UNIVERSITY OF CALIFORNIA SAN DIEGO

SAN DIEGO STATE UNIVERSITY

Coral Reef Arks: Molecular mechanisms underlying the demise and recovery of coral reef ecosystems

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Biology

by

Jason Lajos Baer

Committee in charge:

University of California San Diego

Professor Andrew Allen
Professor James Golden

San Diego State University

Professor Forest L. Rohwer, Chair
Professor David Lipson
Professor Antoni Luque
Professor Uduak George

2024

The dissertation of Jason Lajos Baer is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

Chair

University of California San Diego

San Diego State University

2024

DEDICATION

To my family, and to the sea.

EPIGRAPH

“It is a strange thing that most of the feeling we call religious, most of the mystical outcrying which is one of the most prized and used and desired reactions of our species, is really the understanding and the attempt to say that man is related to the whole thing, related inextricably to all reality, known and unknowable. This is a simple thing to say, but the profound feeling of it made a Jesus, a St. Augustine, a St. Francis, a Roger Bacon, a Charles Darwin, and an Einstein. Each of them in his own tempo and with his own voice discovered and reaffirmed with astonishment the knowledge that all things are one thing and that one thing is all things—plankton, a shimmering phosphorescence on the sea and the spinning planets and an expanding universe, all bound together by the elastic string of time. It is advisable to look from the tide pool to the stars and then back to the tide pool again.”

-John Steinbeck, *The Log from the Sea of Cortez*

TABLE OF CONTENTS

LIST OF ABBREVIATIONS

ADCP	Acoustic doppler current profiler
ADV	Acoustic doppler velocimeter
AMG	Auxiliary metabolic gene
ARMS	Autonomous reef monitoring structures
ATP	Adenosine triphosphate
BGE	Bacterial growth efficiency
CARICOOS	Caribbean coastal ocean observing system
CCA	Crustose coralline algae
DDAM	Dissolved organic carbon, disease, algae, microbes
DDO	Daytime dissolved oxygen
DNA	Deoxyribonucleic acid
DNER	Department of natural and environmental resources
DO	Dissolved oxygen
DOC	Dissolved organic carbon
DOD	Department of defense
DOM	Dissolved organic matter
ED	Entner Doudoroff [pathway]
e^-DAR	Electron donor to acceptor ratio
EMP	Embden Meyerhof Parnas [pathway]
ESTCP	Environmental security technology certification program
FRP	Fiberglass-reinforced polyester
HDPE	High-density polyethylene

MDA	Mean decrease in accuracy
NDO	Nighttime dissolved oxygen
NOAA	National oceanographic and atmospheric administration
OM	Organic matter
OMZ	Ocean minimum zone
OOB	Out-of-bag error
PAM	Pulse amplitude modulated [fluorometry]
PAR	Photosynthetically active radiation
PC	Parametric control
PCA	Principal coordinate analysis
PEG	Polyethylene glycol
PES	Polyethyl sulfone
PHC	Physical habitat control
PPP	Pentose phosphate pathway
PTFE	Polytetrafluoroethylene
PVC	Polyvinyl chloride
SC	State control
SCTLD	Stony coral tissue loss disease
SCUBA	Self-contained underwater breathing apparatus
SINDy	Sparse identification of nonlinear dynamics
SPH	Smooth particle hydrodynamics
SST	Sea surface temperature
TEP	Transparent exopolymer particles

USA	United States of America
UXO	Unexploded ordnance
VLP	Virus-like particle
VMR	Virus-to-microbe ratio
VNTR	Vieques naval training range

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEGEMENTS

The work of this dissertation would not have been possible without a vast number of people. To all who have been part of my journey, thank you for your support, knowledge, optimism, passion, insight, and friendship.

They say rough seas make stronger sailors, but so do good Dive Safety Officers. I'd like to thank Mike Anghera for unlocking my passion for underwater power tools, for honing my dive skills, and for trusting my instincts when it was time to make my own calls. Similarly, I wouldn't be the diver (or marine scientist) I am today without Constance Gramlich, who shaped my understanding of marine ecology and my love for temperate coastal ecosystems. Some of the fondest days of my PhD were wrapped in neoprene and pelted by sun on the deck of the *Squilla*, picking through kelp holdfasts with one of the world's few remaining great naturalists.

Field science is in equal parts sweaty, exhausting, and exhilarating, and I owe a huge debt of gratitude to the scientists that accompanied me into the field and tolerated my dynamism, which at times bordered on the deranged. Thank you to the Curacao crew – Will Barnes, Lars ter Horst, Emily Nixon, Kristen Marhaver, Mark Vermeij, Joaquin Yus, Andi Haas, Ben Darby, and many more – for interesting conversations, tiny beers, incredible diving, and good company over long nights of spawning work. Thank you to the Rohwer labbies – Jenna Aquino, Anneke van der Geer, Ashton Ballard, Mark Little, and Andrés Sánchez-Quinto – for accompanying me on a combined nine challenging, rewarding, chaotically entertaining, and bioluminescent trips to the homey island of Vieques. Finally, to Ahmi Cacapit for an incredible journey into the untouched waters of Micronesia. They were among the best of times.

I owe sincere thanks to the people who helped the Arks projects get done – shipping construction materials all over the world is no easy feat. Thank you to Gina Spidel, a true logistical force of nature, and to Rafa Baron, who fielded calls from distant time zones at all hours of the night and always got us home.

I am the scientist and person I am today, at least in part, because of the Hatays. Thanks to Mark Hatay, who turned a wayward biologist with an almost physical repulsion to mathematics into something of a marine engineer. Thanks also to Mary Hatay, for tolerating Mark and I as we talked shop over countless lunches in Alpine, and to providing me with a home away from home. To them both, for inspiring me to reach new creative heights, for little gifts, and for becoming a support system akin to family.

I consider myself extremely fortunate to have such a widespread and loving network of friends and family, to whom I owe my heartfelt thanks. To my roommates in the Mansion, who cooked with me, listened to me, explored with me, inspired me, and coexisted with me as I learned some of life's great lessons. To my friends, for their unconditional support, much needed distractions, frequent visits to San Diego and frequent excuses to leave. Finally, to my family – Sydney, Mackenzie, Cami, Eddie, and Drew – for that seemingly bottomless well of love and devotion that kept me anchored in high seas and kept wind in the sails as I navigated the lows. I made it to this milestone, truly, standing on their shoulders.

Finally, I get to thank my mentors, who laid the cobblestones in the path I walked that led to my PhD. To Linda Wegley-Kelly, for her enduring optimism and kindness, and for providing a counterweight to Forest's chaos. To Jessica Carilli and Aaron Hartmann, for their wise counsel, esprit de corps, moral support, and truly remarkable patience with

me as we tackled challenge after herculean challenge with our small but mighty team. And finally, to Forest, who first led me, and then accompanied me, on a journey into the unknown. They say temperature and pressure forge the hardest minerals, and Forest definitely applied both. The six, stimulating years I spent thinking, arguing, failing, observing, philosophizing, diving, chatting, and building with Forest forged my capacity and my scientific mind. It is him I can thank for the opportunities to see some of the world's most beautiful underwater landscapes, and the resources to try and rebuild them. Thank you, Forest, for guiding my evolution, and for never letting my curiosity reach deaf ears.

For financial support I acknowledge the Gordon and Betty Moore Foundation, the National Science Foundation, the Environmental Security and Technology Certification Program, the Achievement Rewards for College Scientists (ARCS) Foundation, and the SDSU University Graduate Fellowship.

Chapter 1, in full, has been accepted for publication of the material by Nature Springer as a special issue on microbial mechanisms of coral reef degradation. Jason L Baer and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

Chapter 2, in full, is a reprint of the material as it appears in the Journal of Visualized Experiments (JoVE). Jason L Baer, Jessica Carilli, Bart Chadwick, Mark Hatay, Anneke van der Geer, Yun Scholten, Will Barnes, Jenna Marie Cruz Aquino, Ashton Ballard, Mark Little, Jared Brzenski, Xiaofeng Liu, Gunther Rosen, PF Wang, Jose Castillo, Andreas Haas, Aaron Hartmann, and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

Chapter 3 is currently being prepared for submission for publication of the material. Jason L Baer, Mark Little, Jenna Marie Cruz Aquino, Anneke van der Geer, Ashton Ballard, Andrés Sánchez-Quinto, Jessica Carilli, Aaron Hartmann, and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

Chapter 4, in full, has been accepted for publication of the material by the journal PeerJ. Jessica Carilli*, Jason L Baer*, Jenna Marie Cruz Aquino, Mark Little, Bart Chadwick, Forest Rohwer, Gunther Rosen, Anneke van der Geer, Andrés Sánchez-Quinto, Ashton Ballard, and Aaron Hartmann. The dissertation author was the co-primary investigator and co-first author of this paper.

Chapter 5 in full, is a reprint as it was submitted to the journal Nature Ecology and Evolution. Jason L Baer, Aaron Hartmann, and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

VITA

2024 Doctor of Philosophy in Biology, University of California San Diego and San Diego State University

2017 Bachelor of Science in Marine Science (Biology track), Eckerd College

2017 Bachelor of Arts Spanish Language and Literature, Eckerd College

PUBLICATIONS

Baer, J; Little, M; Cruz Aquino, JM; van der Geer, A; Ballard, A; Sánchez-Quinto, A; Carilli, J; Rohwer, F; Hartmann, A. *Escaping the microbialized benthos with Coral Reef Arks: Effects on microbial ecology and biogeochemistry.* (in prep)

Baer, J; Ashworth, H; Yus, J; van der Geer, A; Ballard, A; Roach, T; Nixon, E; van Bendegom, D; Teague, J; Rohwer, F. *Sunlight, grazing, and material composition differentially drive the development of coral reef fouling communities.* (in prep)

Baer, J; Hartmann, A; Rohwer, F. *A control theoretic framework and in situ experimental platform for active restoration of coral reefs.* Nature Ecology and Evolution. (in review)

Carilli, J*; **Baer, J*;** Cruz Aquino, JM; Little, M; Chadwick, B; Rohwer, F; Rosen, G; van der Geer, A; Sánchez-Quinto, A; Ballard, A; Hartmann, A. *Escaping the microbialized benthos with Coral Reef Arks: Effects on coral translocation and fish biomass.* PeerJ. (in press)

Baer, J; Rohwer, F. *Viralization and microbialization shape coral reef health, stability, and resilience.* Nature Springer: Coral Reef Microbiome. (in press)

Baer, J; Carilli, J; Hartmann, A; Chadwick, B; Hatay, M; van der Geer, A; Aquino, J; Ballard, A; Scholten, Y; Barnes, W; Little, M; Brzenski, J; Haas, A; Rohwer, F. (2023). *Coral Reef Arks: An in situ mesocosm and toolkit for assembling reef communities.* Journal of Visualized Experiments (JoVE), 191, e64778.

Rojas, M. I., Giles, S. S., Little, M., Baron, R., Livingston, I., Dagenais, **Baer, J;** T. R., ... & Rohwer, F. (2021). *Swabbing the Urban Environment-A Pipeline for Sampling and Detection of SARS-CoV-2 From Environmental Reservoirs.* Journal of Visualized Experiments (JoVE), 170, e62379.

ABSTRACT OF THE DISSERTATION

Coral Reef Arks: Molecular mechanisms underlying the demise and recovery of coral reef ecosystems

by

Jason Lajos Baer

Doctor of Philosophy in Biology

University of California San Diego, 2024
San Diego State University, 2024

Professor Forest L. Rohwer, Chair

Viruses and microbes are foundational to the healthy functioning of coral reef ecosystems. However, dysregulation among viral and microbial communities owing to global and local pressures is driving widespread coral reef collapse. The objective of this dissertation was to investigate the drivers of this ecosystem degradation process,

termed *microbialization*, on coral reefs and to identify mechanisms associated with ecosystem recovery from microbialized states.

To begin the dissertation, I review the biochemistry underlying coral reef function and describe how ecosystem energy is differentially stored in predominantly the macroorganisms on healthy coral reefs versus the microbes on degraded coral reefs as a result of positive feedback loops. In this review, I develop hypotheses concerning how microbes, organic matter, and oxygen interact to drive shifts to microbialized states and propose a tool to manipulate reef biochemistry to counter microbialization. To begin testing these hypotheses, I build midwater mesocosm tools called Coral Arks, develop protocols for designing, deploying, and monitoring them *in situ*, and demonstrate their structural integrity in the marine environment. Next, I use Coral Arks in a long-term field experiment, demonstrating that microbial ecology, water quality, and biogeochemistry are improved on Arks relative to seafloor sites at the same depth. Lower microbialization on the Arks enhanced survival and growth of transplanted corals and recruited diverse assemblages of reef organisms, including fish and benthic invertebrates. These findings highlight the role of microbes in shaping the coral reef abiotic environment and suggest microbialization can be countered by reducing organic matter inputs, enhancing dissolved oxygen, and reinstating viral predatory control over microbes. Lastly, I discuss the future of coral reef restoration, identify explicit goals for reinstating reef ecosystem services, and through a literature review, summarize potential interventions for manipulating coral reefs. Using this information, I propose a restoration framework based in control theory that uses Coral Arks as experimental platforms for identifying effective restoration interventions and scaling these interventions to a natural reef.

Chapter 1

CORAL REEF MICROBIALIZATION AND VIRALIZATION SHAPE ECOSYSTEM HEALTH, STABILITY, AND RESILIENCE

ABSTRACT

Microbes mediate the flow of organic carbon through aquatic ecosystems, and the structure of microbial communities is linked to ecosystem health and functioning. Globally increased inputs of organic matter (OM) over the past several decades have resulted in widespread degradation and trophic simplification of aquatic ecosystems, including coral reefs. As ecosystems degrade, they become increasingly dominated by microbial biomass (usually enriched with potential pathogens) and energy use, a phenomenon termed microbialization. The enhanced microbial respiration of OM that underlies microbialization results in deoxygenation, acidification, and increased outbreaks of disease that, in turn, cause mortality of macrofauna and erode benthic structural complexity. In this chapter, we review the biochemical drivers and impacts of microbialization on coral reefs and discuss how microbialization is reinforced by biological feedbacks and global climate change. We also introduce the countering process of viralization and discuss how *in situ* experimental tools may improve reef health.

INTRODUCTION

Healthy ecosystems are organized hierarchically in trophic levels, enabling energy fixed by primary producers to be channeled between the microbes and the macrobes (Odum 1968). Ecosystems degrade when this organization is disrupted,

resulting in a shift in ecosystem energy allocation from larger organisms and the macro-scale processes they support to the microbes. This shift in ecosystem trophic structure towards higher microbial activity and energy use is known as microbialization and is a prominent mediator of decline in coral reef ecosystems (Haas et al., 2016). Microbes, owing to their sheer numbers and high metabolic rates relative to their size (DeLong et al., 2010), are the primary agents of energy transfer in ecosystems and determine the biogeochemical landscape of coral reefs (Carlson et al., 2007; Moriarty, 1979; reviewed in Nelson et al., 2023). When tightly regulated through trophic control, coral reef microbes recycle essential nutrients and shunt energy in the form of dissolved organic matter (DOM) up to higher trophic levels, facilitating high productivity and biodiversity in nutrient-poor waters (Odum and Odum 1955). Yet, coral reef microbialization has shifted the role of microbes from trophic links to energy sinks, diverting the flow of ecosystem energy into the microbial food web at the expense of the macrobes (Haas et al., 2016). Threats currently facing coral reefs, including deoxygenation, acidification, and trophic downgrading, are a consequence of this microbial expansion.

Coral reef ecosystems generate more than $400 billion in annual revenue by way of ecosystem services that provide food, coastal protection, and tourism to coastal communities (Moberg and Folke 1999; De Groot et al., 2012; Costanza et al., 2014). Coral reefs are currently in decline globally, with reef-building corals being replaced by alternative benthic assemblages composed of turf- and fleshy-macroalgae (Hughes 1994; Smith et al., 2016). Transitions to algal dominance facilitate coral reef microbialization via the DDAM positive feedback system (dissolved organic carbon (DOC), disease, algae, and microorganisms (Kuntz et al., 2005; Kline et al., 2006;

Barott and Rohwer 2012). DDAM is initiated by local eutrophication and overfishing (McCook 1999; Zaneveld et al., 2016), which release controls on algal growth and enable macroalgae to dominate over corals on the reef benthos **(**Figure 1.1**)**. Macroalgae release labile organic carbon and bubble off photosynthetic oxygen, creating a benthic environment rich in electron donors (DOC) and depleted of electron acceptors (O_2). The increased electron donor to acceptor ratio (e^-DAR) in reef water provides an abundant carbon source for microbial consumption with relatively less oxygen; conditions that favor rapid microbial growth (Haas et al., 2011; Silveira et al., 2019). Increased e^-DAR selects for copiotrophic, virulent microbial communities that create suboxic zones and cause disease, contributing to coral mortality and freeing up benthic space for further algal overgrowth (Smith et al., 2006; Haas et al., 2013a; Silveira et al., 2019, 2020). The loss of corals and other sessile benthic invertebrates, which prey on microbes via suspension feeding, reduces organic matter (OM) recycling to higher trophic levels and compromises benthic-pelagic coupling processes connecting reef biogeochemical cycles (Bak et al., 1998; McNally et al., 2017).

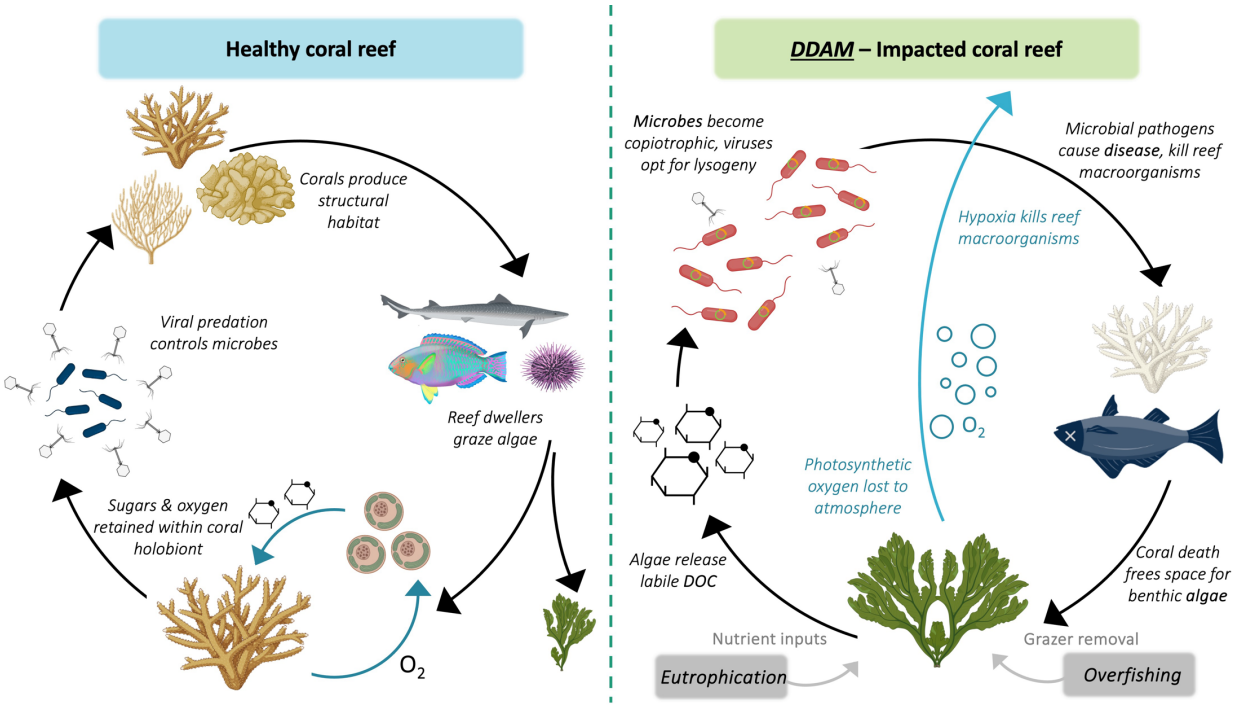


Figure 1.1 Positive feedback loops reinforcing coral reef health (left) and degradation (right). (Left Panel) On healthy coral reefs, corals use sugars and oxygen produced by photosynthesis in endosymbiotic zooxanthellae to build three-dimensional habitat for reef macrofauna, including herbivorous invertebrates and fish. Herbivory pressure keeps the cover of turf- and fleshy-macroalgae low, facilitating coral dominance. Coral reef microbes are maintained under trophic control by lytic viruses. (Right Panel) Reefs degrade according to the DDAM positive feedback loop. Local overfishing of herbivores and eutrophication enable the overgrowth of fleshy macroalgae, which release dissolved organic carbon, stimulating the growth of heterotrophic microbes which reduce oxygen concentrations and cause disease, killing corals and freeing space for further algal overgrowth. A switch among coral reef viruses to lysogeny facilitates further microbial community expansion, shunting algal photosynthetic production into the microbial food web and preventing transfer to higher trophic levels.

One initiating factor for DDAM is a loss of predation pressure by fish, preventing the transfer of photosynthetically fixed carbon between the microbial and macrobial food webs. Predation pressure is a stabilizing force in coral reef ecosystems: at the macro-scale, predation by large fish controls the abundance and distribution of smaller fish (DeMartini et al., 2008; Sandin et al., 2008; Boaden and Kingsford 2015), including reef herbivores, which facilitate the transfer of algal production to higher trophic levels (Mumby et al., 2006; Zgliczynski and Sandin 2017; McCauley et al., 2018). At the micro-

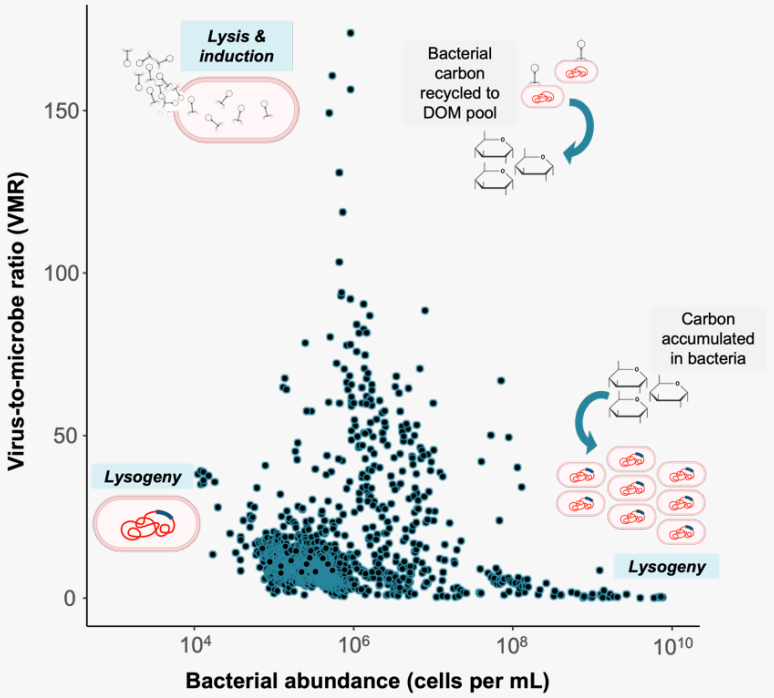
scale, viral predation via viral lysis controls microbial densities, preventing energy from accumulating in the microbial food web (Wilhelm and Suttle 1999; Suttle 2007). Indeed, coral cover has been observed to be highest on reefs with high predator fish biomass and high virus-to-microbe ratios (VMRs, Box 1), indicating the combined effects of predation pressure by fish and viruses are instrumental in coral reef health and stability (Silveira et al., 2023). However, herbivory pressure by fish and lytic predation by viruses are reduced on overfished, algal-dominated reefs, accelerating transitions to algal and microbial dominance. Coral reefs experience viralization, the counter process to microbialization, when viral control of microbial growth and a robust and structured fish community retains up to 100% of ecosystem energy in the macrobial food web. Reef transitions from healthy, viralized states to degraded, microbialized states are thus initiated by a loss of algal grazing pressure, mediated by resulting shifts in reef biochemistry towards high e^-DAR, and accelerated by the loss of viral predatory control on microbial expansion. These transitions to high e^-DAR and microbialization can likely also be initiated by other stressors, such as ocean warming events and hurricanes, which cause widespread mortality and divert organic carbon flows into the microbes.

