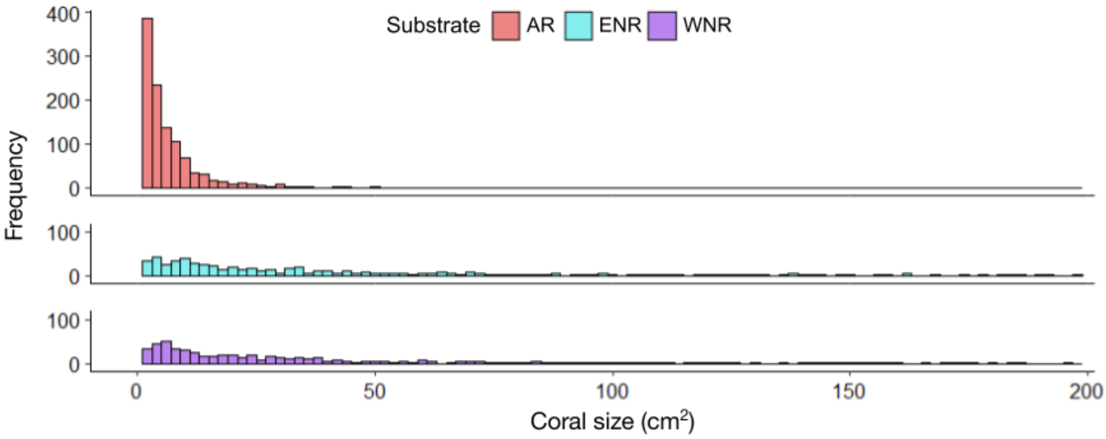

Figure 7. Size frequency distribution of coral size on artificial reefs, East and West natural reefs. Large corals (>200 cm^2) were only found in the natural reef sites and here 93 large corals are omitted for clarity (see Appendix 2 for complete figure). Corals found in the sand site have also been omitted and are as follows: 1.2, 1.3, 2.1, 5.1, 6.7, and 11.3 cm^2. Number of histogram bins = 100.

However, the density of corals in the artificial reef was significantly higher than the density found in all other sites (AR: 129.2 colonies ± 5.9 SEM m^{-2}; S: 0.6 ± 0.4 m^{-2}; ENR: 64.8 ± 4.3 m^{-2} and WNR: 62.6 ± 3.3 m^{-2}, one-way ANOVA, F(1, 3) = 171.4, $p < 0.05$) (Fig. 8B) (Table 2). More specifically, *Porites*, *Pocillopora*, and *Acropora* were the most abundant coral genera in the artificial reef and the densities of these corals was higher in the artificial reef than in all other sites (Fig. 9) (Table 2.)

Coral cover was significantly lower on artificial reefs compared to that in the east and west natural reef sites but significantly higher than the coral cover in the sand (AR: 7.1 ± 0.7 %; S: 0.03 ± 0.02 %; ENR: 52 ± 3 % and WNR: 39.5 ± 2.9 %, one-way ANOVA, F(1, 3) = 369.25, $p < 0.05$) (Fig. 8C). The percentage cover of EAM was significantly higher on the artificial reef than all other sites (AR: 53.8 ± 2.56 %; S: 0 ± 0 %; ENR: 20.8 ± 1.93 % and WNR: 32.4 ± 2.07 %, one-way ANOVA, F(1, 3) = 139, $p < 0.05$) (Fig. 8D).

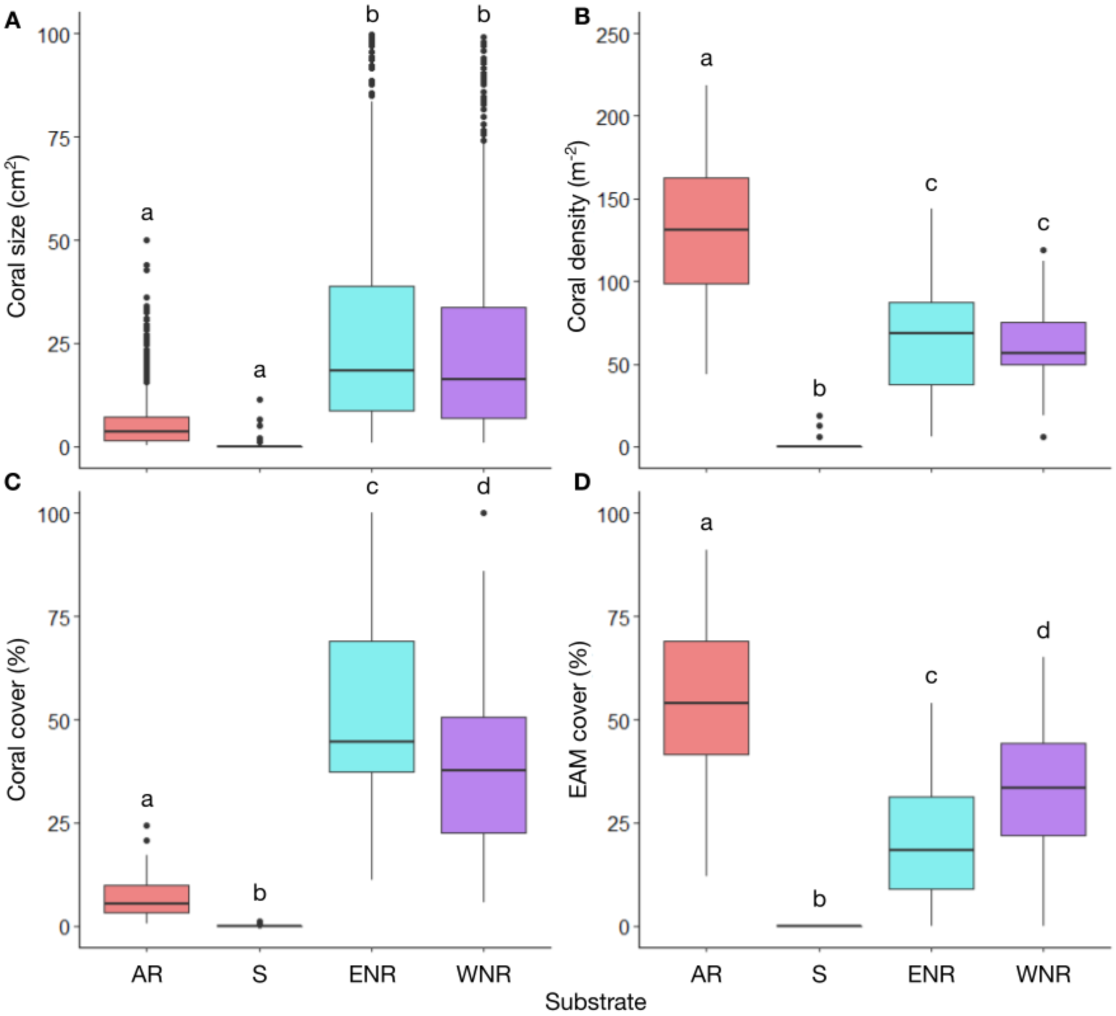

Figure 8. Boxplots showing coral size (A), coral density (number of colonies m^{-2}) (B), coral cover (C), and EAM cover (D) at different sites. Corals >100 cm^2 were only found in the natural reef sites and have been omitted from plot A for clarity (see Appendix 3 for complete figure). Letter groupings represent Tukey's pairwise post-hoc test results whereby sites sharing the same letter are not significantly different ($p < 0.05$). Boxplots show the median (horizontal middle line), the first and third quartiles (box), the lower and upper extremes (vertical lines), and the black dots represent outlying values (>1.5 interquartile range).

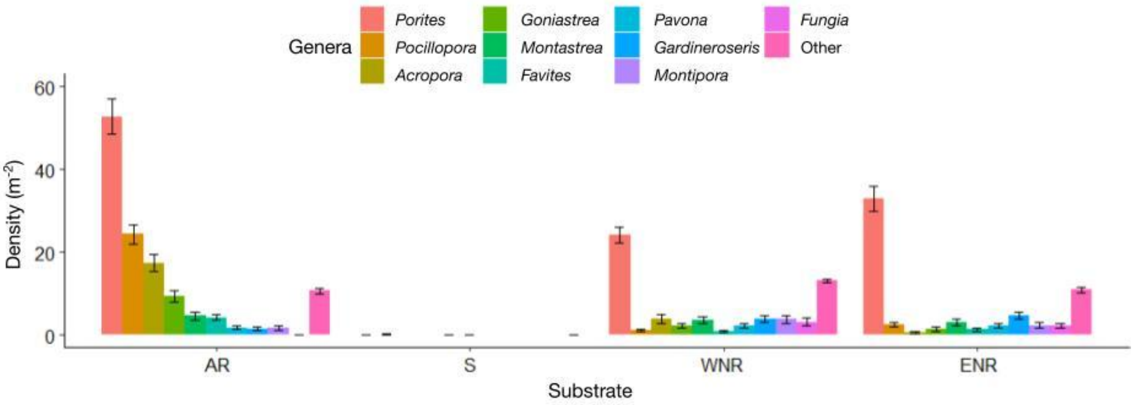

Figure 9. Bar plot of coral community composition on different sites. Error bars show ± SEM. The ten most abundant coral genera are shown in the plot while all other genera are grouped into 'Other'. The genera pooled into 'Other' are: *Psammocora, Leptoseris, Leptoria, Leptastrea, Turbinaria, Favia, Platygyra, Merulina, Lobophyllia, Symphyllia, Diploastrea, Echinopora, Galaxea, Stylophora, Coscinarea, Millepora, Plesiastrea*, *Podabacia* and unknown corals.

Table 2. Average density of corals sampled within four different sites. * Coral genera grouped into the "other" category.

