ARTIFICIAL REEFS AS A PLATFORM FOR RESEARCH AND CONSERVATION IN CORAL REEF ECOSYSTEMS

by

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This thesis is for my mother, who completed a Master's degree while raising two tireless young children and working full-time.

I was in awe then; I am even more amazed now.

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ABSTRACT

Artificial reefs (ARs) increasingly are being deployed to mitigate damage to coral reef ecosystems from local anthropogenic stressors and climate change. Evaluating the efficacy of ARs in enhancing or sustaining reef assemblages is key to assessing their role in conservation or management. In this thesis, I review global patterns of AR deployment and monitoring in coral ecosystems, and evaluate their success in achieving conservation objectives. I also present results of a 13-month field experiment that compared patterns of colonization on settlement collectors (ceramic tiles) on ARs and natural reefs at Eilat, Gulf of Aqaba. I found that the composition of algal and invertebrate colonists differed with collector aspect (top or underside) and between reef types (ARs vs. natural reef) in shaded microhabitats (undersides). Invertebrate biomass also tended to be greater on ARs than natural reefs, suggesting that ARs can potentially enhance the abundance of certain reef-associated assemblages.

LIST OF ABBREVIATIONS USED

Abbreviation	Description
et al.	et alia
AR	artificial reef
NR	natural reef
e.g.	for example
i.e.	that is
m	meter(s)
n	sample size
no	number
y	year(s)
Inverts	Invertebrates
SST	Sea surface temperature
km	kilometer(s)
vs	versus
mo	month(s)
FER	Floating Experimental Reef
IGL	Igloo Reef
IUI	Interuniversity Institute Reef
OBS	Observatory Reef
N	North
E	East
cm	centimeter(s)
h	hour(s)
d	day(s)
mm	millimeter(s)
g	gram(s)
min	minute(s)
MB	megabyte(s)
PERMANOVA	Permutational Multivariate Analysis of Variance

Abbreviation	Description
ANOVA	Analysis of Variance
α	Significance level
LSD	Least Significant Difference
nMDS	Non-metric Multidimensional Scaling Analysis
SIMPER	Similarity Percentage Analysis
PERMDISP	Test of Homogeneity of Dispersions
log	Logistic
SD	Standard deviation
T	Top surface of experimental collectors
U	Under surface of experimental collectors
Oct	October
Nov	November
SE	Standard error
P	P-value
F	ANOVA Fisher statistic
df	Degrees of freedom
MS	Mean square
Pseudo-F	PERMANOVA Fisher statistic
p(perm)	Permutated p-value
t	test statistic
spp	Species
sp	Specie
PVC	Polyvinyl chloride

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CHAPTER 1

INTRODUCTION

1.1 CLIMATE CHANGE AND RESTORATION STRATEGIES FOR CORAL REEFS

Ecological restoration and remediation strategies are being implemented globally at an increasing rate with the acceleration of climate change (Harris et al. 2006). The extent to which these strategies are capable of restoring or rehabilitating select structural and functional variables of degraded ecosystems is poorly understood and spatially and temporally variable (Moberg & Rönnbäck 2003; Adger et al. 2005). Successful restoration strategies depend on the life histories and functional roles of dominant and foundation species in the recipient ecosystem (Walther et al. 2002). Success also relies on historical environmental conditions, including the frequency and severity of natural and anthropogenic disturbances and the propensity of the ecosystem to shift between alternative stable states (Suding et al. 2004; Elliot et al. 2007). In addition, perceptions of restoration success are affected by the desired, socially-constructed ecosystem baseline used by managers and researchers (Higgs 2003).

Marine tropical ecosystems have experienced high rates of change in sea surface temperatures, severe storms, and ocean acidification since the 1980s (Doney et al. 2012), resulting in loss of species and changes to marine food webs (Hoegh-Guldberg & Bruno 2010). Coral reefs, mangroves, and tropical seagrass beds are some of the world's most biodiverse and environmentally sensitive ocean ecosystems and are located in marine realms experiencing the highest reported rates of change (Short & Neckles 1999; Doney et al. 2012). Moreover, these ecosystems frequently occur in developing countries where resources for implementing and evaluating restoration strategies are limited (Kaly & Jones 1998). Peer-reviewed studies comparing restoration sites to adjacent control sites are necessary for discerning the overall efficacy of restoration initiatives and informing adaptive management plans for degraded ecosystems. Additionally, synthesizing existing results from published studies can bring new insights to ongoing restoration projects and provide suggestions for addressing or navigating existing knowledge gaps.

Coral reefs, which directly or indirectly support more than 25% of all life in the oceans (Plaisance et al. 2011), have been severely impacted by climate change (Hughes et al. 2017). Hermatypic (reef building) corals are foundation species that support a diverse assemblage of fish and invertebrates by creating a structurally complex biogenic habitat (Graham & Nash 2013). Coral reefs also provide many ecosystem services with 800 million people relying on goods and services provided by coral reefs globally (Rogers et al. 2015; Pendleton et al. 2016). In recent decades, coral reefs have suffered disproportionally to other ecosystems from acute and chronic environmental stressors. Many regions have lost more than 50% of hard coral cover since the 1970s (Bruno & Selig 2007; De'ath et al. 2012), and more than 30% of scleractinian coral species are estimated to be at risk of extinction under predicted climate scenarios (Carpenter et al. 2008). As a result, conservation and restoration strategies are being implemented worldwide to protect existing reefs and rehabilitate degraded ones.

Conservation strategies have varied markedly over time and across marine realms (Spalding et al. 2007). Despite their increasing implementation, coral reefs have continued to decline globally (Hughes et al. 2017). In response, researchers and ecosystem managers have adopted active or manipulative restoration strategies to prevent further deterioration of these valuable habitats (Rinkevich 2015). The most common active restoration strategies used on coral reefs are coral transplantation (Harriot & Fisk 1988; Guzmán 1991) and deployment of artificial reefs (ARs) (Pickering et al. 1999; Abelson 2006). Transplantation seeks to restore or enhance existing coral cover by attaching coral colonies or fragments of colonies to the seafloor. Transplantation projects on coral reefs are expensive and logistically difficult to deploy and monitor, particularly for nations with limited resources allocated for conservation (Harriot & Fisk 1988; Yeeman et al. 2006). The success of these projects can be limited by the increasing frequency of natural and anthropogenic disturbances (Edwards & Clark 1999; McClanahan et al. 2005).

Since the 1960s, thousands of ARs have been purposefully deployed on coral reefs worldwide in an effort to restore select ecosystem metrics, such as increasing the abundance of commercially or socio-culturally important species (Jan et al. 2003; Ali et al. 2013), adding colonizable substrate or increasing structural complexity on denuded reefs (Perkol-Finkel & Benayahu 2005), and mitigating effects of recent physical or chemical anthropogenic disturbances (Edwards et al. 2001; Spieler et al. 2001). Many AR programs in the past two decades have borrowed design applications from silviculture and mariculture that have been specifically adapted to address reef conservation objectives (Rinkevich 2005). The purported benefits of ARs as a coral reef restoration strategy depend on the assumption that these man-made structures develop similar biological communities to natural reefs (Carr & Hixon 1997; Perkol-Finkel et al. 2006). However, many studies have found that ARs develop distinct benthic communities, often dominated by fouling species that favour artificial substrates and shaded microhabitats (Perkol-Finkel & Benayahu 2007; Higgins et al. submitted). The role of ARs as a source or sink for fish populations also remains unresolved in the peer-reviewed literature (Brickhill et al. 2005). Overall, the success of ARs towards meeting their initial conservation objectives has been poorly documented.

1.2 Outline of the Thesis

The overarching aim of my thesis is to examine artificial coral reefs as a platform for scientific experimentation and remediation of damage to coral reef ecosystems. Chapter 2 reviews the success of artificial coral reefs as a restoration strategy within the peer-reviewed literature. I describe global patterns of AR deployment and monitoring on coral reef ecosystems over time and discuss the reported success of ARs in meeting conservation objectives of deployment. I conclude that ARs are most successful when addressing well-defined, small-scale objectives. In Chapter 3, I examine the succession and colonization of sessile benthic invertebrates on artificial reefs in the Gulf of Aqaba, Red Sea over 13 months. I show that artificial and natural reefs can form distinct benthic communities and follow different patterns of succession, particularly in shaded microhabitats. This thesis contributes to a growing body of literature calling for proper evaluation and monitoring of restoration strategies. The conclusions drawn here about the design and implementation of ARs to address regional conservation objectives can be integrated into adaptive management plans for coral reefs on a global scale.

CHAPTER 2

ARTIFICIAL REEFS AS PLATFORMS FOR CORAL REEF RESEARCH AND CONSERVATION

2.1 INTRODUCTION

Globally, scleractinian coral cover has declined dramatically since 1985 due to synergistic effects of increased ocean temperatures and acidification, predation, biological invasions, mechanical damage, and disease (Heron et al. 2016; Hughes et al. 2017). The increasing frequency and intensity of natural and anthropogenic stressors has altered coral reefs, contributing to large-scale phase shifts in some regions to alternative stable communities dominated by fleshy macroalgae (Done 1992; Hughes et al. 2007), soft corals, corallimorpharia, or sponges (Norström et al. 2009). It has been estimated that more than 800 million people worldwide depend on coral reefs for food, coastal protection, and tourism (Burke et al. 2011; Rogers et al. 2015; Pendleton 2016), and that the persistence of alternative stable states will cause a significant reduction in these ecosystem services (Bellwood et al. 2004).

Traditional conservation measures (e.g. no take-zones, reserves, and marine protected areas) have been used on coral reefs for decades (Allison et al. 1998; Hoegh-Guldberg et al. 2007; Almany et al. 2009), but attention has been progressively shifting toward manipulative or active restoration methods as a consequence of accelerating coral decline (McClanahan et al. 2006; Rinkevich 2008). Active restoration strategies seek to rehabilitate ecosystems by restoring select structural and functional variables to a defined pre-disturbance state (Rinkevich 2014). Artificial coral reefs have been deployed globally to address many conservation objectives, including enhancing fish and invertebrate biomass (Ali et al. 2013), increasing habitat quantity and structural complexity of denuded reefs (Clark 1999; Gratwicke & Speight 2005), conservation of target species (Edwards et al. 2001; Hartati et al. 2017), and as nursery habitat for transplantation initiatives (Amar & Rinkevich 2007). Examining spatio-temporal patterns of the objectives of artificial coral reefs, success in meeting these objectives, and assessing their potential benefits as a restoration strategy can inform management decisions in different regions and under projected climate scenarios.

Artificial reefs (ARs) can provide benefits to both benthic and pelagic communities by supplying additional hard substrate for settlement (Bombace et al. 1994), reducing fishing and tourism pressure on natural reefs (Baine 2001), increasing heterogeneity of natural substrata (Abelson & Shlesinger 2002, Perkol-Finkel et al. 2006), and providing shelter from predators and human disturbances (Pickering & Whitmarsh 1997, Svane & Petersen 2001). However, there is concern that the scale of ARs is too small to have long-term impacts on the conservation or restoration of target species and their functional relationships (Edwards & Gomez 2007). It has been argued that ARs introduce alien materials onto reefs and can harm the recipient community by leaking toxic compounds (Collins et al. 2002) or scouring natural reef sites during coastal storms (Ingsrisawang et al. 1995). Additionally, there is debate as to whether ARs act as a source or sink for fish and invertebrate populations (Grossman et al. 1997; Brickhill et al. 2005).

To assess the functional importance of ARs, an understanding of the dynamics of established benthic communities and their relationship with demersal and pelagic species is imperative (Svane & Petersen 2001). Deploying ARs for restoration of coral ecosystems is a relatively new strategy, and most research to date largely has been descriptive (Seaman 2002), with few replicated comparisons to natural reefs (Carr & Hixon 1997). For example, there is increasing evidence that fish and invertebrate assemblages on ARs deployed in coral ecosystems do not mimic those on natural reefs (Thanner et al. 2006; Perkol-Finkel & Benayahu 2009; Higgins et al. submitted). Additionally, the role of ARs for colonization by reef invertebrates is unknown (Svane & Petersen 2001). Long-term data on species' residence time, growth and survival, and production patterns on adjacent natural coral reefs rarely are collected during studies of ARs (Pickering & Whitmarsh 1997; Brickhill et al. 2005).

In this chapter, I review objectives of existing ARs for conservation of coral ecosystems and assess the success of ARs in meeting those objectives. For ARs in tropical and subtropical coral ecosystems, I describe the spatio-temporal patterns of deployment, areal scale, monitored taxa, and study duration over the past hundred years. I also evaluate and discuss the reported success of ARs for each listed objective and identify factors that may limit the attainment of objectives. I propose that among all prospective conservation objectives for artificial coral reefs, the provision of nursery habitats and additional hard substrate for colonization, and the promotion of local socio-cultural values are the most likely to achieve conservation success.

2.2 METHODS

2.2.1 Literature search and data extraction

I conducted searches in ISI Web of Science Core Collection (1900–2018), Scopus (https://www.scopus.com), and Google Scholar (https://scholar.google.ca) for peer-reviewed publications that measured or monitored ecological and socio-cultural variables on ARs deployed in tropical and subtropical coral reef ecosystems (up to 35° latitude). In each database, I adapted the following general search terms to account for syntax differences: (TITLE-ABS-KEY ((artificial* OR "man-made" OR construct*) W/2 (coral* OR reef* OR habitat* OR nurser*)) AND TITLE-ABS-KEY (coral* OR tropic* OR subtropic*)). The first two sets of search terms were optimized to return studies that incorporate purposefully-designed and *de facto* AR structures. The last set narrowed the scope of the search to articles pertaining to ARs deployed in coral ecosystems. Studies on both vertebrate and invertebrate groups were included. Searches in all databases were completed between 12 August 2016 and 15 May 2018.

Over all databases, the search terms returned 2228 articles after duplicates were removed. All article citations and abstracts were imported into the web-based software review program Covidence (https://www.covidence.org), their titles and abstracts were screened, and 629 studies were extracted that included research on AR structures in coral reef ecosystems. A full text review was conducted for a sample of 430 articles, and data were extracted from 105 that met the following secondary inclusion criteria: 1) included a date, precise location, and depth of deployment, 2) included the precise dimensions and number of ARs in the study, and 3) stated an objective of AR deployment.

Articles were divided into two categories: 1) those that directly measured the success of meeting the objective(s) of ARs, and 2) those that were deployed for the purposes of scientific experiments or as *de facto* submergences (e.g. accidental ship groundings, dumping vehicles or building materials as waste). All 105 studies from both categories were surveyed for 1) duration of study, 2) clear description of AR dimensions, 3) targeted taxonomic groups, and 4) socio-cultural and ecological response variables used to assess whether the objective of the AR was being met. Latitude and longitude were extracted for each AR and then categorized into marine realms as defined in Spalding et al. (2007). All 105 studies were used to examine spatio-temporal patterns of AR deployments as presented in the scientific literature. All structures clearly defined as ARs by study authors and with a minimum area of ≥ 0.25 m^2 were included in analyses of global AR abundance over time to ensure accurate representation of all structures currently considered ARs in the scientific literature.

Studies reporting on progress towards attaining conservation objectives of deployed ARs were subjected to additional inclusion criteria to ensure that conclusions about conservation success were ecologically relevant. Studies were included if the monitored ARs were ≥ 1 m^2 to allow for comparison with natural reef formations and knolls. For studies reporting on multiple ARs, individual AR structures were defined as such if they were at least 2 m from the nearest adjacent AR (n = 30 studies). This spacing reflects what is considered an AR by study authors and the methods used to ensure connectivity of motile organisms and larvae between ARs. It has been shown that ARs >2 m apart can form distinct benthic communities (Huntington and Lirman 2012).

2.2.2 Classification of deployment objectives and response variables

Studies monitoring the success of an AR towards achieving one or more conservation objectives were further sub-classified into 9 categories of objectives: increase fish abundance, increase coral cover, conservation of target species (i.e. reef species of significant ecological or socio-cultural importance), socio-cultural value (e.g. economic evaluation, attractiveness to divers or tourists), source population, nursery or coral garden, increase habitat quantity, and stressor mitigation (i.e. deployment following catastrophic events, such as bleaching, severe tropical storms, and dredging). The ecological response variables used to assess success in meeting the conservation objective(s) of ARs were categorized according to the measurements taken (abundance, diversity, cover, recruitment, biomass, size distributions, survival/mortality, growth and reproduction rates, species turnover, connectivity/space use, and structural complexity) and by broad taxonomic groups (fish, coral, other invertebrates, and algae).

2.3 AR Deployments on Coral Reefs

2.3.1 Definitions of AR

There is little standardization or agreement about the definition of AR in the scientific literature. Definitions within the studies examined in this review were disparate or absent. Authors reported on a vast array of structures, from *de facto* or accidental deployments (i.e. shipwrecks, bridges, cars) to purposefully designed and deployed ARs. Purposefully deployed ARs ranged from piles of tires on the seafloor (Campos & Gamboa 1989) to specifically engineered structures optimized for recruitment of target species for conservation (Amar & Rinkevich 2007; Blakeway et al. 2013). I used a broad AR definition when examining spatio-temporal patterns of AR deployment to accurately characterize the wide variety of structures that are currently being categorized as ARs in the peer-reviewed literature.

There is also little consistency in AR size within the peer-reviewed literature. Deployments of ARs for conservation purposes were conducted on a larger scale than ARs deployed for scientific experimentation. Most ARs used in experimental studies

(74%) were 1–5 m^2 (Table 2.1), while more than a third (37%) of ARs with conservation objectives were >150 m^2 (Table 2.2). This likely reflects logistical constraints of monitoring large reef structures in scientific experiments or of experimentally controlling and disentangling confounding abiotic effects of reef development on larger ARs (Edwards & Gomez 2007). Spacing between individual ARs is not well reported in studies examining structures with conservation objectives, which often neglect to distinguish between ARs and AR modules. All studies that monitored communities on *de facto* reefs reported that the structures were >150 m^2; only two studies also monitored response variables on ARs of smaller area (Table 2.1).

Table 2.1. AR deployment for scientific experimentation or *de facto* ARs deposited as marine waste or accidental submergences (n = 65 studies). Response variables, study duration (mean, range), AR size, and marine realm (see Fig. 2.1 for bioregions) are given for each objective. Numbers in parentheses are studies per variable or category. See Appendix A.1 for reference list.

Objective	**No. of studies**	**Response variables**	**Study duration (y)**	**Reef area (m^2)**	**Marine realm**
Scientific experimentation	46	Fish density (21), fish diversity (12), fish recruitment (7), invertebrate density (5), coral recruitment (4), coral diversity (3), coral cover (3), invertebrate diversity (4), fish size-distributions (3), fish biomass (2), structural complexity (2), invertebrate biomass (1), coral density (1), coral survival/mortality (2), invertebrate survival/mortality (1), fish survival/mortality (2), invertebrate cover (1), coral growth (1), fish connectivity/ space use (2), species turnover (1), other ecological response variables (2)	1.8, 0.08–8.33	1–5 (34) 5–25 (6) 75–150 (2) >150 (6)	Tropical Atlantic (22) Western Indo-Pacific (11) Central Indo-Pacific (8) Eastern Indo-Pacific (2) Temperate N. Atlantic (1) Tropical E. Pacific (1) Temperate Australasia (1)
De facto	19	Fish diversity (8), fish density (8), coral cover (7), coral diversity (6), coral density (4), coral recruitment (2), coral size distributions (2), fish size distributions (2), invertebrate density (1), invertebrate diversity (1), invertebrate cover (1), fish biomass (1), coral survival/mortality (1), coral growth (1), coral genetics (1), socio-cultural variables (1), other ecological response variables (1)	1.55, 0.002–10.97	25–75 (1) 75–150 (1) >150 (19)	Western Indo-Pacific (8) Temperate N. Atlantic (4) Tropical Atlantic (4) Central Indo-Pacific (2) Temperate N. Pacific (1)

Table 2.2. AR deployment for conservation objectives (n = 30 studies). Response variables, study duration (mean, range), AR size, reported success rate (%), and reported reasons for limited success are given for each objective. Numbers in parentheses are studies per variable or category. See Appendix A.2 for reference list.