Microbialization is a natural feature of ecosystems with consistent inputs of organic matter (OM) and can play an important role in OM recycling and biogeochemical cycles. However, globally increased inputs of OM to coastal environments have shifted the role of microbialization from a localized and transient phenomenon to a widespread and persistent threat to coastal ecosystems. On degraded coral reefs, the microbial food web is predicted to process and accumulate almost 100% of ecosystem energy (McDole et al., 2012; Somera et al., 2016), leading

to losses in the diversity of macrobes, acute and chronic conditions of hypoxia and microbial acidification, and more recently to tropical dead zones (Altieri et al., 2017; Alteri et al., 2019). Here, we place coral reef degradation in the much wider context of global microbialization and show that seemingly disparate phenomena mediating ecosystem decline are linked to the unchecked expansion of the microbes. We show how an increase in e^-DAR, caused by algal release of labile carbon and several mechanisms of deoxygenation, reshape the biochemical reef environment to favor microbial dominance. Next, we present Coral Reef Arks, an experimental tool to reduce e^-DAR, and thus microbialization, on coral reefs and discuss potential interventions for restoring ecosystems in a microbial world.

Box 1 – Virus-to-microbe ratio and coral reef microbialization

The virus-to-microbe ratio (VMR) is an outcome of the interactions between microbes and their viral predators and is used as a proxy for microbialization (McDole et al., 2012; Silveira et al., 2023). Calculated as a ratio of the abundance of free viruses to microbial cells, VMR can be used to approximate the relative frequency of two dominant modes of viral infection, lysogeny and lysis, among microbial communities. While canonical Lotka-Volterra predator-prey dynamics predicted the frequency of lysogenic infections in a microbial community to decrease with increasing microbial abundance (more prey encounters = more lysis), analysis of VMRs from diverse global environments provided evidence that VMR decreases with increasing cell densities (Knowles et al., 2016a). This finding led to the development of the Piggyback-the-Winner hypothesis, which predicts viral lysis as a dominant infection strategy at intermediate bacterial densities (Thingstad 2000) and predicts lysogeny to dominate at both high and low bacterial densities (Figure 2, Knowles et al., 2016a; reviewed in Silveira et al., 2021).



Coral reefs experiencing microbialization display reduced VMRs relative to healthy sites (Knowles et al., 2016a), suggesting a decrease in viral lytic predation pressure which facilitates microbial expansion. Metagenomes from reefs with low VMRs are enriched in prophages and phage-encoded virulence genes, confirming the increase in the frequency of lysogenic infection on these reefs and highlighting lysogeny as a primary driver of coral reef microbialization and decline (Knowles et al., 2016a; Touchon et al., 2016; Little et al., 2020). While VMR serves as a useful proxy for viral lytic/temperate dynamics and thus for the magnitude of viral predation pressure on microbial communities, genomic markers including the presence of integrases, excisionases, lysis repressors and known prophage sequences are still the best proxies to identify lysogens and temperate phages in ecosystems (Luo et al., 2020; Silveira et al., 2020).

Figure 1.2 Virus-to-microbe ratio and coral reef microbialization

ORGANIC CARBON AND THE TRANSFER OF ENERGY THROUGH ECOSYSTEMS

Dissolved organic carbon (DOC) the largest reservoir of organic matter on Earth, and its use and reuse in ecosystems is mediated by microbes. By consuming DOC and incorporating it as biomass in the microbial loop (Azam et al., 1983; Hollibaugh and Azam 1983), microbes serve as a trophic link that transfers organic carbon to higher trophic levels. Predation of microbes by benthic suspension feeders and nanoflagellate planktonic protists mediates this transfer and prevents organic carbon from accumulating in the microbial food web. On coral reefs, the DOC pool is continuously replenished by benthic primary production, whose rates range from 256 to 1696 mmol C m^{-2} d^{-1} and compare to those of tropical rain forests (Odum and Odum 1955; Crossland et al., 1991; Williams et al., 2004; Cardini et al., 2016). Benthic primary producers, including corals, algae, and crustose coralline algae, differ in their rates of DOC production and release, and the relative proportions of each group on a reef benthos can have a substantial influence on the quantity and composition of reef DOC available for microbial consumption (Cardini et al., 2016; reviewed in Nelson et al., 2023, 2013; Wegley Kelly et al., 2022). For instance, whereas corals invest up to 50 to 80% of the photosynthetically fixed carbon from their endosymbionts into growth and calcification (Hatcher 1988; Falkowski et al., 1993; Houlbrèque and Ferrier-Pagès 2009; Tremblay et al., 2012a, b), algae release as much as 60% of their fixed carbon into the surrounding seawater (Jokiel and Morrissey 1986; Crossland 1987; Cheshire et al., 1996). High release rates of DOC by fleshy algae enrich overlying reef water with a high energy food source for microbes, increasing e^{-}DAR and serving as the first step in a regime of degradative microbial phase shifts that reinforce DDAM (reviewed in Silveira et al.,

2017). Increasing e^-DAR drives microbial expansion by (1) selecting for microbial communities dominated by super-heterotrophs, (2) shifting microbial carbon metabolism to low efficiency strategies that increase microbial biomass, (3) facilitating shifts in viral infection strategies that remove top-down control on microbial expansion, and (4) contributing to the rise of pathogens.

Microbial community structure and biomass

Coral and macroalgae differentially shape the taxonomic structure of reef-associated microbial communities through the release of DOC (Barott et al., 2011; Hester et al., 2016; Walter et al., 2016). Coral-derived DOC, in the form of mucus, is rich in lipids and proteins and selects for mainly oligotrophic microbial taxa (Ducklow and Mitchell 1979; Meikle et al., 1988; Haas and Wild 2010; Nelson et al., 2013). Reefs with high coral cover support highly diverse microbial communities enriched in Synechococcus and taxa within the Alphaproteobacteria such as Sphingomonadales, Rhodobacterales, and SAR11 (Nelson et al., 2013; McNally et al., 2017). In contrast, macroalgae release up to seven times as much DOC as coral, and exudates rich in labile carbohydrates and depleted in organic nutrients stimulate rapid consumption by microbial heterotrophs (Ducklow and Mitchell 1979; Meikle et al., 1988; Haas and Wild 2010; Nelson et al., 2013; Wegley Kelly et al., 2022). Algal-dominated reefs support low diversity, copiotrophic microbial communities enriched in Bacteroidetes, Betaproteobacteria, and Gammaproteobacteria such as Alteromonadales, Pseudomonadales, and Vibrionales (Nelson et al., 2013; Haas et al., 2016; Zaneveld et al., 2016; Meirelles et al., 2018). Reef benthic cover of coral and macroalgae, and thus the quantity and composition of DOC available to reef microbes, is consistently one of

the strongest predictors of microbial community taxonomic composition in overlying reef water (Dinsdale et al., 2008; Haas et al., 2016; Kelly et al., 2014; reviewed in Silveira et al., 2017).

The enrichment of reefs with macroalgal DOC also stimulates the growth and increased abundances of physically larger microbes. A survey of microbial abundance and cell size on coral reefs across the Pacific Ocean found that degraded, eutrophied reefs supported higher microbial densities and total community biomass relative to coral-dominated sites (McDole et al., 2012). This increase in microbial biomass can be partially explained by the shift in microbial taxonomic composition on algal-dominated reefs, as microbial “super-heterotrophs” have higher growth rates, larger genomes, and are larger in size than oligotrophic taxa (McDole et al., 2012; Haas et al., 2016). The high free energy content of macroalgal exudates, which contain a high proportion of reduced sugars and are depleted in organic nutrients (Kelly et al., 2022), increases the carrying capacity of the ecosystem, supporting higher microbial abundances that increase total community biomass. Considering nearly 100% of available metabolic energy in the water column on degraded reefs is allocated to the microbes, this small increase in total microbial biomass represents a large shift in the distribution of reef energy (DeLong et al., 2010; McDole et al., 2012; Haas et al., 2016). Yet, microbial abundances and taxon-dependent size differences are not alone sufficient to explain the increase in microbial biomass at degraded sites.

Microbial metabolism

A shift in microbial carbon metabolism towards anabolic pathways is the primary mechanism by which microbial biomass is accumulated on degrading reefs (Haas et al.,

2016; Somera et al., 2016). Metabolic shifts were observed on coral reefs through changes in bacterial growth efficiency (BGE), or the amount of bacterial biomass produced per unit of organic carbon consumed (Haas et al., 2011; Haas et al., 2013). BGE on coral exudates can exceed 18% but is reduced to as low as 6% on algal exudates (Nelson et al., 2013), indicating a decoupling between catabolic (energy-producing) and anabolic (energy-consuming) processes among microbial communities (Del Giorgio and Cole 1998; Carlson et al., 2007). Using metagenomics, Haas et al., showed that microbial communities at coral-dominated sites encode genes for the energy efficient Embden-Meyerhof-Parnas (EMP) glycolytic pathway but shift to the less efficient Entner-Doudoroff (ED) and Pentose Phosphate (PP) pathways as benthic algal cover increases (Haas et al., 2016; Silveira et al., 2019). These measurements of BGE and genomic indicators of microbial metabolism suggest that microbes respond to a surplus of labile carbon by switching from highly efficient metabolic pathways that maximize the use of limited carbon substrates to less efficient, faster pathways in a canonical yield-to-power switch (Flamholz et al., 2013; Lipson 2015; Haas et al., 2016; Roach et al., 2017). The canonical EMP route generates more ATP and NADH, driving metabolic pathways towards oxidative phosphorylation and the complete oxidation of the carbon substrate to CO_2 (Figure 1.3, Russell and Cook 1995; Pollak et al., 2007; Spaans et al., 2015). This strategy is well-suited to environments with limited organic carbon supply and abundant oxygen, such as oligotrophic coral reefs and the open ocean. Microbes in these systems devote available energy towards maintenance costs, preserving cellular function and integrity (De Mattos and Neijssel 1997; Hoehler 2004).

Microbes growing on the abundant labile carbon in macroalgal exudates preferentially utilize the alternative ED and PP glycolytic pathways, which produce less ATP and more NADPH (Figure 1.3, Russell and Cook 1995). Abundant NADPH and depleted ATP drive pathways related to overflow metabolism, which shunt excess organic carbon into biosynthesis as opposed to being oxidized to CO_2 (Basan et al., 2015; reviewed in Russell and Cook, 1995). This switch enables microbes in eutrophic environments to metabolize the excess organic carbon faster, at the expense of metabolic efficiency (Stettner and Segrè 2013; Lipson 2015). Because microbes utilizing overflow metabolism do not fully oxidize the available carbon substrate, they consume less oxygen relative to organic carbon and store a larger fraction of the available carbon as biomass. This reduced oxygen consumption per unit carbon would suggest an increase in available oxygen relative to organic carbon in algae-stimulated microbial communities, or a decrease in e^-DAR. However, enhanced rates of respiration and DOC consumption coupled with increased microbial abundance and community biomass ensure a net depletion of oxygen relative to DOC, increasing e^-DAR.

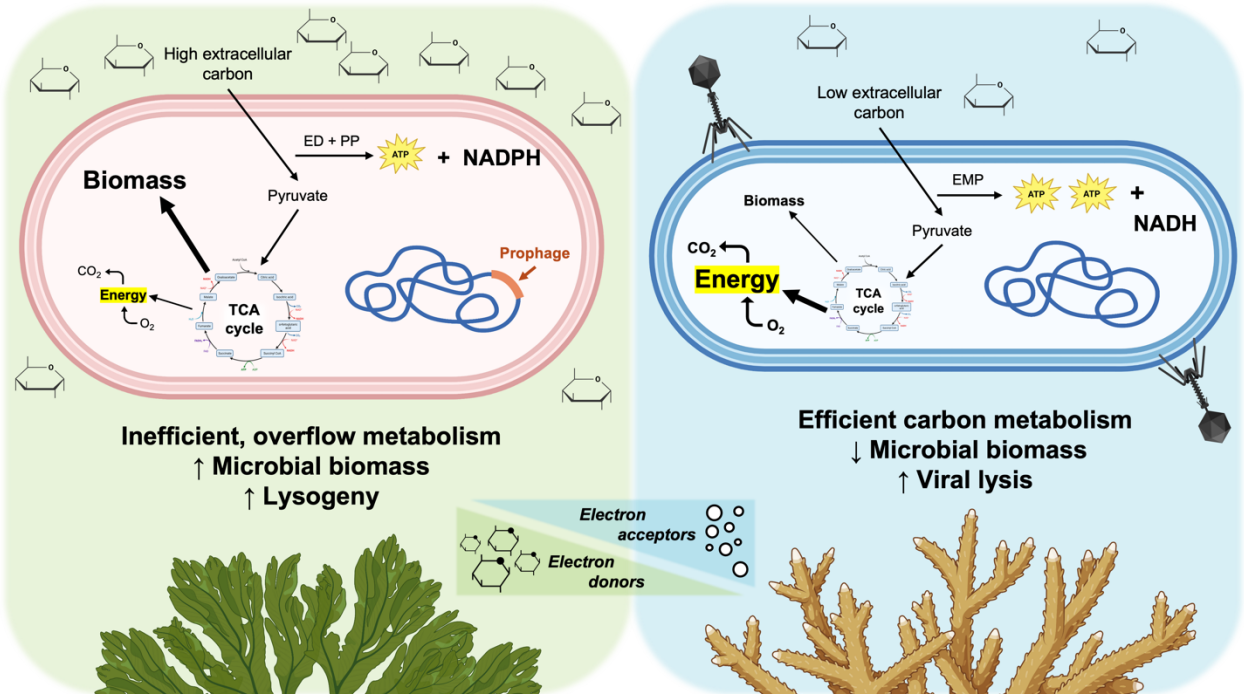


Figure 1.3 The role of e⁻DAR in determining microbial community structure and function on coral reefs. (Left Panel) At high e⁻DAR (abundant electron donors relative to acceptors, i.e., algal-dominated reefs), microbes preferentially use the fast, but inefficient Entner Doudoroff (ED) and Pentose Phosphate (PP) pathways for metabolizing carbon substrates. Shifts to overflow metabolism result in incomplete carbon oxidation and shunt excess carbon into biosynthesis, increasing microbial biomass. High concentrations of NADPH and relatively less ATP in the intracellular environment favor viral integration into host genomes as prophages. (Right Panel) At low e⁻DAR (abundant electron acceptors relative to donors, i.e., coral-dominated reefs), microbes preferentially use the energy efficient Embden-Meyerhof-Parnas (EMP) pathway for metabolizing carbon substrates, which results in full oxidation of carbon substrates to CO_2. High production of ATP and NADH are used for maintenance costs and favor viral lysis, which serves as a trophic control on microbial community growth.

Viral predation

Increased microbial abundances and metabolic switching at high e⁻DAR modulates microbial interactions with viral predators which result in the loss of viral predation pressure on reefs (Figure 1.3). Viruses utilize two dominant modes of infection: a lytic strategy which terminates in lysis of the bacterial host, or a dormant lysogenic strategy in which viruses establish a long-term relationship with the bacterial host by integrating into the host genome as a prophage (reviewed in Howard-Varona et

al., 2017). Coral-dominated reefs support high viral lytic production and relatively lower microbial abundances (Payet et al., 2014; Silveira et al., 2015), implicating viral lysis as a major trophic control of reef microbes (Thurber et al., 2017). The release of bacterial cell contents through viral lytic predation in the so-called viral shunt reduces the transfer of OM to higher trophic levels and instead recycles bacterial carbon back to the DOC pool, where it enhances primary productivity in planktonic food webs (Suttle 2005, 2007). In contrast, high bacterial abundances on algal-dominated reefs are accompanied by an increased frequency of lysogeny and the abundance of temperate phages (Knowles et al., 2016a), which act to enhance microbial loop activity and cause OM to accumulate in microbial biomass.

The lysis-lysogeny decision is driven primarily by the metabolic state of the host cell, in which high energy conditions inside the cell (high ATP) tend to favor lysis and low energy conditions inside the cell (low ATP) tend to favor lysogeny (Echols 1986; Kobiler et al., 2004; Laganenka et al., 2019). At the ecosystem level, the energy state of host cells is related to microbial density, with low intracellular ATP conditions, and therefore lysogeny, more common at high and low host densities (Figure 1.2, Knowles et al., 2017a, 2016a; reviewed in Silveira et al., 2021). When resource poor conditions support low host densities ($>10^4$ mL^{-1}), such as in the deep ocean, slow-growing, starved, and ATP-depleted microbes favor lysogeny in the Refugium Hypothesis (Silveira et al., 2021). At intermediate bacterial densities (10^5 -10^6 mL^{-1}), such as those found in the open ocean, higher viral-bacterial encounter rates and high intracellular ATP concentrations favor viral lysis in the Kill-the-Winner strategy (Box 1, Cheng et al., 1988; Thingstad 2000; Thingstad et al., 2014). However, at high host densities ($>10^6$

mL^{-1}) in microbialized systems, microbes using anabolic pathways with low ATP yield and increased production of NADPH create an intracellular environment favoring the buildup of phage repressors, which stimulate new lysogenic infections and maintain existing prophages (Silveira et al., 2021). The increased frequency of lysogeny at high host densities is referred to as the Piggyback-the-Winner hypothesis and has been observed in ecosystems ranging from aquatic and terrestrial systems to holobionts in both virus-to-microbe ratios (Box 1) and metagenomes (Knowles et al., 2016a; Touchon et al., 2016). Note that recent research supporting the Piggyback-the-Winner hypothesis suggests that bacterial growth rates, and not densities, are the primary factor mediating the switch between lytic and lysogenic life cycles (Roughgarden 2023). The implications of the lysis-lysogeny decision on reef biogeochemistry are substantial, with viral lysis removing up to half of bacterial standing stock each day in healthy reef systems (Suttle 2007; Payet et al., 2014; Bouvy et al., 2015; Breitbart et al., 2018) and acting as a primary top-down control on microbialization (McDole et al., 2012; Silveira et al., 2023). In contrast, lysogeny facilitates microbial community persistence and expansion on reefs, and contributes to the death of reef macrofauna through the rise of pathogens.

Rise of pathogens

Lysogeny reinforces microbial dominance on degrading reefs by enhancing bacterial fitness and removing top-down predatory control by other viruses and by protist grazers, accelerating the positive feedback loop of microbial biomass accumulation (Silveira et al., 2017). Prophages encode auxiliary metabolic genes (AMGs) that modulate existing host functions or confer new abilities that improve the chances of survival of the virus-host pair (Canchaya et al., 2003; Feiner et al., 2015;

Howard-Varona et al., 2017). Phage-encoded virulence factors enable microbes to recognize and invade metazoan hosts, and are commonly involved in eukaryotic host attachment, invasion, immune system evasion, and toxin production (Silveira et al., 2020). These genes enable microbes to expand their niche, as well as to evade predation by single-celled protistan grazers, which contribute to up to 50% of bacterial predation and transfer bacterial carbon to higher trophic levels (Sherr and Sherr 2002). Reefs with high microbial densities display an increased abundance of phage-encoded virulence genes (Brüssow et al., 2004; Knowles et al., 2016a; Cárdenas et al., 2018; Silveira et al., 2020), providing a mechanism to explain the increased abundance of microbial pathogens on degrading reefs. With phage-mediated enhancements in fitness and a suite of virulence factors, reef-associated microbes become agents of disease, contributing to coral death. Further, prophages protect their hosts against infection and lytic predation by other viruses through a defense strategy known as superinfection exclusion, facilitating persistence of the lysogen (Sternberg et al., 1978; Bondy-Denomy et al., 2016; Dedrick et al., 2017). This loss of predatory control over microbial communities by viruses and protists serves as the proverbial “nail in the coffin” for reefs, accelerating transitions to higher microbial energy use.

In summary, changes in e^-DAR represent a substantial shift in an ecosystem’s carbon budget and are linked to the physical structure and function of coral reefs. In coral-dominated systems, carbon fixed in photosynthesis provides the energy required for corals to build complex and foundational habitats through calcification. In contrast, the fate of algal-derived carbon does not contribute to an ecosystem-building process (Hughes et al., 2007a), but instead feeds into the microbial food web. As a result of

shifts in microbial community structure and metabolism, a large fraction of this surplus carbon is stored in microbial biomass (Haas et al., 2016). Temperate viruses, sensing the shifted energetic environment within microbial hosts, opt to integrate into host genomes, and carry virulence genes to enhance host fitness and evade predation (Knowles et al., 2016b; Silveira et al., 2023). The loss of controls on microbial growth prevents the transfer of microbially-incorporated carbon back up the trophic web, further accumulating ecosystem energy in the microbial food web.

DEOXYGENATION IN AQUATIC SYSTEMS – A MICROBIAL MATTER

Oxygen is a primary electron acceptor driving aerobic respiration in nearly all marine organisms, and its abundance is regulated primarily by metabolism (reviewed in Nelson and Altieri, 2019). While photosynthesis enriches water with oxygen, respiration depletes it, and influxes of organic matter (OM) that stimulate microbial respiration can result in imbalances in net metabolism that cause deoxygenation. OM is not evenly distributed across ecosystems: it is incorporated in microbial biomass during growth, transferred up trophic levels, released in pulses as organisms die, and accumulated in sediments and at hydrological and geomorphological boundaries. Sites of OM accumulation are hotspots of microbial activity and the resulting deoxygenation drives shifts in ecosystem trophic structure, energy utilization, and biogeochemical cycling. By limiting aerobic respiration, deoxygenation constrains an ecosystem's energetic potential, because the alternative energy producing pathways and electron acceptors associated with anoxic conditions yield less energy (Falkowski et al., 2008; Wright et al., 2012), and explicitly favor microbial communities capable of sustained anaerobic metabolism over macrobes. As such, ecosystem energy previously allocated to

expensive macroecological interactions, such as predation and competition, is transferred to the microbes as ecosystems become deoxygenated (Figure 1.6).

Microbial degradation of OM depletes electron acceptors available for aerobic respiration, increasing e^-DAR and reinforcing transitions to higher microbial energy use (i.e., microbialization). This section emphasizes the relationship between OM, microbes, and deoxygenation in aquatic systems. On coral reefs, sporadic and natural influxes of OM can cause (1) local and acute hypoxic episodes, but enhanced OM loading to coastal ecosystems and resulting microbial community responses have sparked a paradigm of (2) chronic deoxygenation on coral reefs. In addition to consuming oxygen, enhanced respiration of OM decreases seawater pH locally through the production of CO_2, causing (3) acidification and metabolic dissolution that further compromise the growth and survival of reef macrobes, particularly those of calcifiers. Ecosystems at the extremes of OM accumulation, deoxygenation, and acidification may become (4) permanently microbialized, and microbial processes therein play a key role in global biogeochemical cycling. However, expansion of these zones due to (5) climate change and globally increased OM inputs have increased the incidence and scale of coastal "dead zones," and will intensify microbialization processes to the detriment of coastal ecosystem health and productivity.