Genus	Average coral density (m^{-2}) (± SEM)			
	Artificial Reef	Sand	East Natural Reef	West Natural Reef
Porites	52.8 ± 4.2	0.1 ± 0.1	32.9 ± 3	24.3 ± 1.9
Pocillopora	24.5 ± 2.3	0.21 ± 0.21	2.5 ± 0.52	1.1 ± 0.31
Acropora	17.5 ± 2	-	0.73 ± 0.26	3.9 ± 1.1
Goniastrea	9.5 ± 1.3	-	1.5 ± 0.45	2.3 ± 0.44
Montastrea	4.7 ± 1	0.1 ± 0.1	3.1 ± 0.9	3.6 ± 0.8
Favites	4.3 ± 0.72	0.1 ± 0.1	1.4 ± 0.42	0.94 ± 0.33
Pavona	1.9 ± 0.5	-	2.4 ± 0.58	2.3 ± 0.47
Gardineroseris	1.6 ± 0.44	-	4.8 ± 0.83	4 ± 0.7
Montipora	1.7 ± 0.53	-	2.4 ± 0.6	3.9 ± 0.9
Fungia	0.1 ± 0.1	-	2.2 ± 0.53	3.2 ± 0.87
Psammocora *	2.8 ± 0.73	-	1.9 ± 0.62	1.5 ± 0.45
Leptoseris *	0.21 ± 0.15	-	-	0.21 ± 0.15
Leptoria *	0.63 ± 0.24	-	0.63 ± 0.24	0.73 ± 0.4
Leptastrea *	1.3 ± 0.38	-	0.21 ± 0.15	-
Turbinaria *	-	-	0.73 ± 0.3	1 ± 0.4
Favia *	0.2 ± 0.15	-	0.63 ± 0.29	1.1 ± 0.35
Platygyra *	0.63 ± 0.29	-	1.1 ± 0.41	1.5 ± 0.73
Merulina *	-	-	1.1 ± 0.38	0.73 ± 0.54
Lobophyllia *	-	-	1.4 ± 0.47	0.63 ± 0.29
Symphyllia *	-	-	0.31 ± 0.18	0.63 ± 0.24
Diploastrea *	-	-	0.31 ± 0.18	0.21 ± 0.15
Echinopora *	0.1 ± 0.1	-	0.42 ± 0.42	0.1 ± 0.1
Galaxea *	-	-	0.1 ± 0.1	0.31 ± 0.18
Stylophora *	-	-	-	0.1 ± 0.1
Coscinarea *	-	-	-	0.1 ± 0.1
Millepora *	-	-	-	0.31 ± 0.18
Plesiatrea *	2.4 ± 0.74	-	0.63 ± 0.24	1.67 ± 0.44
Podabacia *	-	-	-	0.1 ± 0.1
Unknown *	2.5 ± 0.58	0.1 ± 0.1	1.5 ± 0.48	2.2 ± 0.63
Total	129.2 ± 5.9	0.6 ± 0.4	64.8 ± 4.3	62.6 ± 3.3

East and West natural reef sites had the highest coral community Shannon-Wiener biodiversity indices (2.4 and 2.1 respectively) while the coral biodiversity was slightly lower on the artificial reef (1.9) and the sand was the lowest (1.6).

The coral composition was significantly different between sites (PERMANOVA, F(1,3) = 9.3, $p < 0.001$). While the respective coral compositions of the two natural reef sites were not significantly different to each other, the benthic community sampled on the artificial reef and that of the sand were significantly different to each other and the natural reef sites (Fig. 10).

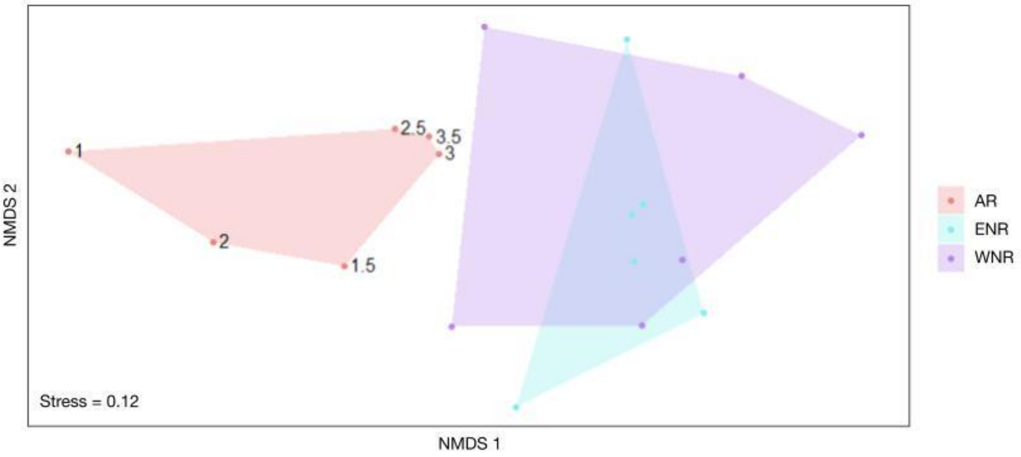

Figure 10. Multidimensional scaling plot of coral community composition in three sites: artificial reef, east natural reef and west natural reef. The coral community on the sand site has been omitted for clarity due to the low number of corals present (n = 6). The age of the artificial reef in years has been labelled.

2.4.2. Benthic Community in the Artificial Reef

The 1,240 corals counted in the six artificial reefs of different ages belonged to 18 genera. Corals on the older artificial reef (≥3 years) were significantly larger than corals on newer artificial reef (<3 years) (1: 2.4 ± 0.2 SEM cm^2; 1.5: 3.1 ± 0.2 cm^2; 2: 4.1 ± 0.3 cm^2; 2.5: 4.4 ± 0.3 cm^2; 3: 8.2 ± 0.4 cm^2 and 3.5: 7.8 ± 0.4 cm^2, one-way ANOVA, F(1,5) = 65, $p < 0.05$) (Fig. 11) (Fig. 12A).

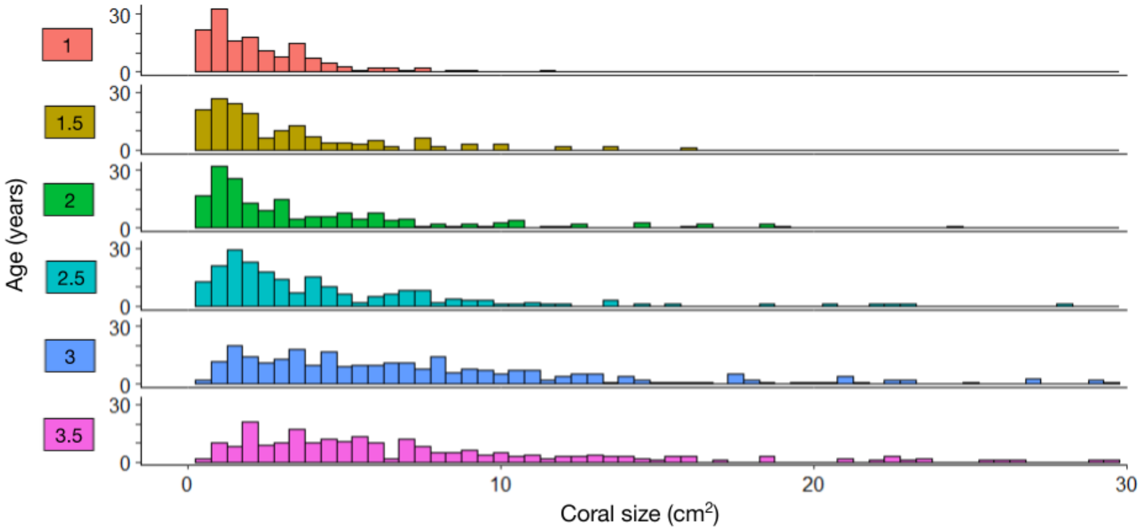

Figure 11. Size frequency distribution of corals on artificial reefs of different ages. Corals larger than $30cm^2$ from 3 & 3.5 years were omitted for clarity (see Appendix 4 for full figure). Number of bins = 60.

The newest artificial reef (1 year) had a significantly lower coral density than the older artificial reefs (≥3 years) (1: 93.1 colonies ± 13.6 SEM m^{-2}; 1.5: 102.5 ± 9.4 m^{-2}; 2: 116.9 ± 10.2 m^{-2}; 2.5: 133.8 ± 11.9 m^{-2}; 3: 181.3 ± 11.4 m^{-2} and 3.5: 147.5 ± 11.7 m^{-2}, one-way ANOVA, F(1,5) = 8, $p < 0.05$) (Fig. 12B) (Fig. 13) (Table 3). More specifically, *Porites, Pocillopora*, and *Acropora* were the most abundant coral genera in the artificial reef (Table 3). The density of *Porites* corals was lowest in the newest artificial reef and generally increased as the age of the structure increased, but this trend was not present in *Pocillopora* or *Acropora* corals (Fig. 13). Both *Pocillopora* and *Acropora* recruited to the newest structures in high densities but were less abundant in older structures (Fig. 13) (Fig. 14).

The older artificial reefs (≥3 years) had a significantly higher average coral cover percentage than the newer artificial reefs (<3 years) (1: 2.2 ± 0.5 SEM %; 1.5: 3.2 ± 0.4 %; 2: 4.8 ± 0.6 %; 2.5: 5.8 ± 0.5 %; 3: 14.8 ± 1.7 % and 3.5: 11.4 ± 1 %, one-way ANOVA, F(1,5) = 39.3, $p < 0.05$) (Fig. 12C). The newer artificial reefs (≤3 years) had a significantly higher average EAM cover percentage than the older artificial reefs (>3 years) (1: 80.6 ± 2.4 SEM %; 1.5: 50.8 ± 4.9 %; 2: 56.8 ± 3.9 %; 2.5: 55.4 ± 4.9 %; 3: 34.1 ± 6.2 % and 3.5: 44.9 ± 4 %, one-way ANOVA, F(1,5) = 11.8, $p < 0.05$) (Fig. 12C).

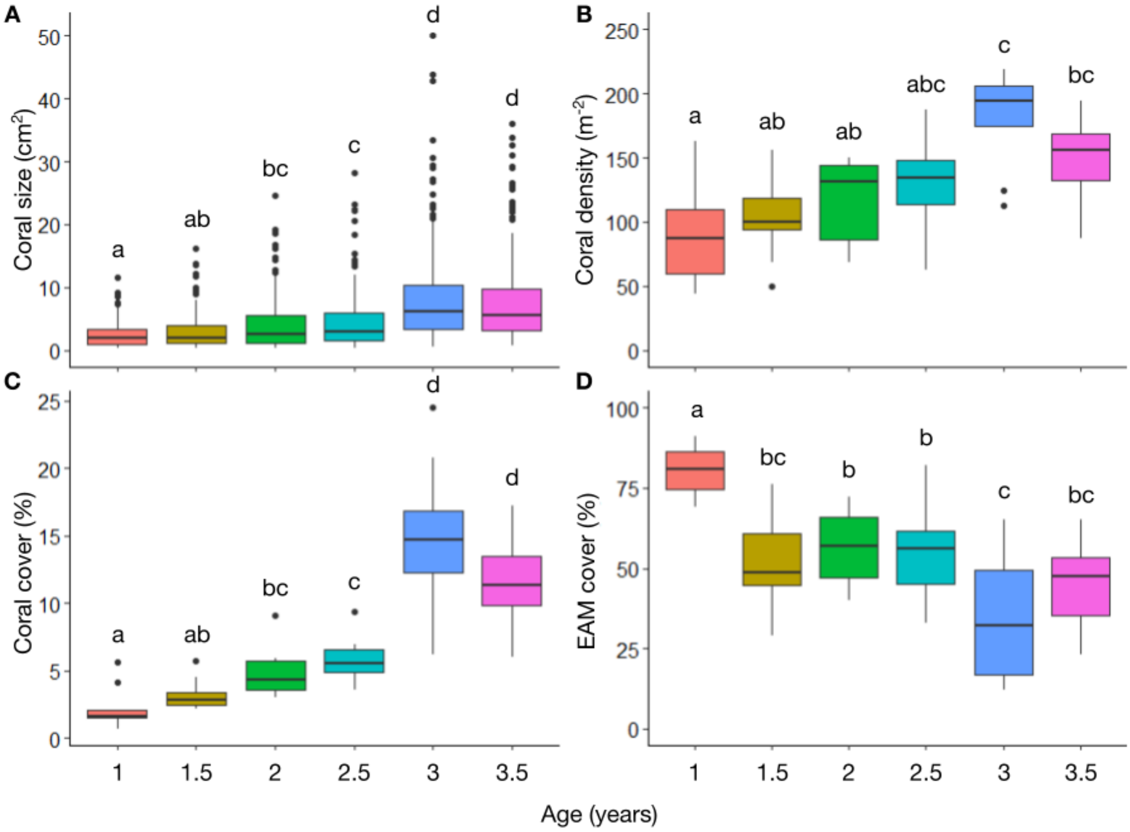

Figure 12. Boxplots showing coral size (A), coral density (B), relative coral cover (C), and relative EAM cover (D) on artificial reefs of different ages (legend shows age in years). Letter groupings represent Tukey's pairwise post-hoc test results whereby age groups sharing the same letter are not significantly different ($p < 0.05$). Boxplots show the median (horizontal middle line), the first and third quartiles (box), the lower and upper extremes (vertical lines), and the black dots represent outlying values (>1.5 interquartile range).