AR objective	**No. of studies**	**Response variables that address objective**	**Study duration (y)**	**Reef area (m^2)**	**Reported success rate (%)**	**Reasons for limited success**
Increase fish abundance	16	Fish density (10), diversity (10), biomass (3), size distribution (2), recruitment (1)	1.2, 0.01–3	1–5 (1) 5–25 (3) 25–75 (5) 75–150 (6) >150 (7)	56	Poor design for target species (2), colonization interference by invasive species (1), extensive bleaching during study (1), conclusions made about another conservation objective (3)
Increase coral cover	10	Coral diversity (4), recruitment (2), density (2), cover (2), growth (1), survival (3), biomass (1), reproduction (1)	2.1, 0.58–4	1–5 (1) 5–25 (3) 25–75 (4) 75–150 (4) >150 (1)	60	Extensive bleaching during study (1), conclusions made about another conservation objective (3)
Conservation of target species	11	Coral recruitment (6), fish recruitment (1), coral diversity (5), invertebrate diversity (2), fish diversity (3), fish density (3), coral density (6), invertebrate density (2), coral cover (2), invertebrate cover (2), coral size distribution (1), coral survival (2), coral growth (3), coral biomass (1), invertebrate biomass (1), fish biomass (1), coral reproduction (1)	2.1, 0.55–3.5	1–5 (1) 5–25 (1) 25–75 (4) 75–150 (4) >150 (1)	54	Poor design for target species (1), extensive bleaching during study (2), colonization interference by invasive species (1)

AR objective	No. of studies	Response variables that address objective	Study duration (y)	Reef area (m^2)	Reported success rate (%)	Reasons for limited success
Socio-cultural value	5	Diver behaviour and attitudes towards ARs (1), diving tourism/public education (3), cost-benefit analysis (1)	3.0, 0.002–10	1–5 (2) 5–25 (1) 25–75 (2)	40	Conclusions made about another conservation objective (3)
Provide nursery area	6	Coral growth (4), reproduction (1), survival (5)	1.1, 0.70–2.0	1–5 (3) 5–25 (2) 75–150 (1)	67	Extensive bleaching during study (1), conclusions made about another conservation objective (1)
Increase habitat quantity	6	Coral recruitment (4), coral diversity (3), fish diversity (3), fish density (3), coral mortality (3), coral growth (2), invert diversity (1), invert cover (1), fish biomass (1), fish recruitment (1), fish size distributions (1), structural complexity (1), other ecological response variable (1)	2.8, 2–3.5	5–25 (1) 75–150 (4)	67	Extensive bleaching during study (2)
Stressor mitigation	8	Fish diversity (4), coral cover (4), fish density (3), coral recruitment (3), coral growth (2), coral mortality (2), invertebrate cover (1), invertebrate diversity (1), coral diversity (5), coral density (3), structural complexity (2)	2.3, 0.7–5	1–5 (4) 5–25 (1) 25–75 (2) >150 (2)	63	Extensive bleaching during study (2), conclusions made about another conservation objective (1)

2.3.2 Spatio-temporal patterns in deployments of ARs

There were only 2 reports of AR deployments in the scientific literature until the mid-twentieth century. More than 2000 ARs were deployed in the 1960s, all in Hawaii in the Eastern Indo-Pacific (Fig. 2.1). Comparatively few deployments were recorded from the 1970s to the 1990s, with a greater than 2-fold increase (relative to the 1960s) in the 2000s (Fig. 2.1). This increase corresponds with the increased focus on effects of climate change on coral reefs in the late 1990s following the first major global bleaching event in 1998 (Goreau et al. 2000). Currently, the Tropical Atlantic region has the highest recorded number of deployed ARs globally, with 4208 cumulative deployments reported in the peer-reviewed literature to date. The higher abundance of ARs from the Tropical Atlantic and Eastern Indo-Pacific may be the product of the high intensity of study and frequency of publication from the southern United States (particularly Florida and Hawaii) from the 1960s onward (Leeworthy et al. 2006; Arena et al. 2007). Both Hawaii and Florida have long histories of AR deployment, and these reefs are often made from cheap waste materials (tires, metal construction materials, automotive parts) or *de facto* structures (sunken vessels, planes) (Bohnsack & Sutherland 1985).

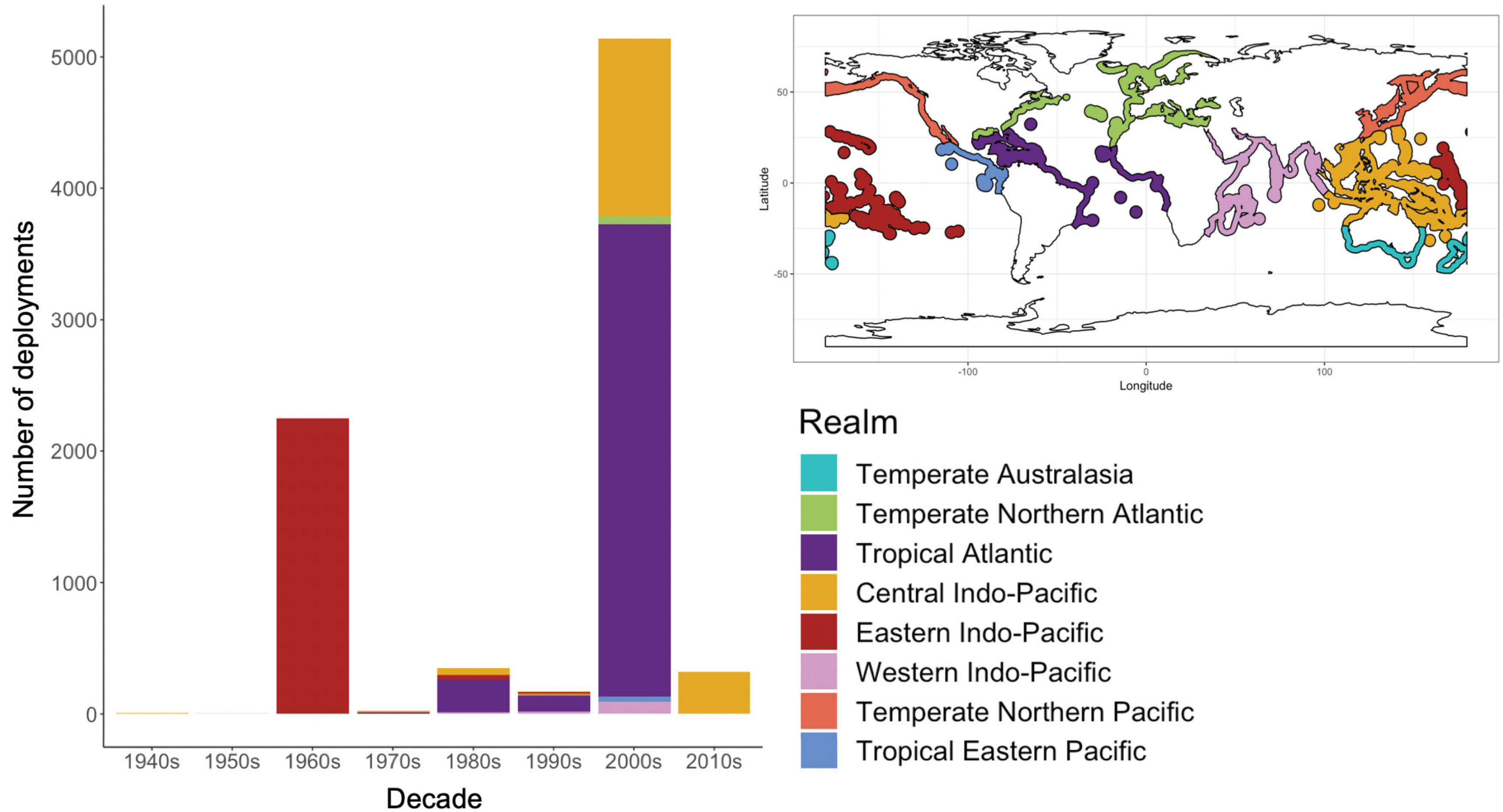

Fig. 2.1. Abundance of tropical and subtropical (up to 35° latitude) deployments of ARs in each marine realm by decade from 1940s to 2010s (to May 2018). Inset shows marine realms defined by Spalding et al. (2007).

2.3.3 Scientific experimentation and *de facto* AR deployments

Studies reporting on ARs that did not have a direct conservation-oriented objective were classified as either scientific experimentation or *de facto* submergences (Table 2.1) and were not included in analyses of AR conservation objectives (Table 2.2). Nearly half (44%) of the studies examined in this review (46 out of 105) reported on scientific experiments conducted on ARs, and 48% of these 46 studies were conducted in the Tropical Atlantic (Florida and the Gulf of Mexico). Overall, studies addressing only scientific objectives were marginally shorter than conservation-oriented projects, with mean study durations of 1.7 y (Table 2.1) and 2.0 y (Table 2.2), respectively. ARs recorded in peer-reviewed literature and deployed in the 1940s and 1950s were unplanned ship groundings that later were observed to have an AR effect by attracting fish and invertebrate colonizers (Fowler & Booth 2012). *De facto* ARs are the most variable in terms of study duration (Table 2.1), ranging from 1 day to 11 y, reflecting largely opportunistic monitoring and research of their effects.

The Tropical Atlantic and Central Indo-Pacific have the highest number of AR deployments for scientific objectives or *de facto* deployments, with 383 and 362 respectively. In the past decade, all records of AR deployments are from the Central Indo-Pacific, which has been an ocean warming hotspot since 1998 (Graham et al. 2008). Additionally, abundance of ARs deployed is not proportional to the area of coral reefs in each marine realm (Fig. 2.1). Australia has the second largest area of coral reefs in the world (Sheppard et al. 2012), but only 4 AR deployments were documented in the peer-reviewed literature. No-take reserves and marine protected areas are more common conservation strategies employed on the Great Barrier Reef (Fernandes et al. 2005).

2.3.4 Conservation based AR deployments

2.3.4.1 Conservation objectives of ARs

Less than a third (31.5 %) of all articles reviewed (30 out of 105) monitored progress towards achieving the initial conservation objectives of the AR and adhered to the secondary inclusion criteria used in my review. The three most commonly cited conservation objectives of ARs were increasing fish abundance (53%), conserving target species (37%), and increasing coral cover (33%) (Table 2.2). These conservation objectives were most common in the Western and Central Indo-Pacific, Temperate North Atlantic, and Tropical Atlantic (Fig. 2.2). Many of these ARs are in countries with relatively large sums of government funding dedicated to research and conservation purposes, notably the USA (Florida and Gulf of Mexico) and Israel. In addition, these highly cited conservation objectives reflect a concentration on remediation of natural and anthropogenic effects on economically valuable species, such as commercial fish species and hermatypic corals. Fewer studies reported on ARs deployed for objectives related to rehabilitation of deteriorated natural reefs, such as mitigation of environmental stressors (27%), increasing habitat (20%) and provision of coral nurseries (20%), a relatively new restoration technique (Shaish et al. 2008). These AR conservation objectives are particularly common in the Central and Western Indo-Pacific (Fig. 2.2). Studies addressing socio-cultural value and economic analyses on ARs (17%) were conducted only in the Western Indo-Pacific. More specifically, 8 out of 30 studies were from the Middle East, where sea surface temperatures (SST) have increased more than 3 times the global average since 1985 (Heron et al. 2016). This region is a global hotspot for AR research, dominating all categories of conservation objectives (Fig. 2.2). Two studies (both from Malaysia) stated their conservation objective was to deter fishing trawlers and were not included in Table 2.2.

2.3.4.2 Taxonomic groups monitored on ARs

Globally, coral and fish were the taxonomic groups monitored in most (93%) studies assessing progress in achieving conservation objectives of an AR, and half of these studies were conducted in the Western Indo-Pacific and Tropical Atlantic (Fig. 2.3). Publications in these regions were most frequently from Florida, Jordan, and Israel, indicating publication biases in the AR conservation literature.

ARs have been deployed on coral reefs to assess and increase abundance of fish populations since the 1980s (Fig. 2.4), and fish taxa were monitored in 50% of studies (n = 30) evaluating the conservation success of ARs (Fig. 2.3). This is largely in response to declining fisheries on coral reefs due to overfishing and harmful fishing practices that have had catastrophic effects on coral reef fish since the 1980s, such as cyanide and dynamite fishing (Edinger et al. 1998; Hughes et al. 2017). Many studies have focused on the population dynamics and behaviour of commercially or recreationally desirable fish species on and near ARs (Bohnsack 1989; Burt et al. 2009b). In the 1980s and 1990s, publications focused on protecting and increasing target fish species on reefs (Bohnsack 1983; Bohnsack et al. 1994; Brock & Kam 1994). From the 2000s onward, there has been less focus on fish taxa in the conservation literature, and more on the use of ARs to rehabilitate reef-forming foundation species on degraded reef sites (Fig. 2.4).

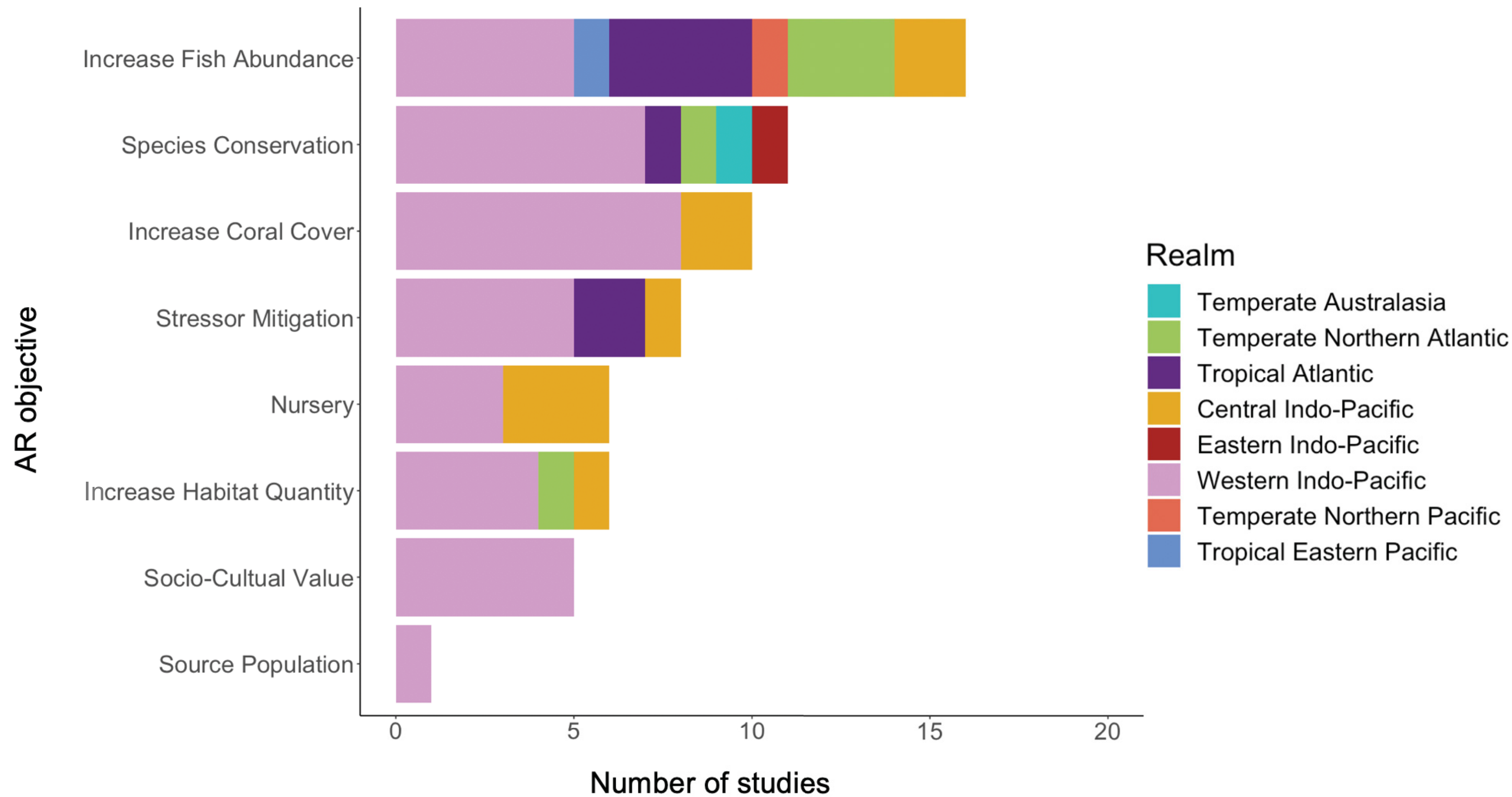

Fig. 2.2. Number of studies that measured each objective by marine realm (Temperate Australasia, n=1 study; Temperate Northern Atlantic, n=3; Tropical Atlantic, n=6; Central Indo-Pacific, n=6; Eastern Indo-Pacific, n=1; Western Indo-Pacific, n=11; Temperate Northern Pacific, n=1; Tropical Eastern Pacific, n=1) in ARs reporting success in meeting conservation objectives. See Fig. 2.1 for map of bioregions.