Acute deoxygenation on coral reefs

Coral reefs have a net metabolic balance close to zero (Crossland et al., 1991), with rates of high primary production met with equally high rates of consumption, decomposition, and recycling. Despite this relative balance between autotrophy and heterotrophy (Alldredge et al., 2013; Naumann et al., 2013; Rix et al., 2015), diel and

seasonal fluctuations in physical factors, nutrient inputs, and biogeochemistry can temporarily shift reef metabolism in favor of heterotrophy. Periods of net heterotrophy are commonly driven by an accumulation of OM over relatively short time scales or in shallow, stratified, or confined water masses. Rapid microbial decomposition of this accumulated OM can result in the formation of suboxic conditions at the coral reef benthos and throughout the water column that can last for several days (Figure 1.4, Best et al., 2007). Episodic microbial deoxygenation on coral reefs has been documented following coral larval slicks (Glud et al., 2008; Patten et al., 2008; Wild et al., 2008), extreme tidal fluctuations (Simpson et al., 1993; Villanueva et al., 2005; Hobbs and Macrae 2012), phytoplankton blooms resulting from nutrient-rich terrestrial runoff (reviewed in Fabricius 2005; Kealoha et al., 2020), sewage pollution (Smith et al., 1981; Jokiel et al., 1993), mariculture effluent (Loya 2004; Villanueva et al., 2005), and coastal upwelling (Genin et al., 1995; Laboy-Nieves et al., 2001).

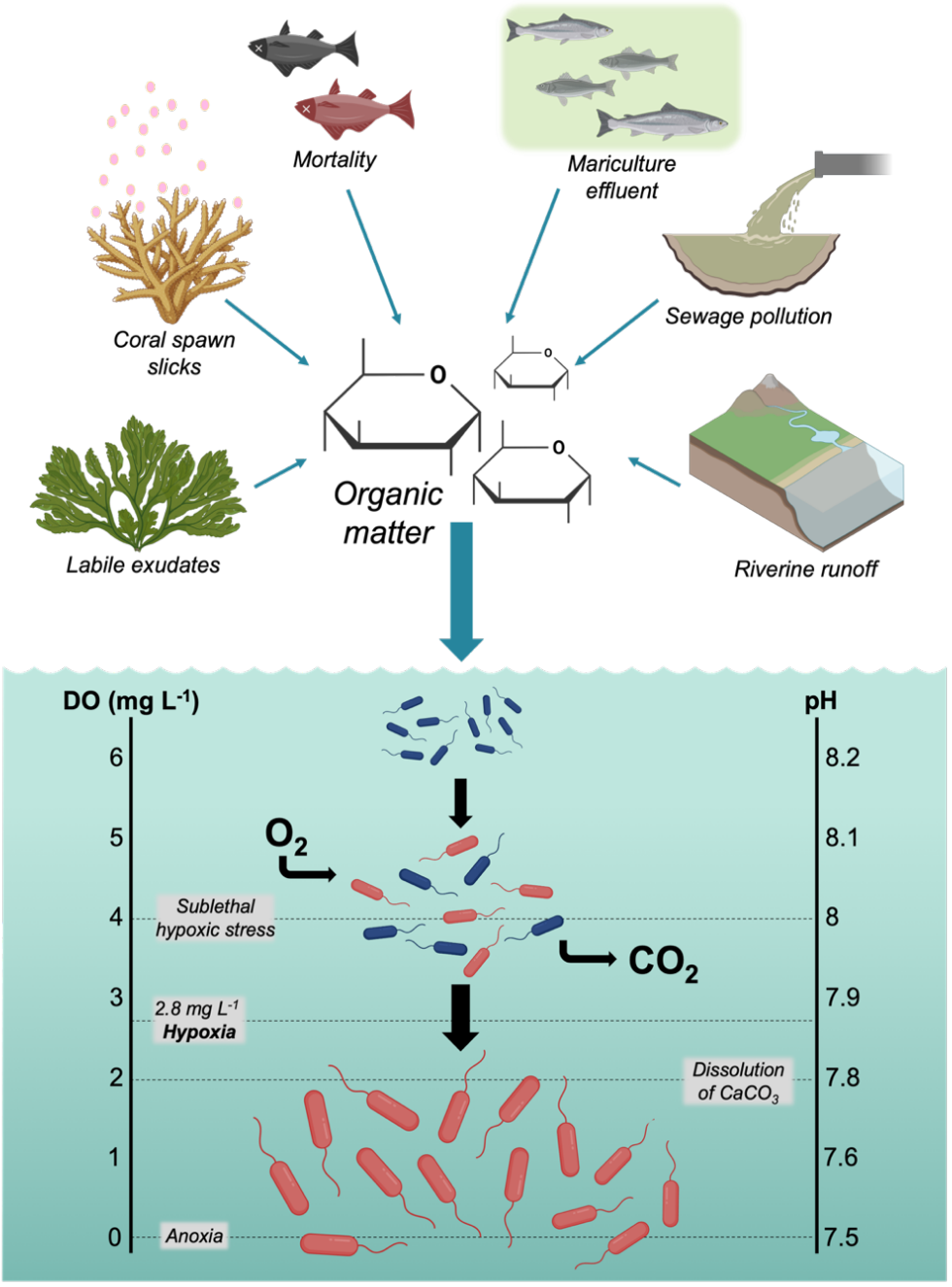


Figure 1.4 Organic matter inputs as a driver of deoxygenation and acidification in aquatic systems. Microbial degradation of (1) labile macroalgae exudates, (2) larval biomass following coral spawning events, (3) dead and decaying reef organisms, (4) nutrient-rich effluent from fisheries, (5) anthropogenic wastewater, and (6) terrestrial and agricultural runoff from river discharge can reduce local oxygen concentrations and pH to lethal levels for reef macrofauna. Persistent OM inputs, combined with local geomorphological characteristics which prevent mixing with more oxygenated waters, can result in long-term or permanent conditions of hypoxia and reduce the aragonite saturation state below thresholds necessary for calcification processes.

Hydrological and geomorphological characteristics of reefs can enhance their susceptibility to acute suboxic events by facilitating OM accumulation and reducing the replenishment of oxygen depleted by microbial respiration. Shallow, semi-enclosed sites with restricted water flow such as lagoons (Camp et al., 2017), reef flats (Guadayol et al., 2014), atolls (Andréfouët et al., 2015), embayments, and tide pools routinely experience periods of suboxia (<2-3 mg/L O_2), which can become hypoxic during tidal and seasonal warming events that increase basal rates of respiration and microbial oxygen demand (Meire et al., 2013). Risk of deoxygenation is further compounded at sites in close proximity to terrestrial inputs and with limited flushing from the surrounding ocean (Kraines et al., 1996; Diaz and Rosenberg 2008; Andréfouët et al., 2015; Altieri et al., 2021). Suboxic and hypoxic events are more common during calm weather, when light winds, reduced current speeds, and low swell cause the water column to stratify, reducing mixing and the transfer of oxygenated surface water to deeper layers (Simpson et al., 1993; Hobbs and Macrae 2012; reviewed in Gobler and Baumann 2016).

Acute microbial deoxygenation is an agent of stress and mortality for reef macrobes and can impact local benthic community structure. Reef organisms display a wide range of tolerance to suboxic conditions and are accustomed to some natural variation in dissolved oxygen (DO) concentrations due to diel and seasonal fluctuations (Altieri et al., 2021; Diaz and Rosenberg, 1995; reviewed in Nelson and Altieri, 2019). Broadly, periodic hypoxia affects marine organisms by altering behavior and immune responses, enhancing susceptibility to disease, and impairing growth and reproduction (reviewed in Breitburg et al., 2018 and Nelson and Altieri 2019). In corals specifically,

low oxygen conditions can cause bleaching, tissue loss, DNA damage, and shifts in metabolism, photosynthetic capacity, and calcification rates which compromise coral health and function (see Pezner et al., 2023 and citations therein). Depending on the duration, frequency, and magnitude of the suboxic conditions, many reef organisms can recover from episodes of acute microbial deoxygenation. Johnson et al., 2021 documented the recovery of a coral reef community following a severe, multi-day hypoxic event and found that while water column microbial communities rebounded to pre-hypoxic states within days, changes to benthic communities persisted for more than a year, with marked losses in coral cover and invertebrate diversity (Johnson et al., 2021). These findings indicate a decoupling in ecological trajectories between microbes and macrobes following disturbance (Johnson et al., 2021). Due to a combination of global climate change and increased OM inputs to coastal ecosystems, acute deoxygenation events are becoming more frequent, severe, and longer in duration on coral reefs (Figure 1.5, Breitburg et al., 2018; Alteri et al., 2019), with 15% of coral reefs estimated to be at an elevated risk of hypoxia (Altieri et al., 2017; Hughes et al., 2020). Increasing e^-DAR on reefs as a result of increasing OM inputs and active oxygen loss will contribute to a chronic paradigm of deoxygenation challenging the recovery of degraded reef communities.

Chronic deoxygenation of coral reefs

Reefs under phase shift towards macroalgal dominance are threatened by chronic deoxygenation. Algae-dominated reefs have lower DO standing stocks, with nighttime respiratory drawdown causing DO to approach hypoxia at many sites (Wild et al., 2010; Haas et al., 2013a; Altieri et al., 2021; Pezner et al., 2023). This observation is

counter to experimental studies of oxygen production by benthic primary producers, which show turf- and fleshy- macroalgae release up to three times as much oxygen into the surrounding seawater as calcifying organisms (Naumann et al., 2010; Haas et al., 2011; Nelson et al., 2013; Silveira et al., 2019). These findings can be explained by two mechanisms which result in (1) active loss and (2) increased consumption of oxygen on algae-dominated reefs. Silveira et al., described a biophysical mechanism by which photosynthetically produced oxygen supersaturates at the surface of fleshy algae, forming bubbles through heterogeneous nucleation, which, when liberated from the algal surface, are lost to the atmosphere (Figure 1.5, Odum and Odum 1955; Kraines et al., 1996; Freeman et al., 2018; Silveira et al., 2019). In contrast, 78-90% of the photosynthetic oxygen produced by endosymbiotic microalgae living within coral tissues is provided to the coral host to sustain the energetic demands of respiration and calcification (Al-Horani et al., 2003b, a), thus retaining oxygen within the benthic community. The process of oxygen bubbling, known as ebullition, has been documented in several aquatic systems and is predicted to account for the loss of up to 37%, 21%, and 20% of gross oxygen production in lakes (Koschorreck et al., 2017), salt marshes (Howard et al., 2018), and algal-dominated reefs (Silveira et al., 2019), respectively.

By releasing oxygen through ebullition and retaining labile carbon exudates in solution, algae increase e^-DAR and create a high energy, low oxygen environment which stimulates microbial heterotrophic metabolism (Haas et al., 2010, 2011; Wild et al., 2010; Nelson et al., 2013; Kelly et al., 2014). The resulting increase in microbial heterotrophy is the second mechanism contributing to oxygen loss on coral reefs: microbialization increases a reef's baseline biological oxygen demand (Figure 1.5). In

mesocosm incubations, microbial communities growing on labile macroalgal exudates had higher respiratory demand and consumed 10 times more oxygen than those growing on coral exudates (Silveira et al., 2019). At the coral-algae interface, this increased microbial growth and oxygen demand can cause suboxic zones which result in coral death (Barott et al., 2009; Gregg et al., 2013; Haas et al., 2013a, b, 2014; Roach et al., 2017). The formation of microbially mediated suboxic zones through the release of labile DOC has been implicated as a major strategy for turf- and fleshy-macroalgae to gain a competitive advantage over corals in the struggle for benthic space. At the scale of a reef, microbial respiration can consume up to 47% of the oxygen produced by benthic primary producers and, together with ebullition, may result in the loss of almost two thirds of gross oxygen production on reefs (Silveira et al., 2019).

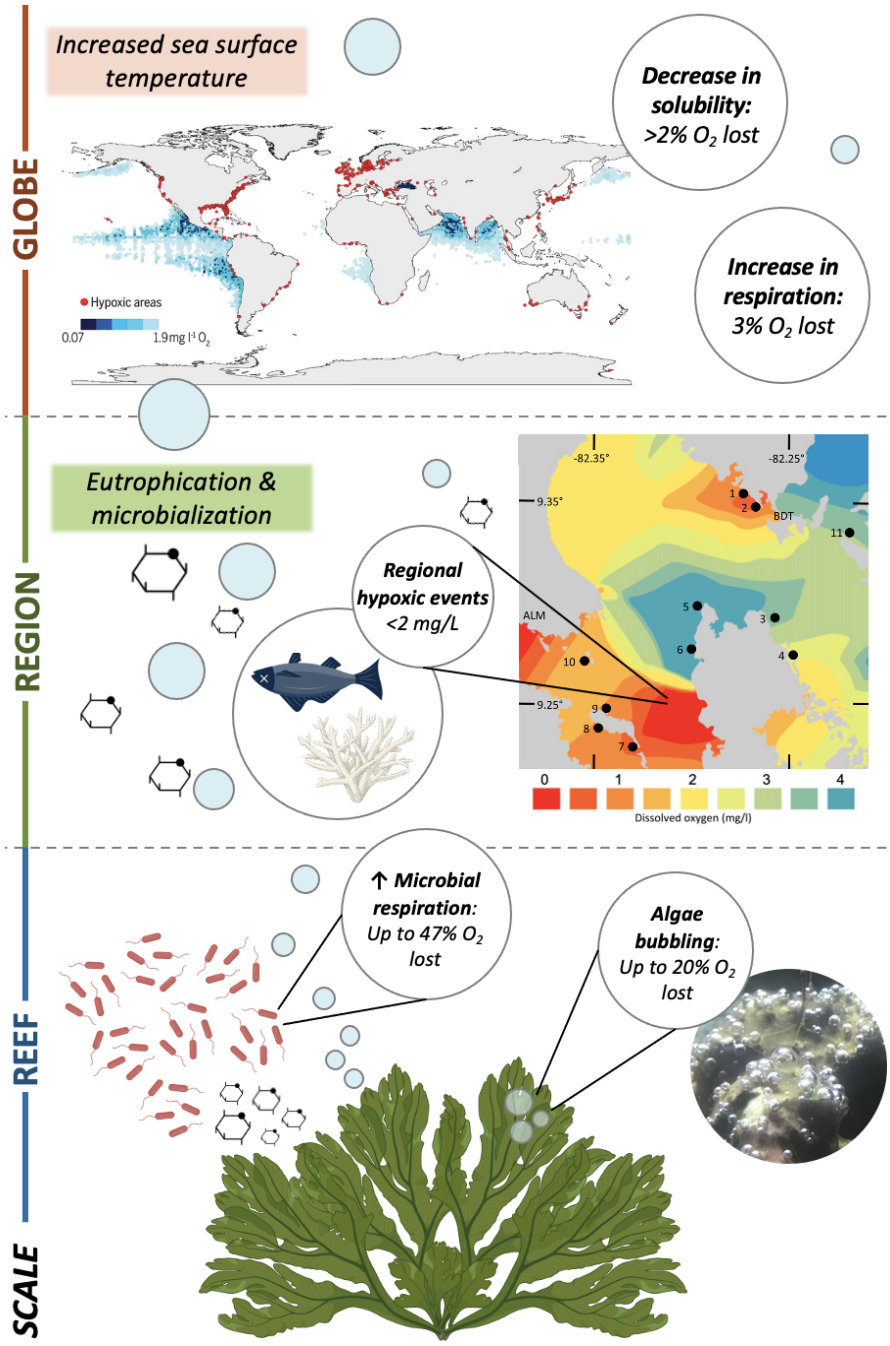


Figure 1.5 Microbial deoxygenation as a feature of coastal ecosystems spanning multiple scales, driven by anthropogenic inputs of organic matter and climate change. At local reef scales, the overgrowth of fleshy macroalgae can result in the loss of up to 67% of gross oxygen production through ebullition and enhanced microbial respiration of algal-derived organic matter. At regional scales, terrestrial inputs of organic matter and accompanying microbial decomposition can result in suboxic events which kill benthic invertebrates, including corals. At the global scale, increases in sea surface temperature result in global ocean deoxygenation through reduced oxygen solubility and increased respiratory demand of micro- and macroorganisms. World map figure (top panel) adapted from Breitburg et al., 2018. Map of Panama (middle panel) adapted from Altieri et al., 2017.

Microbial acidification

The consequences of enhanced microbial heterotrophy during microbialization often focus on depletion of oxygen and overlook the production of carbon dioxide (CO_2), which reduces seawater pH and drives acidification. Open ocean pH is controlled primarily by atmospheric exchange of CO_2, leading to relatively low interannual variation in pH (<0.1 unit) (Caldeira and Wickett 2003). In contrast, pH in highly productive coastal ecosystems is strongly regulated by metabolism and displays diel and seasonal fluctuations up to an order of magnitude higher than open ocean systems, with daily ranges of up to 1 pH unit observed on coral reefs (Borgesa and Gypensb 2010; Hofmann et al., 2011; reviewed in Duarte et al., 2013). Photosynthesis and respiration modify local pH through the consumption and production of CO_2, respectively, and elevated microbial respiration of OM reduces both pH and the availability of carbonate ions (CO_3^{2-}) essential to calcification (Feely et al., 2008; Cai et al., 2011; Wallace et al., 2014). This “metabolic acidification” reduces the saturation state for $CaCO_3$ minerals such as aragonite, negatively affecting $CaCO_3$ production in calcifying organisms and accelerating reef bioerosion and dissolution (Yeakel et al., 2015). In eutrophied coastal areas, seasonal and sometimes daily levels of CO_2, aragonite saturation, and pH already exceed (1) thresholds that are known to reduce growth and survival in marine organisms and (2) predicted extremes in the open ocean due to ocean acidification (Melzner et al., 2013; Wallace et al., 2014). While hypoxia and acidification tend to co-occur following episodes of enhanced microbial respiration, low pH conditions persist longer than hypoxia due to differences in rates of CO_2 and O_2 diffusion and solubility (Wallace et al., 2014). The combined effects of these processes dampen net reef

accretion by enhancing metabolic dissolution (Eyre et al., 2014; Cyronak and Eyre 2016), negatively impact the growth and survival of calcifying organisms (Mccoy and Kamenos 2015; Steckbauer et al., 2020), and exacerbate organismal responses to deoxygenation (see for citations Breitburg et al., 2018; Steckbauer et al., 2020), reinforcing transitions from biodiverse, accreting reefs dominated by calcifiers to low diversity, actively dissolving reefs dominated by algae and microbes (Yates et al., 2017).

Metabolic acidification may also enhance positive feedback to higher e^-DAR by altering the composition of DOC available for microbial consumption. The DOC pool comprises an immense diversity of chemical compounds whose residence time in seawater is determined by their ability to be degraded by microbes, with highly labile carbon compounds degraded easily on the order of minutes to hours and refractory carbon compounds resisting degradation and persisting in seawater over much longer timescales (Carlson and Ducklow 1996; Carlson et al., 2007). Efforts to balance carbon budgets in terrestrial systems led to the discovery of the priming effect, in which the addition of labile organic carbon compounds induce co-metabolism interactions among microbial communities which enable them to degrade more refractory organic carbon (reviewed in Guenet et al., 2010). The priming effect “diversifies the menu” for microbes, facilitating the consumption of more of the DOC pool and, in marine systems, results in measured values of DOC inventory that are lower than expected given organic carbon inputs (Thingstad et al., 2008; Guenet et al., 2010; Haas et al., 2016). Reduced seawater pH enhances both (1) the production of labile organic carbon sources such as transparent exopolymer particles (TEP) and (2) the net rates of organic carbon loss (Engel et al., 2004; Riebesell et al., 2007), suggesting acidification may enhance the

lability of the DOC pool and, through the priming effect, the amount of the DOC pool respired to CO_2. Intensification of the priming effect via increased inputs of CO_2 and OM may therefore serve as a feedback loop that amplifies metabolic deoxygenation and acidification in eutrophied coastal systems.

Microbial hotspots – life at the e^-DAR extremes

Where consistently high OM inputs combine with physical features restricting water movement and mixing, ecosystems can become permanently microbialized and commonly experience hypoxic and acidified conditions for extended periods of time or in perpetuity. At these extreme ends of the e^-DAR spectrum, ecosystem energy use is dominated by microbes, and low oxygen conditions support microbial processes that are major contributors to global biogeochemical cycles (reviewed in Wright et al., 2012). In oceanic oxygen minimum zones (OMZs), microbial degradation of OM from nutrient-rich, upwelled deepwater and a rain of decaying OM from productive surface waters create near-anoxic conditions that facilitate anaerobic processes normally absent in oxic surface waters (Ulloa et al., 2012). As oxygen is depleted, aerobic respiration is replaced by processes including denitrification, anaerobic ammonium oxidation (annamox), and sulfate reduction, which use nitrate (NO_3^-) and nitrite (NO_2^-), ammonium (NH_4^+), and sulfate (SO_4^{2-}) as alternate electron acceptors to degrade OM, respectively. Remineralization of OM by denitrification and annamox to dinitrogen gas (N_2) in OMZs represents up to 50% of bioavailable (fixed) nitrogen loss in the oceans (Codispoti et al., 2001). Denitrification also produces N_2O, a potent greenhouse gas, and OMZs are estimated to account for at least one third of global N_2O emissions (Codispoti et al., 2001; Wright et al., 2012). In the open ocean, microbialization

processes driving OMZs are essential to the remineralization and redistribution of inorganic nutrients in the oceans, facilitate the export of OM from surface waters in the biological carbon pump, and impact atmospheric concentrations of gases affecting the global climate.

Microbial degradation of OM also shapes ecological and biogeochemical landscapes in coastal ecosystems. Estuaries are net heterotrophic systems, with high delivery of labile OM via eutrophied river plumes supplementing internal OM accumulation from high primary production rates (Del Giorgio and Williams 2005; Gobler and Baumann 2016). Persistently hypoxic conditions in sediments and stratified bottom water layers of estuaries can expand to affect the entire water column in warmer, summer months (Soertaert et al., 2006), supporting similar anaerobic OM degradation pathways as in OMZs. High denitrification rates in estuaries reduce the concentration of terrestrially derived organic nitrogen by more than 70%, thus helping to mitigate eutrophication to adjacent oceanic ecosystems and serving as a buffer for globally increased anthropogenic inputs of nitrogen (Barbier et al., 2011; Smyth et al., 2013; Pennino et al., 2016). As a sink for terrigenous N, microbialized estuaries control the flux of nutrients to the oceans and can limit the amount of organic nitrogen available for primary production (Seitzinger 1987; Cornwell et al., 1999). However, global increases in temperature and anthropogenic inputs of OM have overwhelmed the capacity of many estuaries to regulate eutrophication, thus expanding microbialization to the coastal ocean and altering global biogeochemical cycles.