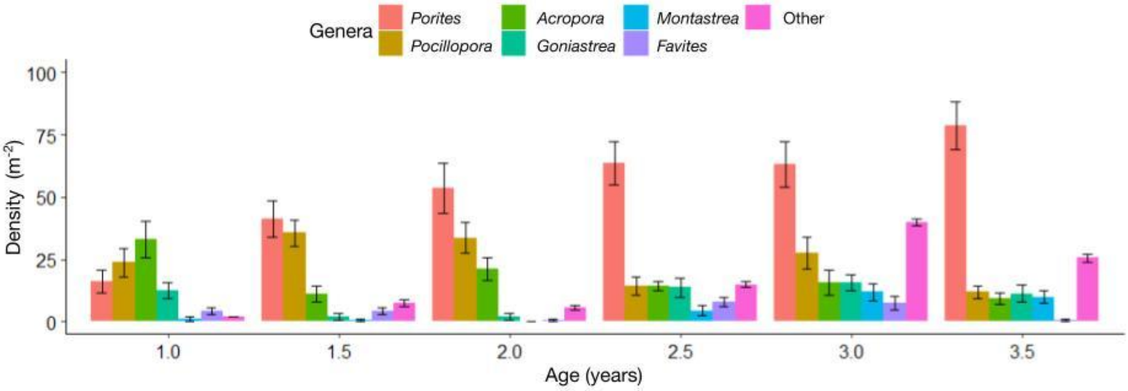

Figure 13. Bar plot of the coral community composition on artificial reefs of different ages. Error bars show ± SEM. The six most abundant coral genera are shown in the plot while all other genera are grouped into 'Other'. The genera pooled into 'Other' are: *Pavona, Gardineroseris, Montipora, Fungia, Psammocora, Leptoseris, Leptoria, Leptastrea, Favia, Platygyra, Echinopora*, *Plesiastrea,* and unknown corals.

The Shannon-Wiener biodiversity index of coral genera was lower in the newer structures (≤2 years) compared to the older structures (>2 years). 1 year – 1.6, 1.5 years – 1.5, 2 years – 1.3, 2.5 years – 1.8, 3 years – 2.2, 3.5 years – 1.8.

Table 3. Average density of coral recruits on artificial reef structures of different ages (years). * Coral genera grouped into the "other" category.

Genus	Average coral density (m^{-2}) (± SEM)					
Age (years)	1	1.5	2	2.5	3	3.5
Porites	16.3 ± 4.6	41.3 ± 7.2	53.8 ± 10	63.8 ± 8.6	63.1 ± 9.2	78.8 ± 9.8
Pocillopora	23.8 ± 5.7	35.6 ± 5.4	33.8 ± 6	14.4 ± 3.5	27.5 ± 6.3	11.9 ± 2.5
Acropora	33.1 ± 7.3	11.3 ± 3.2	21.3 ± 4.6	14.4 ± 1.9	15.6 ± 5	9.4 ± 2.3
Goniastrea	12.5 ± 3.2	1.9 ± 1.3	1.9 ± 1.3	13.8 ± 3.8	15.6 ± 3.3	11.3 ± 3.5
Montastrea	1.3 ± 0.83	0.63 ± 0.63	-	4.4 ± 2.1	11.9 ± 3.5	10 ± 2.5
Favites	4.4 ± 1.3	4.4 ± 1.3	0.63 ± 0.63	8.1 ± 1.9	7.5 ± 2.6	0.63 ± 0.63
Pavona *	-	2.5 ± 1.4	1.9 ± 1	1.9 ± 1.3	1.9 ± 1.3	3.1 ± 1.7
Gardineroseris *	-	0.63 ± 0.63	-	0.63 ± 0.63	5 ± 1.6	3.1 ± 1.4
Montipora *	0.63 ± 0.63	1.9 ± 0.95	1.3 ± 0.83	0.63 ± 0.63	3.8 ± 2.7	1.9 ± 0.95
Fungia *	-	0.63 ± 0.63	-	-	-	-
Psammocora *	-	0.63 ± 0.63	0.63 ± 0.63	2.5 ± 1	11.9 ± 2.5	1.3 ± 1.3
Leptoseris *	-	-	-	-	-	1.3 ± 1.3
Leptoria *	-	0.63 ± 0.63	-	0.63 ± 0.63	1.9 ± 0.95	0.63 ± 0.63
Leptastrea *	-	-	-	3.1 ± 1	2.5 ± 1.4	1.9 ± 0.95
Favia *	-	-	-	0.63 ± 0.63	0.63 ± 0.63	-
Platygyra *	-	-	-	0.63 ± 0.63	1.9 ± 1.3	1.3 ± 0.8
Echinopora *	-	-	-	0.63 ± 0.63	-	-
Plesiatrea *	-	-	1.3 ± 1.3	0.63 ± 0.63	6.3 ± 3.2	6.3 ± 2.1
Unknown *	1.3 ± 1.3	0.63 ± 0.63	0.63 ± 0.63	3.1 ± 1.7	4.4 ± 2.1	5 ± 1.3
Total	93.1 ± 13.6	102.5 ± 9.4	116.9 ± 10.2	133.8 ± 11.9	181.3 ± 11.4	147.5 ± 11.7

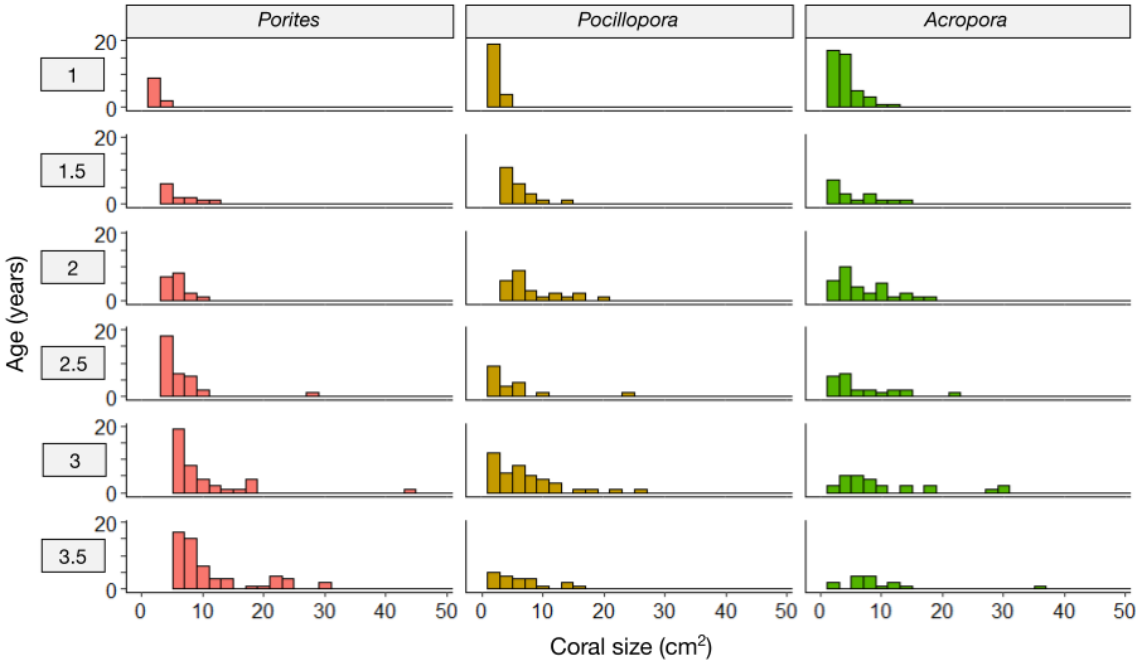

Figure 14. Size frequency distribution for three coral genera on artificial reefs of different ages (years). Number of histogram bins = 30.

2.4.3. Fish Community at Different Sites

In total, 11,383 individual fish representing 137 species were counted during the underwater visual census stationary point counts at all four sites (Appendix 6). The highest densities of fish were found in the East and West natural reef sites while the fish densities in the artificial reef and sand were significantly lower (AR: 11.8 fish ± 2.8 SEM m^{-2}; S: 6.4 ± 1 m^{-2}; ENR: 30.6 ± 6.8 m^{-2}; WNR: 26.8 ± 4.4 m^{-2}, one-way ANOVA, F(1,3) = 17.7, $p < 0.001$) (Fig. 15) (Fig. 16) (Table 4). Piscivores were the most abundant feeding guild in the artificial reef while planktivores were more abundant in the natural reef sites (Fig. 16) (Table 4).