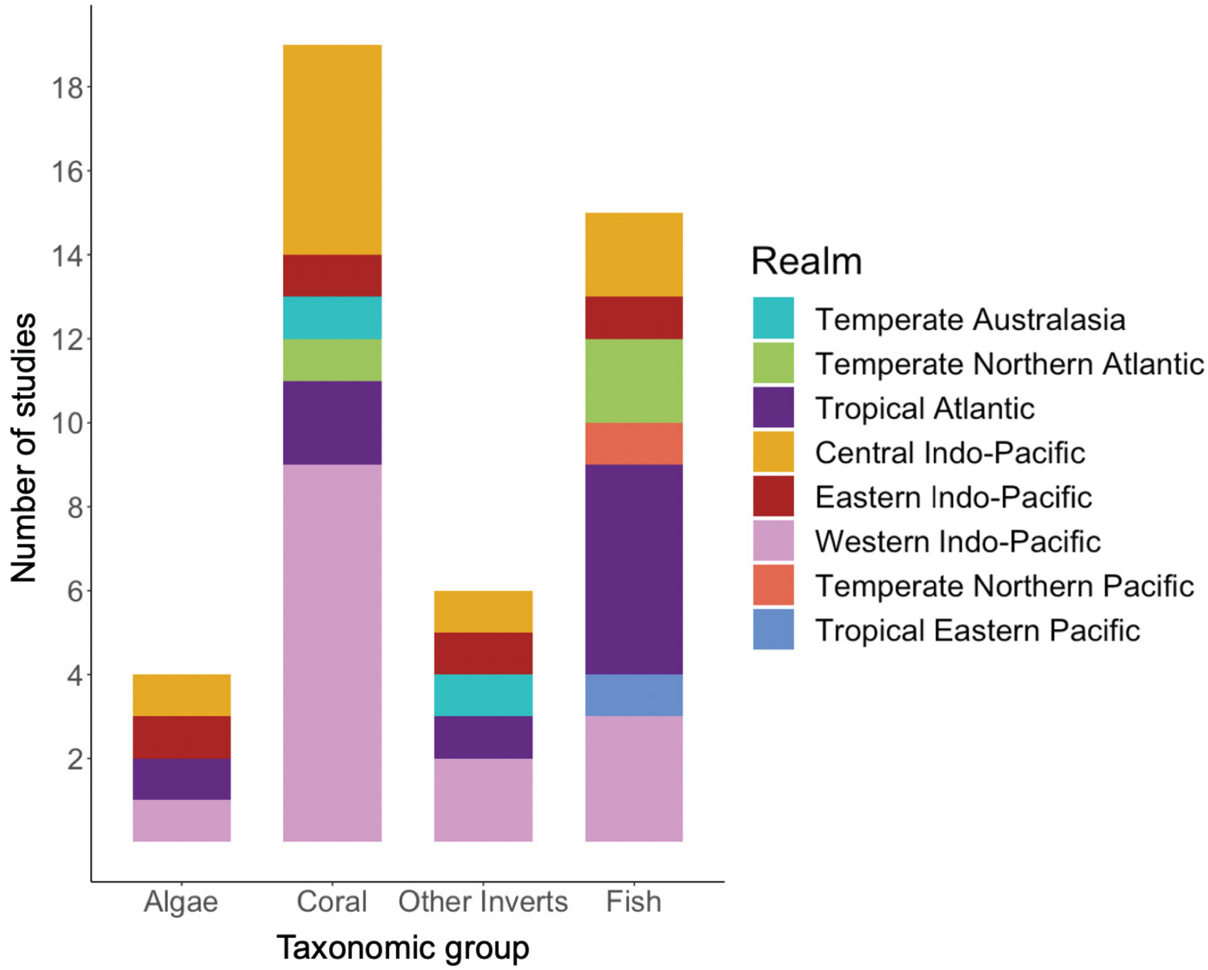

Fig. 2.3. Number of studies monitoring conservation success of an AR (n = 30 studies) that measured ecological response variables for 4 taxonomic groups (Benthic Algae, Coral, Other Invertebrates, Fish) for each marine realm. See Fig. 2.1 for map of bioregions.

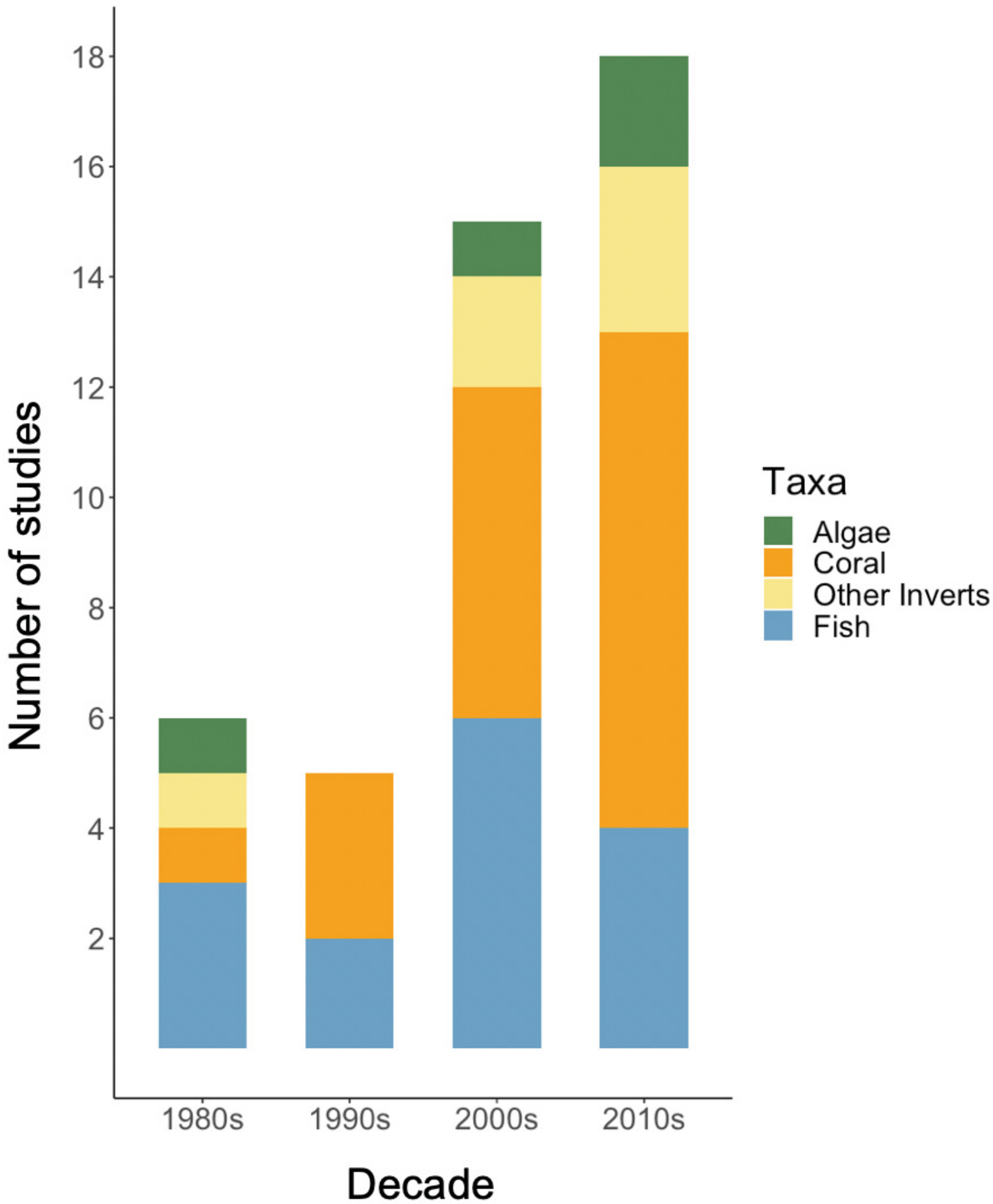

Fig. 2.4. Number of studies (n = 30) that measured ecological response variables for 4 taxonomic groups (Benthic Algae, Coral, Other Invertebrates, Fish) on ARs by decade from 1980s to 2010s (to May 2018).

Despite the long history of monitoring fish population metrics on ARs in the peer-reviewed literature, scleractinian corals were the most frequently monitored (63%) taxonomic group. The number of studies monitoring coral communities nearly doubled every decade from the 1990s onward (Fig. 2.4), reflecting the growing catastrophic and irreversible effects climate change has on coral reefs (Oliver et al. 2018). Due to the alarming decline in coral cover and associated biodiversity worldwide, objectives of ARs that focus on coral conservation are continuing to increase in frequency (Fig. 2.5), for example, as nurseries for coral transplantation (Allison et al. 1998; Rinkevich 2015).

Invertebrates other than corals and benthic algae were the least monitored taxonomic groups on ARs (Fig. 2.3). Understanding the successional patterns of these organisms on different AR structures is important because they can attract or deter target species (Svane & Petersen 2001). Monitoring frequency of both of these underrepresented groups has increased since the 1990s, but they were still only measured in 7–10% of studies by the 2010s (Fig. 2.4). Although there may be increasing awareness of the importance of these groups for attaining conservation objectives of ARs, monitoring is still lacking in many regions. Non-coral invertebrate groups were monitored in 17% of studies in all Indo-Pacific marine realms, the Tropical Atlantic, and Temperate Australasia (Fig. 2.3). Only 13% of studies measured benthic algae, all from the Western, Central, or Eastern Indo-Pacific, and Tropical Atlantic. Fouling invertebrates and macroalgae growing on ARs can attract fish and motile invertebrate grazers (Gilinsky 1984; Hixon & Brostoff 1996; Osman & Whitlatch 2004). It has been suggested that structures designed to support the growth of these organisms on coral reefs can enhance the consumer population (Reyes & Martens 1996). Alternatively, it also has been shown that excessive fouling by toxic invertebrates (e.g. ascidians and sponges) and some species of macroalgae deter coral larvae from settling and increase post-recruitment mortality rates (Russ 1982; Miller et al. 2009; Dixson et al. 2014). Therefore, ARs designed to promote fouling communities for attracting target fish species may not be conducive to coral recruitment.

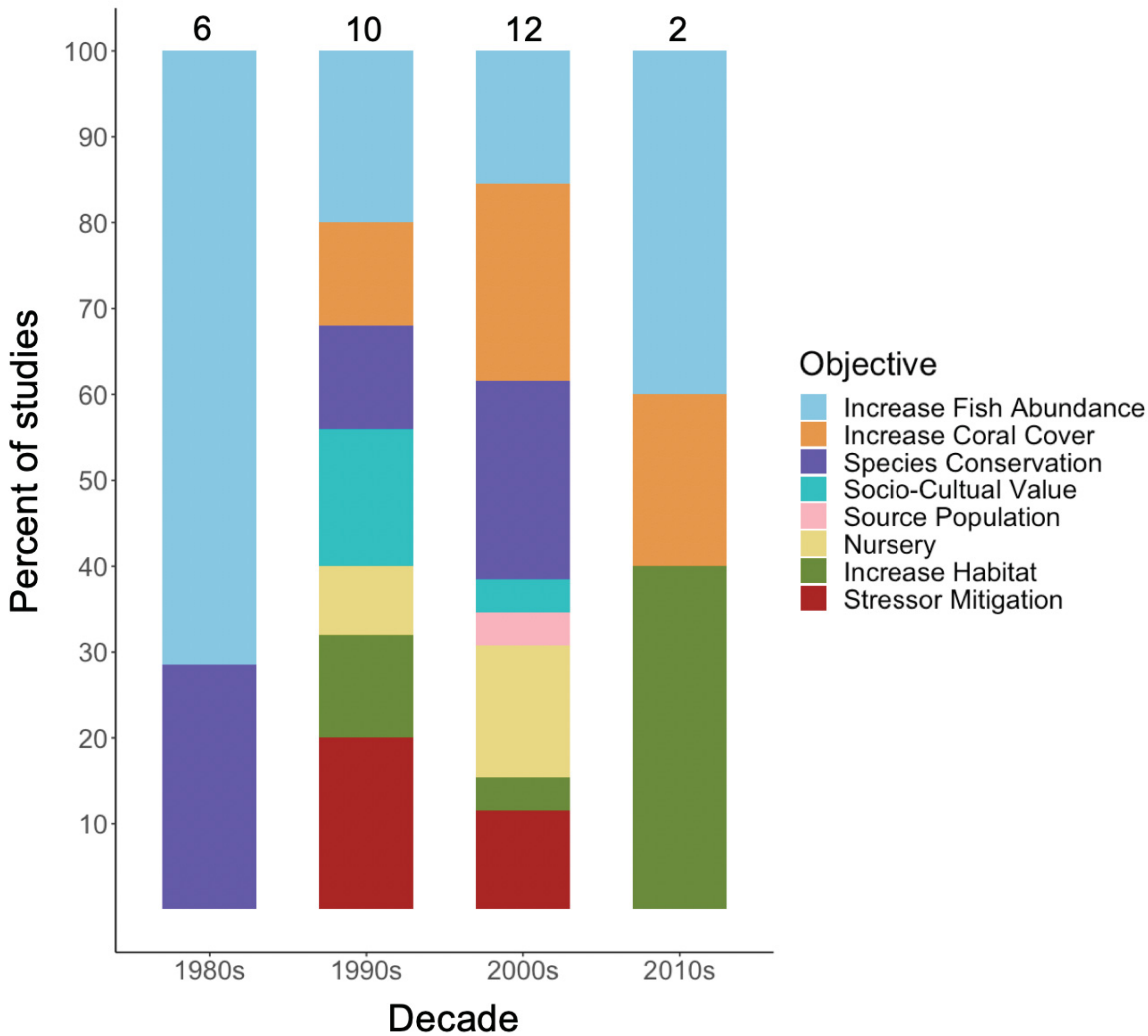

Fig. 2.5. Percent of studies citing each category of AR conservation objective (n = 30 studies) by deployment decade from 1980s to 2010s (to May 2018). Numbers above bars are number of studies.

2.4 Potential of ARs as a Conservation or Restoration Strategy on Coral Reefs

2.4.1 Reported success of achieving AR conservation objectives

Deployment of ARs with specific conservation objectives has varied over time (Fig. 2.5) and geographic locations (Fig. 2.2), and only 29% of all studies examined in this review (30 out of 105) monitored the success of ARs in meeting their conservation objective(s). Of these studies, 63% reported success or progress towards achieving the conservation objective of AR deployment. Nearly half reported success for increasing fish abundance (56%) and conserving target species (54%), and 60% for increasing coral cover (Table 2.2). ARs deployed for provision of nursery or additional habitat for colonization, or for mitigating the effects of environmental impacts, were reported successful in 67% and 63% of studies, respectively. Attainment of socio-cultural objectives (e.g. appropriate diver behaviour on ARs, generating diving tourism or public education, evaluating economic benefits) was reported as successful in only 40% of studies. Overall, the most commonly cited reasons for not achieving conservation objectives were poor AR design for target species and extensive bleaching during the study period, reported in 10% and 20% of studies, respectively (Table 2.2). Effective AR design considerations can be integrated into management strategies and deployment plans, however reducing the level of extensive bleaching on artificial and natural reefs will require global cooperation for reducing carbon emissions (Hansen et al. 2013).

Many studies reported multiple conservation objectives for each AR (Table 2.2), and 37% did not draw conclusions on all stated objectives. For example, if an AR was deployed for both increasing fish abundance and mitigating an environmental stressor, researchers may have recorded progress towards attaining only one of the two objectives due to constraints of logistics or expertise. I found no case of multiple studies investigating different conservation objectives on the same AR in my review. Deploying ARs with multiple conservation objectives may reduce the likelihood of evaluating success or measuring ecological function of the AR. The limited success of ARs deployed to achieve multiple conservation objectives may be due to logistical constraints or trade-offs in AR structure design or monitoring program to accommodate various objectives. This underscores the need for strategic planning prior to deployment of ARs with multiple conservation objectives to limit ambiguous conclusions about success.

2.4.2 Evaluation of reported success in achieving AR conservation objectives

While ARs have been deployed to increase fish abundance since the 1980s, many studies monitoring their success did not measure appropriate ecological response variables for detecting increased fish production on the reef (Fig. 2.6). For example, few studies examining the success of ARs in increasing fish abundance effectively monitored fish recruitment and movement between natural reefs and ARs. Therefore, authors are not able to distinguish whether ARs are attracting fish from adjacent habitats or enhancing abundance of resident populations. The three-dimensional structure and physical relief of the AR plays a significant role in attracting adult and juvenile fish from the water column (Pickering & Whitmarsh 1997; Rilov & Benayahu 2000; Sherman et al. 2002). Factors that contribute to the species composition of the colonizing fish community on ARs include distance from suitable substrate, distance from source populations, access by predators, access to food, and shelter for protection and egg-laying (Bohnsack 1989; Pickering & Whitmarsh 1997). Disentangling whether ARs actually enhance production of fish or simply redistribute them within the ecosystem would enable researchers to evaluate whether ARs can be used to increase absolute fish abundance on coral reefs. This knowledge gap is well cited within the AR literature (Pickering & Whitmarsh 1997; Brickhill et al. 2005), but my results indicate that it remains poorly addressed.

Increasing coral cover has been a relatively successful AR conservation strategy (Table 2.2). Overall, peer-reviewed studies used appropriate monitoring strategies for determining the success of this objective, however there is regional variation in the measured response variables. For most marine realms, studies focused on diversity of coral and abundance of coral species; however, for marine realms that encompassed ocean warming hotspots (Western and Central Indo-Pacific), studies concentrated on response variables pertaining to specific coral life history events (e.g. recruitment, survival/mortality, reproduction, and growth) (Fig. 2.6). As with fish abundance, the scale of ARs has been too small to address regional losses in coral cover. In addition, the study duration has been too short to adequately assess a sustained increase in coral cover (Table 2.2), which can take decades to detect (Baker et al. 2008; Knowlton & Jackson 2008). However, small-scale rehabilitation projects using ARs to increase coral cover in denuded areas might be successful if proper design considerations and environmental stressors are taken into account. For example, suspended ARs could be deployed on shallow water reefs and moved to deeper or cooler water during periods of peak SST to avoid bleaching.

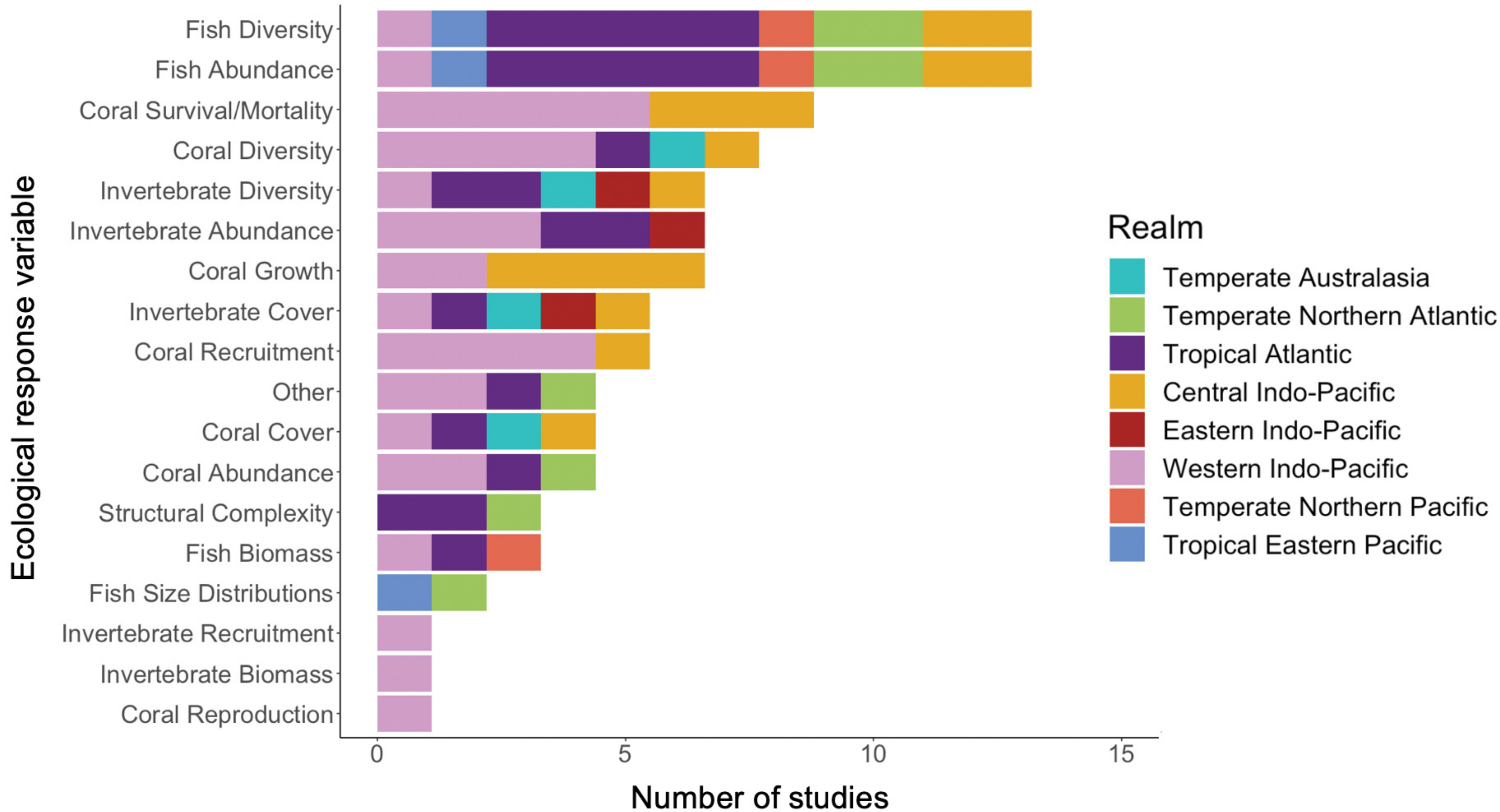

Fig. 2.6. Number of studies that measured each ecological response variable by marine realm (Temperate Australasia, n=1 study; Temperate Northern Atlantic, n=3; Tropical Atlantic, n=6; Central Indo-Pacific, n=6; Eastern Indo-Pacific, n=1; Western Indo-Pacific, n=11; Temperate Northern Pacific, n=1; Tropical Eastern Pacific, n=1) in ARs reporting success in meeting conservation objectives. See Fig. 2.1 for map of bioregions.