Global changes and dead zones

Global changes in climate patterns and ocean conditions will exacerbate and amplify the effects of microbial deoxygenation and acidification in coastal environments (Breitburg et al., 2018; Hughes et al., 2020). Dissolved oxygen concentrations are in decline across global aquatic ecosystems: the open ocean has lost more than 2% of its oxygen content in the past 50 years (Schmidtko et al., 2017) and is expected to lose an additional 3-5% by 2100 (Bopp et al., 2013; Pezner et al., 2023). Oxygen losses are more pronounced in the coastal ocean due to close proximity to terrestrial OM inputs and increased warming of shallower water over continental shelves (Gilbert et al., 2010). Increased precipitation due to ocean warming is enhancing riverine discharge to coastal ecosystems (Justić et al., 1996; Fabricius 2005; Solomon 2007), compounding already considerable OM inputs from anthropogenic activities. Globally increased sea surface temperatures (SST) both reduce oxygen solubility in seawater and increase organismal metabolic rates (Brown et al., 2004; reviewed in Keeling et al., 2010; Vaquer-Sunyer et al., 2012), thus increasing biological oxygen demand while simultaneously reducing its availability. Indeed, hypoxia and acidification at eutrophied sites reach peak highs during warmer summer months, as rapid microbial respiration rates consume oxygen and produce CO_2 faster than they can be replenished and exported, respectively (Wallace et al., 2014).

As warm, fresh water is less dense than cold and salty water, rising SST and increased precipitation act to increase water column stratification of the coastal ocean (Keeling et al., 2010). Stratification isolates deeper water layers from oxygenated surface waters, preventing mixing that would otherwise replenish oxygen consumed by microbial degradation of OM (Sotto et al., 2014). Reduced oxygen resupply to the ocean

interior owing to increased thermal stratification has caused open ocean OMZ suboxic boundaries to expand into shallower depths (Whitney et al., 2007), causing habitat compression for pelagic species. By increasing the strength of offshore winds, ocean warming is also increasing coastal upwelling, resulting in the expansion of coastal OMZ onto continental shelves (Stramma et al., 2008, 2010). This “shoaling” of OMZs transports low-oxygen, acidified water to coastal ecosystems and can result in major losses to benthic macrofauna (Chan et al., 2008; Feely et al., 2008; Sydeman et al., 2014). Hypoxia-induced mass mortality of macrobes then provides a rich source of OM for microbial decomposition, creating a feedback loop in which eukaryotic secondary production is vastly reduced and virtually all ecosystem OM is remineralized by the microbes (Diaz and Rosenberg 2008). Collectively, these factors are increasing microbialization in coastal environments by creating OM rich, oxygen depleted, and poorly mixed zones dominated by microbial processes and hostile to macrobial life.

Ecosystems in which severe, prolonged suboxic conditions cause mass mortality or migration of macrobes are known as dead zones (Figure 1.5, Diaz and Rosenberg 1995; Rabalais et al., 2002), representing the extreme end of the microbialization regime. Anthropogenic OM inputs and climate change have increased the incidence and severity of dead zones in temperate and tropical ecosystems (Figure 1.5, Diaz and Rosenberg 2008; Rabalais et al., 2014; Altieri and Gedan 2015; Breitburg et al., 2018), with major consequences to coastal fisheries (Diaz and Rosenberg 2008) and ecosystem services. Ecosystem models of hypoxia show that in oxygenated conditions, up to 75% of the energy produced via primary production is allocated to mobile predators (Diaz and Rosenberg 2008), while under conditions of hypoxia, energy is

diverted into microbial pathways and away from higher trophic levels (Pearson and Rosenberg 1992; Baird et al., 2004). Yet, despite drastic reductions in macrofaunal biomass and diversity, dead zones are hotspots of microbial life and activity. Globally increased coastal dead zones are expected to impact biogeochemical cycles in similar ways to other highly microbialized habitats, potentially by enhancing losses of bioavailable N and increasing production of greenhouse gases, including N_2O and methane, that impact global climate.

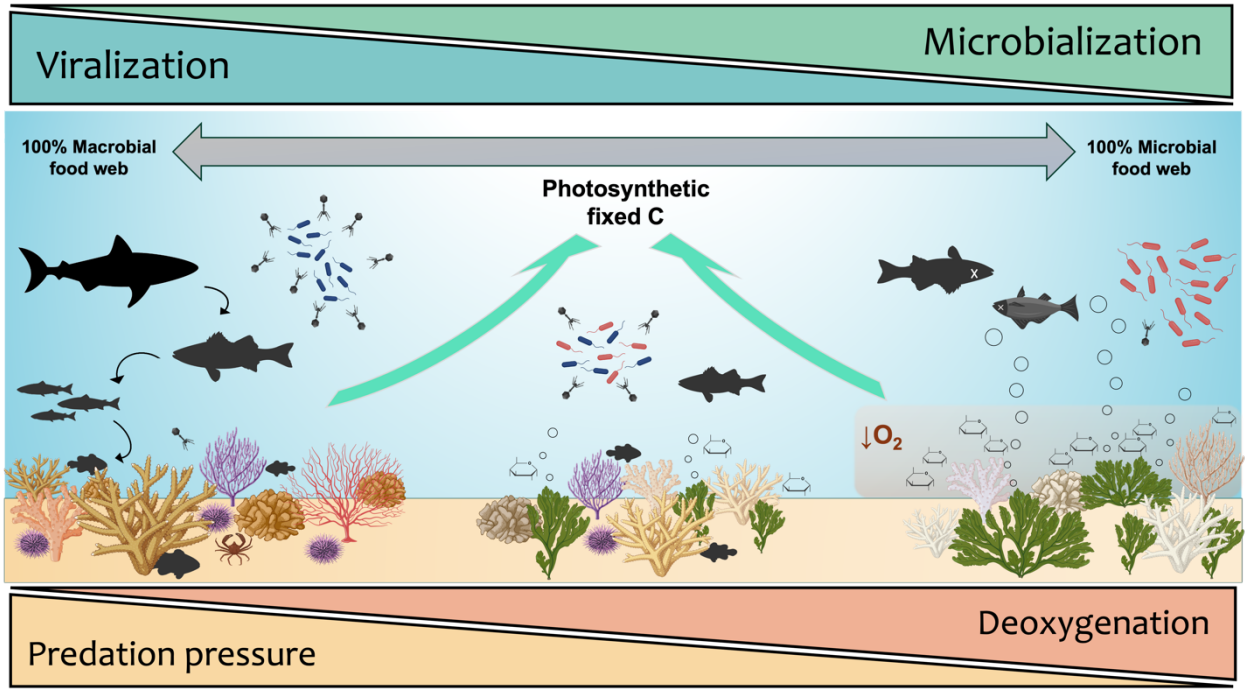


Figure 1.6 Viralization vs microbialization on coral reefs. On viralized reefs dominated by corals, predation pressure by fish and viruses transfers photosynthetically fixed carbon up to higher trophic levels, maintaining up to 100% of ecosystem energy in the macrobial food web. On microbialized reefs dominated by algae, macroalgal carbon is fed directly into the microbial food web, diverting ecosystem energy away from higher trophic levels. Deoxygenation from algal oxygen bubbling and microbial respiration kill reef macrobes and reinforce microbial dominance. Here, blue microbes represent beneficial or neutral taxa, while red microbes represent copiotrophs and potential pathogens.

Coral reef microbialization is a global phenomenon and on many reefs has progressed to a stage at which natural recovery processes will not be sufficient to reinstate reef functions, even in the absence of continued anthropogenic impact. At these sites, active and targeted interventions will be necessary to restore and reshape reef ecosystems to the point of self-sufficiency. Early coral reef restoration efforts adopted techniques from forest restoration to create a marine silviculture paradigm known as “coral gardening” (Guzmán 1991; Rinkevich 1995; Epstein et al., 2003), which despite limited efficacy remains a leading practice used today. Current restoration interventions center primarily around the propagation and active translocation of corals to denuded sites, the artificial augmentation of reef three-dimensional framework, and the enhancement of coral sexual reproduction through larval rearing and dispersal (Rinkevich 2019; Boström-Einarsson et al., 2020; Randall et al., 2020; Higgins et al., 2022). Yet, efforts to restore coral reef function and reinstate valuable ecosystem services have not achieved much success (Boström-Einarsson et al., 2020).

How to restore a reef?

In this chapter, we have provided evidence that coral reef microbialization is initiated by the loss of predation pressure by fish and viruses and mediated by a change in reef biochemistry through increased e-DAR (Figure 1.6). Solutions for restoring reefs may involve combatting these processes by (1) reinstating fish and viral predation pressure or (2) reducing e-DAR. Both can be addressed in part through active management: enforcement of fishing regulations can reduce local overfishing (Hilborn et al., 2020), and improved methods of wastewater treatment can reduce anthropogenic

OM inputs to marine ecosystems (Smith et al., 1981; Kemp et al., 2009). Indeed, active management of nutrient and organic carbon inputs has reduced microbial biological oxygen demand, reestablished oxic conditions, and eliminated dead zones from several coastal and aquatic ecosystems (Diaz and Rosenberg 2008; Kemp et al., 2009). Well-designed and enforced fishing regulations can contribute to the recovery of reef fish populations (Di Franco et al., 2016), which increase coral cover and slow phase shifts to macroalgal states (Hughes et al., 2007b). No such methods exist yet for reinstating viral predatory control over microbes, though the enhancement of lytic production and induction among environmental viruses represents a fruitful avenue for research. Engineering solutions have also been proposed to combat deoxygenation, typically involving mechanisms which enhance vertical and horizontal mixing of the water column or resupply oxygen via mechanical air bubbling (Stigebrandt and Gustafsson 2007; Conley et al., 2009), but none have yet been brought to scale.

Reducing e^-DAR using Coral Arks

Active restoration interventions on coral reefs will benefit from integrating the above goals of reinstating predation pressure and reducing e^-DAR into management plans. Locally reducing e^-DAR on reefs may be achieved simply by moving vertically out of the reef boundary layer. Changes in e^-DAR are most pronounced at the benthic interface, where the concentration of organic carbon exuded by primary producers, microbial activity, and oxygen consumption are at a maximum. Reef e^-DAR is therefore highest at the reef-water interface and decreases with distance from the benthos, suggesting that biochemical conditions may be improved by relocating a portion of the reef community from the benthos to the overlying water column. Baer et al., 2023

demonstrated the use of a seafloor-tethered, midwater platform called Coral Reef Arks to support the growth and propagation of coral reef biodiversity (Baer et al., 2023). Survival rates of translocated corals on Coral Arks after one year were three times higher than for corals translocated to nearby denuded seafloor sites. The midwater Coral Arks environment displayed higher dissolved oxygen concentrations, flow speeds, virus-to-microbe ratios (VMRs), and lower DOC concentrations relative to the seafloor control sites (Figure 1.7), indicating an environment with reduced e^-DAR and enhanced viral predation pressure (Baer et al., 2023). Similarly, the Mars Assisted Reef Restoration System (MARRS) improved environmental conditions for corals by escaping the boundary layer and facilitated rapid accretion on “Reef Stars,” leading to reef recovery at highly degraded sites (Williams et al., 2019; Lange et al., 2024).

Population enhancement and restocking of reefs via *in situ* propagation of corals and keystone reef herbivores (i.e., *Diadema antillarum* in the Caribbean) is underway and will benefit from new methods to enhance survival despite deteriorating ecological conditions. Relocating a portion of the reef community to improved conditions in the midwater may be a viable first step for coral reef restoration projects. Escaping the reef boundary layer dampens diel fluctuations in DO and pH which result in nighttime hypoxia and respiratory acidification on algal-dominated reefs. This can be achieved through the use of positively buoyant, fully midwater structures such as Coral Arks, or seafloor-attached structures (such as MARRS’ reef stars) with sufficient height off the benthos to locally reduce e^-DAR (Baer et al., 2023; Lange et al., 2024) (Figure 1.7). Species which play a disproportionate role in maintaining ecosystem functioning, such as corals and grazing invertebrates, are good candidates for translocation to these local

biochemical hotspots on an otherwise microbialized benthos. Coral Arks and similar methodologies which enhance reef biochemical conditions while providing habitat for reef macrofauna will support the success of coral restoration efforts and help conserve reef biodiversity while the factors driving global microbialization, namely OM inputs, overfishing, and CO_2 emissions, can be addressed.

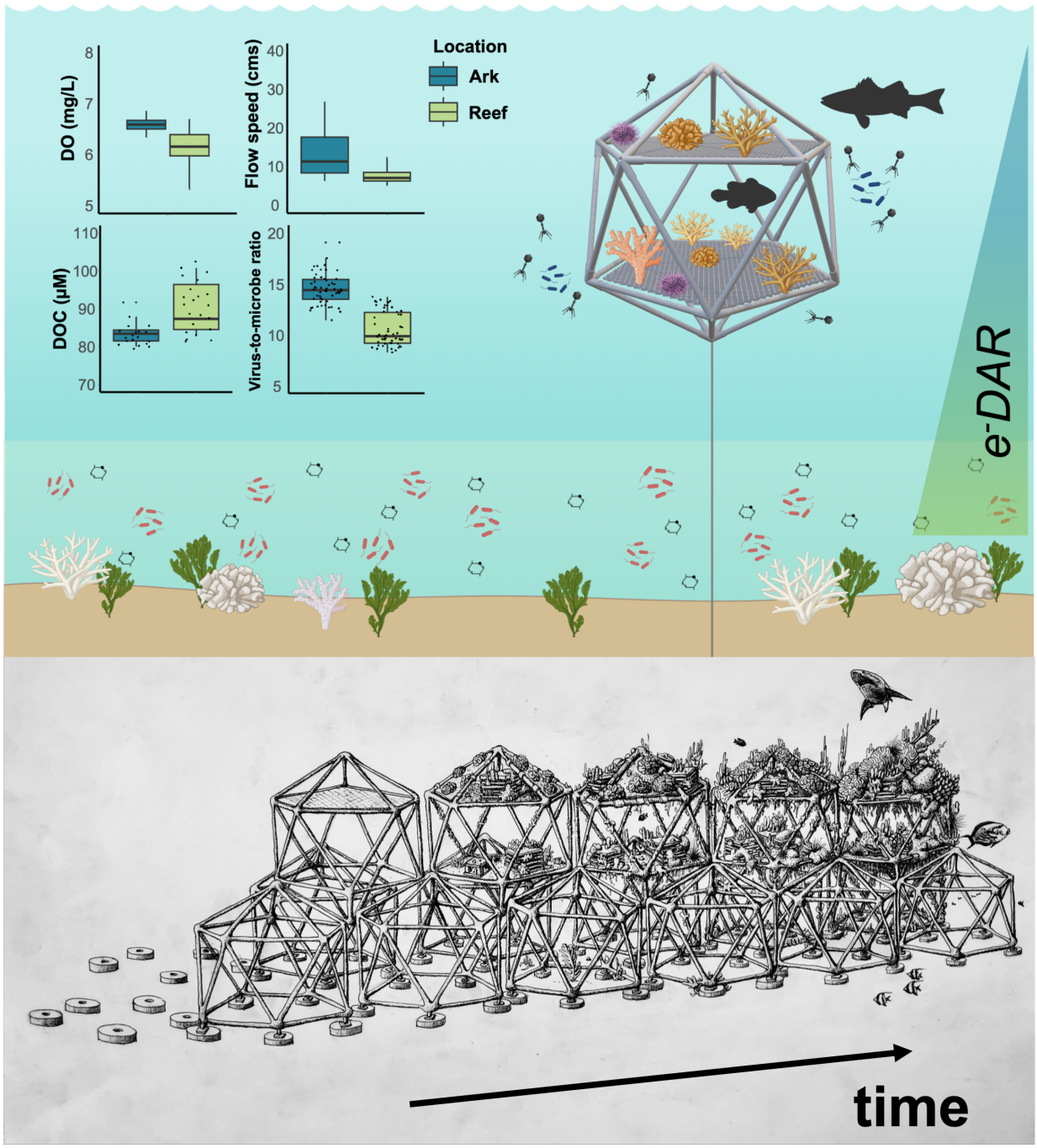


Figure 1.7 Coral Reef Arks as seafloor-tethered, midwater platforms for recruiting and propagating coral reef biodiversity and reducing microbialization. (Top Panel) By elevating reef communities above the microbialized benthos, Coral Arks provide enhanced oxygen, higher flow speeds, and reduced DOC concentrations (reducing e-DAR overall relative to the benthos). Arks also display higher virus-to-microbe ratios (VMR), indicating enhanced viral lytic control over microbial communities. (Bottom Panel) Arks can be constructed into seafloor-attached, living breakwalls to provide improved habitat for reef species while reinstating reef framework for wave dissipation and coastal protection. Bottom panel illustrated by Ben Darby.

CONCLUSIONS

Microbes are the engines that drive Earth's biogeochemical cycles (Falkowski et al., 2008), supporting the global recycling and redistribution of carbon and nutrients across ecosystems. Organic matter represents the energy source feeding microbial engines in aquatic systems and its consumption by microbes, which are in turn consumed by planktonic protists and benthic suspension feeders, transfers this energy up through the trophic web. The high productivity and biodiversity of coral reefs rely on low influxes of OM, efficient trophic transfer of microbially-incorporated carbon via microbial predation, and abundant oxygen. However, global increases in labile OM inputs and decreases in oceanic oxygen content have enhanced processes associated with microbial expansion and diminished those processes integrating microbes into reef macrobial food webs. This microbialization of coral reefs represents a redistribution in ecosystem energy from supporting high macrofaunal biomass, ecological interactions such as predation and symbiosis, and energy intensive processes such as calcification to trophically simplified, oxygen-limited, and eutrophied microbial reactors.

Microbialization is driven by an increase in the ratio of electron donors (i.e., labile organic carbon) to electron acceptors (i.e., oxygen), or e^-DAR, in aquatic systems. Increased labile organic carbon causes shifts in microbial community structure that enhance microbial carbon consumption at the expense of metabolic efficiency, reduces connectivity with reef food webs by evading predation, and exacerbates climate change-driven losses in oxygen by increasing biological oxygen demand. Resulting decreases in oxygen, which further increase e^-DAR, limit aerobic respiration and divert energy away from macrofauna and into microbial metabolism. This positive feedback between

organic matter, microbial metabolism, and deoxygenation reinforces microbial dominance and makes microbialized systems increasingly stable over time, locking resources in the microbial food web. Dead zones represent an extreme outcome of these changes; increases in the incidence and severity of these zones in coastal ecosystems will alter ocean productivity, biodiversity, biogeochemical cycling, and human livelihoods by compromising food security, coastal protection, and other reef ecosystem functions. Efforts to mitigate coral reef microbialization should aim to reduce e^-DAR and reinstate predation by herbivorous fish and viruses to control macroalgae and microbes and redirect photosynthetically fixed carbon back up the trophic web.

ACKNOWLEDGEMENTS

We thank Heather Maughan and the editors for the manuscript revision. Chapter 1, in full, has been accepted for publication of the material by Nature Springer as a special issue on microbial mechanisms of coral reef degradation. Jason L Baer and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

REFERENCES

Al-Horani, F. A., Al-Moghrabi, S. M., & De Beer, D. (2003a). Microsensor study of photosynthesis and calcification in the scleractinian coral, *Galaxea fascicularis*: Active internal carbon cycle. *Journal of Experimental Marine Biology and Ecology*. https://doi.org/10.1016/S0022-0981(02)00578-6

Al-Horani, F. A., Al-Moghrabi, S. M., & De Beer, D. (2003b). The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Marine Biology*. https://doi.org/10.1007/s00227-002-0981-8

Alldredge, A. L., Carlson, C. A., & Carpenter, R. C. (2013). Sources of organic carbon to coral reef flats. *Oceanography*. https://doi.org/10.5670/oceanog.2013.52

Alteri, A., Nelson, H., & Gedan, K. (2019). The significance of ocean deoxygenation for tropical ecosystems - corals, seagreasses and mangroves. In *Ocean deoxygenation: everyone's problem. Causes, impacts, consequences and solutions*.

Altieri, A. H., & Gedan, K. B. (2015). Climate change and dead zones. *Global Change Biology*, *21*(4), 1395–1406. https://doi.org/10.1111/gcb.12754

Altieri, A. H., Harrison, S. B., Seemann, J., Collin, R., Diaz, R. J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1621517114

Altieri, A. H., Johnson, M. D., Swaminathan, S. D., Nelson, H. R., & Gedan, K. B. (2021). Resilience of tropical ecosystems to ocean deoxygenation. *Trends in Ecology and Evolution*, *36*(3), 227–238. https://doi.org/10.1016/j.tree.2020.11.003

Andréfouët, S., Dutheil, C., Menkes, C. E., Bador, M., & Lengaigne, M. (2015). Mass mortality events in atoll lagoons: environmental control and increased future vulnerability. *Global Change Biology*, *21*(1), 195–205.

Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L., & Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, *10*(3), 257–263. https://doi.org/10.3354/meps010257

Baer, J. L., Carilli, J., Chadwick, B., Hatay, M., van der Geer, A., Scholten, Y., Barnes, W., Aquino, J., Ballard, A., Little, M., Brzenski, J., Liu, X., Rosen, G., Wang, P. F., Castillo, J., Haas, A. F., Hartmann, A. C., & Rohwer, F. (2023). Coral Reef Arks: An *in situ* mesocosm and toolkit for assembling reef communities. *Journal of Visualized Experiments*, *2023*(191). https://doi.org/10.3791/64778

Baird, D., Christian, R. R., Peterson, C. H., & Johnson, G. A. (2004). Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecological Applications*, *14*(3), 805–822.

Bak, R. P. M., Joenje, M., De Jong, I., Lambrechts, D. Y. M., & Nieuwland, G. (1998). Bacterial suspension feeding by coral reef benthic organisms. *Marine Ecology Progress Series*, *175*, 285–288.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193.

Barott, K. L., Rodriguez-Brito, B., Janouškovec, J., Marhaver, K. L., Smith, J. E., Keeling, P., & Rohwer, F. L. (2011). Microbial diversity associated with four functional groups of benthic reef algae and the reef-building coral *Montastraea annularis*. *Environmental Microbiology*. https://doi.org/10.1111/j.1462-2920.2010.02419.x

Barott, K. L., & Rohwer, F. L. (2012). Unseen players shape benthic competition on coral reefs. In *Trends in Microbiology*. https://doi.org/10.1016/j.tim.2012.08.004

Barott, K., Smith, J., Dinsdale, E., Hatay, M., Sandin, S., & Rohwer, F. (2009). Hyperspectral and physiological analyses of coral-algal interactions. *PLoS ONE*, *4*(11). https://doi.org/10.1371/journal.pone.0008043

Basan, M., Hui, S., Okano, H., Zhang, Z., Shen, Y., Williamson, J. R., & Hwa, T. (2015). Overflow metabolism in *Escherichia coli* results from efficient proteome allocation. *Nature*, *528*(7580), 99–104. https://doi.org/10.1038/nature15765

Best, M. A., Wither, A. W., & Coates, S. (2007). Dissolved oxygen as a physico-chemical supporting element in the Water Framework Directive. *Marine Pollution Bulletin*, *55*(1–6), 53–64. https://doi.org/10.1016/j.marpolbul.2006.08.037

Boaden, A. E., & Kingsford, M. J. (2015). Predators drive community structure in coral reef fish assemblages. *Ecosphere*, *6*(4), 1–33.