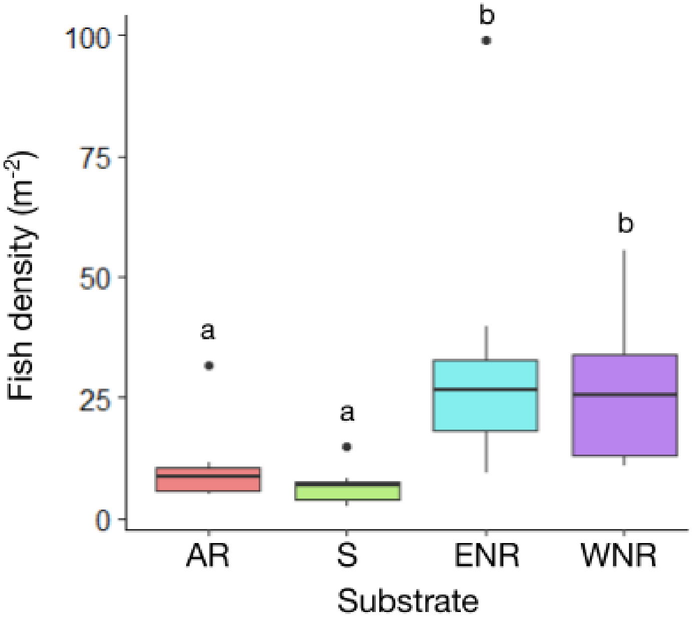

Figure 15. Box plot of fish density at different sites. Letter groupings represent Tukey's pairwise post-hoc test results whereby sites sharing the same letter are not significantly different ($p < 0.05$). Boxplots show the median (horizontal middle line), the first and third quartiles (box), the lower and upper extremes (vertical lines), and the black dots represent outlying values (>1.5 interquartile range).

Fish communities on the artificial reef, sand, East and West natural reef sites had Shannon-Wiener biodiversity indices of 2.8, 2.9, 2.5, and 2.7 respectively.

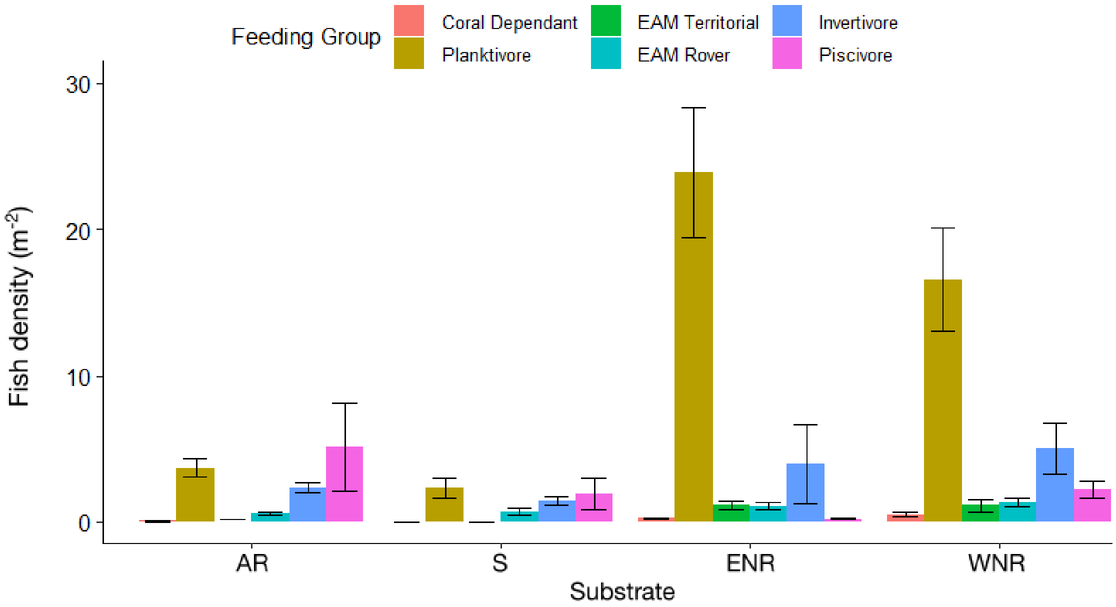

Figure 16. Bar plot of fish community composition on different sites. Fish have been categorised into their respective feeding guilds.

Table 4. Average density of fish feeding guilds within fish communities at four different sites.

Trophic group	Average fish density (m^{-2}) (± SEM)			
	Artificial Reef	Sand	East Natural Reef	West Natural Reef
Coral Dependant	0.04 ± 0.02	0.007 ± 0.007	0.25 ± 0.06	0.5 ± 0.2
Planktivore	3.71 ± 0.7	2.3 ± 0.7	23.9 ± 4.5	16.6 ± 3.6
EAM Territorial	0.01 ± 0.01	-	1.2 ± 0.3	1.1 ± 0.4
EAM Rover	0.5 ± 0.09	0.7 ± 0.2	1.1 ± 0.3	1.3 ± 0.3
Invertivore	2.3 ± 0.3	1.5 ± 0.3	4 ± 2.7	5 ± 1.8
Piscivore	5.1 ± 3	1.9 ± 1	0.2 ± 0.05	2.2 ± 0.6
Total	11.8 ± 2.8	6.4 ± 1	30.6 ± 6.8	26.8 ± 4.4

The fish composition was significantly different between sites (PERMANOVA, F(1,3) = 4, $p < 0.001$). While the respective fish compositions of the two natural reef sites were not significantly different to each other, the fish community sampled on the artificial reef and that of the sand were significantly different to each other and the natural reef sites (Fig. 17).

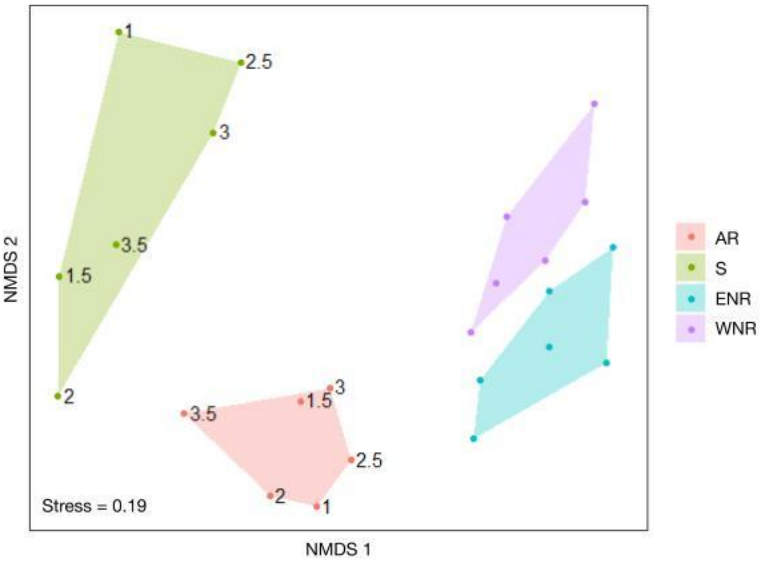

Figure 17. Multidimensional scaling plot of fish community composition in four sites: Artificial Reef (AR), Sand (S), East Natural Reef (ENR) and West Natural Reef (WNR). The age of the artificial reef and the sand site to which it was paired have been labelled.

2.4.4. Fish Community in the Artificial Reef

In total, 1,773 individual fish representing 70 species were counted within the artificial reef across all six groups. The newest artificial reefs (1 year) had significantly higher densities of fish than all older artificial reefs (1: 31.7 fish ± 0.04 SEM m^{-2}; 1.5: 5.25 ± 0; 2 m^{-2}: 10.9 ± 0.8 m^{-2}; 2.5: 7.4 ± 1.3 m^{-2}; 3: 7 ± 1.9 m^{-2} and 3.5: 8.3 ± 1.5 m^{-2}, one-way ANOVA, F(1,5) = 16.5, $p < 0.01$) (Fig. 18) (Fig. 19) (Table 5). More specifically, the high densities of piscivores were responsible for the generally high fish densities at the newest structures (Fig. 19).

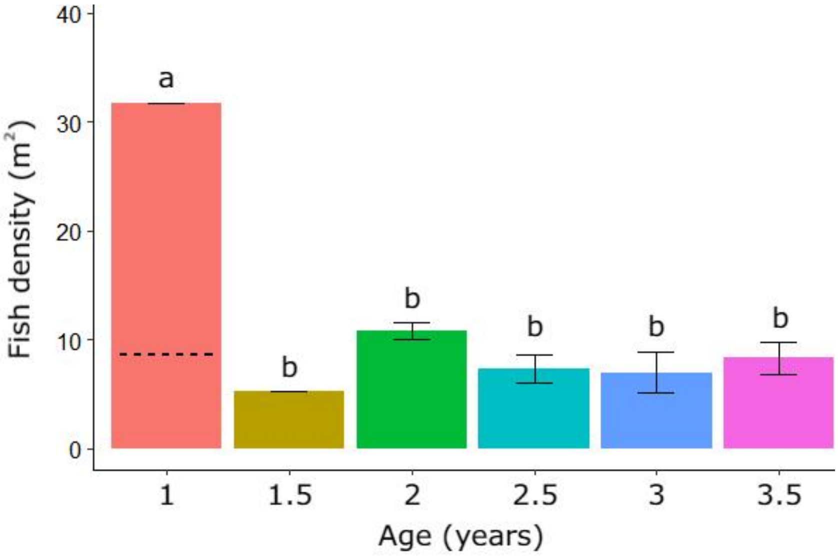

Figure 18. Bar plot of fish density on artificial reefs of different ages. Dashed line represents the density of fish at the newest artificial reef with *Lutjanus rufolineatus* excluded. Letter groupings represent Tukey's pairwise post-hoc test results whereby age groups sharing the same letter are not significantly different ($p < 0.05$).

In terms of biodiversity, Shannon-Wiener biodiversity indices were calculated and are as follows: 1 year – 1.2, 1.5 years – 3.1, 2 years – 2.8, 2.5 years – 2.1, 3 years – 3.1, and 3.5 years – 2.5.

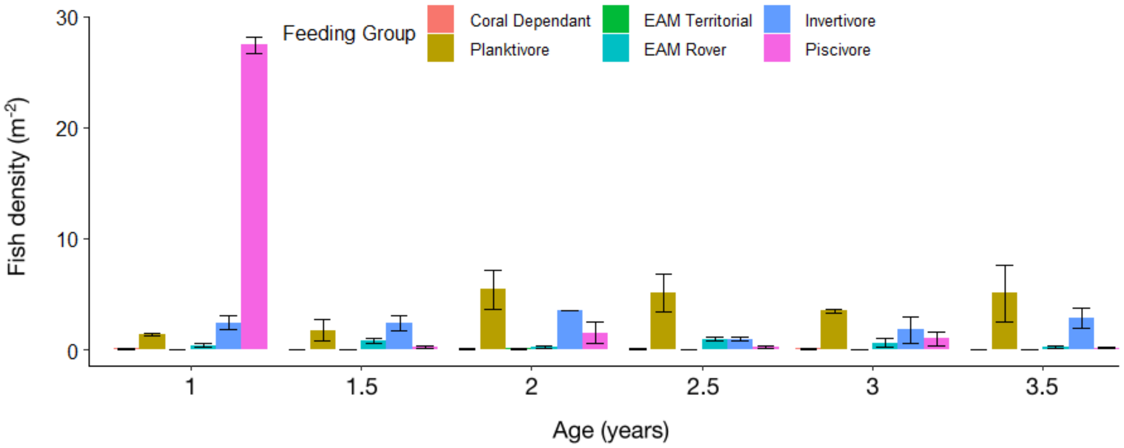

Figure 19. Bar plot of the fish community composition on artificial reefs of different ages. Fish have been categorised into their respective feeding guilds.