Protecting select ecologically and socio-culturally important species was addressed by way of the objective of conserving target species. Authors reported limited success for this objective (54%), with one study citing inappropriate design for target species as the reason (Table 2.2). One study reported that colonization of target fish species was interrupted by the presence of invasive lionfish (Dahl et al. 2016). Structural design and site selection must be considered using species-specific requirements to increase the overall success of this conservation objective. ARs deployed for the purpose of restoring, rehabilitating, or mitigating reef degradation for conservation of selected species need to be specifically engineered to enhance settlement and survival of targeted species (Sherman et al. 2002).

Stressor mitigation has been increasingly used as a conservation objective for ARs over the past two decades (Fig. 2.5). This is most likely a response to the increasing frequency and severity of coral bleaching events and concurrent climate change perturbations since the 1990s (Heron et al. 2016; Cantin & Spalding 2018; Oliver et al. 2018). My results suggest that this objective experience limited success when ARs are deployed to address ecosystem-wide stressors. This likely is because ARs operate on a much smaller scale (m – 100s m) than natural reefs (10s – 100s km). Both scientific and conservation projects on ARs can be interrupted by large-scale bleaching events during the study period, making it difficult or impossible to assess the efficacy of ARs in mitigating stressors (Edwards et al. 2001; Fadli et al. 2012). Also, ARs do not directly alleviate underlying environmental stressors, and may only be effective at remediating damages once the original perturbation has been substantially reduced or removed (Abelson 2006).

Arguably the most successful application of ARs is as nursery habitat for coral transplantation or source populations and specific and appropriate ecological response variables (i.e. coral growth, reproduction, and survival) were used to determine success (Table 2.2). As long as coral colonies or fragments of colonies experience low mortality, there is the potential for increased larval production and a high yield of functional adult colonies with low environmental impact (Rinkevich 2005; Forsman et al. 2006). Native species that are predicted to respond well to anticipated climatic changes can be selectively bred as a biological bank to re-populate natural reefs after disturbances (van Oppen et al. 2015). If ARs are suspended or designed to detach from the seafloor, they also can be moved horizontally or vertically to avoid unfavorable growing conditions (Shaish et al. 2008). While nurseries operate on a relatively small scale compared to natural reefs, the likelihood of an AR functioning as a small source population in the region can be maximized by seeding it with high densities of coral species (Amar & Rinkevich 2007). As with many studies published on active coral restoration strategies, publications examining the success of ARs as coral nurseries were exclusively from the Western and Central Indo-Pacific (Fig. 2.2).

ARs deployed to increase habitat have been largely successful, likely because they add hard substrate to the benthic environment, making this a relatively attainable objective (Abelson et al. 2005; Glassom et al. 2004; Seaman 2002). Measured response variables focused on benthic community development and fish presence at the AR (Table 2.2). Study durations for this objective were too short (2 to 3.5 y) to characterize success beyond initial recruitment and colonization phases for fish and invertebrates (Bohnsack & Sutherland 1985). However, increasing hard substrate is not considered a high priority in reef conservation compared to addressing large-scale tissue loss of scleractinian corals caused by ocean acidification and warming (Edwards & Gomez 2007).

Overall, deployment of ARs for a variety of socio-cultural purposes was unsuccessful as a conservation strategy if additional objectives were included (Table 2.2). In all cases where meeting socio-cultural objectives was the primary goal of the AR, the ARs were monitored appropriately and can be considered successful. However, when studies were examining a socio-cultural objective in combination with an ecological objective, conclusions were only made about the latter. Studies that monitored AR success using socio-cultural objectives employed a variety of socio-cultural variables, which can be separated into those monitoring human behaviour and emotions relative to ARs and those concerned with economic valuation (Table 2.2). In the Western Indo-Pacific, researchers surveyed the attractiveness of ARs to divers and diver behaviour on ARs (Belhassen et al. 2017). Some studies examining the economic value of ARs lacked secondary inclusion criteria for this review, but conducted a cost-benefit analysis (Chen et al. 2013) or estimated gross revenue generated from commercial fisheries as a consequence of ARs (Brock 1994).

2.4.3 Limitations of ARs and current knowledge gaps

Overall, my results indicate that ARs have limited success in meeting regional-scale conservation objectives, such as increasing abundance of coral and fish species or stressor mitigation. Nonetheless, these objectives are being increasingly cited in studies examining AR success, likely because of the acceleration of coral decline globally and the increasing call for remediating losses with active restoration strategies (Rinkevich 2008). Because ARs operate on a much smaller scale than natural reefs, their success in addressing large-scale objectives must be assessed. While it has been suggested that larger ARs (>150 m^2) support higher fish abundances (Ali et al. 2013), the extent to which ARs function as a source of fish production remains poorly understood (Pickering & Whitmarsh 1997; Brickhill et al. 2005). Further, larger ARs are logistically difficult to fund, deploy, and monitor. The introduction of networks of ARs to regions with minimal environmental stressors may increase the success of abundance-oriented conservation objectives (i.e. increasing fish abundance and coral cover) by increasing colonizable reef area while fostering connectivity of fish and invertebrate species between degraded natural reefs (Abelson 2006). Overall, small-scale objectives of ARs (e.g. increasing public education, selective coral breeding programs, training scientific and recreational divers) are far more achievable because they do not require additional intensive, long-term studies to determine their contribution to reef conservation and are generally successful when well defined and monitored.

Among all studies considered in this review, more than 90% spanned less than 3 years, which is too short to elucidate or predict long-term shifts in coral reef populations. Studies that examined the success of ARs in meeting conservation objectives spanned 1 week to 5 y. This is sufficient time for monitoring colonization patterns in most short-lived organisms, such as reef-associated invertebrates (e.g. ascidians, bryozoans, and some sponges), that can settle, reproduce, and die on a substrate within months (Stoner 1990; Przeslawski et al. 2008; Higgins et al. submitted). These durations also may be effective for monitoring fish populations on ARs, as many species of fish have a life expectancy of <5 y due to their lifespan or high rates of juvenile mortality (Aldenhoven 1986; Rocha et al. 2005; Almany & Webster 2006). However, changes in coral community composition and dynamics take much longer to detect (Bruno & Selig 2007;

Palandro et al. 2008). For example, scleractinian coral communities require multidecadal monitoring to properly assess ecologically relevant trends in coral cover and species composition (Baker et al. 2008; Knowlton & Jackson 2008). Therefore, future studies examining the success of ARs in achieving coral-oriented conservation objectives must increase study duration accordingly. Alternatively, ARs can be seeded with fragments of adult coral colonies grown *ex situ* to evaluate the potential beneficial effects of creating additional coral-dominated habitat on degraded reefs.

2.5 CONCLUSIONS

Of all studies examined in this review, less than half measured the success of ARs in meeting their conservation objectives. Most artificial coral reefs were deployed in the 2000s, and nearly half of the studies conducted since 2000 monitored coral performance. Overall, increases in fish abundance and coral cover were the most frequently documented conservation objectives of ARs, although success in meeting these objectives has been limited due to the difficulty in isolating biological mechanisms of change (i.e. attraction vs. production) and because of environmental perturbations (e.g. bleaching, invasive species). The objective of using ARs to address ecosystem-wide restoration goals, such as increasing coral cover and stressor mitigation, has also been met with limited success. A few studies reported on the success of smaller-scale ARs deployed as nurseries, for socio-cultural values, and to increase habitat quantity.

Many studies examined here reported that ARs were unsuccessful due to improper design and loss of AR communities due to severe environmental perturbations. Future studies aiming to increase the efficacy of ARs for conservation purposes should choose a structure and site(s) that are tailored for specific conservation objectives. While nearly all AR projects are relatively small compared to adjacent natural reefs, they can address local, conservation-specific objectives. I propose that ARs are most likely to achieve their conservation objectives and aid in coral reef conservation and restoration by: 1) providing nursery habitat for rearing target reef species, and 2) supplying additional hard substrate for settlement and recruitment of corals and other marine organisms. Promoting local socio-cultural values, such as increasing public awareness of coral reef decline, also has the potential to be a successful AR conservation objective if it is prioritized and properly monitored. Deploying ARs with multiple conservation objectives may reduce overall success or fail to quantify the ecological function of an AR if structure design and monitoring are not carefully planned. While ARs may not be effective at achieving regional-scale conservation objectives in a changing climate, their integration into a larger restoration program may prove beneficial. Further research should focus on the benefits of using ARs in conjunction with other restoration strategies, such as the creating of MPAs or coral transplantation projects.

CHAPTER 3

BENTHIC COMMUNITY SUCCESSION ON ARTIFICIAL AND NATURAL CORAL REEFS IN THE NORTHERN GULF OF AQABA, RED SEA[1]

3.1 INTRODUCTION

Coral reefs are deteriorating due to multiple natural and anthropogenic stressors (Heron et al. 2016; Hughes et al. 2017, 2018). Increasing ocean temperature and acidification, coupled with localized pollution, eutrophication, and harmful fishing practices, have accelerated the loss of structural and biological complexity on reefs worldwide (Jackson et al. 2001; Knowlton 2001; Hughes et al. 2003). Artificial reefs (ARs) are being used increasingly to mitigate impacts on coral ecosystems. These reefs are human-made structures, sometimes with established coral colonies or fragments attached, intended to mimic natural reefs and enhance habitat availability for corals and reef-associated invertebrates and fish (Seaman 2002; Abelson 2006; Thanner et al. 2006). Specific conservation goals of artificial coral reefs include: restoration of 3-dimensional structure on degraded reefs (Rinkevich 2005); enhancement of local biodiversity and survival of reef species (Chua & Chou 1994; Svane & Petersen 2001; Perkol-Finkel & Benayahu 2009); accumulation of commercially important fish and invertebrates (Svane

[1] Higgins E, Scheibling RE, Desilets KM, Metaxas A. Benthic community succession on artificial and natural coral reefs in the northern Gulf of Aqaba, Red Sea. PLoS One. Submitted January 28, 2019.

My coauthors Drs. Robert Scheibling and Anna Metaxas supervised the design and analysis of the experiment, and edited the manuscript. My coauthor Kelsey Desilets contributed to field data collection.

& Petersen 2001; Bohnsack 1989); and provision of nursery sites for coral transplantation (Epstein et al. 2001, 2003).

A variety of algal and invertebrate taxa colonize ARs within weeks of deployment (Bailey-Brock 1989; Bohnsack et al. 1994; Plass-Johnson et al. 2016). Composition and abundance of the resulting community depends on reef size (Bohnsack et al. 1994), proximity of source populations (Burt et al. 2009a), local hydrodynamics (Baynes & Szmant 1989), and the composition (Brown 2005; Ushiama et al. 2016) and orientation of settlement substrates (Connell 1999; Glasby 1999, 2000). The developing assemblage on artificial substrates can affect other reef-associated fauna, including fish and marine reptiles, although it may not resemble assemblages on adjacent natural reefs (Svane & Petersen 2001; Carr & Hixon 1997; Connell & Glasby 1999). Comparisons of the pattern and process of succession between ARs and adjacent natural reefs is a critical first step in assessing the efficacy of ARs as conservation tools.

On natural coral reefs, filamentous algae are early macroscopic colonizers on light-exposed surfaces, followed by crustose coralline algae and fleshy and foliose brown algae (Lewis 1986; Hughes et al. 1987; Steneck & Dethier 1994). Sessile suspension and filter-feeding invertebrates generally colonize shaded and sheltered microhabitats (Plass-Johnson et al. 2016; Díaz-Castañeda et al. 1999, Knott et al. 2004). Reef-associated fishes and large mobile invertebrates, such as sea urchins and gastropods, can directly (as predators) or indirectly (as grazers) regulate recruitment and abundance of algae and sessile invertebrates (Hixon & Brostoff 1996; Burkepile & Hay 2006). Herbivorous fish play a key role in limiting algal biomass on coral reefs (Carr & Hixon 1997; Thacker et al. 2001): when abundant, they can denude the substratum of most algae (Steneck 1983). In contrast, turf-forming filamentous algae persist (Bailey-Brock 1989; McClanahan

1997) and larger macroalgal forms proliferate (Hughes 1994, Lirman 2001) when herbivores are absent or at low abundance.

Coral reefs in the northern Gulf of Aqaba, Red Sea, have long been exposed to natural and anthropogenic perturbations, including extreme low tide events, oil spills, eutrophication, and diving tourism (Loya 2004; Hasler & Ott 2008). To date, conservation strategies used in the region include preservation through marine reserves, and restoration using ARs and coral transplantation (Epstein et al. 2001). These ARs, which include shipwrecks, stone structures, oil platforms, and designed frameworks, can support vibrant and diverse fish and invertebrate communities (Shenkar et al. 2008), which in some cases surpass those on adjacent natural reefs in abundance (Perkol & Benayahu 2007). ARs suspended above the seafloor have been deployed in the last two decades in the northern Gulf of Aqaba (Amar & Rinkevich 2007; Shaish et al. 2008; Shafir & Rinkevich 2010).

Suspended structures are a novel conservation tool in coral ecosystems that can be isolated from localized perturbations or disturbances (Rinkevich 2006). Invertebrate fouling communities that develop on suspended structures (e.g. pontoons) can differ from those on seafloor structures (e.g. vessels, pilings, concrete blocks) or adjacent natural reefs (Connell 2001; Glasby 2001; Perkol-Finkel et al. 2008), according to differences in environmental conditions related to depth or isolation from the benthos (Perkol-Finkel et al. 2008; Holloway & Connell 2002). Suspended artificial structures may recruit and attract different fish species than natural reefs or structures on the seafloor (Thanner et al. 2006; Chandler et al. 1985), depending on their spatial orientation and height above bottom (Rilov & Benayahu 1998; Rilov & Benayahu 2000), habitat complexity (Alevizon & Gorham 1989; Gratwicke & Speight 2005), and degree of fouling (Rooker et al. 1997).

Suspended structures tend to attract more transient pelagic fish and fewer demersal fish than reefs on the seafloor (Rooker et al. 1997).

The main objective of my study was to compare the development of the benthic assemblage on different types of ARs to that on neighbouring natural reefs, and thereby examine the effects of recipient community and environmental context on patterns of colonization. To address this objective, I measured the pattern and rate of development of the benthic assemblage, on the exposed upper surface of settlement collectors (ceramic tiles) and the shaded/sheltered underside, in a mensurative experiment at four sites in the Gulf of Aqaba: a suspended AR in open water, a seafloor AR, and two natural reefs (one contiguous with the seafloor AR). Both ARs had transplanted coral colonies attached to their framework upon deployment and were naturally accumulating corals and other sessile invertebrates and algae over time. I predicted that the composition or abundance of colonizing invertebrates would not differ between reef sites, either on the topsides or on the undersides of collectors, because the sites were in close proximity (< 7 km), collectors were deployed at a similar depth, and artificial and natural reefs harbored similar coral and invertebrate species. I also predicted that different assemblages would develop between shaded and light-exposed microhabitats provided by my collectors, and that undersides would support a greater abundance of sessile invertebrates, as evidenced in previous empirical studies in this region and elsewhere. The overarching goal of my study is to inform the use of ARs as a potential mitigation tool for reef recovery through enhanced recruitment of corals and other benthic invertebrates.

3.2 MATERIALS AND METHODS

3.2.1 Study sites and surveys of background community

I measured colonization and succession of algae and invertebrates for 13 mo (October 2015–November 2016) on artificial collectors on a suspended AR (Floating Experimental Reef, FER), a seafloor AR (Igloo, IGL), and two natural reef sites (Interuniversity Institute Reef, IUI; Observatory Reef, OBS) in the northern Gulf of Aqaba (Appendix B.1). The structure at FER was deployed ~350 m off the northern shore of the Gulf (29°32'28.56"N, 34°58'25.38"E) in 2010 (Fig. 3.1). It is suspended at 11-m depth on a framework (8 x 8 m) of large, air-filled polyethylene tubes. Plastic trays or mesh panels are attached to the upper surface of the suspended reef and contain transplanted and naturally recruited colonies of coral and other benthic invertebrates. The Igloo was deployed in 2001 within 20 m of OBS reef. It is a domed stainless-steel structure, 10 m in diameter and 3 m in height, at 10–13 m depth. Study areas on natural reefs at IUI (29°30'03.45"N, 34°55'01.62"E) and OBS (29°30'12.50"N, 34°55'08.42"E) were constrained to the 10–13 m depth contour, comparable to the depth range of the two ARs (Fig. 3.1). The natural reefs are part of a fringing reef system in the Coral Beach Nature Reserve established in 1967.