Bondy-Denomy, J., Qian, J., Westra, E. R., Buckling, A., Guttman, D. S., Davidson, A. R., & Maxwell, K. L. (2016). Prophages mediate defense against phage infection through diverse mechanisms. *ISME Journal*, *10*(12), 2854–2866. https://doi.org/10.1038/ismej.2016.79

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., & Seferian, R. (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, *10*(10), 6225–6245.

Borgesa, A. V, & Gypensb, N. (2010). Carbonate chemistry in the coastal zone responds more strongly to eutrophication than ocean acidification. *Limnology and Oceanography*, *55*(1), 346–353.

Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C. A., Hancock, B., Harrison, P., Hein, M., & Shaver, E. (2020). Coral restoration–A systematic review of current methods, successes, failures and future directions. *PloS One*, *15*(1), e0226631.

Bouvy, M., Got, P., Bettarel, Y., Bouvier, T., Carré, C., Roques, C., Rodier, M., Lopé, J.-C., & Arfi, R. (2015). Importance of predation and viral lysis for bacterial mortality in a tropical western Indian coral-reef ecosystem (Toliara, Madagascar). *Marine and Freshwater Research*, *66*(11), 1009–1017.

Breitbart, M., Bonnain, C., Malki, K., & Sawaya, N. A. (2018). Phage puppet masters of the marine microbial realm. *Nature Microbiology*, *3*(7), 754–766.

Breitburg, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalais, N. N., Roman, M. R., Rose, K. A., Seibel, B. A., … Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science*, *359*(6371). https://doi.org/10.1126/science.aam7240

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789.

Brüssow, H., Canchaya, C., & Hardt, W.-D. (2004). Phages and the evolution of bacterial pathogens: from genomic rearrangements to lysogenic conversion. *Microbiology and Molecular Biology Reviews*, *68*(3), 560–602.

Cai, W.-J., Hu, X., Huang, W.-J., Murrell, M. C., Lehrter, J. C., Lohrenz, S. E., Chou, W.-C., Zhai, W., Hollibaugh, J. T., & Wang, Y. (2011). Acidification of subsurface coastal waters enhanced by eutrophication. *Nature Geoscience*, *4*(11), 766–770.

Caldeira, K., & Wickett, M. E. (2003). Anthropogenic carbon and ocean pH. *Nature*, *425*(6956), 365.

Camp, E. F., Nitschke, M. R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S. G., Smith, D. J., Zampighi, M., & Suggett, D. J. (2017). Reef-building corals thrive within hot-acidified and deoxygenated waters. *Scientific Reports*, *7*(1), 1–9. https://doi.org/10.1038/s41598-017-02383-y

Canchaya, C., Fournous, G., Chibani-Chennoufi, S., Dillmann, M.-L., & Brüssow, H. (2003). Phage as agents of lateral gene transfer. *Current Opinion in Microbiology*, *6*(4), 417–424.

Cárdenas, A., Neave, M. J., Haroon, M. F., Pogoreutz, C., Rädecker, N., Wild, C., Gärdes, A., & Voolstra, C. R. (2018). Excess labile carbon promotes the expression of virulence factors in coral reef bacterioplankton. *ISME Journal*. https://doi.org/10.1038/ismej.2017.142

Cardini, U., Bednarz, V. N., van Hoytema, N., Rovere, A., Naumann, M. S., Al-Rshaidat, M. M. D., & Wild, C. (2016). Budget of primary production and dinitrogen fixation in a highly seasonal Red Sea coral reef. *Ecosystems*, *19*(5), 771–785. https://doi.org/10.1007/s10021-016-9966-1

Carlson, C. A., del Giorgio, P. A., & Herndl, G. J. (2007). Microbes and the dissipation of energy and respiration: From cells to ecosystems. *Oceanography*, *20*(SPL.ISS. 2), 89–100. https://doi.org/10.5670/oceanog.2007.52

Carlson, C. A., & Ducklow, H. W. (1996). Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquatic Microbial Ecology*. https://doi.org/10.3354/ame010069

Chan, F., Barth, J. A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W. T., & Menge, B. A. (2008). Emergence of anoxia in the California current large marine ecosystem. *Science*, *319*(5865), 920.

Cheng, H. H., Muhlrad, P. J., Hoyt, M. A., & Echols, H. (1988). Cleavage of the cII protein of phage lambda by purified HflA protease: control of the switch between lysis and lysogeny. *Proceedings of the National Academy of Sciences*, *85*(21), 7882–7886.

Cheshire, A. C., Westphalen, G., Wenden, A., Scriven, L. J., & Rowland, B. C. (1996). Photosynthesis and respiration of phaeophycean-dominated macroalgal communities in summer and winter. *Aquatic Botany*, *55*(3), 159–170. https://doi.org/10.1016/S0304-3770(96)01071-6

Codispoti, L. A., Brandes, J., Christensen, J. P., Devol, A. H., Naqvi, S. W. A., Paerl, H., & Yoshinari, T. (2001). The oceanic fixed nitrogen and nitrous oxide budgets: moving targets as we enter the Anthropocene? *Scientia Marina*, *65*(S2), 85–105.

Conley*, D. J., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hansson, L.-A., Rabalais, N. N., Voss, M., & Zillén, L. (2009). Tackling hypoxia in the Baltic Sea: is engineering a solution? ACS Publications.

Cornwell, J. C., Kemp, W. M., & Kana, T. M. (1999). Denitrification in coastal ecosystems: Methods, environmental controls, and ecosystem level controls, a review. *Aquatic Ecology*, *33*(1), 41–54. https://doi.org/10.1023/A:1009921414151

Costanza, R., De Groot, R., Sutton, P., Van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., & Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, *26*, 152–158.

Crossland, C. J. (1987). *In situ* release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. *Coral Reefs*. https://doi.org/10.1007/BF00302210

Crossland, C. J., Hatcher, B. G., & Smith, S. V. (1991). Role of coral reefs in global ocean production. *Coral Reefs*, *10*, 55–64.

Cyronak, T., & Eyre, B. D. (2016). The synergistic effects of ocean acidification and organic metabolism on calcium carbonate (CaCO3) dissolution in coral reef sediments. *Marine Chemistry*, *183*, 1–12. https://doi.org/10.1016/j.marchem.2016.05.001

De Groot, R., Brander, L., Van Der Ploeg, S., Costanza, R., Bernard, F., Braat, L., Christie, M., Crossman, N., Ghermandi, A., & Hein, L. (2012). Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services*, *1*(1), 50–61.

De Mattos, M. J. T., & Neijssel, O. M. (1997). Bioenergetic consequences of microbial adaptation to low-nutrient environments. *Journal of Biotechnology*, *59*(1–2), 117–126.

Dedrick, R. M., Jacobs-Sera, D., Guerrero Bustamante, C. A., Garlena, R. A., Mavrich, T. N., Pope, W. H., Cervantes Reyes, J. C., Russell, D. A., Adair, T., Alvey, R., Bonilla, J. A., Bricker, J. S., Brown, B. R., Byrnes, D., Cresawn, S. G., Davis, W. B., Dickson, L. A., Edgington, N. P., Findley, A. M., … Hatfull, G. F. (2017). Prophage-mediated defense against viral attack and viral counter-defense. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2016.251

Del Giorgio, P. A., & Cole, J. J. (1998). Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics*, *29*(1), 503–541.

Del Giorgio, P., & Williams, P. (2005). *Respiration in aquatic ecosystems*. OUP Oxford.

DeLong, J. P., Okie, J. G., Moses, M. E., Sibly, R. M., & Brown, J. H. (2010). Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(29), 12941–12945. https://doi.org/10.1073/pnas.1007783107

DeMartini, E. E., Friedlander, A. M., Sandin, S. A., & Sala, E. (2008). Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series*, *365*, 199–215. https://doi.org/10.3354/meps07501

Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, N. L., Jeudy de Grissac, A., Koutsoubas, D., Milazzo, M., & Otero, M. del M. (2016). Five key attributes can increase marine protected areas performance for small-scale fisheries management. *Scientific Reports*, *6*(1), 38135.

Diaz, R. J., & Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology. An Annual Review*, *33*(245), 3.

Diaz, R. J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, *321*(5891), 926–929. https://doi.org/10.1126/science.1156401

Dinsdale, E. A., Pantos, O., Smriga, S., Edwards, R. A., Angly, F., Wegley, L., Hatay, M., Hall, D., Brown, E., Haynes, M., Krause, L., Sala, E., Sandin, S. A., Thurber, R. V., Willis, B. L., Azam, F., Knowlton, N., & Rohwer, F. (2008). Microbial ecology of four coral atolls in the Northern Line Islands. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0001584

Duarte, C. M., Hendriks, I. E., Moore, T. S., Olsen, Y. S., Steckbauer, A., Ramajo, L., Carstensen, J., Trotter, J. A., & McCulloch, M. (2013). Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuaries and Coasts*, *36*, 221–236.

Ducklow, H. W., & Mitchell, R. (1979). Bacterial populations and adaptations in the mucus layers on living corals. *Limnology and Oceanography*, *24*(4), 715–725. https://doi.org/10.4319/lo.1979.24.4.0715

Engel, A., Delille, B., Jacquet, S., Riebesell, U., Rochelle-Newall, E., Terbrüggen, A., & Zondervan, I. (2004). Transparent exopolymer particles and dissolved organic carbon production by *Emiliania huxleyi* exposed to different CO2 concentrations: a mesocosm experiment. *Aquatic Microbial Ecology*, *34*(1), 93–104.

Eyre, B. D., Andersson, A. J., & Cyronak, T. (2014). Benthic coral reef calcium carbonate dissolution in an acidifying ocean. *Nature Climate Change*, *4*(11), 969–976. https://doi.org/10.1038/nclimate2380

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*(2), 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Falkowski, P. G., Fenchel, T., & Delong, E. F. (2008). The microbial engines that drive earth's biogeochemical cycles. *Science*, *320*(5879), 1034–1039. https://doi.org/10.1126/science.1153213

Feely, R. A., Sabine, C. L., Hernandez-Ayon, J. M., Ianson, D., & Hales, B. (2008). Evidence for upwelling of corrosive" acidified" water onto the continental shelf. *Science*, *320*(5882), 1490–1492.

Feiner, R., Argov, T., Rabinovich, L., Sigal, N., Borovok, I., & Herskovits, A. A. (2015). A new perspective on lysogeny: prophages as active regulatory switches of bacteria. *Nature Reviews Microbiology*, *13*(10), 641–650.

Flamholz, A., Noor, E., Bar-Even, A., Liebermeister, W., & Milo, R. (2013). Glycolytic strategy as a tradeoff between energy yield and protein cost. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1215283110

Freeman, S. E., Freeman, L. A., Giorli, G., & Haas, A. F. (2018). Photosynthesis by marine algae produces sound, contributing to the daytime soundscape on coral reefs. *PLoS ONE*, *13*(10), 1–14. https://doi.org/10.1371/journal.pone.0201766

Genin, A., Lazar, B., & Brenner, S. (1995). Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature*, *377*(6549), 507–510.

Gilbert, D., Rabalais, N. N., Diaz, R. J., & Zhang, J. (2010). Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences*, *7*(7), 2283–2296.

Glud, R. N., Eyre, B. D., & Patten, N. (2008). Biogeochemical responses to mass coral spawning at the Great Barrier Reef: Effects on respiration and primary production. *Limnology and Oceanography*, *53*(3), 1014–1024. https://doi.org/10.4319/lo.2008.53.3.1014

Gobler, C. J., & Baumann, H. (2016). Hypoxia and acidification in ocean ecosystems: Coupled dynamics and effects on marine life. *Biology Letters*, *12*(5). https://doi.org/10.1098/rsbl.2015.0976

Gregg, A. K., Hatay, M., Haas, A. F., Robinett, N. L., Barott, K., Vermeij, M. J. A., Marhaver, K. L., Meirelles, P., Thompson, F., & Rohwer, F. (2013). Biological oxygen demand optode analysis of coral reef-associated microbial communities exposed to algal exudates. *PeerJ*. https://doi.org/10.7717/peerj.107

Guadayol, Ò., Silbiger, N. J., Donahue, M. J., & Thomas, F. I. M. (2014). Patterns in temporal variability of temperature, oxygen and pH along an environmental gradient in a coral reef. *PLoS ONE*, *9*(1). https://doi.org/10.1371/journal.pone.0085213

Guenet, B., Danger, M., Abbadie, L., & Lacroix, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology*, *91*(10), 2850–2861.

Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y. W., Maughan, H., Pantos, O., Roach, T. N. F., Sanchez, S. E., Silveira, C. B., Sandin, S., Smith, J. E., & Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2016.42

Haas, A. F., Gregg, A. K., Smith, J. E., Abieri, M. L., Hatay, M., & Rohwer, F. (2013). Visualization of oxygen distribution patterns caused by coral and algae. *PeerJ*. https://doi.org/10.7717/peerj.106

Haas, A. F., Jantzen, C., Naumann, M. S., Iglesias-Prieto, R., & Wild, C. (2010). Organic matter release by the dominant primary producers in a Caribbean reef lagoon: Implication for *in situ* O2 availability. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps08631

Haas, A. F., Nelson, C. E., Kelly, L. W., Carlson, C. A., Rohwer, F., Leichter, J. J., Wyatt, A., & Smith, J. E. (2011). Effects of coral reef benthic primary producers on dissolved organic carbon and microbial activity. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0027973

Haas, A. F., Nelson, C. E., Rohwer, F., Wegley-Kelly, L., Quistad, S. D., Carlson, C. A., Leichter, J. J., Hatay, M., & Smith, J. E. (2013). Influence of coral and algal exudates on microbially mediated reef metabolism. *PeerJ*. https://doi.org/10.7717/peerj.108

Haas, A. F., Smith, J. E., Thompson, M., & Deheyn, D. D. (2014). Effects of reduced dissolved oxygen concentrations on physiology and fluorescence of hermatypic corals and benthic algae. *PeerJ*. https://doi.org/10.7717/peerj.235

Haas, A. F., & Wild, C. (2010). Composition analysis of organic matter released by cosmopolitan coral reef-associated green algae. *Aquatic Biology*. https://doi.org/10.3354/ab00271

Hatcher, B. G. (1988). Coral reef primary productivity: A beggar's banquet. In *Trends in Ecology and Evolution*. https://doi.org/10.1016/0169-5347(88)90117-6

Hester, E. R., Barott, K. L., Nulton, J., Vermeij, M. J. A., & Rohwer, F. L. (2016). Stable and sporadic symbiotic communities of coral and algal holobionts. *ISME Journal*, *10*(5), 1157–1169. https://doi.org/10.1038/ismej.2015.190

Higgins, E., Metaxas, A., & Scheibling, R. E. (2022). A systematic review of artificial reefs as platforms for coral reef research and conservation. *PLoS ONE*, *17*(1 January), 1–23. https://doi.org/10.1371/journal.pone.0261964

Hilborn, R., Amoroso, R. O., Anderson, C. M., Baum, J. K., Branch, T. A., Costello, C., De Moor, C. L., Faraj, A., Hively, D., Jensen, O. P., Kurota, H., Little, L. R., Mace, P., McClanahan, T., Melnychuk, M. C., Minto, C., Osio, G. C., Parma, A. M., Pons, M., … Ye, Y. (2020). Effective fisheries management instrumental in improving fish stock status. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(4), 2218–2224. https://doi.org/10.1073/pnas.1909726116

Hobbs, J.-P. A., & Macrae, H. (2012). Unusual weather and trapped coral spawn lead to fish kill at a remote coral atoll. *Coral Reefs*, *31*(4), 961.

Hoehler, T. M. (2004). Biological energy requirements as quantitative boundary conditions for life in the subsurface. *Geobiology*, *2*(4), 205–215.

Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., Paytan, A., Price, N. N., Peterson, B., & Takeshita, Y. (2011). High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PloS One*, *6*(12), e28983.

Hollibaugh, J. T., & Azam, F. (1983). Microbial degradation of dissolved proteins in seawater. *Limnology and Oceanography*. https://doi.org/10.4319/lo.1983.28.6.1104

Houlbrèque, F., & Ferrier-Pagès, C. (2009). Heterotrophy in tropical scleractinian corals. In *Biological Reviews*. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Howard, E. M., Forbrich, I., Giblin, A. E., Lott III, D. E., Cahill, K. L., & Stanley, R. H. R. (2018). Using noble gases to compare parameterizations of air-water gas exchange and to constrain oxygen losses by ebullition in a shallow aquatic environment. *Journal of Geophysical Research: Biogeosciences*, *123*(9), 2711–2726.

Howard-Varona, C., Hargreaves, K. R., Abedon, S. T., & Sullivan, M. B. (2017). Lysogeny in nature: Mechanisms, impact and ecology of temperate phages. In *ISME Journal*. https://doi.org/10.1038/ismej.2017.16

Hughes, D. J., Alderdice, R., Cooney, C., Kühl, M., Pernice, M., Voolstra, C. R., & Suggett, D. J. (2020). Coral reef survival under accelerating ocean deoxygenation. *Nature Climate Change*, *10*(4), 296–307. https://doi.org/10.1038/s41558-020-0737-9

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, *265*(5178), 1547–1551.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*. https://doi.org/10.1016/j.cub.2006.12.049

Johnson, M. D., Scott, J. J., Leray, M., Lucey, N., Bravo, L. M. R., Wied, W. L., & Altieri, A. H. (2021). Rapid ecosystem-scale consequences of acute deoxygenation on a Caribbean coral reef. *Nature Communications*, *12*(1), 1–12. https://doi.org/10.1038/s41467-021-24777-3

Jokiel, P. L., Hunter, C. L., Taguchi, S., & Watarai, L. (1993). Ecological impact of a fresh-water “reef kill” in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs*, *12*, 177–184.
Jokiel, P. L., & Morrissey, J. I. (1986). Influence of size on primary production in the reef coral *Pocillopora damicornis* and the macroalga *Acanthophora spicifera*. *Marine Biology*. https://doi.org/10.1007/BF00397566

Jorissen, H., Skinner, C., Osinga, R., De Beer, D., & Nugues, M. M. (2016). Evidence for water-mediated mechanisms in coral–algal interactions. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2016.1137

Justić, D., Rabalais, N. N., & Turner, R. E. (1996). Effects of climate change on hypoxia in coastal waters: a doubled CO2 scenario for the northern Gulf of Mexico. *Limnology and Oceanography*, *41*(5), 992–1003.

Kealoha, A. K., Doyle, S. M., Shamberger, K. E. F., Sylvan, J. B., Hetland, R. D., & DiMarco, S. F. (2020). Localized hypoxia may have caused coral reef mortality at the Flower Garden Banks. *Coral Reefs*, *39*, 119–132.

Keeling, R. F., Körtzinger, A., & Gruber, N. (2010). Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, *2*(1), 199–229. https://doi.org/10.1146/annurev.marine.010908.163855

Kelly, L. W., Nelson, C. E., Petras, D., Koester, I., Quinlan, Z. A., Arts, M. G. I., Nothias, L. F., Comstock, J., White, B. M., Hopmans, E. C., van Duyl, F. C., Carlson, C. A., Aluwihare, L. I., Dorrestein, P. C., & Haas, A. F. (2022). Distinguishing the molecular diversity, nutrient content, and energetic potential of exometabolomes produced by macroalgae and reef-building corals. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(5). https://doi.org/10.1073/PNAS.2110283119

Kelly, L. W., Williams, G. J., Barott, K. L., Carlson, C. A., Dinsdale, E. A., Edwards, R. A., Haas, A. F., Haynes, M., Lim, Y. W., McDole, T., Nelson, C. E., Sala, E., Sandin, S. A., Smith, J. E., Vermeij, M. J. A., Youle, M., & Rohwer, F. (2014). Local genomic adaptation of coral reef-associated microbiomes to gradients of natural variability and anthropogenic stressors. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1403319111

Kemp, W. M., Testa, J. M., Conley, D. J., Gilbert, D., & Hagy, J. D. (2009). Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences*, *6*(12), 2985–3008.

Knowles, B., Bailey, B., Boling, L., Breitbart, M., Cobián-Güemes, A., Del Campo, J., Edwards, R., Felts, B., Grasis, J., Haas, A. F., Katira, P., Kelly, L. W., Luque, A., Nulton, J., Paul, L., Peters, G., Robinett, N., Sandin, S., Segall, A., … Rohwer, F. (2017). Variability and host density independence in inductions-based estimates of environmental lysogeny. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2017.64

Knowles, B., Silveira, C. B., Bailey, B. A., Barott, K., Cantu, V. A., Cobian-Guëmes, A. G., Coutinho, F. H., Dinsdale, E. A., Felts, B., Furby, K. A., George, E. E., Green, K. T., Gregoracci, G. B., Haas, A. F., Haggerty, J. M., Hester, E. R., Hisakawa, N., Kelly, L. W., Lim, Y. W., … Rohwer, F. (2016). Lytic to temperate switching of viral communities. *Nature*, *531*(7595), 466–470. https://doi.org/10.1038/nature17193

Koschorreck, M., Hentschel, I., & Boehrer, B. (2017). Oxygen ebullition from lakes. *Geophysical Research Letters*, *44*(18), 9372–9378.

Kraines, S., Suzuki, Y., Yamada, K., & Komiyama, H. (1996). Separating biological and physical changes in dissolved oxygen concentration in a coral reef. *Limnology and Oceanography*. https://doi.org/10.4319/lo.1996.41.8.1790

Laboy-Nieves, E. N., Klein, E., Conde, J. E., Losada, F., Cruz, J. J., & Bone, D. (2001). Mass mortality of tropical marine communities in Morrocoy, Venezuela. *Bulletin of Marine Science*, *68*(2), 163–179.

Lipson, D. A. (2015). The complex relationship between microbial growth rate and yield and its implications for ecosystem processes. *Frontiers in Microbiology*. https://doi.org/10.3389/fmicb.2015.00615

Loya, Y. (2004). *The coral reefs of Eilat—past, present and future: three decades of coral community structure studies*. Springer.

Luo, E., Eppley, J. M., Romano, A. E., Mende, D. R., & DeLong, E. F. (2020). Double-stranded DNA virioplankton dynamics and reproductive strategies in the oligotrophic open ocean water column. *ISME Journal*, *14*(5), 1304–1315. https://doi.org/10.1038/s41396-020-0604-8

McCauley, D. J., Gellner, G., Martinez, N. D., Williams, R. J., Sandin, S. A., Micheli, F., Mumby, P. J., & McCann, K. S. (2018). On the prevalence and dynamics of inverted trophic pyramids and otherwise top-heavy communities. *Ecology Letters*, *21*(3), 439–454.