Table 5. Average density of fish sampled on artificial reef structures of different ages (years).

Trophic group	Average fish density (m^{-2}) (± SEM)					
	1	1.5	2	2.5	3	3.5
Coral Dependant	0.08 ± 0.08	-	0.04 ± 0.04	0.04 ± 0.04	0.08 ± 0.08	-
Planktivore	1.4 ± 0.1	1.8 ± 1	5.4 ± 1.8	5.1 ± 1.7	3.5 ± 0.16	5.1 ± 2.6
EAM Territorial	-	-	0.08 ± 0.08	-	-	-
EAM Rover	0.4 ± 1.6	0.84 ± 0.2	0.24 ± 0.08	0.96 ± 0.16	0.6 ± 0.24	0.24 ± 0.08
Invertivore	2.4 ± 0.6	2.4 ± 0.68	3.6 ± 0	0.96 ± 0.16	1.8 ± 1.2	2.8 ± 0.92
Piscivore	27.4 ± 0.76	0.24 ± 0.08	1.5 ± 0.96	0.28 ± 0.12	1 ± 0.6	0.16 ± 0.08
Total	31.7 ± 0.04	5.3 ± 0	10.9 ± 0.8	7.4 ± 1.3	7 ± 1.9	8.3 ± 1.5

2.5. Discussion

This study clearly reveals the potential of artificial reefs as a conservation tool for habitat restoration and recovery in a severely degraded coral reef ecosystem. The comparison of natural reef sites to artificial reef sites of increasing time since deployment contextualises an important long-term goal and can provide an insight into the reef communities developing on the artificial reef over time. Although they are currently distinct, the coral community developing on the artificial reef does show a general trend towards resembling coral communities found in the natural reefs.

A higher density of corals was found on the artificial reef than the natural reef, showing that, where sites are not recruitment limited, artificial reef structures can be an effective way to facilitate coral recruitment. Here, the new substrate provided by the artificial reef allowed for coral recruits to settle and survive in an area where they would have otherwise been smothered in the sand substrate (Brown and Dunne, 1988). The monitoring of the change in coral community over time is key to understanding coral reef succession and here the sampling of artificial reef structures deployed 6 months apart illustrates this change. The increase in coral density on older structures suggests that coral recruits will continue to settle onto the artificial reef over time.

The density of corals on artificial reefs within the same year since deployment (1-1.5, 2-2.5, & 3-3.5 years) was not significantly different, suggesting that they experienced the same number of spawning events. However, the major mass spawning event in this area usually takes place in November (Keith *et al.,* 2016) (one month after the 1.5, 2.5, and 3.5 reefs were deployed) and so despite being in the water for one month prior to the spawning event these reefs were not significantly different to the reefs deployed six months later in April. This gives an insight into the conditioning period required on bare substrates before coral larvae will settle (Grigg and Maragos, 1974; Pearson, 1981). Clark and Edwards (1994) suggest that artificial reefs should be deployed three months before a spawning event to allow for biofilm development and optimise coral recruitment.

The average density of coral recruits on this artificial reef at one year since deployment (93.1 ± 13.6 SEM m^{-2}) is comparatively high compared to others within the Indo-Pacific with the same time since deployment (Fadli *et al.,* 2012: 53 ± 3.2 SEM m^{-2}), suggesting that the design and location of this artificial reef allowed for particularly effective coral recruitment. Although the density was high, the small size of corals means that the coral cover of artificial reefs is not yet comparable to that of the natural reefs which is to be expected given the relatively short time since deployment. Pearson (1981) recorded a similar pattern on *Acanthaster planci* denuded natural reefs which were quickly recolonised by coral recruits resulting in a high density of relatively small corals. Three years after the disturbance coral cover was still low (2.6%) but this quickly increased and within six years of the original disturbance coral cover was recorded at 60% (Pearson, 1981). This is consistent with the two-phase recovery pattern often found in recovering reef systems in which an initial phase of slow recovery post disturbance is followed by a second phase of rapid increases in coral cover (Warne *et al.,* 2021). These observations of coral recovery dynamics in natural reefs suggest that the coral community trajectories seen here in the artificial reef may not remain linear and could become more similar to the natural coral reef communities sooner than would be expected.

Further monitoring of the artificial reef can evaluate the survival of coral recruits over longer timescales. Where post-settlement mortality is low it would be expected that the benthic succession would continue with corals growing larger and new coral recruits settling onto the substrate, leading to an increase in coral cover (Halford *et al.,* 2004; Gilmour *et al.,* 2013). In all cases where the quadrat overlapped a coral, only the coral area within the bounds of the quadrat was measured. This caused the average coral size to be underestimated at all sites as only the visible section of a coral was measured (Leujak and Ormond, 2007). This effect was greatest in the natural reef as many corals found there were much larger than the quadrat and in some cases completely filled the quadrat boundaries, resulting in a maximum coral size of 1600 cm^2 and a coral cover of

100%, while the density was 1. Despite this underestimate of coral size the corals in the natural reef were still significantly larger than those in the artificial reef.

Here, the average size of corals on the artificial reef generally increased as the time since deployment increased. This suggests that, not only are the artificial reefs effective in facilitating coral recruitment, the survivorship of coral recruits is also high enough to an extent where they can grow to significantly larger sizes. The conservation value of an artificial reef is greatly increased where corals grow to the point where they reach sexual maturity and become a source of coral recruits. Sexually propogated *Acropora* corals have been recorded reaching sexual maturity after three years (Wallace, 1985) with a minimum diameter of 12.3 cm (Baria *et al.,* 2012), suggesting that coral communities on artificial reefs are likely to reach sexual maturity before the development of the climax community.

Nevertheless, the coral community recorded on the artificial reef was found to be less biodiverse and significantly different to that of the natural reef. This is likely due to the absence of some coral genera that are found in the natural reef but have not yet been recorded on the artificial reef. Grigg and Maragos (1974) found some coral species such as *Montipora verrucosa* were absent on lava flows younger than 10 years indicating that reef substrates may need to be 'conditioned' before some species can settle. The general positive trajectory of coral community development on the artificial reef suggests the artificial reef coral communities will become more similar to those found on the natural reef over time. As an artificial reef experiences more coral spawning events, the recruitment of new corals would be expected to increase the biodiversity of coral communities and become more similar to the coral communities found in the natural reefs (Thanner *et al.,* 2006). The identification of corals to genus level in this present study limited the recorded coral biodiversity at all sites and if corals were identified to species level the biodiversity for all sites would likely be higher.

The epilithic algal matrix in the artificial reef covered significantly more area per m^2 than on natural reefs due to the input of new hard substrate and complex topography of the artificial reef (Young *et al.,* 2015). While this algae matrix does compete with corals for space on the substrate, these pioneer species play an important role in coral reef succession. The presence of this algal matrix is important for herbivorous reef species (Pratchett *et al.,* 2008) which graze on the algae, creating space and allowing corals to settle (Smith *et al.,* 2010; Doropoulos *et al.,* 2016; Holbrook *et al.,* 2016). Analogous to natural reef recovery (Pearson, 1981; Sato *et al.,* 2018), the continued recruitment of new corals and the growth of settled corals on artificial reefs over time leads to increased coral cover and biodiversity while reducing the EAM cover. This trend was evident from the analyses of artificial reef structures deployed at 6-month intervals. In general, as the time since deployment increased, the coral cover increased, the EAM cover decreased, and the biodiversity increased. This pattern is likely due to the recruitment of new corals which out-compete the early pioneer algae and can increase coral biodiversity where the new recruits belong to a genus previously absent from the artificial reef (Clark and Edwards, 1994).

Due to the limited space on artificial reefs, at some point the successional pattern of increased coral cover and richness over time will slow and stabilise to reach the climax community as recorded on lava flows in Hawaii (Grigg and Maragos, 1974). As the corals grow they limit the settlement of new coral recruits and can even out-compete other corals through overtopping (Sheppard, 1979) or direct-contact competition (Lang, 1973), potentially leading to a reduction in coral density. Over time, the stabilisation of successional processes could cause the artificial reef benthic community structure and composition to become more similar to the climax coral community recorded here in the natural reef. This pattern of succession was recorded by Pearson (1981) on *Acanthaster planci* denuded reefs in which the number of corals had increased to 528, coral cover had risen to 60.0% and average colony size was 11.6 cm after six years but in less than one year later the number of corals fell to 119 while cover cover increased to 80% and average coral size increased to 36.7 cm. Over a time frame of seven years, this recovering coral community became more similar to the climax communities found in natural, undisturbed reefs, with a relatively low coral density due to the greater coral cover and average colony size.

Porites, *Acropora* and *Pocillopora* are the most abundant coral genera in the artificial reef and *Porites* is also abundant in the natural reef sites. However, *Pocillopora* and *Acropora* were both relatively rare in the natural reefs, suggesting that these corals have a relatively high fecundity and consequently have the ability to colonise new substrates to a greater extent. This could be particularly true for the *Pocillopora* coral genus in which some species utilise ‘brooding’ reproductive techniques with relatively fewer, larger, and less mobile asexual larvae that limited to recruitment over short distances (Jones *et al.,* 2009). Alternatively, these less abundant corals may have recruited from further reefs within the metacommunity by employing ‘broadcasting’ reproductive techniques. Some coral species belonging to *Pocillopora* and *Acropora* coral families have been identified as ‘broadcasting’ corals whose relatively smaller, highly mobile larvae disperse in large numbers over tens of kilometres (Jones *et al.,* 2009) and have been shown to maintain coral populations within the metacommunity (Ayre *et al.,* 1997). At the very least, the physical and/or demographic factors that naturally resulted in the coral composition found in the natural reef, could now be driving coral community composition developing on the artificial reef. Physical factors such as high wave action and the associated sedimentation, which was found to limit the settlement of *Acropora millepora* (Ricardo *et al.,* 2017), could reduce the number of competitors and lead to a higher density of *Porites* corals. Demographically, there could be an abundance of *Porites* corals within the reef metacommunity which supply greater numbers of recruits to these reefs.

There was also a clear pattern in terms of the change in coral communities on artificial reefs over time. The density of *Porites* corals increased as the time since artificial reef deployment increased, perhaps due to the survival of settled corals and the further recruitment of new individuals over time. Meanwhile, the densities of *Acropora* and *Pocillopora* corals did not share this pattern of increasing density and instead showed little difference over time. One explanation for this difference is that these coral genera are pioneer coral recruits, colonising the substrate very effectively within the first year of deployment where there is relatively little competition (Wallace, 1983; Clark and Edwards, 1994). *Pocillopora* corals specifically have been identified as an opportunistic genus with life history traits that allow for the quick colonisation of newer substrates (Jouval *et al.,* 2020). The further colonisation of these pioneer corals may be limited by the presence of settled coral colonies or by the growth of the epilithic algal matrix.