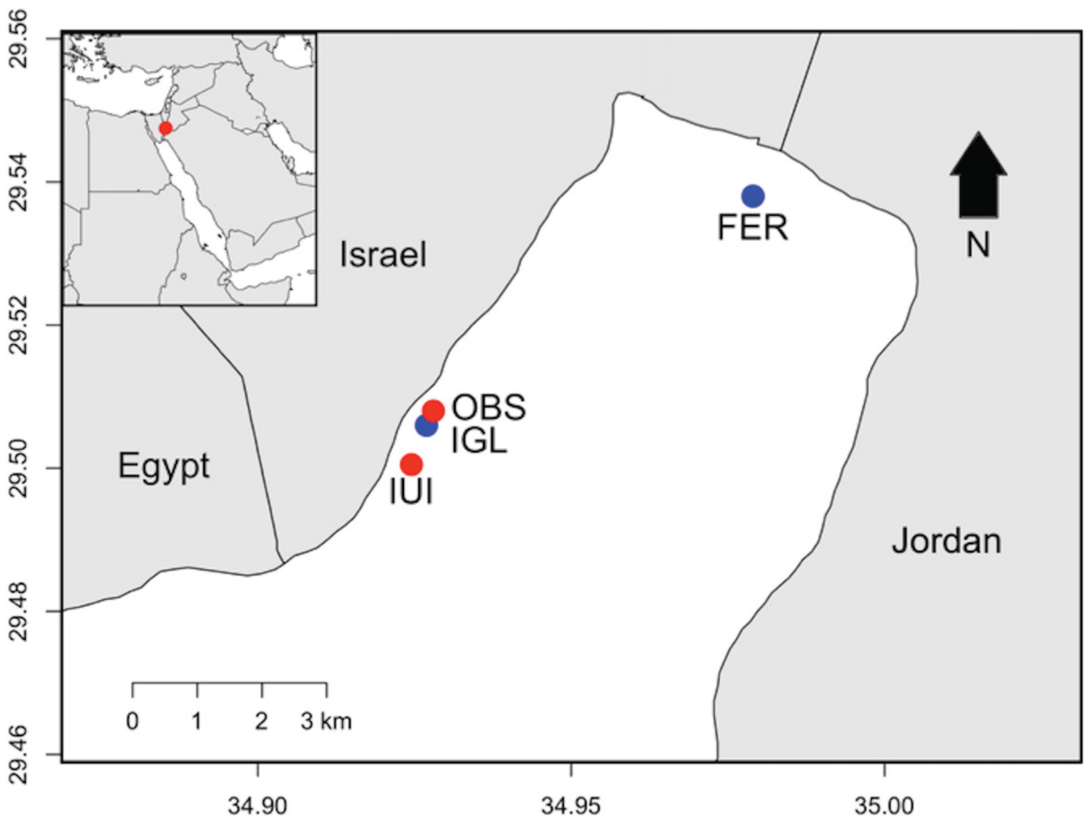

Fig. 3.1. Map of Northern Gulf of Aqaba showing study sites. Suspended AR (FER) and seafloor AR (IGL) in blue, and two natural reef sites in red (IUI, OBS). Inset shows location of the Gulf in the Red Sea.

To quantify the biotic assemblage on artificial and natural reefs at my study sites and provide context for the experiment, these areas were surveyed photographically using diver-operated cameras (Canon S100, Canon S110) in June 2015. The entire upper surface of FER was sampled with still photographs taken by divers swimming ~1 m above the reef platform. The shaded underside of the framework and cryptic microhabitats beneath it (undersides of plastic trays or the tubes that suspended the reef) were sampled similarly, using flash photography as necessary. At IGL, the entire outer surface was surveyed in a series of video transects conducted by divers swimming parallel to and at a constant distance from the evenly-spaced circular metal bands that supported the structure, from bottom to top. The underside of the IGL also was sampled systematically along these bands using flash photography. Structural elements on the ARs provided scale for the photographs. At both IUI and OBS, a 100 x 0.8 m video belt-transect was conducted by divers swimming along the 10–13 m depth contour. A metal washer (4.5 cm in diameter) attached to a plumb line was used to maintain the camera at a fixed distance (2 m) above the seafloor and provide scale.

Videos were imported into GoPro Studio where contiguous, non-overlapping frames were extracted for each transect, and individual frame captures randomly selected to quantify percent cover of algae, stony corals, soft corals, and other sessile benthic invertebrates. Uncolonized frame area consisted of "bare" (without visually detectable fauna or flora) hard substratum (e.g. artificial structures, cobble, coral rubble and standing skeletons), sand (at natural reefs), and gaps (open water between artificial or biogenic structures at the ARs). Frame captures on natural reefs (IUI: n = 12; OBS: n = 12) encompassed 28.8 m^2 of the seafloor at each site. Still images of the upper platform (n = 30) and shaded underside (n = 30) at FER and frame captures of the outer surface (n = 30) and underside (n = 30) at IGL encompassed a total of 14.4 m^2 and 4.8 m^2 in reef surface area, for each side of each AR, respectively. All images were analyzed using ImageJ64 (1.47v). Percent cover of taxonomic groups (see *Sampling and analysis of experimental collectors*) was calculated by superimposing a uniform array of 100 points on the image. Points were disqualified if the substratum was obscured by a motile invertebrate.

3.2.2 Experimental design

Settlement collectors were deployed at FER, IGL, IUI and OBS on 11–14 October 2015 (Permit no: 2015/41064). Two identical settlement surfaces were created on each collector by gluing 2 ceramic tiles (20 x 20 cm) together with the unfinished terracotta surfaces exposed. Topsides were exposed to light and accessible to all consumers, and undersides created a sheltered and shaded microhabitat. At the ARs (FER and IGL), I attached paired collectors mounted at an angle of 45° (to limit sediment accumulation) on L-shaped frames of galvanized steel mesh and attached with plastic cable ties to form an array (Fig. 3.2A). At each AR, 10 arrays were dispersed around the upper surface of the structure at ~10 m depth and attached with cable ties to galvanized mesh (IGL) or metal posts (FER) to raise them 10–30 cm into the water column (Fig. 3.2A). Due to permitting restrictions at IUI and OBS, single arrays included 4 collectors attached to large triangular frames of galvanized mesh (Fig. 3.2B). Holes were cut out of the mesh to accommodate each collector. Five of these arrays were deployed at each site with 2 collectors spaced 35 cm apart and affixed to each side at a 45° angle. The apex of each array was 50 cm above the seafloor and the arrays were anchored on sandy bottom with buried concrete blocks. At each natural reef site, the arrays were spaced at 15–20 m-intervals along a 10–13 m-depth contour.

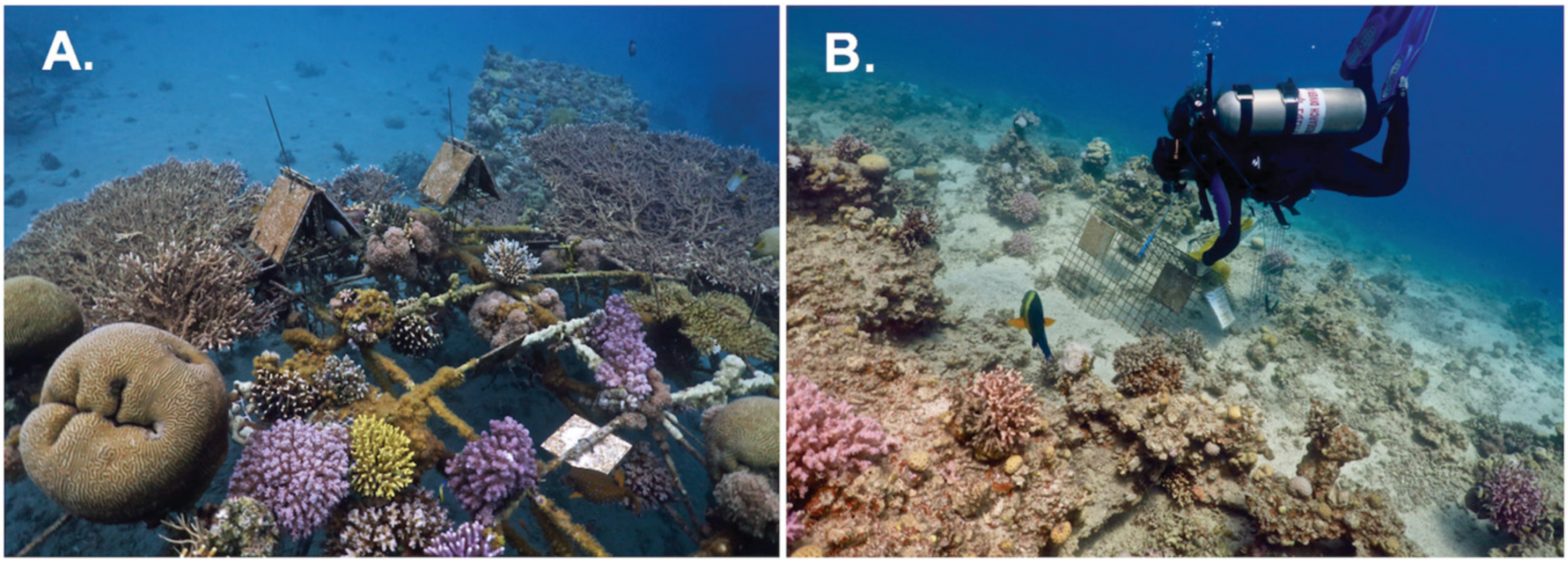

Fig. 3.2. Experimental units and arrays at artificial and natural reefs. (A) 2-collector arrays at an AR (IGL) and (B) a 4-collector array at a natural reef (IUI). Each collector (ceramic tile) in an array had 2 settlement surfaces (topside, underside).

3.2.3 Sampling and analysis of experimental collectors

Topsides and undersides of collectors were photographically sampled at monthly intervals, using a metal framer fitted to the camera housing (Canon S100 with Fish Eye housing) to ensure the lens was centered and perpendicular to the collector surface at a fixed distance. To photograph the underside, divers cut a cable tie securing the collector to the top of the frame, allowing it to flip downwards.

At the end of the experiment, all collectors were recovered to measure the composition and abundance of the attached invertebrate assemblage. Collectors were recovered from FER, IGL, IUI, and OBS between 25 October and 15 November 2016. Collectors were photographed directly before collection (the final *in situ* photographic sample) and placed in sealed plastic bags *in situ* for delivery to a research vessel where they submerged in seawater in large plastic bins. To prevent damage to colonizing communities on the surfaces, each collector was isolated and placed upright on an edge. Collectors were transferred within < 1 h to flow-through seawater tables at the Interuniversity Institute, also individually isolated and upright, until processing.

Collectors were assigned random number designations and processed within 5 d of recovery. Sessile macroinvertebrates (> 2 mm in maximum dimension) were manually removed by scraping with a scalpel under a dissecting microscope. Each individual was identified as a basal species (or morphospecies) or epibiont, and photographed upon removal for future reference or identification. Biomass was not recorded for algal films or turfs, encrusting sponges (≤ 3 mm thick), small oysters (< 5 mm) and sessile polychaetes (< 1 cm) because they could not be effectively removed from collectors. Cover of encrusting sponges was negligible or low on collector topsides at all reefs (< 1%) and undersides at natural reefs (< 4%), but formed a thin film on undersides at ARs (17–23%; estimated biomass based on volume, 0.28–0.38 g). Therefore, exclusion of encrusting sponges did not appreciably underestimate my measures of sponge biomass. For the other taxa that could not be effectively removed from collectors, small individuals constituted ≤ 4% of oyster cover on artificial and natural reefs, and ≤ 3% and ≤ 1% of sessile polychaete cover on artificial and natural reefs, respectively.

Invertebrates were blotted on paper toweling for ~5 min before biomass (wet weight, g 400 cm^{-2}) was recorded on a top-loader electronic scale (precision, 0.01 g). Collectors were submerged in flow-through seawater tables periodically during processing to prevent desiccation. Individuals were identified to the lowest possible taxonomic level by visual inspection in the laboratory during processing of collectors (Appendix B.2). A photographic catalogue was kept for all invertebrate taxa in both experiments. Samples of individuals that could not be identified to genus or species based on available taxonomic keys or local expertise were sent to experts for assistance. Coral recruits were measured (colony diameter, mm) and the number of polyps per recruit recorded. Recruits were counted on each collector surface to calculate density.

Photographs of individual collectors (image size: 4000 x 3000 pixels, 46 MB) from monthly samples were processed using ImageJ64 (1.47v). Percent planar cover of colonist taxonomic groups were analyzed by superimposing 100 uniformly spaced points across the collector surface. Points were excluded where the tile surface was obscured by a cable tie or motile invertebrate. Microbial or algal taxonomic groups included biofilms (bacteria, microalgae); algal matrix (conglomerate of filamentous turf-forming algae, sediment and detritus); macroalgae (non-coralline fleshy or foliose brown algae, e.g. *Lobophora* spp., *Padina* spp.); and encrusting coralline algae. Invertebrate groups included ascidians; bivalves; polychaetes; bryozoans; corals; and anemones. The only vertebrate group was damselfish eggs.

3.2.4 Statistical analysis

Given the non-independence of exposed and cryptic surfaces on the same collectors, and expected large differences in assemblages between these surfaces, topsides and undersides of collectors were analyzed separately. Given the difference in array structure between artificial and natural reefs, I averaged the abundance (planar cover or biomass) of each taxonomic group across collectors (topside or underside) in each array (ARs: $n = 2$ collectors; natural reefs: $n = 4$ collectors) for all analyses. I used PERMANOVA with Bray-Curtis similarity matrices to examine the effect of site (fixed factor, 4 levels: FER, IGL, OBS, IUI) on the final composition of the entire assemblage (planar cover) and of invertebrate colonists (biomass). I used ANOVA to examine the effect of site on total invertebrate biomass or coral recruit density at the end of the experiment. I conducted post-hoc comparisons of sites ($\alpha = 0.05$) using PERMANOVA pairwise t-tests and Fisher's LSD test for ANOVA.

I examined temporal changes in composition of the assemblage (planar cover) during the experiment, and differences in composition (planar cover, biomass) among sites at the end of the experiment, using non-metric multidimensional scaling (nMDS), also using Bray-Curtis similarity matrices. I used site means (average of array means within a site) to represent community composition at each time interval for each site for temporal analysis. Analysis of similarity percentage (SIMPER) was used to identify taxonomic groups that contributed most to differences in composition between sites.

Planar cover of taxonomic groups was arcsine transformed and biomass of invertebrate groups was fourth-root transformed for PERMANOVA. PERMDISP test for PERMANOVA indicated that transformation succeeded in homogenizing variance (α = 0.05) for cover and biomass. Total invertebrate biomass and coral recruit density were log-transformed for ANOVA to satisfy Levene's test for homogeneity of variance (α = 0.05). PERMANOVA, PERMDISP, nMDS, and SIMPER analyses were computed in Primer v7.0 (Plymouth Routines in Multivariate Ecological Research) with PERMANOVA+ (PRIMER-E Ltd, Plymouth, UK).

3.3 RESULTS

3.3.1 Community structure at artificial and natural reefs

At the start of my study in June 2015, coral cover (stony and soft coral combined) on the substratum surface was 3- to 5-fold greater on ARs (IGL, 28%; FER, 43%) than natural reefs (IUI/OBS, 9%) (Fig. 3.3). Stony corals dominated the cover at FER (35.5%), while soft corals dominated at IGL (24.2%). Stony corals also accounted for most of the coral cover at natural reefs (IUI, 7.8%; OBS, 6.0%). Cover of other sessile benthic invertebrates, including sponges, ascidians, bryozoans and bivalves, was low on the surface at ARs (FER, 6.8%; IGL, 3.3%) and negligible at natural reefs. Macroalgae were observed only at FER (10.7%). Corals and other sessile invertebrates extensively covered the undersides of ARs (FER, 83.7%; IGL, 59.4%) (Fig. 3.3). Coral cover (stony and soft coral combined) on undersides was 3-fold greater at IGL (44.3%) than FER (12.7%), with soft corals dominating at IGL (29.9%).

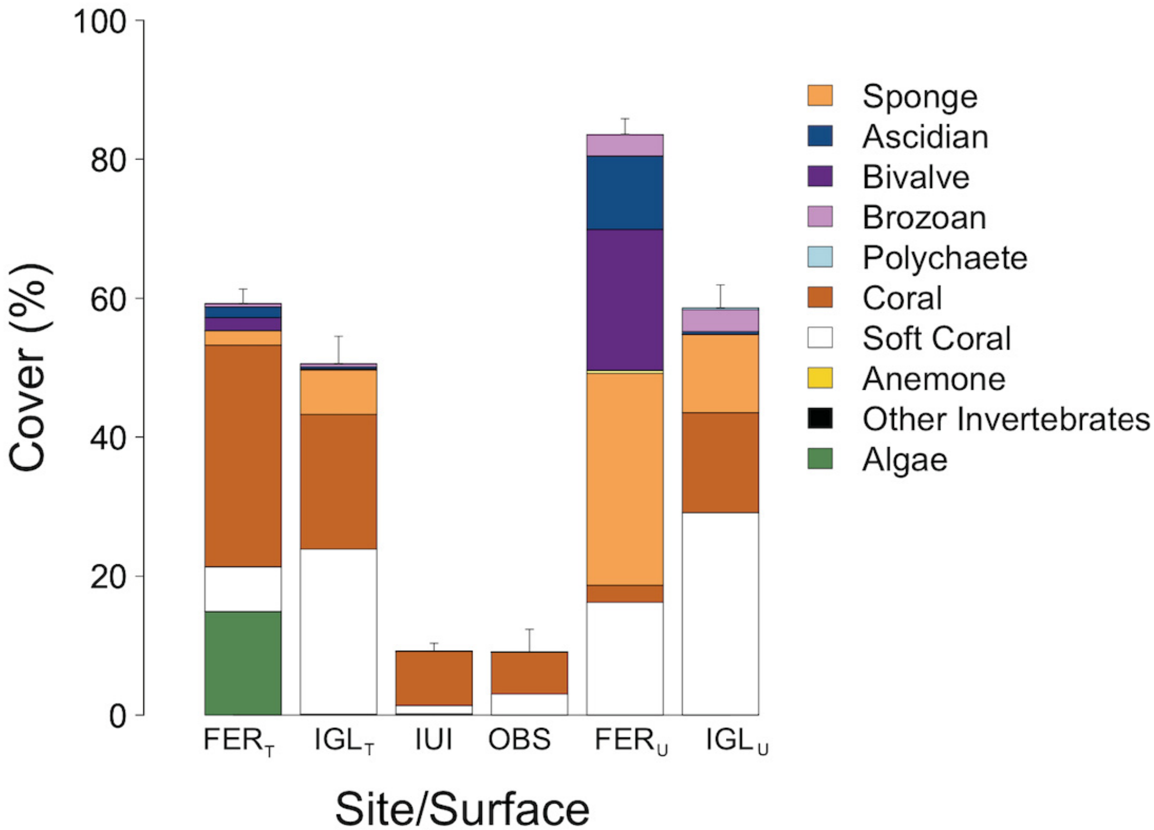

Fig. 3.3. Background community composition on artificial and natural reefs. Mean (+SD) planar cover (%) and composition of sessile benthic organisms on upper (top) surface (FER_T, IGL_T: n = 30 frames) and underside (FER_U, IGL_U: n = 30 frames) of the platform on ARs, and on upper surface of natural reefs (IUI_T, OBS_T: n = 12 frames), in June 2015.

3.3.2 Cover of the colonizing community

On collector topsides, planar cover of the colonizing community on artificial and natural reefs was dominated by algal matrix and biofilm throughout the experiment (Fig. 3.4). Coralline algae increased in cover after 3 mo at IUI and IGL, respectively, but were rare at FER and OBS. Invertebrates colonized after 1 mo reaching maxima that were 1–2 orders of magnitude greater at ARs than natural reefs. FER had the greatest cover of invertebrates (Appendix B.1), mainly polychaetes (from 2–6 mo), bryozoans, and bivalves (from 6–13 mo). Invertebrates were rare at IGL until 8 mo, when sponges and bivalves colonized. At natural reefs, invertebrates were rare throughout the experiment. nMDS showed that trajectories of change in community composition on topsides were most divergent at FER and OBS, while trajectories at IGL and IUI converged after 4 mo, when collectors were colonized by coralline algae (Fig. 3.5).