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*, *18*(4), 357–367. https://doi.org/10.1007/s003380050213

Mccoy, S. J., & Kamenos, N. A. (2015). Coralline algae (Rhodophyta) in a changing world: Integrating ecological, physiological, and geochemical responses to global change. *Journal of Phycology*, *51*(1), 6–24. https://doi.org/10.1111/jpy.12262

McDole, T., Nulton, J., Barott, K. L., Felts, B., Hand, C., Hatay, M., Lee, H., Nadon, M. O., Nosrat, B., Salamon, P., Bailey, B., Sandin, S. A., Vargas-Angel, B., Youle, M., Zgliczynski, B. J., Brainard, R. E., & Rohwer, F. (2012). Assessing coral reefs on a Pacific-wide scale using the microbialization score. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0043233

McNally, S. P., Parsons, R. J., Santoro, A. E., & Apprill, A. (2017). Multifaceted impacts of the stony coral *Porites astreoides* on picoplankton abundance and community composition. *Limnology and Oceanography*. https://doi.org/10.1002/lno.10389

Meikle, P., Richards, G. N., & Yellowlees, D. (1988). Structural investigations on the mucus from six species of coral. *Marine Biology*, *99*(2), 187–193. https://doi.org/10.1007/BF00391980

Meire, L., Soetaert, K. E. R., & Meysman, F. J. R. (2013). Impact of global change on coastal oxygen dynamics and risk of hypoxia. *Biogeosciences*, *10*(4), 2633–2653. https://doi.org/10.5194/bg-10-2633-2013

Meirelles, P. M., Soares, A. C., Oliveira, L., Leomil, L., Appolinario, L. R., Francini-Filho, R. B., De Moura, R. L., De Barros Almeida, R. T., Salomon, P. S., Amado-Filho, G. M., Kruger, R., Siegle, E., Tschoeke, D. A., Kudo, I., Mino, S., Sawabe, T., Thompson, C. C., & Thompson, F. L. (2018). Metagenomics of coral reefs under phase shift and high hydrodynamics. *Frontiers in Microbiology*. https://doi.org/10.3389/fmicb.2018.02203

Melzner, F., Thomsen, J., Koeve, W., Oschlies, A., Gutowska, M. A., Bange, H. W., Hansen, H. P., & Körtzinger, A. (2013). Future ocean acidification will be amplified by hypoxia in coastal habitats. *Marine Biology*, *160*, 1875–1888.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*. https://doi.org/10.1016/S0921-8009(99)00009-9

Moriarty, D. J. W. (1979). Biomass of suspended bacteria over coral reefs. *Marine Biology*, *53*(2), 193–200. https://doi.org/10.1007/BF00389189

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., Holmes, K. E., Mendes, J. M., Broad, K., Sanchirico, J. N., Buch, K., Box, S., Stoffle, R. W., & Gill, A. B. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*. https://doi.org/10.1126/science.1121129

Naumann, M. S., Haas, A., Struck, U., Mayr, C., el-Zibdah, M., & Wild, C. (2010). Organic matter release by dominant hermatypic corals of the Northern Red Sea. *Coral Reefs*. https://doi.org/10.1007/s00338-010-0612-7

Naumann, M. S., Jantzen, C., Haas, A. F., Iglesias-Prieto, R., & Wild, C. (2013). Benthic primary production budget of a Caribbean reef lagoon (Puerto Morelos, Mexico). *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0082923

Nelson, C. E., Goldberg, S. J., Wegley Kelly, L., Haas, A. F., Smith, J. E., Rohwer, F., & Carlson, C. A. (2013). Coral and macroalgal exudates vary in neutral sugar composition and differentially enrich reef bacterioplankton lineages. *ISME Journal*. https://doi.org/10.1038/ismej.2012.161

Nelson, C. E., Wegley Kelly, L., & Haas, A. F. (2023). Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. *Annual Review of Marine Science*, *15*, 431–460. https://doi.org/10.1146/annurev-marine-042121-080917

Nelson, H. R., & Altieri, A. H. (2019). Oxygen: the universal currency on coral reefs. In *Coral Reefs*. https://doi.org/10.1007/s00338-019-01765-0

Odum, E. P. (1968). Energy flow in ecosystems: A historical review. *Integrative and Comparative Biology*, *8*(1), 11–18. https://doi.org/10.1093/icb/8.1.11

Odum, H. T., & Odum, E. P. (1955). Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs*. https://doi.org/10.2307/1943285

Patten, N. L., Mitchell, J. G., Middelboe, M., Eyre, B. D., Seuront, L., Harrison, P. L., & Glud, R. N. (2008). Bacterial and viral dynamics during a mass coral spawning period on the Great Barrier Reef. *Aquatic Microbial Ecology*, *50*(3), 209–220. https://doi.org/10.3354/ame01179

Payet, J. P., McMinds, R., Burkepile, D. E., & Vega Thurber, R. L. (2014). Spatial and short-term temporal sampling reveals high viral abundance and lytic activity in coral reef waters of the South Pacific Ocean. *Frontiers in Microbiology*. https://doi.org/10.3389/fmicb.2014.00493

Pearson, T. H., & Rosenberg, R. (1992). Energy flow through the SE Kattegat: a comparative examination of the eutrophication of a coastal marine ecosystem. *Netherlands Journal of Sea Research*, *28*(4), 317–334.

Pennino, M. J., Kaushal, S. S., Murthy, S. N., Blomquist, J. D., Cornwell, J. C., & Harris, L. A. (2016). Sources and transformations of anthropogenic nitrogen along an urban river–estuarine continuum. *Biogeosciences*, *13*(22), 6211–6228.

Pezner, A. K., Courtney, T. A., Barkley, H. C., Chou, W.-C., Chu, H.-C., Clements, S. M., Cyronak, T., DeGrandpre, M. D., Kekuewa, S. A. H., Kline, D. I., Liang, Y.-B., Martz, T. R., Mitarai, S., Page, H. N., Rintoul, M. S., Smith, J. E., Soong, K., Takeshita, Y., Tresguerres, M., … Andersson, A. J. (2023). Increasing hypoxia on global coral reefs under ocean warming. *Nature Climate Change*, *13*(April). https://doi.org/10.1038/s41558-023-01619-2

Pollak, N., Dölle, C., & Ziegler, M. (2007). The power to reduce: Pyridine nucleotides - Small molecules with a multitude of functions. *Biochemical Journal*, *402*(2), 205–218. https://doi.org/10.1042/BJ20061638

Rabalais, N. N., Cai, W. J., Carstens, J., Conley, D. J., Fry, B., Hu, X., Quiñones-Rivera, Z., Rosenberg, R., Slomp, C. P., Turner, R. E., Voss, M., Wissel, B., & Zhang, J. (2014). Eutrophication-driven deoxygenation in the coastal ocean. *Oceanography*, *27*(1), 172–183. https://doi.org/10.5670/oceanog.2014.21

Rabalais, N. N., Turner, R. E., & Wiseman Jr, W. J. (2002). Gulf of Mexico hypoxia, aka "The dead zone." *Annual Review of Ecology and Systematics*, *33*(1), 235–263.
Randall, C. J., Negri, A. P., Quigley, K. M., Foster, T., Ricardo, G. F., Webster, N. S., Bay, L. K., Harrison, P. L., Babcock, R. C., & Heyward, A. J. (2020). Sexual production of corals for reef restoration in the Anthropocene. *Marine Ecology Progress Series*, *635*, 203–232. https://doi.org/10.3354/MEPS13206

Riebesell, U., Schulz, K. G., Bellerby, R. G. J., Botros, M., Fritsche, P., Meyerhöfer, M., Neill, C., Nondal, G., Oschlies, A., Wohlers, J., & Zöllner, E. (2007). Enhanced biological carbon consumption in a high CO2 ocean. *Nature*, *450*(7169), 545–548. https://doi.org/10.1038/nature06267

Rinkevich, B. (2019). The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. *Journal of Marine Science and Engineering*, *7*(7). https://doi.org/10.3390/jmse7070201

Rix, L., Bednarz, V. N., Cardini, U., Van Hoytema, N., Al-Horani, F. A., Wild, C., & Naumann, M. S. (2015). Seasonality in dinitrogen fixation and primary productivity by coral reef framework substrates from the northern Red Sea. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps11383

Roach, T. N. F., Abieri, M. L., George, E. E., Knowles, B., Naliboff, D. S., Smurthwaite, C. A., Kelly, L. W., Haas, A. F., & Rohwer, F. L. (2017). Microbial bioenergetics of coral-algal interactions. *PeerJ*. https://doi.org/10.7717/peerj.3423

Roughgarden, J. (2023). Holobiont Evolution: Model of Phage/Bacteria Dynamics With Implications for the Lytic to Lysogenic Transition. *BioRxiv*, 2001–2023.

Russell, J. B., & Cook, G. M. (1995). Energetics of bacterial growth: Balance of anabolic and catabolic reactions. In *Microbiological Reviews*. https://doi.org/10.1128/mmbr.59.1.48-62.1995

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., Konotchick, T., Malay, M., Maragos, J. E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R. E., Walsh, S., Jackson, J. B. C., Knowlton, N., & Sala, E. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0001548

Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature*. https://doi.org/10.1038/nature21399
Seitzinger, S. P. (1987). Nitrogen biogeochemistry in an unpolluted estuary: the importance of benthic denitrification. *Marine Ecology Progress Series. Oldendorf*, *41*(2), 177–186.

Sherr, E. B., & Sherr, B. F. (2002). Significance of predation by protists in aquatic microbial food webs. *Antonie Van Leeuwenhoek*, *81*, 293–308.

Silveira, C. B., Cavalcanti, G. S., Walter, J. M., Silva-Lima, A. W., Dinsdale, E. A., Bourne, D. G., Thompson, C. C., & Thompson, F. L. (2017). Microbial processes driving coral reef organic carbon flow. *FEMS Microbiology Reviews*. https://doi.org/10.1093/femsre/fux018

Silveira, C. B., Coutinho, F. H., Cavalcanti, G. S., Benler, S., Doane, M. P., Dinsdale, E. A., Edwards, R. A., Francini-Filho, R. B., Thompson, C. C., Luque, A., Rohwer, F. L., & Thompson, F. (2020). Genomic and ecological attributes of marine bacteriophages encoding bacterial virulence genes. *BMC Genomics*. https://doi.org/10.1186/s12864-020-6523-2

Silveira, C. B., Luque, A., Haas, A. F., Roach, T. N. F., George, E. E., Knowles, B., Little, M., Sullivan, C. J., Varona, N. S., Wegley Kelly, L., Brainard, R., Rohwer, F., & Bailey, B. (2023). Viral predation pressure on coral reefs. *BMC Biology*, *21*(1), 77. https://doi.org/10.1186/s12915-023-01571-9

Silveira, C. B., Luque, A., Roach, T. N., Villela, H., Barno, A., Green, K., Reyes, B., Rubio-Portillo, E., Le, T., Mead, S., Hatay, M., Vermeij, M. J., Takeshita, Y., Haas, A., Bailey, B., & Rohwer, F. (2019). Biophysical and physiological processes causing oxygen loss from coral reefs. *ELife*. https://doi.org/10.7554/eLife.49114

Silveira, C. B., Luque, A., & Rohwer, F. (2021). The landscape of lysogeny across microbial community density, diversity and energetics. *Environmental Microbiology*, *23*(8), 4098–4111. https://doi.org/10.1111/1462-2920.15640

Silveira, C. B., Silva-Lima, A. W., Francini-Filho, R. B., Marques, J. S. M., Almeida, M. G., Thompson, C. C., Rezende, C. E., Paranhos, R., Moura, R. L., Salomon, P. S., & Thompson, F. L. (2015). Microbial and sponge loops modify fish production in phase-shifting coral reefs. *Environmental Microbiology*. https://doi.org/10.1111/1462-2920.12851

Simpson, C. J., Cary, J. L., & Masini, R. J. (1993). Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs*, *12*(3–4). https://doi.org/10.1007/BF00334478

Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., Lewis, L., Obura, D., Rohwer, F., Sala, E., Vroom, P. S., & Sandin, S. (2016). Re-evaluating the health of coral reef communities: Baselines and evidence for human impacts across the central pacific. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2015.1985

Smith, J. E., Shaw, M., Edwards, R. A., Obura, D., Pantos, O., Sala, E., Sandin, S. A., Smriga, S., Hatay, M., & Rohwer, F. L. (2006). Indirect effects of algae on coral: Algae-mediated, microbe-induced coral mortality. *Ecology Letters*. https://doi.org/10.1111/j.1461-0248.2006.00937.x

Smith, S. V, Kimmerer, W. J., Laws, E. A., Brock, R. E., & Walsh, T. W. (1981). Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation.

Smyth, A. R., Thompson, S. P., Siporin, K. N., Gardner, W. S., McCarthy, M. J., & Piehler, M. F. (2013). Assessing nitrogen dynamics throughout the estuarine landscape. *Estuaries and Coasts*, *36*, 44–55.

Solomon, S. (2007). IPCC (2007): Climate change the physical science basis. *Agu Fall Meeting Abstracts*, *2007*, U43D-01.

Somera, T. M. D., Bailey, B., Barott, K., Grasis, J., Hatay, M., Hilton, B. J., Hisakawa, N., Nosrat, B., Nulton, J., Silveira, C. B., Sullivan, C., Brainard, R. E., & Rohwer, F. (2016). Energetic differences between bacterioplankton trophic groups and coral reef resistance. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2016.0467

Sotto, L. P. A., Jacinto, G. S., & Villanoy, C. L. (2014). Spatiotemporal variability of hypoxia and eutrophication in Manila Bay, Philippines during the northeast and southwest monsoons. *Marine Pollution Bulletin*, *85*(2), 446–454.

Spaans, S. K., Weusthuis, R. A., van der Oost, J., & Kengen, S. W. M. (2015). NADPH-generating systems in bacteria and archaea. *Frontiers in Microbiology*, *6*(JUL), 1–27. https://doi.org/10.3389/fmicb.2015.00742

Steckbauer, A., Klein, S. G., & Duarte, C. M. (2020). Additive impacts of deoxygenation and acidification threaten marine biota. *Global Change Biology*, *26*(10), 5602–5612.

Sternberg, N., Austin, S., Hamilton, D., & Yarmolinsky, M. (1978). Analysis of bacteriophage P1 immunity by using lambda-P1 recombinants constructed in vitro. *Proceedings of the National Academy of Sciences*, *75*(11), 5594–5598.

Stettner, A. I., & Segrè, D. (2013). The cost of efficiency in energy metabolism. In *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1307485110

Stigebrandt, A., & Gustafsson, B. G. (2007). Improvement of Baltic proper water quality using large-scale ecological engineering. *AMBIO: A Journal of the Human Environment*, *36*(2), 280–286.

Stramma, L., Johnson, G. C., Sprintall, J., & Mohrholz, V. (2008). Expanding oxygen-minimum zones in the tropical oceans. *Science*, *320*(5876), 655–658.
Stramma, L., Schmidtko, S., Levin, L. A., & Johnson, G. C. (2010). Ocean oxygen minima expansions and their biological impacts. *Deep Sea Research Part I: Oceanographic Research Papers*, *57*(4), 587–595.

Suttle, C. A. (2005). Viruses in the sea. In *Nature*. https://doi.org/10.1038/nature04160

Suttle, C. A. (2007). Marine viruses - Major players in the global ecosystem. *Nature Reviews Microbiology*. https://doi.org/10.1038/nrmicro1750

Sydeman, W. J., García-Reyes, M., Schoeman, D. S., Rykaczewski, R. R., Thompson, S. A., Black, B. A., & Bograd, S. J. (2014). Climate change and wind intensification in coastal upwelling ecosystems. *Science*, *345*(6192), 77–80.

Thingstad, T. F. (2000). Elements of a theory for the mechanisms controlling abundance, diversity, and biogeochemical role of lytic bacterial viruses in aquatic systems. *Limnology and Oceanography*, *45*(6), 1320–1328. https://doi.org/10.4319/lo.2000.45.6.1320

Thingstad, T. F., Bellerby, R. G. J., Bratbak, G., Børsheim, K. Y., Egge, J. K., Heldal, M., Larsen, A., Neill, C., Nejstgaard, J., Norland, S., Sandaa, R. A., Skjoldal, E. F., Tanaka, T., Thyrhaug, R., & Töpper, B. (2008). Counterintuitive carbon-to-nutrient coupling in an Arctic pelagic ecosystem. *Nature*. https://doi.org/10.1038/nature07235

Thingstad, T. F., Vage, S., Storesund, J. E., Sandaa, R.-A., & Giske, J. (2014). A theoretical analysis of how strain-specific viruses can control microbial species diversity. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1400909111

Thurber, R. V., Payet, J. P., Thurber, A. R., & Correa, A. M. S. (2017). Virus-host interactions and their roles in coral reef health and disease. In *Nature Reviews Microbiology*. https://doi.org/10.1038/nrmicro.2016.176

Touchon, M., Bernheim, A., & Rocha, E. P. C. (2016). Genetic and life-history traits associated with the distribution of prophages in bacteria. *ISME Journal*. https://doi.org/10.1038/ismej.2016.47

Tremblay, P., Grover, R., Maguer, J. F., Legendre, L., & Ferrier-Pagès, C. (2012). Autotrophic carbon budget in coral tissue: A new 13C-based model of photosynthate translocation. *Journal of Experimental Biology*. https://doi.org/10.1242/jeb.065201

Tremblay, P., Naumann, M. S., Sikorski, S., Grover, R., & Ferrier-Pagès, C. (2012). Experimental assessment of organic carbon fluxes in the scleractinian coral *Stylophora pistillata* during a thermal and photo stress event. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps09640

Ulloa, O., Canfield, D. E., DeLong, E. F., Letelier, R. M., & Stewart, F. J. (2012). Microbial oceanography of anoxic oxygen minimum zones. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(40), 15996–16003. https://doi.org/10.1073/pnas.1205009109

Vaquer-Sunyer, R., Duarte, C. M., Jorda, G., & Ruiz-Halpern, S. (2012). Temperature dependence of oxygen dynamics and community metabolism in a shallow Mediterranean macroalgal meadow (*Caulerpa prolifera*). *Estuaries and Coasts*, *35*, 1182–1192.

Villanueva, R. D., Yap, H. T., & Montaño, M. N. E. (2005). Survivorship of coral juveniles in a fish farm environment. *Marine Pollution Bulletin*, *51*(5–7), 580–589.

Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., & Gobler, C. J. (2014). Coastal ocean acidification: The other eutrophication problem. *Estuarine, Coastal and Shelf Science*, *148*, 1–13. https://doi.org/10.1016/j.ecss.2014.05.027

Walter, J. M., Tschoeke, D. A., Meirelles, P. M., De Oliveira, L., Leomil, L., Tenório, M., Valle, R., Salomon, P. S., Thompson, C. C., & Thompson, F. L. (2016). Taxonomic and functional metagenomic signature of turfs in the Abrolhos reef system (Brazil). *PLoS ONE*, *11*(8), 1–20. https://doi.org/10.1371/journal.pone.0161168

Wegley Kelly, L., Nelson, C. E., Petras, D., Koester, I., Quinlan, Z. A., Arts, M. G. I., Nothias, L. F., Comstock, J., White, B. M., Hopmans, E. C., van Duyl, F. C., Carlson, C. A., Aluwihare, L. I., Dorrestein, P. C., & Haas, A. F. (2022). Distinguishing the molecular diversity, nutrient content, and energetic potential of exometabolomes produced by macroalgae and reef-building corals. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(5). https://doi.org/10.1073/pnas.2110283119

Whitney, F. A., Freeland, H. J., & Robert, M. (2007). Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Progress in Oceanography*, *75*(2), 179–199.

Wild, C., Jantzen, C., Struck, U., Hoegh-Guldberg, O., & Huettel, M. (2008). Biogeochemical responses following coral mass spawning on the Great Barrier Reef: Pelagic-benthic coupling. *Coral Reefs*, *27*(1), 123–132. https://doi.org/10.1007/s00338-007-0298-7

Wild, C., Niggl, W., Naumann, M. S., & Haas, A. F. (2010). Organic matter release by Red Sea coral reef organisms-Potential effects on microbial activity and *in situ* O2 availability. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps08653

Wilhelm, S. W., & Suttle, C. A. (1999). Viruses and nutrient cycles in the sea. *BioScience*. https://doi.org/10.2307/1313569

Wright, J. J., Konwar, K. M., & Hallam, S. J. (2012). Microbial ecology of expanding oxygen minimum zones. *Nature Reviews Microbiology*, *10*(6), 381–394.

Yeakel, K. L., Andersson, A. J., Bates, N. R., Noyes, T. J., Collins, A., & Garley, R. (2015). Shifts in coral reef biogeochemistry and resulting acidification linked to offshore productivity. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1507021112

Zaneveld, J. R., Burkepile, D. E., Shantz, A. A., Pritchard, C. E., McMinds, R., Payet, J. P., Welsh, R., Correa, A. M. S., Lemoine, N. P., Rosales, S., Fuchs, C., Maynard, J. A., & Thurber, R. V. (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature Communications*. https://doi.org/10.1038/ncomms11833

Zgliczynski, B. J., & Sandin, S. A. (2017). Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecological Indicators*, *73*, 411–421.

Chapter 2

CORAL REEF ARKS: AN IN SITU MESOCOSM AND TOOLKIT FOR ASSEMBLING REEF COMMUNITIES

ABSTRACT

Coral reefs thrive and provide ecosystem services when they support a multi-level trophic structure and grow in favorable water quality conditions that include high light levels, rapid water flow, and low nutrient levels. Poor water quality and other anthropogenic stressors have caused coral mortality in recent decades, leading to trophic downgrading and the loss of biological complexity on many reefs. Solutions to reverse the causes of trophic downgrading remain elusive, in part because efforts to restore reefs are often attempted in the same diminished conditions that caused coral mortality in the first place.

Coral Arks, positively buoyant, midwater structures, are designed to provide improved water quality conditions and supportive cryptic biodiversity for translocated and naturally recruited corals to assemble healthy reef mesocosms for use as long-term research platforms. Autonomous Reef Monitoring Structures (ARMS), passive settlement devices, are used to translocate the cryptic reef biodiversity to the Coral Arks, thereby providing a “boost” to natural recruitment and contributing ecological support to the coral health. We modeled and experimentally tested two designs of Arks to evaluate the drag characteristics of the structures and assess their long-term stability in the midwater based on their response to hydrodynamic forces.

We then installed two designs of Arks structures at two Caribbean reef sites and measured several water quality metrics associated with the Arks environment over time.

At deployment and 6 months after, the Coral Arks displayed enhanced metrics of reef function, including higher flow, light, and dissolved oxygen, higher survival of translocated corals, and reduced sedimentation and microbialization relative to nearby seafloor sites at the same depth. This method provides researchers with an adaptable, long-term platform for building reef communities where local water quality conditions can be adjusted by altering deployment parameters such as the depth and site.

INTRODUCTION

Across the globe, coral reef ecosystems are undergoing transitions from high-biodiversity, coral-dominated benthic communities to lower-diversity communities dominated by turf- and fleshy macroalgae (Pandolfi et al., 2003; McManus and Polsenberg 2004; Hughes et al., 2007). Decades of progress in characterizing the mechanisms of coral reef degradation have revealed how links between microbial and macro-organismal communities enhance the pace and severity of these transitions. For example, the overfishing of reefs by human populations initiates a trophic cascade in which excess photosynthetically derived sugars from ungrazed algae shunt energy into the reef microbial communities, thus driving pathogenesis and causing coral decline (Dinsdale et al., 2008; Haas et al., 2016; Zaneveld et al., 2016). This trophic downgrading is reinforced by the loss of biodiversity on reefs that results from water quality decline (Estes et al., 2011; Houk and Musburger 2013). Mesocosm-level experiments can be used to better understand and mitigate the trophic downgrading of coral reef communities by enhancing biodiversity and improving water quality, but logistical challenges make these studies difficult to implement *in situ*.