The survival of these species past this early successional stage appears to be lower given the low densities of the larger surviving colonies compared to the high recruit densities. Perhaps over time, with increased competition from coral recruits, the pioneer species are outcompeted. This pattern fits within the competition-colonisation trade-off explained by the patch paradigm of metacommunity theory (Logue *et al.,* 2011). The comparatively low density of *Pocillopora* and *Acropora* corals in the natural reef sites suggests that these corals have a lower competitive ability and so despite their early success their numbers will diminish over time, although not entirely. Alternatively, physical conditions in the reef can reduce the competitive ability of some species as seen following extensive disturbance where recovering coral communities in sheltered reefs were dominated by *Acropora* corals while *Porites* and other species were more abundant in exposed reefs (Tomascik *et al.,* 1996). The high sedimentation associated with wave exposure has been shown to limit the growth of *Acropora* corals in particular (Nakajima *et al.,* 2013) and this reduced competitive ability may help to explain the dominance of *Porites* corals in this area.

While the artificial reef is effective in supplying the base substrate and basic habitat complexity, the absence of large corals means that they cannot match natural reefs where the habitat complexity is provided by climax coral communities. This lesser habitat complexity is perhaps the reason for the significantly lower fish densities found in artificial reefs when compared to the natural reefs (Holbrook *et al.,* 2002; Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006). The comparison of these fish densities to other studies on artificial reefs is challenging due to the difficulty in standardising the varied size of survey areas between studies given the differences in search efficiency (Samoilys and Carlos, 2000). Meanwhile, the density of fish in the artificial reef was found to be not significantly different to that in the sand substrates. In this study, the sand substrate sites are made up of the areas between artificial reef aggregations and these areas can share the large protective space provided by the artificial reefs. As a result of this protective space, the adjacent sand areas can benefit in terms of fish density from the presence of the artificial reef. In terms of this study, the adjacent sand areas used as a representation of habitats pre-deployment were contaminated by the spillover of fish species into sandy areas around the artificial reefs. This shows the value of surveying the planned restoration area beforehand to have a true representation of the effect that restoration efforts have.

At this point we can see that the artificial reef substrate does lack in some aspects of habitat provision given the significant difference between fish communities in the artificial reef compared to the natural sites. This difference is perhaps linked to the lower coral cover in artificial reef groups given that coral dependent fish require higher coral cover (Boström-Einarsson *et al.,* 2018). It may also be the case that the highly competitive territorial species found within the natural reefs have a low colonisation ability and so these species are also absent from the artificial reefs, befitting the patch paradigm of metacommunity theory (Logue *et al.,* 2011). The similarity between artificial reef and sand sites also suggests that the fish inhabiting the artificial reef are not dependent on the coral itself. Perhaps as the corals continue to grow in size and increase coral cover on the artificial reef it would be possible to see the change in the fish community.

While very few coral dependent fish species were recorded on artificial reefs compared to the natural reef, the main difference between these fish populations appears to be the higher density of planktivores in the natural reef sites. Specifically, the large schools of fusiliers (*Caesionidae*) that were often found in natural reefs were less abundant in most artificial reef sites. Interestingly, the planktivorous feeding preferences of these fish would suggest they are not attracted by the higher habitat complexity in the natural reef, or at least not limited by the lesser habitat complexity in the artificial reef given that they feed within the water column. Instead, perhaps the zooplankton upon which these schools feed on accumulate at higher densities in the natural reef, which could explain the high densities of planktivores found at these sites (Hobson and

Chess, 1978). To investigate this further, water column samples could be assessed in terms of biomass within the artificial and natural reefs to determine any differences in the numbers of plankton between the sites.

The density of fish at the one year old artificial reef was significantly higher than all other artificial reef sites, and even higher than most natural reef sites. The community at the newest artificial reef in particular was dominated by large schools of piscivorous snapper (*Lutjanidae*). These piscivore schools were present before the deployment of the one year old structures (pers. obs.) and so their presence is likely a virtue of the older artificial reefs (not surveyed here) adjacent to the newest structures. So, while these populous schools of predators do show that artificial reefs can support large fish populations, their presence is not a result of or limited to the newest artificial reef. In this sense, when assessing fish community compositions on nearby artificial reefs on small scales it may be more effective to assess only the small, cryptic species rather than the larger more mobile species (McClanahan *et al.,* 2007). Nevertheless, these results showcase the ability of artificial reefs to support relatively large populations of fish. Interestingly, the most abundant fish species in the artificial reef (golden-lined snapper - *Lutjanus rufolineatus*) was one of three fish species found in the artificial reef that were not recorded in any of the natural reef surveys.

With the exception of the large school of piscivores in the newest artificial reef, the fish densities on artificial reefs of different ages did not change over time. Artificial reefs have been shown to increase fish populations considerably compared to pre-deployment surveys but then showed little change over time (Clark and Edwards, 1994). The physical differences between artificial reef aggregations including the depth and number of structures did not cause any significant changes to the fish densities recorded here. Perhaps the carrying capacity of these artificial reef aggregations is bottlenecked by the lack of the large corals which are so crucial for habitat provision in natural reef systems (Holbrook *et al.,* 2002). These artificial reefs were purposefully designed to optimise habitat complexity and rugosity but still clearly cannot compare to natural coral reefs in terms of habitat provision for fish. However, the recruitment of corals onto the artificial reef does show the effectiveness of these structures in their ability to facilitate coral recruitment. Where coral mortality is low, it would be expected that these corals would grow to larger sizes, increase habitat complexity and support larger fish populations (Halford *et al.,* 2004).

The high EAM cover on artificial reefs, and the general decrease in EAM cover over time did not lead to any changes in EAM rovers or EAM territorial species. Likely, the numbers of grazing fish are not limited by the lack of available food and instead the populations of these grazing species are influenced by another limiting factor, perhaps structural complexity (Robinson *et al.,* 2020). The relatively low density of grazing species within the artificial reef and the relatively high density of coral recruits shows that even low grazing pressure can still effectively control algal growth and facilitate coral recruitment.

The deployment of an artificial reef in this severely degraded reef area has initiated the recolonisation and recovery of previously absent reef communities. A generally positive trajectory of coral communities was recorded, including increased coral size, density, cover, and richness on artificial reefs with increasing time since deployment. The development of coral communities assessed here on artificial reefs of different ages helps to showcase the potential for artificial reefs to be used as a conservation tool. However, the density of fish on the artificial reef was significantly lower than the natural reef, was not significantly different to the adjacent sand sites and did not increase over time. Given the recruitment and growth of corals on the artificial reef it would be expected that, in the long term, the eventual development of large corals could support larger populations of fish on the artificial reef (Halford *et al.,* 2004). Based on previous estimates of coral community succession, it may take between 10-20 years for the structure and function of a natural reef to be re-established by an artificial reef (Clark and Edwards, 1999; Ampou *et al.,* 2019). While there are currently no records of coral reef restoration outcomes over these timescales, the establishment of this baseline and plans for future monitoring on this artificial reef can help to outline realistic expectations for future restoration efforts.

3. General Discussion

Through the monitoring of the artificial reef in Tianyar, the assessment of coral communities developing here shows promise with increased coral size, density, cover and richness over time. These results support the utilisation of artificial reefs as a conservation tool for habitat restoration and recovery in severely degraded coral reef ecosystems. Despite significant differences between coral and fish populations between the natural and artificial reefs, the trajectory of corals at this relatively early stage is encouraging. Continued monitoring of the artificial reef could identify the point in time in which the succession of the benthic substrate on artificial reefs leads to a complex coral community similar to those seen in the natural reefs here. Previous estimates of coral community succession suggest that it may take between 10-20 years for an artificial reef to re-establish the structure and function of a natural reef (Clark and Edwards, 1999; Ampou *et al.,* 2019). Long term monitoring can also identify the point at which a coral community can sexually reproduce which is another important reef restoration milestone. Sexually propogated *Acropora* corals have been recorded reaching sexual maturity after three years (Wallace, 1985) with a minimum diameter of 12.3 cm (Baria *et al.,* 2012). This is promising for artificial reefs as a restoration tool as it suggests coral communities developing on the artificial reef can quickly become a source of coral larvae for other sites within the metacommunity and can help to bolster distant reef communities.

A key step in understanding the effectiveness of this artificial reef is investigating how the addition of a new habitat is affected by the mechanisms that underlie patterns of species distribution, abundance and interactions both in terms of local interactions between adjacent reefs and regional processes throughout the coral reef metacommunity. The application of metacommunity theory paradigms can aid in the understanding of these aspects of community ecology and so can be used to evaluate an artificial reef in its role as a restoration tool for reef recovery.

The species sorting paradigm suggests that the varying conditions of each artificial reef patch would support a different species composition for any given patch. This suggests that if the environmental conditions between the artificial reef and adjacent natural reefs are similar then communities developing on the artificial reef will also be similar to those in the natural reef. This was recorded here where *Porites* corals grew to dominate the artificial reefs, recruiting to the structures at higher densities than other coral genera. Nevertheless, the communities of both coral and fish recorded on the artificial reef were found to be significantly different to those in the natural reef, explained by the differences in the physical conditions of the two habitats. The understandable lack of large corals on the artificial reef deployed relatively recently explains the lower habitat complexity, which can limit the fish populations here (Holbrook *et al.,* 2002; Graham and Nash, 2013). This lesser habitat complexity could be remedied over time with the generally positive development of the artificial reef coral community, resulting in an artificial reef community akin to that of the natural reefs.

When applied to the input of an artificial reef, the mass effects paradigm explains why competitively weaker species can exist within a patch. Where heterogeneous patches exist within a metacommunity, the dominant species present in each patch can provide a net export of individuals to other patches where they are not dominant. These exported individuals would struggle to independently maintain a population where the conditions limit their competitive ability but may persist where there is a sufficient supply of recruits from further away broodstocks (Logue *et al.,* 2011). When investigating the specific coral genera colonising the artificial reef it was found that *Pocillopora* and *Acropora*, which were both relatively less abundant in the adjacent natural reefs, were recruiting to the artificial reef in high densities. This suggests that mass input effects from further away *Pocillopora* or *Acropora* coral dominated reefs were responsible for this high recruitment despite the dominance by *Porites* corals in the nearby natural reefs.

For the characteristics of the patch-dynamic paradigm to be evident in an artificial reef the community composition of newer structures would have to be significantly different to the composition of species found on older structures, as found in this study. The patch-dynamic paradigm suggests that newer artificial reefs are more likely to be pioneered by superior colonisers while superior competitors are more likely to be found in older artificial reefs (Yu and Wilson, 2001). Over time the superior competitors are more likely to disperse to the newer habitats and outcompete the superior colonisers. In this study, the newest structures were most densely colonised by *Acropora* and *Pocillopora* which were found to be pioneer species (Wallace, 1983; Clark and Edwards, 1994), with a high colonisation ability while older structures were dominated by *Porites* corals, suggesting they are superior competitors in this system. However, the regular addition of new artificial reef patches provides new habitats for superior colonisers, allowing them to avoid being totally outcompeted within the artificial reef by superior competitors. This may also explain potential differences in species composition between the artificial reef and the natural reef with the latter likely being dominated by superior competitors.