On collector undersides, invertebrates began colonizing earlier at ARs (after 2–3 mo) than natural reefs (after 4–5 mo) and maintained a greater total cover at ARs throughout the experiment (Fig. 3.4). Greatest planar cover was observed at ARs by bryozoans between 3 and 6 mo, and ascidians at 8 mo (Appendix B.1). In contrast, at natural reefs, a greater cover of biofilm and algal matrix remained throughout the experiment, peak cover of bryozoans was lower, and bivalves appeared earlier and reached greater peak cover (Fig. 3.4). nMDS showed that trajectories of change in community composition were similar between sites within reef types; reef types diverged after 2–3 mo (Fig. 3.5).

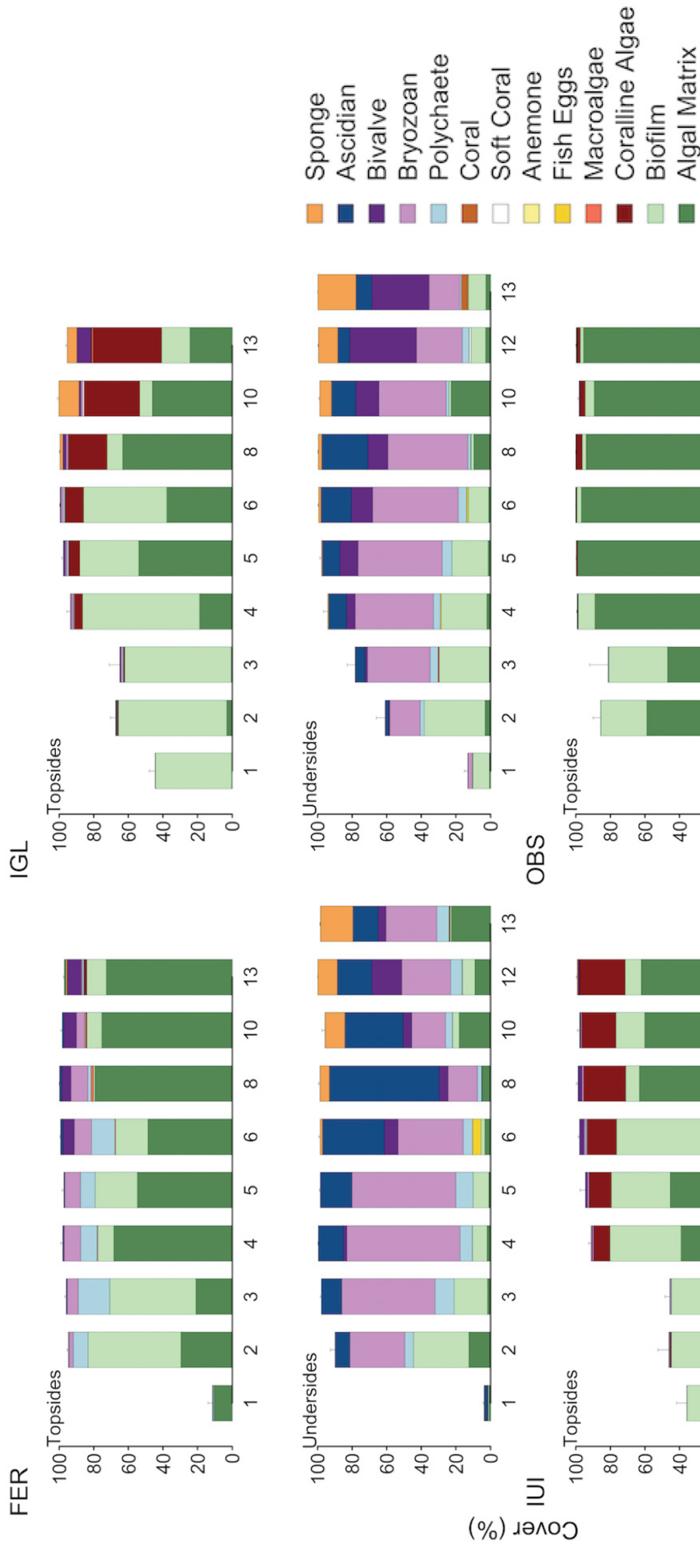
FER
IGL
IUI
OBS
Topsides
Undersides
Cover (%)
Elapsed Time (mo)
Sponge
Ascidian
Bivalve
Bryozoan
Polychaete
Coral
Soft Coral
Anemone
Fish Eggs
Macroalgae
Coralline Algae
Biofilm
Algal Matrix

Fig. 3.4. Spatial and temporal patterns in community composition on artificial and natural reefs. Change in planar cover (%) and composition of taxonomic groups on collector topsides and undersides at a suspended AR (FER), a seafloor AR (IGL), and 2 natural reefs (IUI, OBS) over 13 mo (Oct 2015–Nov 2016). Bar heights are mean (+SE) of 10 arrays (2 collectors averaged per array) for ARs and 5 arrays (4 collectors averaged per array) for natural reefs at each sampling interval.

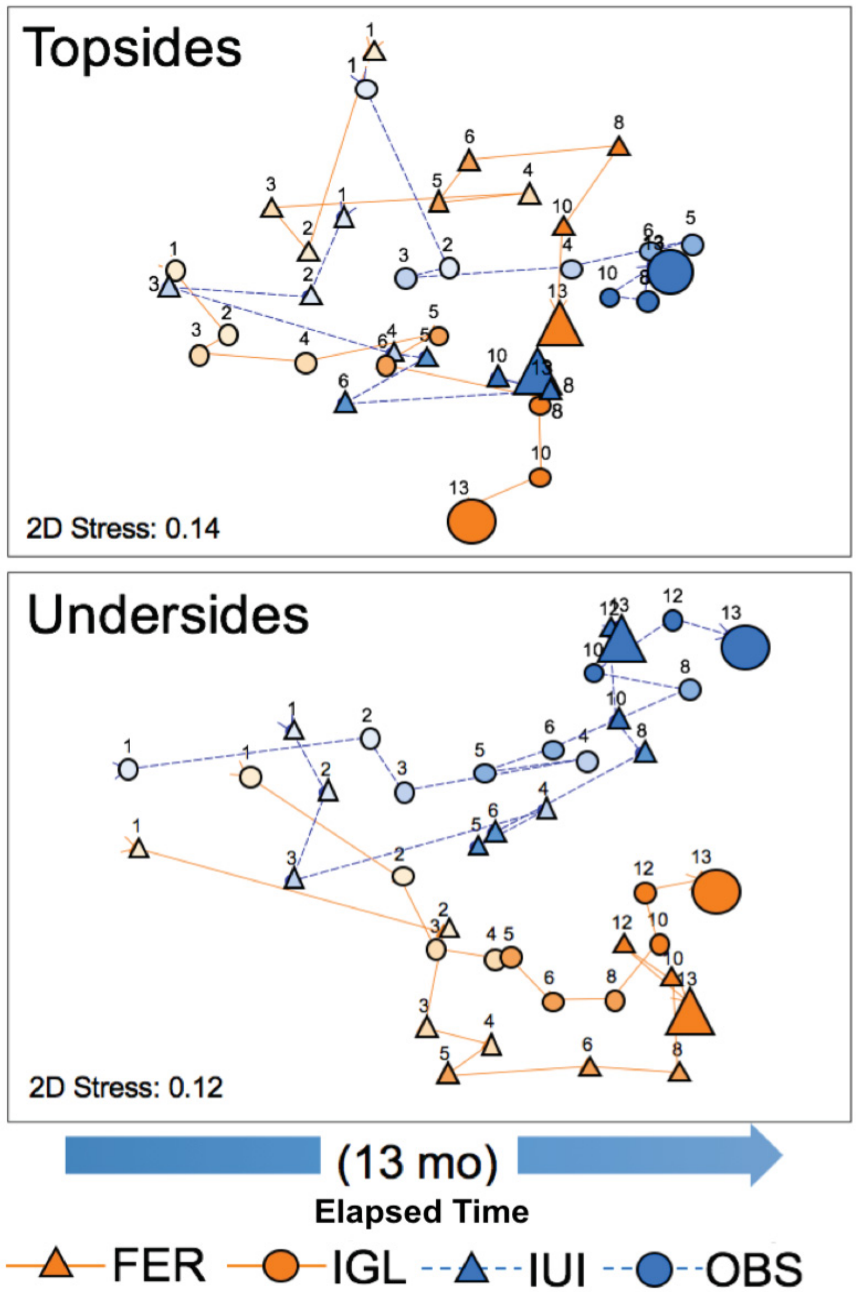

Fig. 3.5. Trajectories of change in community composition among reefs. nMDS plot of community composition as planar cover (%) on collector topsides and undersides for two ARs (FER, IGL) and two natural reefs (IUI, OBS) over 13 mo (Oct 2015–Nov 2016). Each numbered symbol represents the average composition at that sampling interval (elapsed time, mo); symbol colour intensifies with time and symbols for final samples are magnified for clarity (n = 10 arrays for ARs, 5 arrays for natural reefs).

PERMANOVA showed that community composition (arcsine-transformed data) differed significantly ($P < 0.001$) between sites on both topsides and undersides at the end of the 13-mo experiment; pairwise comparisons indicate that all sites differed from one another ($P < 0.01$) in both cases (Table 3.1). Coralline algae and algal matrix accounted for most of the dissimilarity in community composition on topsides between sites, while bivalves, bryozoans and sponges accounted for most of the dissimilarity on undersides (Appendix B.3). nMDS showed that arrays on artificial and natural reefs formed separate clusters at 70% similarity for undersides, but were more interspersed between reef types for topsides (Fig. 3.6A).

Table 3.1. PERMANOVA of community composition. Analysis examines the effect of site (fixed factor: FER, IGL, IUI, OBS) on the composition of planar cover (%) on topsides and undersides of collectors at the end of a 13-mo experiment. Also shown are pairwise comparisons using the PERMANOVA t-statistic. Tests are based on 999 permutations. Significant results in bold.

Source	*df*	MS	*Pseudo-F*	*p(perm)*
Topsides				
Site	3	2328.3	20.4	**0.001**
Residual	26	114.1		
Undersides				
Site	3	3215.7	25.9	**0.001**
Residual	26	124.1		

	t	*p(perm)*
Topsides		
FER vs. IGL	5.2	**0.001**
FER vs. IUI	2.8	**0.001**
FER vs. OBS	3.8	**0.001**
IGL vs. IUI	2.8	**0.007**
IGL vs. OBS	6.8	**0.001**
IUI vs. OBS	3.7	**0.001**
Undersides		
FER vs. IGL	4.4	**0.001**
FER vs. IUI	6.9	**0.002**
FER vs. OBS	6.1	**0.001**
IGL vs. IUI	4.4	**0.001**
GL vs. OBS	4.8	**0.002**
IUI vs. OBS	2.9	**0.007**

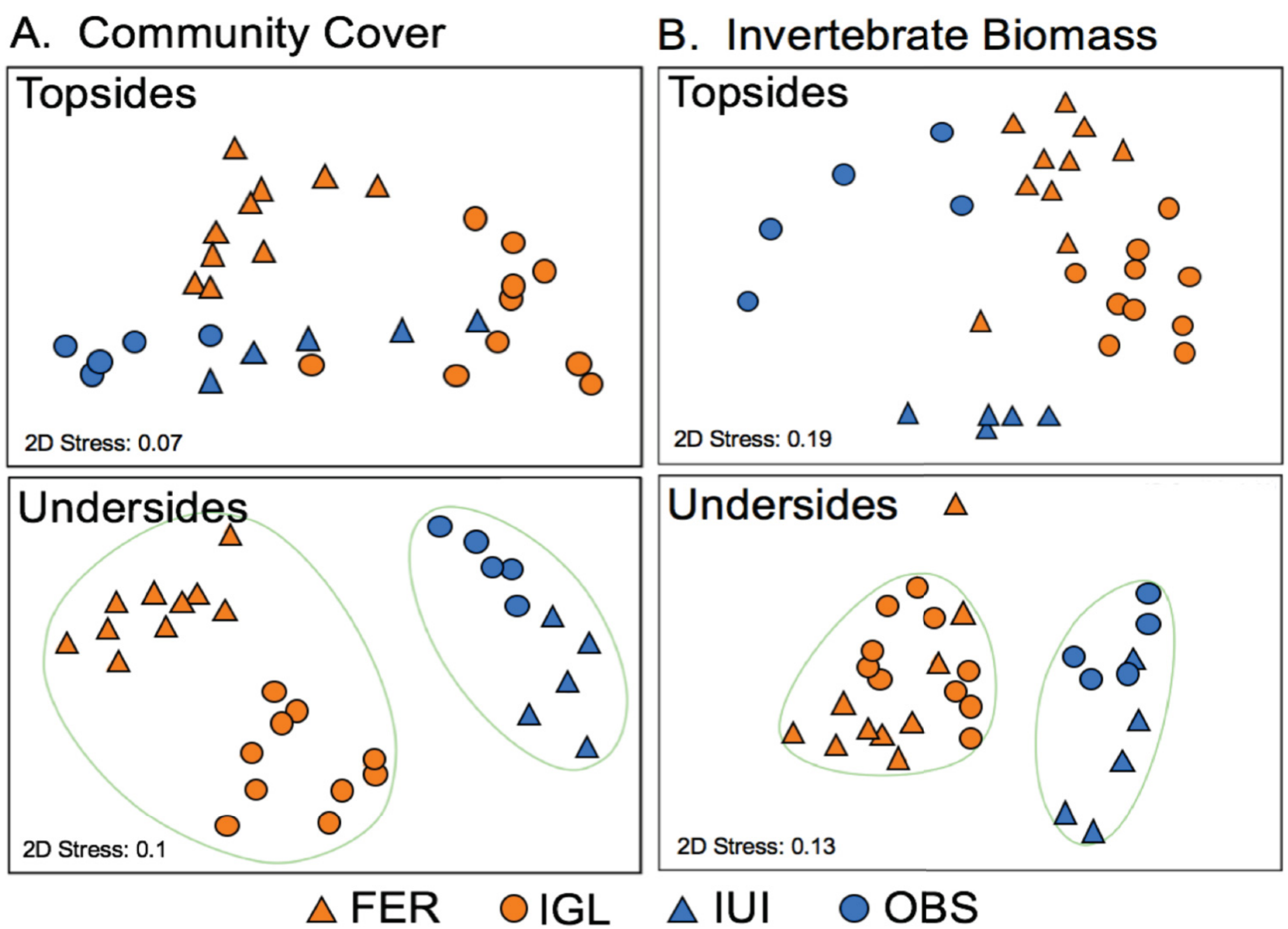

Fig. 3.6. Final community composition on artificial and natural reefs in the mensurative experiment. Non-metric multidimensional scaling (nMDS) plot of (A) community composition as planar cover (%) and (B) invertebrate composition as biomass (g 400 cm^{-2}) on collector topsides and undersides (averaged per array) at two ARs (FER, IGL; orange symbols, n = 10 arrays) and two natural reefs (IUI, OBS; blue symbols, n = 5 arrays) at the end of the experiment (Nov 2016). Ellipses bound groups of arrays of 70 % similarity.

3.3.3 Final biomass of invertebrate colonists

Total biomass was an order of magnitude greater on undersides than topsides across all sites at the end of the experiment (Fig. 3.7). ANOVA showed that biomass (log-transformed data) on topsides differed among sites ($F_{3,26} = 12.9$, $P < 0.001$) and was greater on ARs than natural reefs, but sites within each reef type did not differ (Fisher's LSD test, $\alpha = 0.05$). For undersides, ANOVA yielded a marginally non-significant result for the effect of site ($F_{3,26} = 2.96$, $P = 0.051$), but pairwise comparisons showed that FER, IGL and OBS formed one homogeneous subset, and OBS and IUI another, indicating that biomass at IUI but not OBS was significantly lower than that at the two ARs.

Sponges, bivalves, and ascidians accounted for most of the macroinvertebrate biomass on topsides and undersides of collectors at the end of the experiment (Fig. 3.7). PERMANOVA showed that the composition of invertebrates, as for the entire community, also differed between sites ($P < 0.001$) and in all pairwise combinations ($P < 0.01$) on both topsides and undersides of collectors by the end of the experiment (Table 3.2). Sponges, bivalves and polychaetes accounted for most of the dissimilarity in composition on topsides between sites, while ascidians, bivalves and bryozoans accounted for most of the dissimilarity on undersides (Appendix B.4). nMDS showed that arrays on artificial and natural reefs also formed separate clusters for undersides, with all but 1 array (at FER) clustering at 80% similarity by reef type, but tended to cluster more by site for topsides, with the greatest dissimilarity among arrays at OBS (Fig. 3.6B).

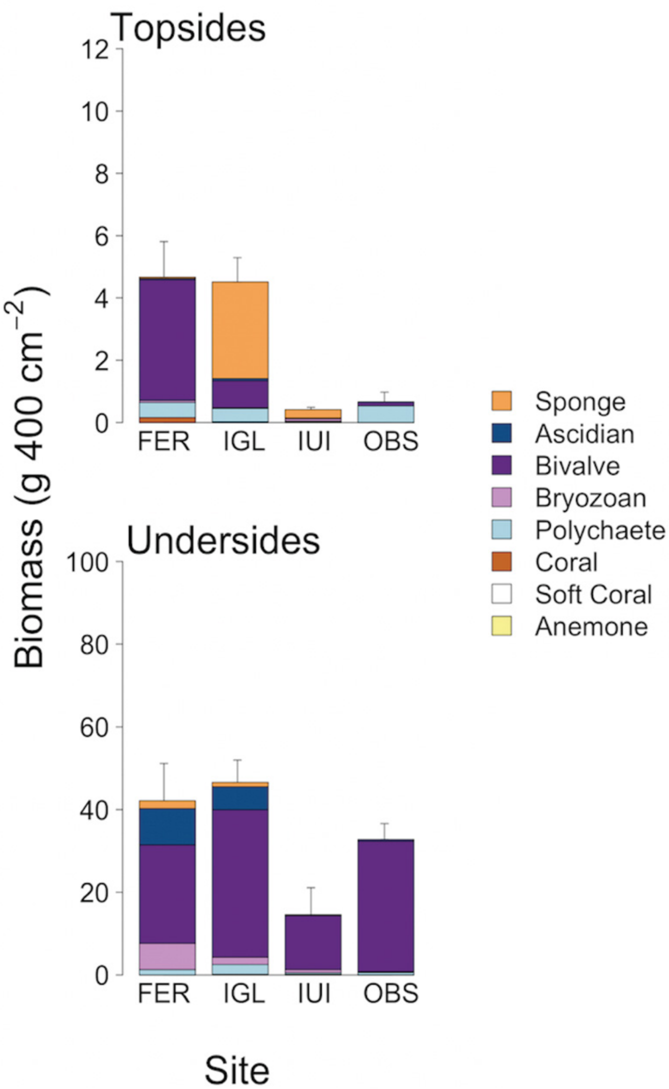

Fig. 3.7. Final biomass of invertebrates on artificial and natural reefs. Biomass (g 400 cm^{-2}) of invertebrate colonists on collector topsides and undersides for two ARs (FER, IGL; n = 10 arrays) and two natural reefs (IUI, OBS; n = 5 arrays) at the end of the experiment (Nov 2016). Bar heights are mean (+SE) total biomass for arrays.