A consequence of trophic downgrading on reefs is the widespread loss of cryptic biodiversity, much of which remains uncharacterized (Estes et al., 2011; Pearman et al., 2016). Corals rely on a diverse suite of cryptic reef organisms (“cryptobiota”) that support their health by playing integral roles in predator defense (Stella et al., 2011), cleaning (Stewart et al., 2006), grazing competing algae (Francis et al., 2019; Williams 2022), and the regulation of reef water chemistry (De Goeij et al., 2013; Rix et al., 2017). Until recently and due to the methodological limitations of visual surveys, reef cryptobiota have been underrepresented and poorly understood in the context of reef ecology, and they are, thus, rarely considered in efforts to restore or rebuild reefs. In the past decade, the use of standardized settlement units called Autonomous Reef Monitoring Structures (ARMS) combined with high-throughput sequencing approaches has enabled the better collection and characterization of reef cryptobiota (Plaisance et al., 2011; Leray and Knowlton 2015). ARMS passively recruit representatives of almost all known coral reef biodiversity and have helped reveal numerous functional roles of cryptic organisms in reef-scale processes (Pearman et al., 2016, 2018, 2019; Hartmann et al., 2017; Pennesi and Danovaro 2017; Ransome et al., 2017; Carvalho et al., 2019). These settlement units, therefore, provide a mechanism to translocate cryptic reef biota alongside corals in order to assemble more intact reef communities with biologically mediated mechanisms, such as grazing, defense, and enhancement of local water quality, that are essential to maintaining the trophic structure.

Coral-dominated reefs thrive in high-light, low-nutrient, and well-oxygenated environments. Human activities such as urbanization, agriculture, and overfishing have reduced the water quality on many coral reefs by increasing the sediment, nutrients,

metals, and other compounds in runoff (Bartley et al., 2014; Häder et al., 2020) and by altering biogeochemical cycling (Bianchi et al., 2021). In turn, these activities degrade reef communities through smothering, energy depletion, the delivery of pollutants associated with sedimentation (Rogers 1990; Fabricius 2005), enhancing the growth of macroalgae that compete with corals (Littler et al., 2006), increasing the abundance of microbial pathogens (Scofield et al., 2015; Zaneveld et al., 2016; Cárdenas et al., 2018), and creating hypoxic zones that kill cryptic invertebrates (Altieri et al., 2017; Johnson et al., 2021). These and other "local impacts" are compounded by regional and global changes in ocean conditions, including increasing temperatures and decreasing pH, further worsening the conditions for corals and other reef organisms (Enochs et al., 2015; Timmers et al., 2021). At the benthic–water interface, specifically, the respiratory and photosynthetic dynamics of benthic communities cause diel fluctuations in the pH and dissolved oxygen, which become more pronounced on highly degraded reefs, thus creating conditions that benthic invertebrates cannot tolerate (Haas et al., 2011; Wallace et al., 2014; Nelson and Altieri 2019; Johnson et al., 2021). Providing appropriate water quality conditions is, therefore, essential for assembling functioning reef communities, but this remains challenging because an increasing number of reefs are trapped in various states of degradation.

Many of the challenges faced by corals and foundational cryptic taxa on the benthos may be overcome *via* relocation to the midwater, defined here as the water column setting between the ocean surface and the seafloor. In the midwater environment, water quality is improved (Shafir et al., 2006; Rinkevich 2019), sedimentation is reduced, and the distance from the seafloor dampens fluctuations in

the parameters associated with benthic metabolism. These characteristics are improved further by moving offshore, where land-based anthropogenic impacts, such as terrestrially derived runoff, become increasingly diluted with distance from the coast. Here, we introduce and provide protocols to build, deploy, and monitor Coral Reef Arks, an approach that leverages improved water quality conditions in the midwater and incorporates cryptic biodiversity on anchored, positively buoyant structures for the assembly of coral reef communities.

Coral Reef Arks systems, or “Arks,” are comprised of two primary components: (1) a suspended rigid geodesic platform elevated above the benthos and (2) organism-covered or “seeded” ARMS that translocate reef cryptobiota from nearby benthic areas, thereby supplementing the natural recruitment processes to provide the translocated corals with a more diverse and functional reef community. A geodesic structure was selected to maximize the strength and minimize the building material (and, thus, the weight), as well as to create an internal, turbulent flow environment analogous to the reef matrix.

Two designs of Arks were successfully installed at two Caribbean field sites and are currently being used for research into reef community establishment and ecological succession **(Figure 2.1)**. Coral Arks structures are intended to be long-term research platforms, and as such, a primary focus of this manuscript is to describe protocols to site, install, monitor, and maintain these structures to maximize their stability and longevity in the midwater environment. A combination of modeling and in-water testing was used to evaluate the drag characteristics of the structures and adjust the design to withstand the anticipated hydrodynamic forces. After installation, reef communities were

established on the Arks and on nearby benthic control sites at the same depth through a combination of active translocation (corals and seeded ARMS units) and natural recruitment. Water quality conditions, microbial community dynamics, and coral survival on the Arks were documented at several time points throughout the early successional period and compared against the benthic control sites. To date, the conditions associated with the midwater Coral Arks environment have been consistently more favorable for corals and their associated cryptic consortia relative to the neighboring benthic control sites at the same depths. The methods below describe the steps required to replicate the Coral Arks approach, including how to select sites and design and deploy Coral Arks structures. Suggested approaches for monitoring Coral Arks are included in **Appendix 1.**

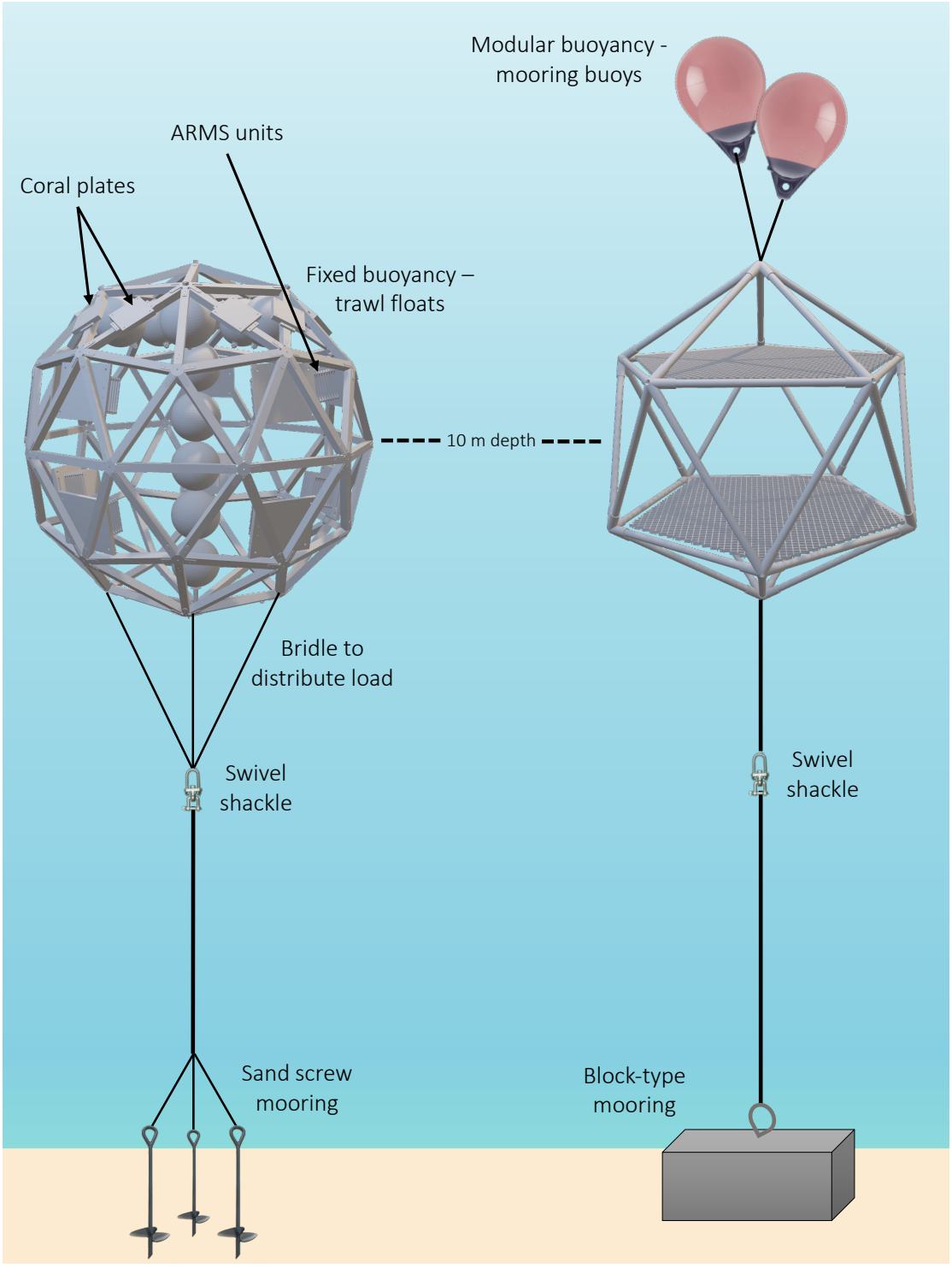


Figure 2.1 Structural components of two fully installed Coral Ark structures. Left, “Shell” and “Two-Platform” (right) Coral Arks structures are shown, together with two methods for providing positive buoyancy and two methods for anchoring. Abbreviation: ARMS = Autonomous Reef Monitoring Structures.

PROTOCOL

NOTE: Detailed information regarding the manufacture, deployment, and monitoring of ARMS and Coral Arks structures, including technical drawings, diagrams, and photos, are provided in **Appendix 1**. Sections of the protocol involving underwater work, including the installation of Arks and ARMS structures, are recommended to be conducted by a team of three divers (on SCUBA) and two surface support personnel.

ARMS assembly and deployment

NOTE: ARMS are approximately 1 ft^3 (30 cm^3) structures made from PVC or limestone base materials that mimic the three-dimensional complexity of reef hardbottom substrates. **Table 2.1** discusses two designs for ARMS given different project considerations. ARMS are recommended to be deployed for 1–2 years prior to transfer to Arks to maximize the colonization by cryptic biota.

Table 2.1 ARMS Assembly and Deployment

Arks type	Two Platform	Shell
Materials Description	1. 1v frequency geodesic sphere assembled from round PVC ‘struts’ (sides) and ‘hubs’ (vertices). 2. Two pentagonal platforms of molded fiberglass grating bisect the sphere horizontally as a mounting and attachment surface. 3. Stainless steel wire rope threaded through geodesic sphere frame for increased structural support, clamped at each vertex. 4. Mooring/buoyancy attachments at top and bottom connect to a central cable via a turnbuckle system. 5. Mooring buoys provide modular positive buoyancy.	1. 2v frequency geodesic sphere assembled from square fiberglass struts and stainless-steel STAR hubs. 2. Fixed buoyancy provided by integrated trawl floats, struts filled with closed-cell foam and sealed using epoxy for added buoyancy. 3. HDPE baseplates added to fiberglass struts for direct attachment of coral plates and PVC ARMSs. 4. Central fiberglass rod allows for addition of buoyancy to compensate for coral growth 5. Mooring/anchoring system attaches to structure using a five-point bridle for redundancy
Intended Use	1. Designed for experimentation. Modification of depth, internal structure, and ecological community structure can enhance understanding of reef systems. 2. Simple, low-cost design - Arks can be deployed en masse as standardized, in situ mesocosms to investigate reef assemblies across disparate sites. 3. Deployment nearshore can support and help set rehabilitation targets for local restoration efforts or provide sources of propagules for out planting. 4. Can build repositories of natural reef biodiversity isolated from degraded systems for conservation.	1. Designed to enhance success in coral mitigation and restoration projects. Attachment of corals and seeded ARMSs onto Arks provides an improved environment for growth. 2. High structural integrity and subsequent high longevity make these structures excellent for long-term projects. 3. Deployment nearshore can support and help set rehabilitation targets for local restoration efforts or provide sources of propagules for out planting. 4. Can build repositories of natural reef biodiversity isolated from degraded systems for conservation.

Table 2.1 ARMS Assembly and Deployment (Continued)

Arks type	Two Platform	Shell
Benefits	1. ***Scalability*** – Low cost, ease of assembly, and accessibility of materials make these Arks optimal as scalable mesocosms. 2. ***Deployment*** – Arks are relatively light and can be deployed with small vessels or from shore by divers dragging it through the water. 3. ***Modularity*** – Geodesic size, interior complexity, and buoyancy are simple to modify for different projects. 4. ***Depth*** – Can be adjusted vertically in the water column to change environmental parameters (O_2, flow, light, temperature). 5. ***Shape*** – Low frequency geodesic sphere can be easily modified for direct attachment to seafloor	1. ***Complexity*** – Higher frequency geodesic has a more turbulent interior. ARMSs deployed in the interior allows natural reef processes to occur (nutrient transformations, shelter) to support corals. 2. ***Strength*** – Fiberglass and stainless-steel design makes these geodesic spheres extremely strong. 3. ***Buoyancy*** – Fixed buoyancy mounted in the interior reduces the vertical profile of Arks and reduces depth concerns associated with navigation and fishing. 4. ***Depth*** – Can be adjusted vertically in the water column to change environmental parameters (O_2, flow, light, temperature).
Drawbacks	1. ***Strength*** – Strength is limited by the central cabling system. Integrating many limestone ARMS, and the requisite buoyancy to support them, may require modifications to ensure structural integrity. 2. ***Materials*** – PVC is not an ideal material for biological colonization. 3. ***Buoyancy*** – Mooring buoys connected to the top of the structure extend the vertical profile of the Arks system with potential depth concerns due to navigation and fishing.	1. ***Weight*** – Heavy weight requires substantial addition of integrated floats for buoyancy offset and requires more involved deployment effort. 2. ***Cost*** – High cost of materials and deployment support make these structures better for long-lasting mitigation and restoration projects. 3. ***Drag*** – Higher frequency geodesic increases drag due to ocean currents, which must be accounted for when designing mooring systems.

PVC ARMS

NOTE: The off-the-shelf components referred to in this protocol (and listed in the **Table of Materials**) are described using imperial units. The fabricated materials are

described using metric units. Detailed fabrication instructions, including technical drawings for the manufacture of the components, are provided in **Appendix 1.**

Assembly

Insert four 1/4 in-20, 8 in long, hex-head bolts through the center holes on a ½ in-thick PVC baseplate, then, invert it such that the bolts face up vertically.

Add a nylon spacer to each bolt, and then add a 1/4 in thick, PVC 9 in x 9 in plate. This creates an open layer between the baseplate and the first stacking plate.

Add a long cross spacer onto two bolts in opposite corners, and then add two short cross spacers onto the remaining bolts such that an “X” is formed. Add another PVC stacking plate to create a closed layer.

Repeat step 1.1.1.2 and step 1.1.1.3, alternating between open and closed layers, until seven to nine plate layers have been added to the bolts (**Appendix 1—Figure S5**).

Add a washer, a hex nut, and a nylon insert locknut to the top of each bolt, and tighten down securely.

For deployment, transport the assembled PVC ARMS to the target deployment site, covering the ARMS with 100 um mesh during the transfer to retain small mobile invertebrates (**Appendix 1—Figure S6**). Locate a patch of reef hardbottom substrate in close proximity to healthy coral reef communities.

NOTE: The specific deployment sites should be selected with consideration of the local regulations and permit stipulations, such as avoiding the critical habitats for Endangered Species Act listed species in US waters.

Using 3 in lengths of 1/2 in rebar and a mallet, secure the ARMS to the benthos at all four corners by pounding the rebar, slightly angled outward, into the base limestone such that the rebar generates tension against the edge of the baseplate (**Figure 2.2A,B**).

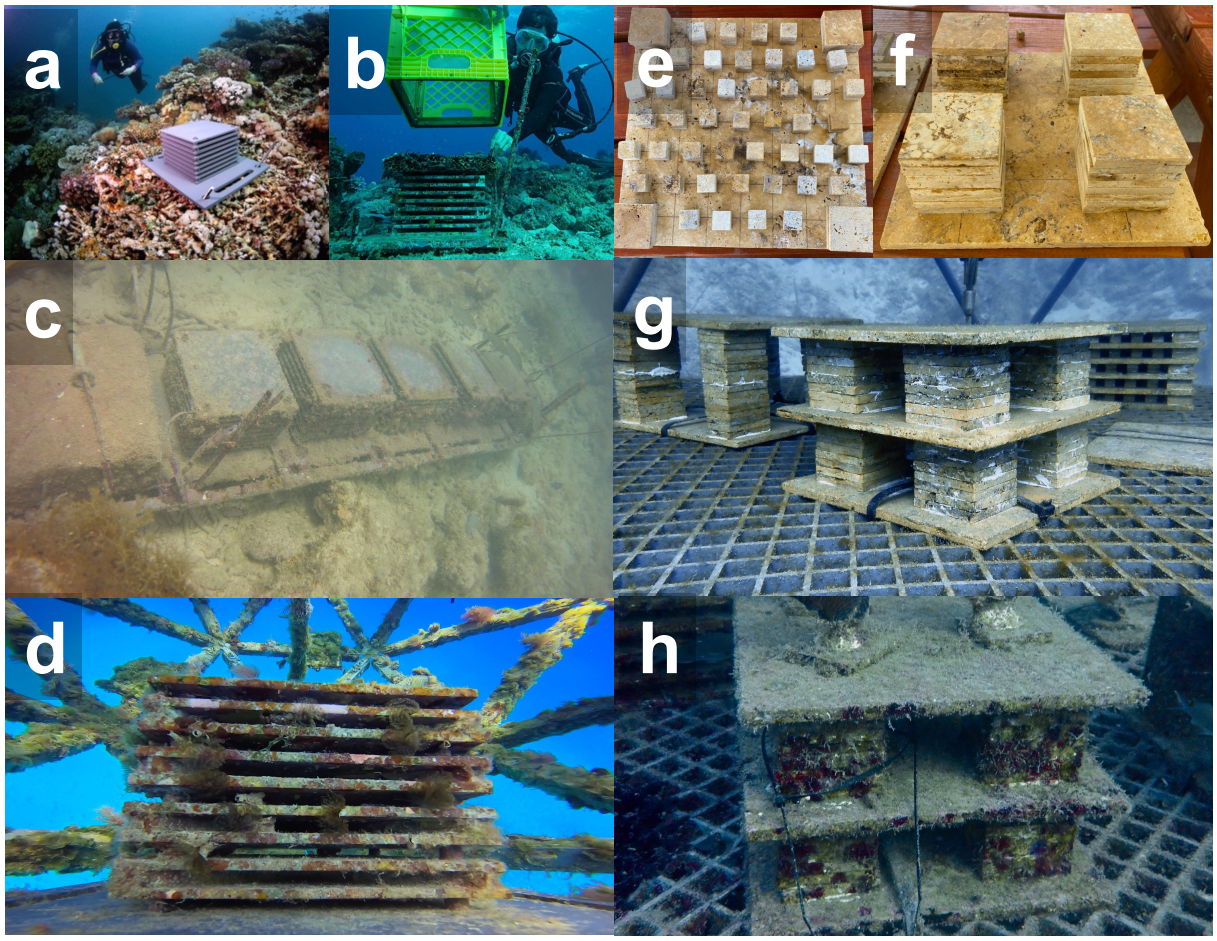


Figure 2.2 Design, deployment, and transfer of ARMS units. (A–D) PVC Autonomous Reef Monitoring Structures (ARMS) and (E–H) Limestone ARMS from seafloor seeding sites to Coral Arks. (A) Photo credit to Michael Berumen. (B) Photo credit to David Littschwager. Abbreviations: PVC = polyvinyl chloride; ARMS = Autonomous Reef Monitoring Structures.

Alternatively, connect the chains of the ARMS using heavy-duty cable ties, and anchor the ends of the chains with hardened concrete bags (**Figure 2.2C** and **Appendix 1—Figure S6**).

Limestone ARMS

For assembly, begin with 12 in x 12 in unfinished limestone or travertine tiles (**Figure 2.2**). Identify the desired complexity of the limestone ARMS interior.

NOTE: It is recommended to use 2 cm3 cubes. Alternative designs and considerations are provided in **Section 2** of **Appendix 1**.

Using a wet tile saw, cut several unfinished tiles into 2 cm2 square spacers (~250).

Cut travertine tiles to the desired shape for the ARMS layers. Similar to the PVC ARMS, use 12 in x 12 in squares, and layer them with spacers to form 1 ft3 cubes (**Appendix 1—Figure S8**).

Using a two-part, non-toxic marine grade epoxy, glue the smaller travertine pieces to a larger travertine layering plate along a pre-drawn grid pattern.

Prepare several layers that, when stacked together, achieve the desired ARMS height. Allow the epoxy to cure based on the manufacturer's recommendations.

Assemble the ARMS stacking plates using epoxy to glue each layer to the one above it.

NOTE: The ARMS height will vary based on the desired weight and internal complexity. A final size of approximately 1 ft3 is recommended.

Allow the epoxy to cure out of direct sunlight for 24 h before deployment.

For deployment, transport the assembled Limestone ARMS to the target deployment site. Locate a patch of reef hardbottom substrate in close proximity to healthy coral reef communities.

NOTE: The specific deployment sites should be selected with consideration of the local regulations and permit stipulations, such as avoiding the critical habitats of Endangered Species Act listed species in US waters.

Transport the ARMS to the benthos using a milk crate and lift bag. Wedge the Limestone ARMS into dead reef matrix (live rock). Avoid sandy bottom habitats and those heavily colonized by turf algae or benthic cyanobacterial mats.

Place the Limestone ARMS next to rocky overhangs and outcrops to protect them from wave action and storm surges.

Coral Arks assembly and deployment

NOTE: **Table 2.2** discusses the design considerations of Coral Arks given different project parameters. The dimensions of the sub-elements (struts, hubs, platforms, mooring components, and positive buoyancy) can be modified depending on the desired size and weight of the final Coral Ark structures.

Table 2.2 Coral Arks Assembly and Deployment

Arks type	Two Platform	Shell
Materials Description	1. Comprised of 7-9 ¼" thick PVC stacking plates. Approximate final size – 1 ft3 2. Plates stacked with ½" gaps in between plates, separated using PVC crossbars and nylon spacers. 3. Stacking plates connected to a larger PVC baseplate by stainless steel rods at all four corners that bolt into the baseplate. 4. Baseplate is attached to the reef by driving rebar posts through gaps on either side of the baseplate.	1. Comprised of 5-7 ½" thick natural limestone or travertine tiles. Approximate final size – 1 ft3 2. Tile layers separated by square tile spacers. Gap size between two plates dependent on desired internal complexity. Tiles and square tile spacers cemented together using a two-part, non-toxic marine grade epoxy. 3. Limestone ARMS wedged into natural crevices in the reef framework for colonization.
Intended Use	1. Census cryptic reef diversity in benthic marine and freshwater ecosystems. 2. Traditionally secured to seafloor for 1-3 years, during which time ARMS passively aggregates organisms. 3. Sampling to determine species diversity via metabarcoding.	1. Long-term conservation and restoration projects. 2. Material more accurately replicates natural ecosystem of hardbottom reef substrates 3. More natural material results in expedited colonization of cryptic biodiversity relative to PVC ARMS 4. Modification of internal complexity allows for targeted recruitment of specific taxa based on body-size ratios.
Benefits	1. Standardization – Each ARMS offers the same amount of settlement surface, thus can be compared across locations. 2. Reusability – After disassembly and sampling, plates can be scraped clean, bleached, and reassembled for another deployment. 3. Durability – Highly durable and can sustain storms and heavy surge. Remain intact even when flipped or buried in sand. 4. Weight – PVC ARMS are light relative to limestone ARMS, allowing for easier transport and deployment.	1. Standardization – Can be designed to provide identical settlement surface and internal volume. 2. Material – Provide a cryptic environment that better replicates the natural habitat of reef cryptobiota. Lacks plastic or metal elements that can leach chemicals or corrode. 3. Location – Limestone can be sourced from quarries on carbonate reef islands and tend to be less expensive than PVC. Cheap cost and ease of assembly allow them to be constructed and deployed en masse with relatively low cost and labor. 4. Weight – Limestone ARMS can be placed onto the seafloor or wedged into existing reef structure without need for sophisticated anchoring methods. 5. Longevity – Can be deployed in the sea in perpetuity.