An understanding of the successional processes outlined by Connell and Slayter (1977) is key for coral reef conservation and restoration efforts as they can provide a valuable insight into the recovery dynamics of a coral reef following disturbances. Here, the abundance and diversity of coral and fish communities in natural reefs and artificial reefs of increasing time since deployment were used as a model system to explore these successional processes within reef ecosystems. The abundance of early successional coral species (*Acropora* and *Pocillopora* spp.) on younger artificial reefs and their subsequent rarity on older artificial reefs supports the facilitation model of ecological succession. However, that is not to say the pioneer corals themselves are solely responsible for the facilitation of later stage colonisers. The presence of corals has been shown to influence the development of biofilms in the surrounding area and the components of these biofilms are known to influence coral recruitment (Weber *et al.,* 2019). Specifically, the presence of crustose coralline algae is highly associated with the production of coral settlement cues and has been shown to significantly increase coral recruitment (Dixson *et al.,* 2014). The development of these complex biofilms may be the ‘conditioning’ requirement suggested by Grigg and Maragos (1974) to explain how some coral species such as *Montipora verrucosa* were absent on newer lava flows.

In this study, *Acropora* and *Pocillopora* corals colonised effectively and were the most abundant coral genera in the newest artificial reefs but were rarer in older artificial reefs where *Porites* had become dominant. These initial colonisers seemed to be outcompeted and replaced by later stage colonisers, contradicting both the tolerance and inhibition models of ecological succession. However, the long-standing theoretical assumptions of ecological succession models were developed in and are often supported by evidence from terrestrial ecosystems (Buma *et al.,* 2017). In coral reef ecosystems, the processes of recruitment and succession can be more complex and stochastic, making it difficult to apply an understanding of these traditional models of ecological succession (Jouval *et al.,* 2020). Sutherland and Karlson (1977) attributed the ill fit of terrestrial succession models in marine environments to the fact that marine organisms are relatively short lived, do not store dormant seeds and generally cannot modify their substrate to the same extent terrestrial plants do.

Further research into the effectiveness of artificial reef structures could look into the ability of an artificial reef to provide coral settlement cues. While the results here clearly show that corals can and do recruit onto artificial reefs, what remains unclear is to what extent the presence of the artificial substrate influences coral recruit settlement preferences. The coral recruitment potential of an area can be sampled using ceramic settlement tiles based on the number of coral recruits found on the tiles. In this way, recruitment potential can be compared between zones in Tianyar but also compared to other sites around the world. Sites in the Komodo islands (Fox, 2004), Spermonde Archipelago (Sawall *et al.,* 2013), Seychelles (Chong-Seng *et al.,* 2013; Montoya-Maya *et al.,* 2016), Palau (Victor, 2008), Australia (Hughes *et al.,* 1999), Caribbean Sea (Kojis and Quinn, 2001), and Red Sea (Higgins *et al.,* 2019) have all been sampled in terms of their coral recruitment potential using settlement tiles. Fox (2004) effectively showed, using coral settlement tiles, that coral reefs damaged by blast fishing in Komodo National Park were subsequently not limited by the number of recruits and instead were found to be limited by the high post-settlement mortality of the remaining unsuitable substrate.

While coral recruitment potential can be a measure of the suitability of an area for restoration, it may also provide a measure for the effectiveness of the restoration technique itself. After a large-scale coral restoration effort in the Seychelles, settlement tiles showed that restored sites had a positive influence on coral recruitment, greater than both unrestored sites and natural reef sites, perhaps due to an increase in settlement cues (Montoya-Maya *et al*., 2016). In Tianyar, settlement tiles deployed in the artificial reef, natural reef and sand sites can measure the recruitment potential of these areas and could be used to investigate to what extent the artificial reef influences coral settlement.

The results of this study give an important insight into what can be expected from the large scale government funded Indonesian Coral Reef Garden (ICRG) programme which created 95,768 artificial reef structures that were deployed in five sites around the island of Bali in late 2020 (Wicaksana, 2020; Suriyani, 2021). Assessment of coral communities developing on the artificial reefs from this major coral restoration programme can expect to find successful coral recruitment over relatively short timescales. However, coral and fish populations on the ICRG artificial reefs are likely to be lesser than those on nearby natural reefs in the short term. Over longer timescales, coral communities can be expected to develop, with corals growing larger, covering more area and increasing habitat complexity which can then support greater and more diverse fish populations. In this way, the assessment of the artificial reef in Tianyar can be used to help outline realistic expectations for future reef restoration programmes.

In Indonesia, the majority of coral reef restoration programmes are financed by large, often single, investments either from the government or private sector (Razak *et al.,* 2022) in which large areas are restored in a short period of time. One drawback of these large-scale projects is the lack of local support after the conclusion of the restoration efforts, which may explain why only 16% of restoration projects in Indonesia reported any post-installation monitoring (Razak *et al.,* 2022). The restoration programme here in Tianyar is markedly different in that it was wholly initiated by members of the local community, Yowana Bhakti Segara (YBS). This reef restoration program is financed by a sustainable ecotourism model supported by international volunteers, who spend up to 6 months volunteering with the local community. Volunteers help the local YBS members construct and deploy the artificial reef which is totally funded by a proportion of the volunteering program fee. In this way, new artificial reefs are deployed in empty sand areas each month and the artificial reef expands slowly over time. The longevity of this program has allowed for the undertaking of this study and can also support further consistent monitoring to assess the effectiveness of the artificial reef in the future.

Within the aims of this study, the deployment of the artificial reef in Tianyar effectively initiated the recolonisation of reef communities previously lost from a severely degraded reef area. The assessment of coral communities developing on the artificial reef showed a generally positive trajectory with increased coral size, density, cover, and richness over time. These results support the use of artificial reefs as a conservation tool for habitat restoration in severely degraded coral reef ecosystems. While the coral and fish communities recorded on the artificial reef were significantly different to those in the natural reefs, the early trajectory of the coral communities on the artificial reef is promising. A lack of artificial reef monitoring records over the multi-decadal timescales required to re-establish the structure and function of coral reefs makes the establishment of this baseline and plans for future monitoring important contributions to the field of coral reef restoration ecology.

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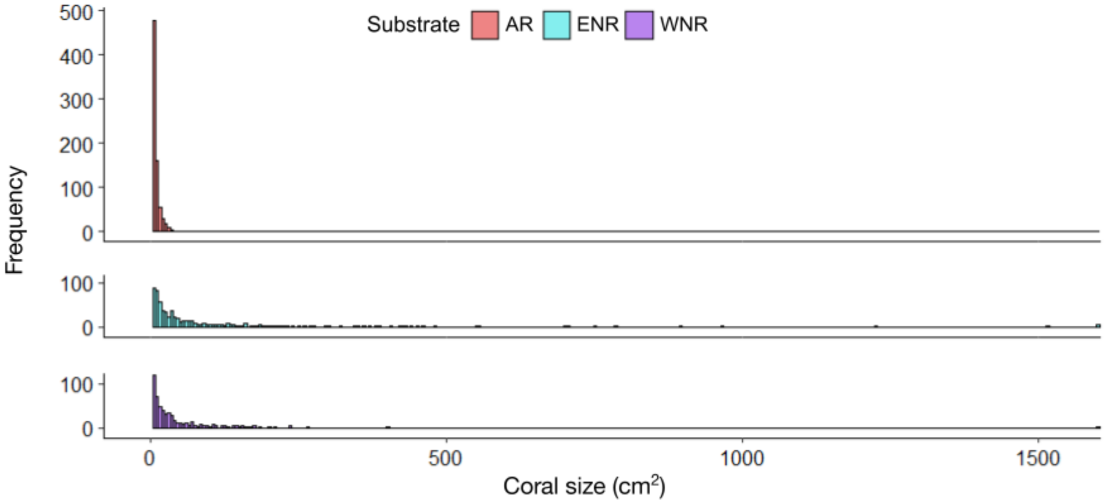
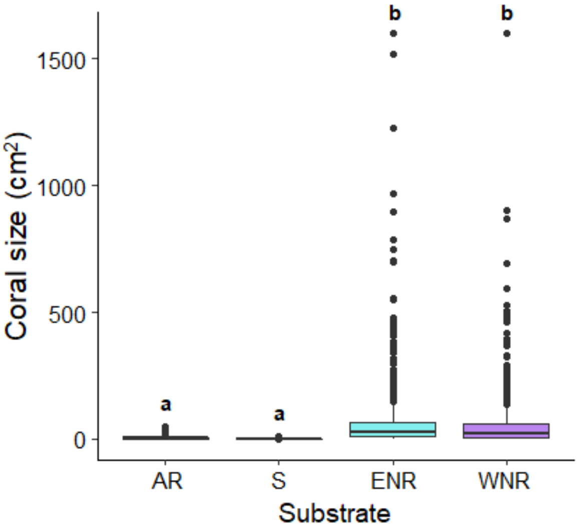
5. Appendices

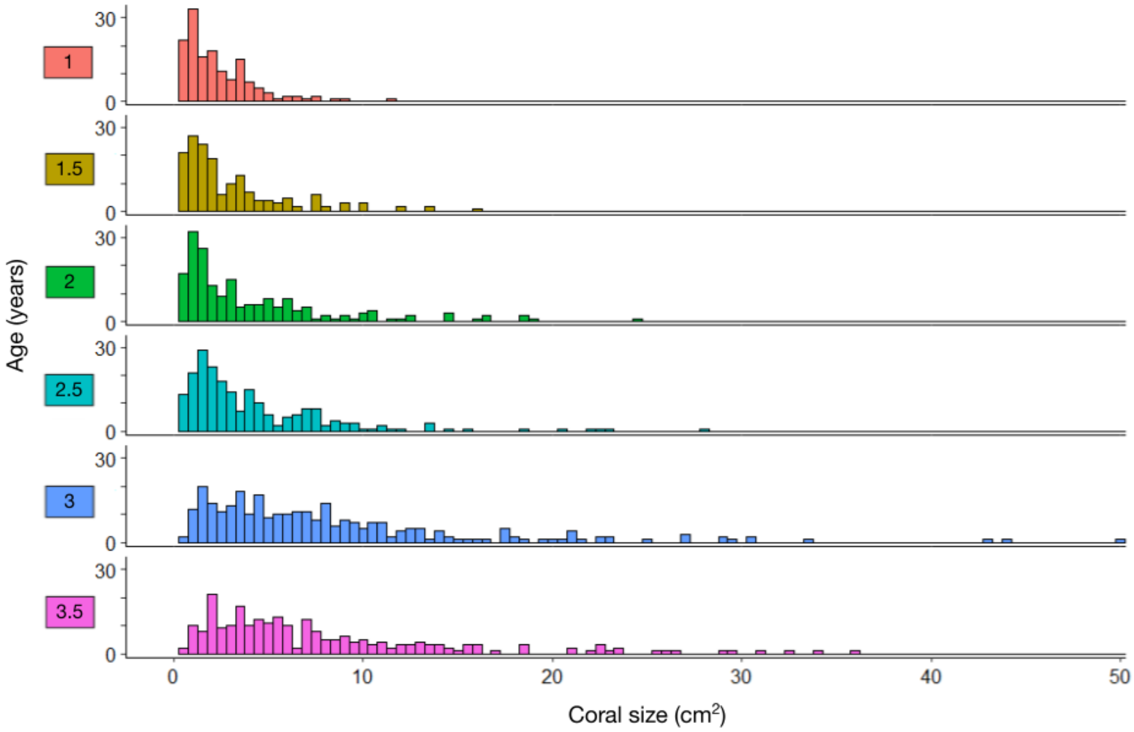
Appendix 1. 3D models of single (A) and aggregated (B) artificial reefs pre-deployment. Dimensions of the above artificial reef structures are 50 x 50 x 50 cm and are representative of the artificial reefs in this study. Models were created using Agisoft Metashape Standard software (version 1.8.2).