Table 3.2. PERMANOVA of invertebrate composition. Analysis examines the effect of site (fixed factor: FER, IGL, IUI, OBS) on the composition of invertebrate biomass (g 400 cm^{-2}) on topsides and undersides of collectors at the end of a 13-mo experiment. Also shown are pairwise comparisons using the PERMANOVA t-statistic. Tests are based on 999 permutations. Significant results in bold.

Source	*df*	MS	*Pseudo-F*	*p(perm)*
Topsides				
Site	3	3739.5	13.9	**0.001**
Residual	26	268.3		
Undersides				
Site	3	1338.5	13.4	**0.001**
Residual	26	100.1		

	t	*p(perm)*
Topsides		
FER vs. IGL	3.7	**0.001**
FER vs. IUI	4.0	**0.002**
FER vs. OBS	3.2	**0.001**
IGL vs. IUI	4.1	**0.001**
IGL vs. OBS	4.2	**0.001**
IUI vs. OBS	3.2	**0.009**
Undersides		
FER vs. IGL	2.1	**0.004**
FER vs. IUI	4.0	**0.003**
FER vs. OBS	4.5	**0.001**
IGL vs. IUI	4.1	**0.002**
GL vs. OBS	4.0	**0.001**
IUI vs. OBS	2.6	**0.009**

3.3.4 Recruitment of stony corals

After 13 months, stony corals accounted for < 3.4% of planar cover. Coral recruits at the end of the experiment (n = 220) were almost exclusively *Stylophora* spp. with one *Seriatopora* sp. and one *Lepastrea* sp. recruit. Recruits ranged in size from 2.0 to 20.7 mm with 4 to 119 polyps. Mean recruit density ranged from 0.4 – 2.2 recruits 400 cm^{-2} on topsides and varied significantly between sites (ANOVA, $F_{3,26} = 3.35$, $P = 0.034$); pairwise comparisons (Fisher's LSD test, $\alpha = 0.05$) showed that FER and IUI formed one homogeneous subset, and IUI, IGL and OBS another, indicating that recruit density was greatest at FER and lowest at IGL and OBS (Fig. 3.8). Mean recruit density was more variable on undersides (0.1 – 4.9 recruits 400 cm^{-2}) and differed significantly between sites (ANOVA, log x+1-transformed data, $F_{3,26} = 51.4$, $P < 0.001$); pairwise comparisons (Fisher's LSD test, $\alpha = 0.05$) showed density at IUI > OBS > IGL = FER (Fig. 3.8).

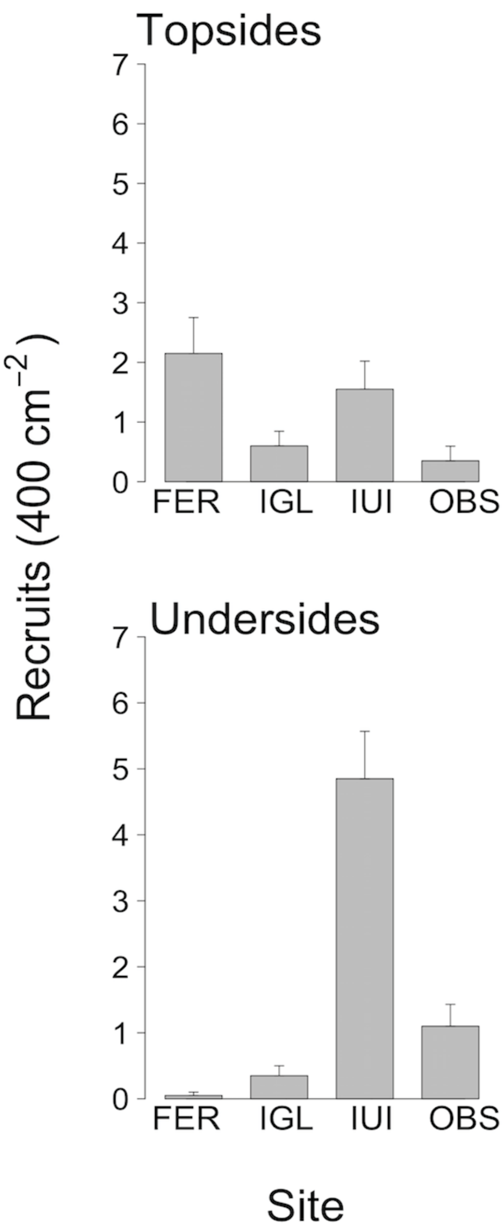

Fig. 3.8. Final coral density on artificial and natural reefs. Mean (+SE) density of stony coral recruits (individuals 400 cm^{-2}) on collector topsides and undersides for two ARs (FER, IGL; n = 10 arrays) and two natural reefs (IUI, OBS; n = 5 arrays) at the end of the experiment (Nov 2016).

3.4 DISCUSSION

3.4.1 Benthic community development and accumulated biomass on artificial and natural reefs

The succession of algae and sessile invertebrates and accumulated cover and biomass after 13 mo differed between reef types (artificial, natural) depending on collector aspect (topside, underside). This is contrary to my prediction that communities would evolve similarly with similar abundances of invertebrates on artificial and natural reefs. On collector undersides, community composition according to cover began to diverge between artificial and natural reefs after 3 mo. By the end of the experiment, sites segregated by reef type in terms of the composition of both cover and invertebrate biomass and accumulated invertebrate biomass. Differences in composition between reef types were less clear on topsides, and there were significant between-site differences within and between reef types. My findings suggest that when free-space is made available on heavily colonized ARs, the emergent benthic assemblages can differ in composition and abundance from those on adjacent natural reefs. This pattern is particularly pronounced when ARs are elevated (IGL) or suspended (FER) off bottom and have luxuriant communities of filter- and suspension-feeding invertebrates (e.g. ascidians, bivalves, bryozoans, and sponges) growing on their undersides, where increased flow and reduced sedimentation are conducive to growth and reproduction of these "fouling species" (Baynes & Szmant 1989; Eckman et al. 1989).

As expected, community composition and invertebrate biomass differed greatly between collector topsides, dominated largely by a filamentous algal matrix, and shaded and sheltered undersides that accumulated a diversity of sessile benthic invertebrates. Similar differences in composition and abundance of colonists depending on collector aspect are well documented in previous studies on temperate (Glasby 2000; Todd & Turner 1986) and tropical reefs (Plass-Johnson et al. 2016; Perkol-Finkel & Benayahu 2007; Field et al. 2007). Light exposure is the key proximate factor accounting for these differences (Glasby 1999; Mundy & Babcock 1998; Ettinger-Epstein et al. 2008). Rapid growth of a dense algal matrix on collector topsides may have inhibited settlement of invertebrate larvae through preemption of space (Davis et al. 1989; Fairfull & Harriott 1999) or chemical deterrence (Arnold et al. 2010; Dixson et al. 2014). An algal matrix also traps sediment that can smother recruits of filter- and suspension-feeding invertebrates (Breitburg 1984), and erect macroalgae can overgrow recruits of corals (Arnold et al. 2010; Birrell et al. 2005) and ascidians (Young & Chia 1984). Competitive interactions among fast-growing algal and invertebrate species result in high species turnover (Plass-Johnson et al. 2016). My findings suggest that ARs that are designed with expanses of shaded, cryptic microhabitats can foster growth of fouling species, such as sponges, bivalves, bryozoans, and ascidians.

Successional patterns within reef types and collector aspects differed between sites despite their proximity and similar depth. Hydrodynamic models of the Gulf of Aqaba describe a chain of gyres (Brenner & Paldor 2004; Ahmed et al. 2012), with the northern section of the gulf dominated by a single gyre throughout the year (Biton & Gildor 2011). This circulation pattern may result in high larval retention (Berman et al. 2000; Kochzius & Blohm 2005), likely from a single larval pool within my general study area, which would lead to similar rates of larval supply to all reefs. This process can explain the relatively high cover of bivalves across all of the reef sites. However, recruitment rates of some fouling species, such as ascidians, bryozoans and sponges, vary at small spatial scales because their short larval duration (minutes to days) resulting in low dispersal distances (10s – 100s m) (Olson 1985; Keough 1989; Stoner 1990; Maldonado 2006). These three taxa constituted a significant component of the recruits on my collectors and of the fouling communities on the structural undersides of IGL and the FER. My results suggest that fouling communities on ARs could be maintained through self-recruitment.

Large mobile consumers can also significantly affect community composition and abundance of sessile invertebrates. Desilets (2017) conducted a concurrent consumer exclusion experiment in the Gulf of Aqaba at the FER and IUI. They found that cover of ascidians on collector undersides was greater in the exclusion treatment than the control after 2 – 3 mo, and accumulated biomass was greater in the exclusion treatment on both topsides and undersides at the end of the experiment, suggesting caging provided a predation refuge that allowed this group to proliferate during their recruitment season (April–August) (Koplovitz et al. 2016). Predation and grazing are considered important sources of mortality for young ascidian recruits (Young & Chia 1984; Osman & Whitlach 2004), and chemically-undefended sponges (Dunlap & Pawlik 1996; Pawlik et al. 2008). However, Schmidt and Warner (1984) suggest that caging collectors also can enhance settlement of ascidian larvae by reducing light intensity and water flow.

Differences in fish assemblages between the artificial and natural reefs in my study likely contributed to differences in patterns of succession and accumulated abundance among sites within and between reef types. Suspended ARs limit access by demersal fish that frequent ARs on the seafloor or natural reefs (Holloway & Connell 2002; Rooker et al. 1997). The FER harbours an abundant and diverse assemblage of planktivorous fish, but demersal fish are rare (Desilets 2017). In contrast, the fish assemblage at IGL and the two natural reefs also includes piscivores and demersal carnivores and herbivores (Genin

& Shaked 2016). Territorial damselfish can be important herbivores on reefs where roving foragers are not present (Gibson et al. 2001). Observations of biting on collectors by scarids and acanthurids at IGL suggest that invertebrate assemblages on seafloor ARs may be exposed to similar grazing pressure as on natural reefs (Desilets 2017); I found that IGL and IUI followed similar trajectories of succession over time on exposed topsides of collectors.

3.4.2 Recruitment of stony corals

Despite their abundance and diversity in the background communities on natural and ARs, the cover of stony corals was low (< 4%) and almost exclusively *Stylophora* spp. in my experiment. Recruit size (2 – 21 mm diameter) at the end of the experiments in November 2016, suggests these corals settled between April and August based on growth rates in the Gulf of Aqaba (Glassom et al. 2004). Recruit density generally was ≤ 2 recruits 400 cm^{-2} across sites and collector aspects, except on undersides at IUI where it reached 4 – 5 recruits 400 cm^{-2}. This is comparable to recruit density previously measured on ceramic (Glassom et al. 2004) and PVC (Perkol-Finkel & Benayahu 2007) recruitment plates in the region. Abelson et al. (2005) documented lower recruitment rates of stony corals (< 1 recruit 400 cm^{-2}), which was attributed to low survival rates and high abundances of fouling species at experimental sites. I also observed the lowest levels of coral recruitment on undersides of ARs, possibly due to the dense cover of fouling species, such as ascidians and sponges that preempted space or inhibited recruitment through allelochemical interactions (Koplovitz et al. 2016; Russ 1982; Watters & van

Den Brenk 1993). In contrast, cover on the undersides at the IUI, where coral recruitment was greatest, was dominated by bivalves, algal matrix and biofilm. Given the relatively slow growth of corals, multi-year studies are required to detect the establishment of adult coral colonies and their eventual dominance on experimental structures (Perkol-Finkel & Benayahu 2005).

3.5 CONCLUSIONS

My experimental results highlight the potential of ARs to enhance cover and biomass of reef-associated assemblages, particularly those occupying sheltered microhabitats. The assemblages of algae and invertebrate colonists that developed on standardized collectors on ARs diverged after 4 months from those on natural reefs and accumulated more invertebrate taxa with greater total biomass. Throughout the experiment, light-exposed and shaded surfaces of collectors supported distinct benthic communities. Dense fouling communities developed on the shaded undersides, although community composition and invertebrate abundance may have been altered by large mobile consumers.

My experiment was relatively short (13 months), making it difficult to discern differences due to seasonality versus length of deployment (Connell & Slatyer 1977; Breitburg 1985; Done 1992). For example, seasonal variation in spawning and recruitment of invertebrate colonizers may have produced different results had the experiment been deployed at different times of year (Glassom et al. 2004). The short duration of the experiment also did not allow me to measure stony coral recruitment effectively, since it appears I only captured a single spawning event. Differences between AR sites, including composition of the resident community, platform structure and elevation above bottom, and proximity to the natural reefs, likely contributed to variation in community composition and accumulated biomass between sites. However, as all sites have a common larval pool for invertebrates with long larval duration, observed differences between artificial and natural reef sites are likely due to variation in the local reef assemblage, particularly of invertebrates with short larval duration, and mobile fish and invertebrate predators.

My findings highlight the importance of strategic design considerations in the deployment of ARs to achieve conservation, management or economic objectives, including: 1) architecture of the physical platform and its elevation above bottom, 2) population of this structure with transplanted colonies of corals and other invertebrates, and 3) positioning of the AR relative to neighbouring natural reefs and propagule sources. An added advantage of suspended ARs, anchored to the seabed, is that of vertical positioning in the water column to optimize the establishment and growth of targeted reef-associated species, and the potential to alter horizontal or vertical position to avoid detrimental changes in environmental conditions (e.g. warming, anoxia) or pulsed disturbances (e.g. pollution events, flash floods, strong storms). In the face of increasing pressures on coral reefs, ARs are being proposed as one mechanism for remediation; however, the variation I observed in my study suggests that the desired conservation outcome needs to be well defined to ensure success of such mitigation efforts.

CHAPTER 4

CONCLUSION

In recent decades, artificial reefs (ARs) increasingly have been deployed to mitigate large-scale environmental stressors such as coral bleaching (Clark 2000), and to increase abundance of commercially and socio-culturally important species on coral reefs (Jan et al. 2003; Al-Horani et al. 2013). My review of the global literature on ARs in coral reef ecosystems has shown that ARs deployed with well defined, small-scale conservation or management objectives are the most likely to report success in meeting those objectives (Chapter 2). ARs often fail to meet their objectives because of large scale environmental disturbances during the study period (Shaish et al. 2010), inadequate design (Adams 2005), or monitoring limitations (Blakeway et al. 2013). The most successful conservation objectives of ARs were the provision of nursery habitat or additional hard substrate for colonization. While ARs often have been deployed to increase fish abundance, direct monitoring of fish movement between ARs and adjacent natural reefs is lacking. Future work should focus on disentangling the effects of behavioural attraction of fish and increased production (Grossman et al. 1997; Brickhill et al. 2005). My review underscores the importance of strategic planning and proper monitoring for artificial coral reefs.

Examining succession and colonization of sessile benthic invertebrates on artificial and natural reefs can inform design and site selection of ARs to achieve the objectives of deployment. The initial development of the benthic community on ARs can influence subsequent establishment of fish and motile invertebrate assemblages (Svane &

Petersen 2001), which in turn determines the success of ARs at conserving these species (Perkol-Finkel & Benyahu 2007; Shenkar et al. 2008). In a mensurative field experiment at Eilat, I showed that colonization on artificial collectors on ARs can surpass that on natural adjacent reefs in terms of invertebrate biomass (Chapter 3). I also found that the species composition of invertebrate assemblages on ARs can differ from that on natural reefs. This pattern is more pronounced when ARs are elevated or suspended above the seafloor, which allows for luxuriant fouling communities to colonize and thrive in shaded and sheltered microhabitats. Suspended frameworks provide a promising platform for experimentation and restoration because they can be repositioned vertically and horizontally in response to changing environmental conditions (Chapter 3).

The accelerating decline of coral reef ecosystems globally demands a timely and effective evaluation of current and planned restoration strategies (Harris et al. 2006). Global syntheses and critical evaluations of restoration data are important tools for informing local management decisions. ARs have been deployed as a restoration strategy on coral reefs at an increasing rate over the past 2 decades (Chapter 2). This thesis examines the success of ARs in meeting conservation objectives and identifies limitations for their use in a changing climate. I've shown that ARs can be a valuable tool for conducting scientific experiments on coral reefs and addressing selective management and conservation targets in small-scale restoration projects. They also are considered a cost-effective restoration strategy relative to coral transplantation projects and large marine reserves (Baine 2001). I propose that ARs can make a meaningful contribution to coral reef restoration when properly designed and monitored to meet specific deployment objectives. Integrating ARs into regional management projects that combine multiple conservation strategies, such as marine reserves and transplantation projects, is likely to yield even higher rates of success.

APPENDIX A

CHAPTER 2

A.1. Reference List for Table 2.1

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Appendix B

Chapter 3

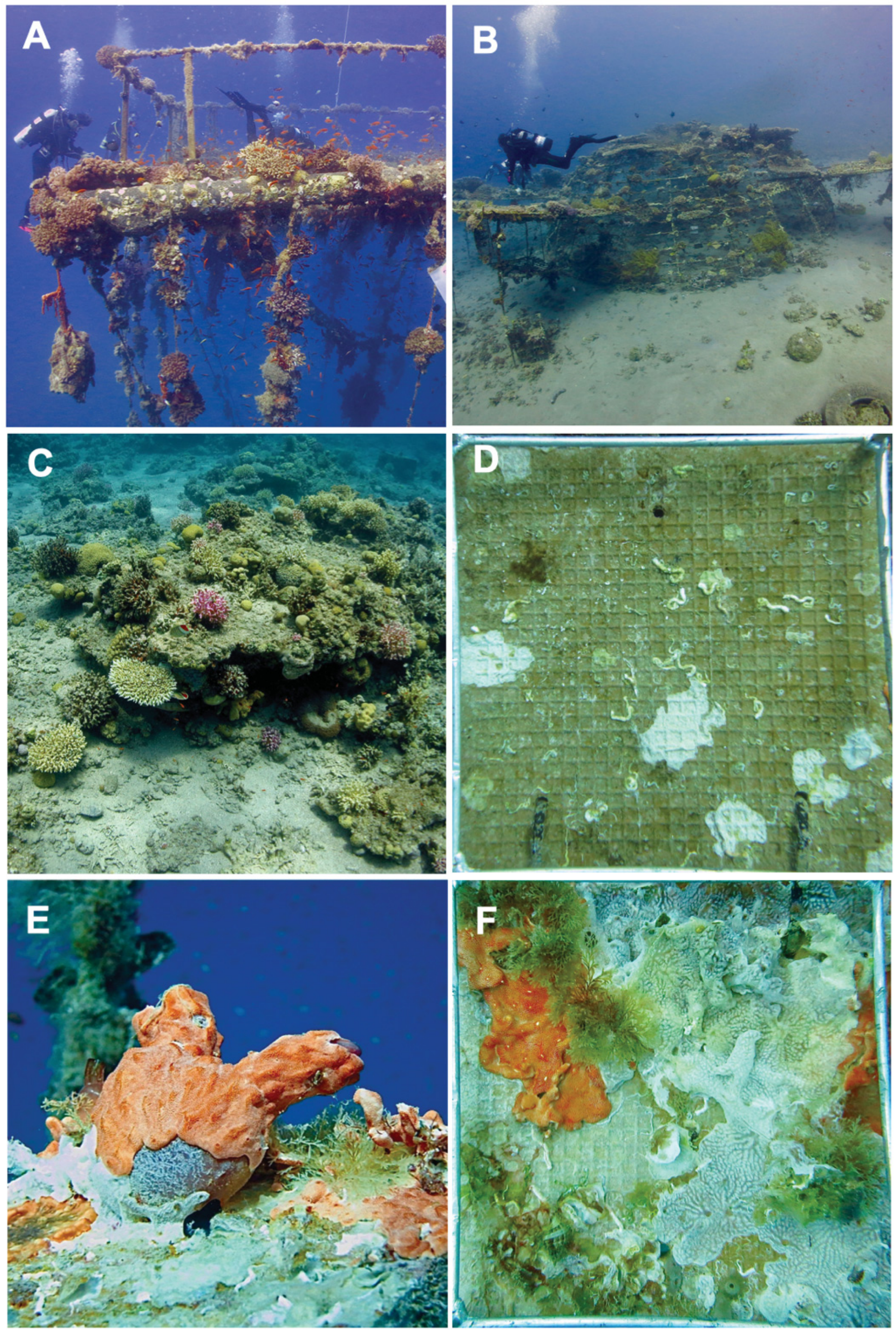

Fig. B.1. Study sites: A) Floating Experimental Reef (FER), B) Igloo (IGL), and C) coral knoll at Interuniversity Institute reef (IUI). Colonization of experimental collectors after 8 mo at FER: D) topside; E, F) undersides.