Appendix 2. Size frequency distribution of coral size on artificial reefs, East and West Natural reefs, including large corals up to 1600 cm^{-2}. Corals found in the sand substrate have been omitted and are as follows: 1.2, 1.3, 2.1, 5.1, 6.7, and 11.3 cm^2. Number of histogram bins = 200.



Appendix 3. Box plot of coral size at different sites, including large corals up to 1600 cm^{-2}. Boxplots show the median (horizontal middle line), the first and third quartiles (box), the lower and upper extremes (vertical lines), and the black dots represent outlying values (>1.5 interquartile range).



Appendix 4. Size frequency distribution of corals on artificial reefs of different ages, including large corals > 30 cm^2. Number of histogram bins = 100.

Appendix 5. Genus level coral count data from four different sites.

Genus	Number of corals			
	Artificial Reef	Sand	East Natural Reef	West Natural Reef
Acropora	168	0	7	37
Pocillopora	235	2	24	11
Porites	507	1	316	233
Goniastrea	27	0	18	14
Montastrea	18	0	23	22
Favites	2	0	0	2
Pavona	6	0	6	7
Gardineroseris	91	0	14	22
Montipora	45	1	30	35
Fungia	41	1	13	9
Psammocora	12	0	2	0
Leptoseris	15	0	46	38
Leptoria	1	0	21	31
Leptastrea	0	0	7	10
Turbinaria	16	0	23	37
Favia	2	0	6	11
Platygyra	6	0	11	14
Merulina	0	0	11	7
Lobophyllia	0	0	13	6
Symphyllia	0	0	3	6
Diploastrea	0	0	3	2
Echinopora	1	0	4	1
Galaxea	0	0	1	3
Stylophora	0	0	0	1
Coscinarea	0	0	0	1
Millepora	0	0	0	3
Plesiatrea	23	0	6	16
Podabacia	0	0	0	1
Unknown	24	1	14	21

Total	1240	6	622	601

Appendix 6. Species level fish count data from four different sites

		Number of fish			
Fish Species	Feeding guild	AR	S	ENR	WNR
C. vagabundus	Invertivore	6	0	7	14
C. auriga	Coral Dependant	2	0	0	0
C. trifascialis	Coral Dependant	0	0	0	2
C. adiergastos	Invertivore	0	2	10	13
C. melannotus	Coral Dependant	0	0	1	7
C. baronessa	Coral Dependant	4	0	6	7
C. lunulatus	Coral Dependant	0	0	3	7
C. speculum	Coral Dependant	0	0	6	1
C. lunula	Invertivore	0	0	0	1
C. kleinii	Invertivore	32	9	16	28
C. rafflesii	Invertivore	0	0	4	4
C. citrinellus	Invertivore	0	0	0	2
C. guttatissimus	Coral Dependant	0	0	0	2
C. ephippium	Invertivore	0	0	3	0
C. ornatissimus	Coral Dependant	0	1	4	0
H. singularius	Invertivore	1	0	0	2
H. chrysostomus	Coral Dependant	0	0	4	11
H. varius	Invertivore	0	0	3	4
F. flavissimus	Invertivore	0	0	5	0
C. bicolor	Invertivore	2	0	0	0
C. tibicen	EAM Rover	3	0	1	0
C. vroliki	EAM Rover	7	0	11	10
P. diacanthus	Piscivore	1	0	0	0
P. imperator	Invertivore	2	0	0	1
P. sextriatus	Invertivore	0	1	0	0
P. teira	Piscivore	2	0	0	0
A. pyroferus	EAM Rover	3	4	13	10
A. nigricans	EAM Rover	5	5	5	0
A. grammoptilus	EAM Rover	16	66	35	49
Z. scopas	EAM Rover	5	2	8	24
Z. veliferum	EAM Rover	0	0	2	0
C. striatus	EAM Rover	29	14	40	57
N. vlamingii	Invertivore	2	3	0	0
N. lituratus	EAM Rover	2	0	7	18
Z. cornutus	Invertivore	9	5	9	12
S. puellus	Invertivore	2	8	7	5
S. guttatus	EAM Rover	0	1	34	0
S. vulpinus	EAM Rover	1	0	0	0
A. vaigiensis	Invertivore	72	105	452	435
A. aureus	Zooplanktivore	0	0	4	0
A. leucogaster	Zooplanktivore	0	0	6	2
A. clarkii	EAM Territorial	0	0	4	5
P. dickii	Coral Dependant	0	0	8	0
P. lacrymatus	EAM Territorial	0	0	8	7
C. talboti	Zooplanktivore	1	0	9	11
D. trimaculatus	Zooplanktivore	63	13	45	0
D. reticulatus	Coral Dependant	0	0	6	41
C. ternatensis	Zooplanktivore	0	0	290	147
C. fumea	Zooplanktivore	17	0	0	0
C. viridis	Phytoplanktivore	0	0	0	300
C. xanthochira	Zooplanktivore	27	19	30	118
C. margaritifer	Zooplanktivore	194	5	1830	1465
C. lepidolepis	Zooplanktivore	45	0	70	0
C. lineata	Zooplanktivore	0	0	31	0
C. retrofasciata	Zooplanktivore	1	0	12	1
Chromis. spp	Zooplanktivore	25	5	0	0
P. coelestis	Zooplanktivore	70	42	25	48
P. vaiuli	EAM Territorial	0	0	2	3
P. bankanensis	EAM Territorial	0	0	3	0
P. lepidogenys	Zooplanktivore	0	0	143	82
P. cuneatus	Zooplanktivore	0	0	0	1
P. moluccensis	EAM Territorial	0	0	157	156
L. kasmira	Piscivore	120	25	0	110
L. quinquelineatus	Piscivore	2	0	0	5
L. rufolineatus	Piscivore	603	210	0	0

L. vitta	Piscivore	4	25	0	0
L. fulvus	Piscivore	6	11	4	143
L. decussatus	Piscivore	0	0	4	3
M. macularis	Piscivore	0	2	1	3
S. bilineatus	Piscivore	2	1	2	5
S. ciliatus	Piscivore	1	3	0	5
S. xenochrous	Invertivore	3	4	0	0
C. crenilabis	Invertivore	0	7	0	0
T. crocodilus	Piscivore	0	0	0	40
P. tile	Zooplanktivore	66	100	370	80
P. pisang	Zooplanktivore	13	10	10	10
C. teres	Zooplanktivore	0	0	0	29
C. lunaris	Zooplanktivore	0	0	60	35
C. caerulaurea	Zooplanktivore	0	92	30	0
P. dispar	Zooplanktivore	0	0	350	0
P. huchti	Zooplanktivore	8	0	187	40
Pseudanthias spp.	Zooplanktivore	30	0	95	130
C. argus	Piscivore	0	2	0	0
C. boenak	Piscivore	1	0	0	0
C. miniata	Piscivore	13	2	2	0
E. fasciatus	Piscivore	0	1	0	1
A. rogaa	Piscivore	6	0	4	1
P. vittatus	Piscivore	2	0	0	0
Scarus spp.	EAM Rover	11	10	9	29
G. varius	Invertivore	0	0	1	1
H. chrysus	Invertivore	24	8	0	0
H. scapularis	Invertivore	2	4	0	0
H. prosopeion	Invertivore	0	1	0	0
H. hortulanus	Invertivore	16	4	6	15
T. hardwicke	Invertivore	0	0	11	8
T. lunare	Invertivore	20	10	4	7
B. axillaris	Invertivore	2	0	0	0
B. mesothorax	Invertivore	1	2	4	0
B. diana	Invertivore	6	1	2	1
L. dimidiatus	Invertivore	23	2	13	7
N. sammara	Piscivore	0	0	5	5
S. caudimaculatum	Piscivore	0	0	1	9
A. cyanosoma	Invertivore	14	0	0	20
A. aureus	Invertivore	63	0	0	30
A. goni	Invertivore	0	0	0	100
A. moluccensis	Invertivore	0	0	0	20
P. evides	Zooplanktivore	0	0	3	2
P. tetracantha	Piscivore	1	4	0	0
S. binotatus	Piscivore	0	1	1	0
V. puellaris	Invertivore	0	2	0	0
E. bicolor	EAM Territorial	2	0	0	0
P. antennata	Invertivore	0	0	1	0
S. diabolus	Piscivore	0	0	0	1
O. meleagris	Invertivore	0	0	0	1
O. cubicus	Invertivore	2	0	0	0
M. flavolineatus	Invertivore	0	7	0	0
P. cyclostomus	Piscivore	0	2	0	0
P. barberinius	Invertivore	0	1	0	5
U. tragula	Invertivore	0	13	2	0
A. chinensis	Piscivore	3	2	9	2
P. vanicolensis	Invertivore	18	0	17	4
B. viridescens	Invertivore	4	0	0	0
P. flavimarginatus	Invertivore	0	1	0	0
B. undulatus	Invertivore	10	2	14	7
S. chrysopterus	Invertivore	3	10	0	3
S. bursa	Invertivore	1	1	2	3
M. vidua	Invertivore	0	0	2	0
O. niger	Invertivore	1	5	2	0
A. stellatus	Invertivore	0	0	0	1
A. nigropunctatus	Invertivore	0	0	1	2
C. valentini	Invertivore	12	3	1	1
D. hystrix	Piscivore	0	0	1	0
G. javanicus	Piscivore	2	0	0	0
H. hassi	Zooplanktivore	0	60	0	0
Total		1,772	961	4,611	4,039