Table B.2. Taxonomic identification of colonizing species. Data are the lowest taxonomic level (Cl, Class; Or, Order; Fa, Family) identified for invertebrates on collector topsides (T) and undersides (U) at the end (Nov 2016) of a 13-mo experiment at a suspended AR (FER), a seafloor AR (IGL), and two natural reefs (IUI, OBS).

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
Porifera			
Cl Calcarea	Or Clathrinida		
	Fa Clathrinidae	*Clathrina coriacea*	IGL-U
		Clarintha sp.	FER-U, IGL-U
	Or Leucosolenida		
	Fa Grantiidae	*Grantia* sp.	
Cl Demospongiae	Or Agelasida		
	Fa Astroscleridae	*Astrosclera* sp.	
	Or Axinellida		
	Fa Raspailiidae	*Ectyoplasia* sp.	FER-T/U, IGL-T/U, IUI-T/U, OBS-T/U
	Or Bubarida		
	Fa Dictyonellidae	*Acanthella* sp.	FER-U, IGL-U
	Or Chondrillida		
	Fa Chondrillidae	*Chondrilla* sp.	FER-T, IGL-T
		sponge 13	FER-U, IGL-U, OBS-U
		sponge 15	FER-U, IUI-U
	Or Clionaida		
	Fa Spirastrellidae	*Spirastrella coccinea*	IGL-U
	Or Dictyoceratida		
	Fa Thorectidae	*Hyrtios* sp.	
	Or Hadromerida		
	Fa Clionaidae	*Cliona* spp.	FER-U, IGL-T/U, IUI-T, OBS-T

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
		Pione spp.	FER-T/U, IGL-T/U, IUI-T/U, OBS-T/U
	Fa Tethyidae	*Tethya* spp.	FER-U, IGL-U, IUI-T/U
	Or Haplosclerida		
	Fa Callyspongiidae	*Callyspongia siphonella*	FER-U, IGL-T/U, IUI-T/U, OBS-T/U
		Callyspongia spp.	FER-U, IGL-U
	Or Poecilosclerida		
	Fa Crellidae	*Crella cyathophora*	IGL-U
	Fa Desmacellidae	*Biemna* spp.	FER-U, IGL-U, IUI-U
	Fa Hymedesmiidae	*Hemimycale arabica*	FER-U, IGL-T/U, IUI-U, OBS-T
	Or Tetractinellida		
	Fa Ancorinidae	sponge 5	FER-U, IGL-U
		sponge 6	IGL-U, IUI-U
		sponge 7	IGL-T/U, IUI-U, OBS-U
		sponge 23	FER-U, IGL-U
		sponge 24	FER-U, IGL-U
		sponge 27	IGL-U
Cnidaria			
Cl Anthozoa	Or Actiniaria		
	Fa Actiniidae	*Anthopleura stellula*	FER-U, IGL-T/U
		Anthopleura sp.	IGL-T/U
	Fa Stichodactylidae	*Heteractis aurora*	IGL-U
	Or Alcyonacea		

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
	Fa Alcyoniidae	*Rhytisma fulvum fulvum*	IGL-U, IUI-U, OBS-U
		soft coral 3b	FER-U
	Fa Nephtheidae	*Dendronephthya* sp.	FER-U
	Fa Xeniidae	*Xenia* spp.	FER-U, IGL-U, OBS-U
	Or Scleractinia		
	Fa Pocilloporidae	*Seriatopora sp.*	IGL-U
		Stylophora spp.	FER-T/U, IGL-T/U, IUI-T/U, OBS-T/U
	Fa Scleractinia incertae sedis	*Leptastrea* sp.	FER-T
<u>Bryozoa</u>			
Cl Stenolaemata	Or Cyclostomata	bryozoan 14	IGL-U
Cl Gymnolaemata	Or Cheilostomata		
	Fa Electridae	*Electra* spp.	FER-U, OBS-U
	Fa Candidae	*Licornia (Scrupocellaria)* spp.	FER-U
	Fa Schizoporellidae	*Schizoporella errata*	FER-U, IUI-U
	Fa Smittinidae	*Parasmittina* spp.	FER-T/U, IGL-T/U, IUI-T/U, OBS-T/U
	Unknown	bryozoan 8	FER-T/U, IGL-T/U, OBS-U
		bryozoan 9	
		bryozoan 10	
		bryozoan 11	
		bryozoan 15	

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
Mollusca			
Cl Bivalvia	Or Arcoida		
	Fa Arcidae	*Barbatia* spp.	OBS-U
	Or Ostreida		
	Fa Pteriidae	*Pteria aegyptiaca*	FER-U, IGL-U
	Or Ostreoida		
	Fa Ostreidae	*Alectryonella* spp.	FER-U, IGL-U
		Dendostrea spp.	FER-T/U, IGL-T/U, IUI-U, OBS-U
		Lopha sp.	FER-U, IGL-U
		Ostrea spp.	FER-T/U, IGL-T/U, IUI-U, OBS-T/U
		Saccostrea spp.	FER-T/U, IGL-T/U
		bivalve 2	FER-U, IUI-T, OBS-T
		bivalve 20	FER-T, IGL-U
		bivalve 32	IGL-U
	Fa Mytilidae	*Modiolus* sp.	
	Or Pectinida		
	Fa Anomiidae	*Anomia* spp.	FER-T/U, IGL-U
	Or Pectinoida		
	Fa Spondylidae	*Spondylus* spp.	FER-U, IGL-U, IUI-U, OBS-U
		bivalve 33	
	Or Pterioida		
	Fa Pinnidae	*Pinna* sp.	
		Streptopinna spp.	FER-U

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
	Fa Pinnoidea	bivalve 40	IGL-U
	Fa Pteriidae	*Pinctada* spp.	FER-T/U, IGL-U
	Or Veneroida		
	Fa Chamidae	*Chama* sp.	FER-U, IGL-U, OBS-U
	Unknown	bivalve 15	
Cl Gastropoda	Or Littorinimorpha		
	Fa Vermetidae	gastropod 4	IGL-T, IUI-T/U, OBS-T/U
		gastropod 12	OBS-U
		gastropod 18	
		gastropod 22	IGL-T
<u>Annelida</u>			
Cl Polychaeta	Or Sabellida		
	Fa Serpulidae	*Hydroides* spp.	FER-T/U, IGL-U, IUI-T/U, OBS-U
		Josephella sp.	IUI-U
		Rhodopsis sp.	IUI-U
		Salmachina sp.	IUI-U
		Serpula spp.	FER-T/U, IGL-T/U
		Spiraserpula spp.	
		Spirobranchus tetraceros	FER-T/U, IGL-T/U, IUI-T/U, OBS-T/U
		Spirobranchus spp.	IGL-U
		Spirorbis spp.	FER-T/U, IGL-T/U, IUI-T/U, OBS-T/U
		Vermiliopsis spp.	IGL-U

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
	Unknown	polychaete 16	FER-T/U, IGL-U
		polychaete 19	IGL-T
Chordata			
Cl Ascidiacea	Or Aplousobranchia		
	Fa Didemnidae	*Didemnum* spp.	FER-T/U, IGL-T/U, IUI-U, OBS-T/U
		Diplosoma simile	IGL-T/U
		*Diplosoma*sp.	FER-T/U, IGL-T/U
	Or Enterogona		
	Fa Ascidiidae	*Phallusia nigra*	FER-U
	Fa Polyclinidae	*Aplidium* sp.	IGL-U
	Or Phlebobranchia		
	Fa Corellidae	*Rhodosoma turcicum*	FER-U, IGL-U
	Or Pleurogona		
	Fa Pyuridae	*Halocynthia spinosa*	FER-U, IGL-U
	Or Stolidobranchia		
	Fa Styelidae	*Eusynstyela latericius* morph 2	IGL-U, IUI-U, OBS-U
		Eusynstyela latericius morph 1	FER-U, IGL-U, IUI-U, OBS-U
		Botrylloides spp.	FER-T/U, IGL-U
		Polycarpa mytiligera	FER-U, IGL-T/U, OBS-U
		Polycarpa spp.	FER-U, IGL-T/U
		Styela canopus	IGL-U
	Fa Pyuridae	*Herdmania momus*	FER-U

Phylum/Class	Order/Family	Genus/Species	Site/Collector Side
	Unknown		
		ascidian 11	
		ascidian 12	
		ascidian 14	
		ascidian 17	OBS-U
		ascidian 19	
		ascidian 25	
		ascidian 27	
		ascidian 32	
		ascidian 33	IGL-U
		ascidian 37	FER-U
		ascidian 38	IGL-U
		ascidian 39	IGL-U
		ascidian 40	IGL-U
		ascidian 41	IGL-U
		ascidian 42	IGL-U
		ascidian 44	IGL-U

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Table B.3. SIMPER analysis of community composition. Analysis indicates the contribution of different taxonomic groups to dissimilarity in the composition of planar cover (%) between combinations of sites (FER, IGL, IUI, OBS), for topsides and undersides of collectors, at the end of a 13-mo experiment.

Topsides

Group	**Average Abundance**	**Average Abundance**	**Average Dissimilarity**	**Dissimilarity/SD**	**Contributing %**	**Cumulative %**
	Group FER	Group IGL				
Coralline algae	0.1	0.7	14.2	3.0	32.9	32.9
Algal matrix	1.0	0.5	13.0	2.3	30.1	63.0
Sponge	0.1	0.2	3.7	1.6	8.6	71.7
	Group FER	Group IUI				
Coralline algae	0.1	0.5	11.1	2.8	34.4	34.4
Algal matrix	1.0	0.9	5.6	1.3	17.4	51.8
Bivalve	0.3	0.1	5.3	1.7	16.3	68.0
Biofilm	0.3	0.3	3.4	1.5	10.6	78.7
	Group FER	Group OBS				
Algal matrix	1.0	1.4	9.1	2.2	26.9	26.9
Bivalve	0.3	0.0	7.0	2.4	20.7	47.6
Biofilm	0.3	0.1	7.0	2.0	20.6	68.2
Coralline algae	0.1	0.1	2.6	1.4	7.7	75.9
	Group IUI	Group OBS				
Algal matrix	0.9	1.4	12.7	1.9	34.8	34.8
Coralline algae	0.5	0.1	11.4	2.8	31.3	66.1
Biofilm	0.3	0.1	6.4	1.7	17.4	83.6
	Group IGL	Group IUI				
Algal matrix	0.5	0.9	11.2	1.7	34.0	34.0

Group	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contributing %	Cumulative %
Coralline algae	0.7	0.5	5.4	1.3	16.2	50.2
Bivalve	0.3	0.1	5.1	1.5	15.4	65.6
Biofilm	0.4	0.3	4.1	1.4	12.5	78.1
	Group IGL	Group OBS				
Algal matrix	0.5	1.4	22.9	3.7	36.6	36.6
Coralline algae	0.7	0.1	14.7	2.9	23.5	60.2
Biofilm	0.4	0.1	8.6	2.3	13.7	73.9

Undersides

Group	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contributing %	Cumulative %
	Group FER	Group IGL				
Bivalve	0.2	0.6	8.9	2.5	22.8	22.8
Algal matrix	0.5	0.1	7.2	2.6	18.5	41.4
Biofilm	0.1	0.3	5.3	2.4	13.8	55.1
Bryozoan	0.6	0.4	4.7	1.2	12.2	67.3
Polychaete	0.3	0.1	3.9	1.5	10.0	77.3
	Group FER	Group IUI				
Bivalve	0.2	0.9	14.2	3.1	23.0	23.0
Bryozoan	0.6	0.2	8.7	1.9	14.2	37.2
Sponge	0.4	0.1	8.3	5.7	13.5	50.6
Ascidian	0.4	0.1	6.8	2.7	11.0	61.7
Biofilm	0.1	0.4	6.4	2.4	10.4	72.0

Group	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contributing %	Cumulative %
	Group FER	Group OBS				
Bivalve	0.2	0.8	12.6	3.3	24.1	24.1
Bryozoan	0.6	0.1	10.8	2.4	20.7	44.8
Ascidian	0.4	0.1	6.4	2.5	12.2	57.0
Sponge	0.4	0.2	5.3	3.7	10.0	67.0
Algal matrix	0.5	0.7	5.0	1.6	9.6	76.7
	Group IUI	Group OBS				
Algal matrix	0.4	0.7	7.1	1.9	23.6	23.6
Biofilm	0.4	0.1	5.0	2.0	16.6	40.2
Bivalve	0.9	0.8	3.8	1.2	12.6	52.8
Sponge	0.1	0.2	3.4	4.2	11.3	64.1
Coralline algae	0.3	0.2	3.3	1.5	11.1	75.2
	Group IGL	Group IUI				
Sponge	0.5	0.1	9.9	3.2	19.5	19.5
Coralline algae	0.0	0.3	6.2	3.5	13.6	33.1
Bryozoan	0.4	0.2	5.7	1.7	12.5	45.6
Bivalve	0.6	0.9	5.4	1.5	11.8	57.4
Algal matrix	0.1	0.4	5.1	1.8	11.1	68.5
Ascidian	0.3	0.1	5.0	2.3	11.0	79.5
	Group IGL	Group OBS				
Algal matrix	0.1	0.7	12.1	3.3	25.9	25.9
Bryozoan	0.4	0.1	7.3	2.0	15.6	41.5
Sponge	0.5	0.2	5.9	2.1	12.7	54.2
Ascidian	0.3	0.1	4.6	2.1	9.8	64.0
Bivalve	0.6	0.8	4.0	1.5	8.5	72.5

Table B.4. SIMPER analysis of invertebrate composition. Analysis indicates the contribution of different taxonomic groups to dissimilarity in the composition of invertebrate biomass (g 400 cm^{-2}) between combinations of sites (FER, IGL, IUI, OBS), for topsides and undersides of collectors, at the end of a 13-mo experiment.

Topsides

Group	**Average Abundance**	**Average Abundance**	**Average Dissimilarity**	**Dissimilarity/SD**	**Contributing %**	**Cumulative %**
	Group FER	Group IGL				
Sponge	0.2	1.2	14.7	2.4	36.6	36.6
Bivalve	1.2	0.9	7.2	1.5	17.8	54.5
Coral	0.6	0.2	5.8	1.7	14.3	68.8
Ascidian	0.2	0.4	4.8	1.5	12.0	80.8
	Group FER	Group IUI				
Bivalve	1.2	0.2	20.3	2.3	36.6	36.6
Polychaete	0.8	0.2	11.3	2.5	20.3	56.9
Sponge	0.2	0.7	10.5	2.0	18.9	75.8
	Group FER	Group OBS				
Bivalve	1.2	0.4	21.1	1.7	35.6	35.6
Coral	0.6	0.1	11.1	1.9	18.6	54.2
Bryozoan	0.4	0.0	9.1	1.7	15.3	69.5
Polychaete	0.8	0.6	9.1	1.3	15.3	84.9
	Group IUI	Group OBS				
Sponge	0.7	0.0	22.5	3.1	29.5	29.5
Polychaete	0.2	0.6	16.0	1.6	21.0	50.5
Bryozoan	0.4	0.0	13.6	1.6	17.8	68.2
Coral	0.4	0.1	12.0	1.6	15.7	84.0
	Group IGL	Group IUI				
Bivalve	0.9	0.2	13.7	2.7	28.2	28.2

Group	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contributing %	Cumulative %
Sponge	1.2	0.7	9.0	1.5	18.7	46.9
Polychaete	0.7	0.2	8.5	1.4	17.6	64.5
Ascidian	0.4	0.0	7.1	1.8	14.8	79.3
	Group IGL	Group OBS				
Sponge	1.2	0.0	24.2	3.2	38.7	38.7
Bivalve	0.9	0.4	12.6	1.5	20.1	58.8
Polychaete	0.7	0.6	8.5	1.2	13.5	72.3

Undersides

Group	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contributing %	Cumulative %
	Group FER	Group IGL				
Bivalve	2.0	2.4	4.0	1.6	21.2	21.2
Ascidian	1.6	1.4	3.4	1.5	18.0	39.2
Bryozoan	1.4	1.1	2.8	1.2	14.8	54.0
Sponge	1.1	0.9	2.2	1.5	12.0	66.0
Soft coral	0.1	0.3	1.9	1.5	9.9	75.9
	Group FER	Group IUI				
Ascidian	1.6	0.5	8.8	2.3	27.8	27.8
Bivalve	2.0	1.7	5.2	1.4	16.5	44.4
Coral	0.0	0.6	5.0	10.3	15.7	60.0
Bryozoan	1.4	0.9	4.7	1.5	14.9	75.0
	Group FER	Group OBS				
Ascidian	1.6	0.8	6.9	2.1	21.7	21.7
Bryozoan	1.4	0.6	6.6	2.3	20.8	42.4
Sponge	1.1	0.3	6.2	2.3	19.3	61.8

Group	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contributing %	Cumulative %
Bivalve	2.0	2.4	4.6	1.7	14.3	76.1
	Group IUI	Group OBS				
Bivalve	1.7	2.4	7.1	1.6	33.2	33.2
Ascidian	0.5	0.8	3.0	2.1	14.1	47.3
Polychaete	0.8	0.7	2.6	1.6	12.3	59.6
Bryozoan	0.9	0.6	2.6	1.3	12.3	71.8
	Group IGL	Group IUI				
Ascidian	1.4	0.5	7.0	2.2	23.9	23.9
Bivalve	2.4	1.7	6.0	1.6	20.6	44.5
Polychaete	1.2	0.8	3.6	3.9	12.2	56.7
Coral	0.2	0.6	3.4	1.8	11.6	68.3
Sponge	0.9	0.6	3.1	2.3	10.8	79.0
	Group IGL	Group OBS				
Ascidian	1.4	0.8	5.0	1.7	19.1	19.1
Sponge	0.9	0.3	4.9	2.2	18.6	37.7
Polychaete	1.2	0.7	4.2	1.8	16.1	53.8
Bryozoan	1.1	0.6	3.8	2.1	14.7	68.5
Coral	0.2	0.4	2.4	2.1	9.2	77.7

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