Table 2.2 Coral Arks Assembly and Deployment (Continued)

Arks type	Two Platform	Shell
Drawbacks	1. PVC and stainless steel are expensive and not readily available everywhere. Require special facilities for precision cutting. 2. Components of PVC ARMS are not natural. 3. PVC ARMS are lightweight and must be secured to the seafloor, limiting possible seeding locations and increasing underwater dive time for deployment.	1. Unfinished tiles contain natural grooves, cavities, and pore spaces each providing a unique microenvironment, and thus are challenging to standardize to the degree of PVC ARMS. 2. Limestone tiles are more brittle than PVC and are at a higher risk of breakage by storms or improper handling during construction and deployment. 3. Limestone is heavier than PVC and can make deployment more logistically challenging.

Installation of the anchoring system

NOTE: Select the anchoring system based on site- and project-specific considerations such as Ark design, storm frequency, bottom type, site exposure, duration of the project, and anticipated forces due to drag, currents, and buoyancy. See PADI (Padi 2005) for insights into mooring system selection.

Use sand screws in sandy bottom and loose rubble habitats.

Transport the sand screws to the benthos. Standing the sand screw upright, twist and bury the sand screw until the first disk has been covered in sand or loose rubble.

Place a 5 feet long metal turning bar through the eye of the anchor such that the majority of the turning bar sticks out of one side of the eye.

Walking or swimming in circles on the benthos, screw the sand screw into the substrate until only the eye remains sticking out of the benthos (**Appendix 1—Figure S20**).

Install three sand screws in a triangular pattern, connected by a chain bridle, for increased holding power (**Appendix 1—Figure S20**).

Use Halas anchors in hardbottom and carbonate base rock habitats.

Transport 9–12 in eyebolts and a submersible drill (electric or pneumatic) to the anchor site.

Use the submersible drill and a 1 in diameter masonry hole saw to drill a 9 in deep and 1 in wide hole into the base rock. Periodically clean out excess substrate from the hole using a turkey baster.

Fill the hole with Portland cement or marine-grade epoxy. Push the eyebolt shaft into the hole and fill the remaining gaps with cement or epoxy.

Let the cement/epoxy cure for 5 days.

For increased holding power, install three Halas anchors in a triangular pattern, connected by a chain bridle.

Use block-type mooring at sites with existing mooring blocks or heavy debris elements.

NOTE: The installation of a new mooring block requires commercial-grade installation equipment such as a barge-mounted crane and is not recommended for projects with a smaller scope.

Attach the mooring system to existing heavy debris elements (sunken vessels, engine blocks) or to existing mooring block eyes *via* hardware and tackle.

Ensure the metal mooring components are made from similar metals and protected against galvanic corrosion using sacrificial anodes.

The 1V frequency structure (Two Platform)

NOTE: Detailed fabrication instructions, including technical drawings for the manufacture of the components, are provided in **Section 4** of **Appendix 11**. The off-the-shelf components referred to in this protocol (and listed in the **Table of Materials**) are described using imperial units.

Assembly of the 1V geodesic frame

Screw a 1/4-20 stainless steel hex nut onto a 1/4-20 2.5 in stainless steel bolt 3/4 of the way to the top of the bolt. Insert the bolt into one of the inside-facing holes on the strut.

Secure a locknut onto the other side of the screw, tightening it down until it mates securely with the PVC to prevent the hub from sliding down the length of the strut.

Repeat for the opposite side of the strut and for the remaining 29 struts.

Push the end of each strut through one of the holes in the hubs and fasten another bolt through the outer hole on the strut, finishing with a locknut to prevent the strut from sliding out of the hub (**Appendix 1—Figure S24**).

Repeat for all five struts in one hub, and then continue to add hubs and struts until the geodesic sphere is assembled (**Appendix 1—Figure S24**).

Unspool the 1/8 in stainless steel wire rope and begin threading it through the struts. Create 12 loops, about the size of a silver dollar, out of nylon cable ties—one for each

hub. As the wire rope is threaded through the struts, pass the rope through the zip tie loop at the hub, and then continue to the next strut.

NOTE: Some struts will be repeated.

Continue threading until the wire rope has been threaded through all the struts, connected in the middle of each vertex by the zip tie loop.

Thread the cable back to the starting point. Using pliers, pull the zip tie loops to shrink them to the smallest size possible, bringing the lengths of wire rope close together. Fit a 1/2 in stainless steel cable clamp onto all the wire rope lengths and tighten down securely.

Repeat for all the vertices of the structure.

Mate the beginning length of the wire rope with the end length, and clamp these together using three 1/2 in cable clamps.

NOTE: The wire rope (breaking strength: 2,000 lb) should now support most of the load placed on the structure, strengthening it considerably.

Add the rigging system, which is composed of two lengths of 3/8 in stainless steel cable hydraulically swaged onto an eye at each end. Fit the PVC endcaps between the swages such that the cable passes through the entire Ark length, with eyes at the top and bottom for the mooring/buoy line attachments. A turnbuckle system in the middle connects the two lengths of stainless cable.

Pass the bottom ends of the cable through the top and bottom of the Ark, fitting the endcaps onto the top and bottom hubs using a mallet. Screw the eyebolts into the turnbuckle and tighten until there is sufficient tension on the structure to make the system rigid (**Appendix 1—Figure S24**).

Add each molded fiberglass grating, cut into two half-pentagons, into the Ark interior using heavy-duty 250 lb zip ties to anchor the sides of the platform to the Ark struts (**Appendix 1—Figure S24**).

Underneath the structure, place one length of fiberglass I-beam so that it joins both halves of the fiberglass platform. Secure to the underside of the platform using two 1/4 in-20 stainless steel U-bolts.

Repeat for the other four I-beams, equally distributing them down the length of the platform. This joins and supports the two halves of the platform, creating a full pentagon.

Tighten the heavy-duty zip ties at the edges of the platform, and clip off the excess. At the end of this step, the internal platform is firmly integrated into the Ark structure (**Appendix 1**—Figure S24).

Use stainless steel mousing wire to mouse the ends of the turnbuckle and all the shackles. At the end of this step, the Ark will have two integrated platforms, top and bottom attachments for hardware attachment, and a central cable that bears the bulk of the tension force placed on the structures *via* anchoring and positive buoyancy.

Attachment of the mooring line to the geodesic frame

NOTE: Mooring systems should be designed such that the breaking strength of all the individual mooring components exceeds the maximum load expected due to ambient and extreme environmental conditions. See the representative results for a description of the use of hydrodynamic modeling in mooring system design. It is recommended to distribute the load across multiple attachment points on the Ark and on the seafloor anchoring system, as this adds redundancy to the system in case of the failure of individual elements.

Design the mooring lines and hardware to ensure secure connections between the Ark base and the anchor system (see **Figure 2.1** for an example).

NOTE: It is recommended to design the mooring system such that the midline of the Ark structure is positioned at a 30 m depth.

Connect the top of a double-spliced line to the base eye of the Ark with a shackle. Connect a high-strength, stainless steel swivel shackle to the base of this line (**Figure 2.1** and **Appendix 1—Figure S25**).

Connect the top of a double-spliced line to the base of the swivel shackle. The bottom of this line will connect to the anchor system (**Figure 2.1** and **Appendix 1—Figure S25**).

Transportation of the Ark to the deployment site

Transport the Ark *via* a flatbed truck to a beach adjacent to the deployment site (nearshore deployment with sand entry) or to a boat launch site (vessel deployment).

Attach a 220 lb lift bag to the top stainless eye of the Ark using a 1/2 in shackle.

Attach a mooring line, including the hardware for attaching to the seafloor anchor, to the base of the Ark.

For deployment from a vessel lacking an A-frame or davit, load the Ark onto the vessel such that it can be easily rolled off the boat and into the water (avoiding bows with high gunnels or sterns with outboard engines).

For deployment from the shore, roll the Ark into the water until a sufficient depth at which the lift bag can be filled with air (**Figure 2.3**).

Swim, tow, or transport the Ark to the anchoring site at the surface (**Figure 2.3**).

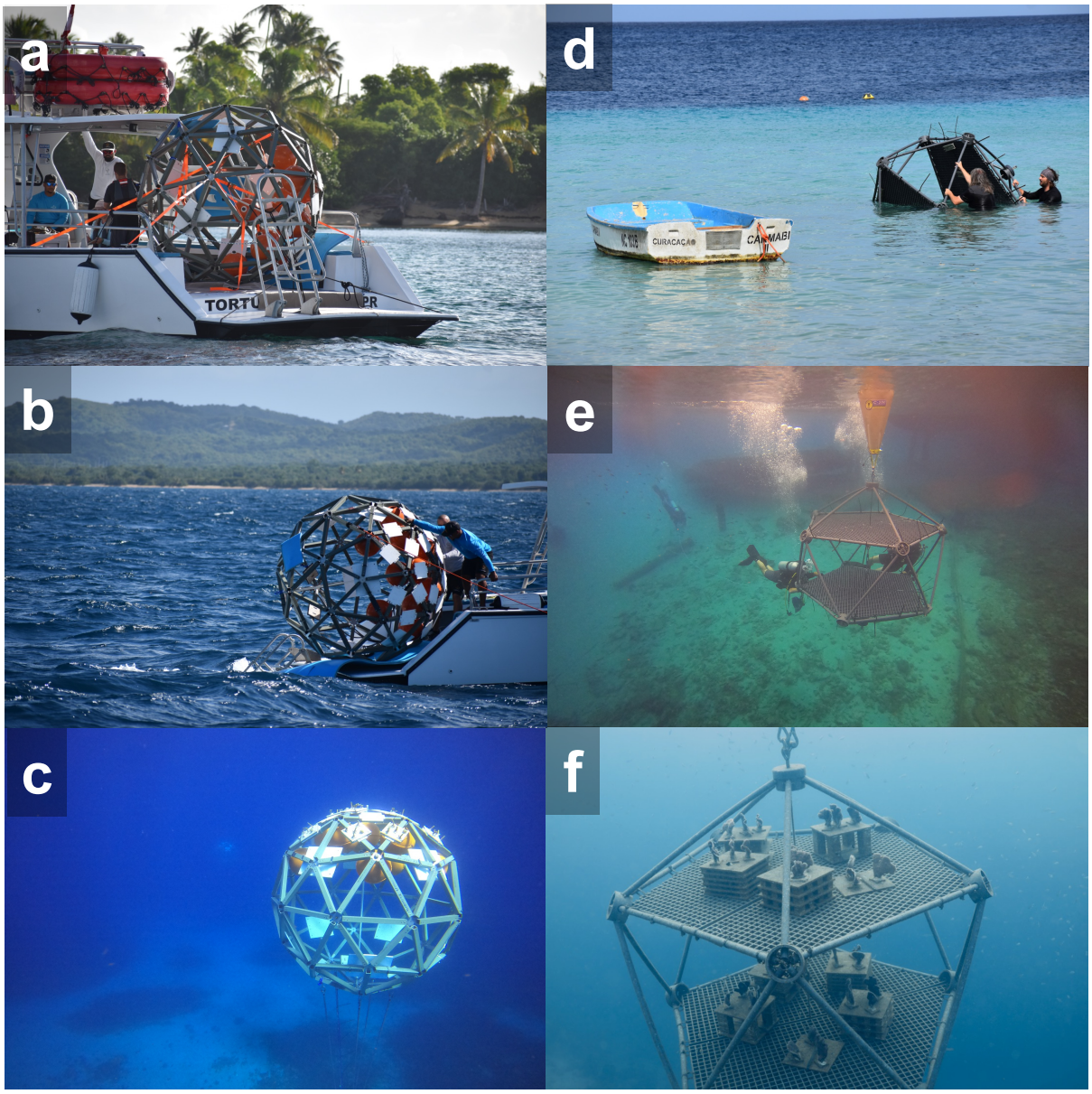


Figure 2.3 Images representing the deployment stages of Coral Arks, including transport to the site and full installation. (A–C) Shell type and (D–F) Two-Platform type systems.

Attachment of the Arks to the mooring system

NOTE: At this stage, the Ark system is floating at the surface above the anchoring site with a lift bag. The following tasks are performed underwater on SCUBA and require a team of at least three divers.

Slowly venting the air from the lift bag, perform a controlled descent to the anchoring system.

Attach the mooring hardware at the base of the Ark to the anchoring system.

Increase the positive buoyancy of the Arks system by filling the lift bag with air, and inspect the monitoring components for structural integrity. Ensure the shackles are seated properly and that the anchors are firmly in place. Use mousing wire to mouse all the shackles.

Connect the eye of a short, double-spliced length of line to the top eye of the Arks system with a shackle. Connect a polyform, inflatable mooring buoy to the other end of this line with a shackle (**Appendix 1—Figure S25**).

Fill the mooring buoy with air using a standard low-pressure air nozzle adapter attached to a pony bottle of compressed air until it is approximately 75% full of air.

Slowly vent the air from the lift bag and remove it from the system.

Add larger or more numerous mooring buoys for Arks systems utilizing limestone ARMS or to compensate for biological mass accumulation.

Attachment of the ARMS to the Arks

Retrieve the ARMS from the seeding location, and place into milk crates lined with 100 µm mesh to prevent the loss of small mobile invertebrates living within the ARMS.

Transfer the ARMS to the Arks sites in tubs of shaded, cool seawater.

Place the ARMS on the top or bottom platform of the Arks, evenly distributing the weight across the platform.

Pass heavy-duty cable ties through both the molded fiberglass platform and the base of the PVC or Limestone ARMS and tighten to secure the ARMS to the Ark frame (**Appendix 1—Figure S25**).

The 2V frequency structure (Shell)

NOTE: Detailed fabrication instructions, including technical drawings for the manufacture of the components, are provided in **Section 3** of **Appendix 1**.

Assembly of the 2V geodesic frame

Assemble the Ark mounting framework according to the provided guide from VikingDome (**Appendix 1—Figure S11**).

Add a washer to a 2.5 in long, 10/32 stainless bolt. Insert the bolt through one of the two holes at the end of a strut, adding a STAR connector to the inside face (hole specific to S1 or S2 struts), and fasten with a locknut.

Repeat for the second bolt hole. Continue without tightening the locknuts until the structure is fully assembled (**Appendix 1—Figure S12**).

Tighten down the Ark mounting framework. At the end of step 2.3.1.1, the strut-STAR connections will be loose and malleable. Begin tightening the locknuts using a socket wrench (10 mm or 3/8 in socket) and a Philips head screwdriver.

Continue throughout the structure until all the locknuts have been tightened, with the nylon insert of the locknut fully engaged on the threads of the bolts.

Add pad eyes for the attachment of the mooring bridle. Add a pad eye to the stainless S1 strut at the base of the Ark, and secure with four 3 in pan head stainless steel bolts.

Add 1/4 in-20 locknuts and tighten down. Repeat for a total of five mooring connection points (**Appendix 1—Figure S17**).

Mount 10 ARMS baseplates to the middle-facing N2 STAR connectors. Place a 3 in pan head bolt through the center hole on the ARMS baseplate. Add a grey PVC standoff to the bolt shaft and place it through the center hole of the N2 STAR connector, with the baseplate inside the structure. Add a washer and a locknut and tighten down.

Add two brackets and use four 3 1/4 in hex head bolts and locknuts to secure the ARMS baseplate to the struts. Tighten down all the locknuts. Maintain the same orientation for all the ARMS baseplates (**Appendix 1—Figure S15**).

Mount 20 coral plate baseplates to the top-facing struts. Place four 3 in hex head bolts through the holes on the coral plate baseplate and fasten to the strut using a bracket and a locknut. Repeat for the other side. Tighten the locknuts to secure (**Appendix 1**—Figure S15).

Add a central rod and trawl float to the central spine of the Ark. Insert an 8 feet long, unthreaded fiberglass rod into the STAR connectors modified with a welded pipe segment at the base of the Ark. Add a 1 in washer and an unmodified trawl float onto

the unthreaded fiberglass rod inside the structure. Finish inserting the rod through the top STAR connector of the Ark.

Fit the bolts through the metal tube on the modified STAR connectors and the locknuts to the lock rod inside the Ark. Add a green tube clamp snugly below the trawl float (top of the Ark) and tighten down.

Mount modified trawl floats inside the top facing N2 and N1 STAR connectors modified with a 1 in center hole. Add a fiberglass washer to the longer end of the exposed threaded fiberglass rod.

Secure through the modified STAR connector hole so that trawl float faces inside the structure. Add another fiberglass washer and a fiberglass hex nut. Tighten down using a wrench and by twisting the floats (**Appendix 1—Figure S16**).

Attachment of the mooring system to the geodesic frame

Design the mooring lines and hardware to ensure secure connections between the Ark base and the anchor system (see **Figure 2.1** for example).

NOTE: It is recommended to design the mooring system such that the midline of the Ark structure is positioned at a 10 m depth.

Connect each pad eye at the base of the Ark structure to the spliced eye at the end of a double-spliced length of a 3/4 in spectra line with a high-strength, 7/16 in stainless steel shackle (**Appendix 1—Figure S17**).

Using a 1/2 in screw pin shackle, connect the other end of each spectra line to one of the two stainless steel Masterlinks, such that each link has two or three connections.

Attach the 3/4 in swivel shackle to the bottom of the Masterlink and the eye of a 1 in nylon line spliced with a stainless-steel thimble.

Attach a 3/4 in shackle to the eye and thimble at the other end of the nylon line. This shackle will connect to the anchor system (**Appendix 1—Figure S17**).

Transportation of the 2V Ark to the deployment site

NOTE: The deployment of the Shell Ark requires a vessel with a flat stern and inboard engines, such that the Ark can be rolled off the boat deck and into the water, or a vessel with a large davit or A-frame.

Transport the Ark *via* a flatbed truck to the dock or marina.

Load the Ark onto the vessel using an appropriately sized forklift (**Appendix 1—Figure S21**).

Attach the mooring lines and hardware, including the downlines and hardware for attaching to the seafloor anchor system, to the base of the Ark.

Transport the Ark to the anchor site (**Figure 2.3**). Prepare a line approximately the same length as the depth of the anchoring system with a shackle at one end and a buoy at the other end.

Attach the shackle end of the line to the anchoring system, with the buoy end floating at the surface.

Roll the Ark safely off the stern deck into the water or deploy the Ark into the water with a davit or A-frame. Attach the buoy end of the line to the positively buoyant Ark such that the structure floats above the anchoring system.

Attachment of the Ark to the mooring system

NOTE: At this stage, the Ark structure is floating at the surface above the anchoring site with the integrated buoyancy elements (floats) providing flotation. The following tasks are completed underwater on SCUBA and require a team of at least three divers and two surface support personnel.

Attach the top block of a block and tackle pulley system to a secure attachment point on the base of the Ark, unspooling the pulley while descending toward the seafloor, and then attach the bottom block to the anchoring system (**Appendix 1—Figure S19**).

Pull the line through the bottom block to engage the pulley, pulling the Ark to depth. The line should be locked into the cleat with each pull (**Appendix 1—Figure S19**).

NOTE: For Arks systems with high initial positive buoyancy, use a 6:1 block and tackle system for maximum purchase. Weights can also be temporarily attached to the Arks system to reduce the buoyant force necessary to sink the structure.

Continue to pull the Ark to depth until the downline and mooring attachment hardware can be connected to the anchor system. Use wire to mouse all the shackles.

Inspect all the mooring components for integrity. Ensure the shackles are seated properly and the anchors are firmly in place.

Slowly transfer the tension from the block and tackle to the mooring system. Remove the block and tackle, weights, and buoy line.

Attachment of the ARMS to the Arks

Retrieve the ARMS from the seeding location, and place into milk crates lined with 100 μm mesh to prevent the loss of small mobile invertebrates living within the ARMS. Transfer the ARMS to the Arks sites in tubs of shaded, cool seawater.

Maneuver the ARMS through one of the larger triangular openings near the midline of the Ark such that the ARMS is inside the structure. Hold the ARMS firmly to one of the white baseplates mounted inside of the Ark framework.

Secure a 1/2 in-13, 1.75 in long, stainless-steel hex head bolt through an open corner hole of the ARMS baseplate and the white, underlying HDPE baseplate, attach a stainless-steel locknut to the bolt protruding through the other side, and tighten down until snug. Repeat for the other three sides (**Figure 2.2D**).

Push the ARMS back and forth to ensure firm attachment.

Attachment of the corals to the Arks

Fasten the coral plates containing corals epoxied to the limestone tile to the coral plate HDPE baseplates on the exterior of the Ark using 2 in long, 1/4 in-20, stainless steel hex head bolts, a washer, and a locknut at all four corners.

Tighten the locknuts using a socket wrench to secure the coral plate in place.

Coral Arks monitoring and maintenance

NOTE: Detailed fabrication instructions, including technical drawings for the manufacture of the components, are provided in **Section 7** of **Appendix 1**.

Measuring the in-water weight of the Arks

Attach the submersible load cell to a block and tackle pulley system for use in temporarily transferring tension on the mooring line to the strain gauge system.

Attach the base of the block and tackle to a secure location on the Ark mooring system, such as an intermediate shackle point or to the seafloor anchor. Attach the top of the load cell to a secure location on the Ark mounting framework (**Appendix 1—Figure S33**).

Without removing or altering the mooring components on the Ark, pull the line through the block and tackle pulley system such that tension is transferred from the Ark mooring system to the pulley system, cleating the line with each pull (**Appendix 1—Figure S33**).

Ensure the mooring line is completely slacked to allow the strain gauge to collect tension measurements (**Appendix 1—Figure S33**).

Slowly transfer the tension from the block and tackle pulley system to the Ark mooring line, checking to ensure the shackles and other mooring components are properly seated and secure.

For long-term data collection, integrate a load cell into the mooring system as an “in-line” component. Periodically switch out the dataloggers to retrieve the data.

Long-term maintenance of the Arks

Perform routine inspections of the Arks mooring system and conduct maintenance work as needed.

NOTE: See **Appendix 1—Figure S18** for an example maintenance checklist. Biannual maintenance is recommended.

Ensure the anchors are continuing to provide maximum holding power (i.e., not backing out of the substrate).

Clean the mooring lines of fouling organisms that can invade and compromise the integrity of the lines.

Replace degrading components, such as the sacrificial anodes, shackles, and mooring lines, as needed (**Appendix 1—Figure S18**).

Add supplemental buoyancy as needed by adding fixed buoyancy floats or air to the existing mooring buoys to compensate for biological mass accumulation.

REPRESENTATIVE RESULTS

The above methods provide assembly and installation instructions for two designs of Coral Arks systems. Prototypes for each design were assembled and field-tested in San Diego, USA, prior to long-term deployment to evaluate the drag characteristics and optimize the structural integrity based on modeled and empirical values of strength. The modeling efforts instrumental to the selection and refinement of both the Arks geometries presented here, including the results from wind tunnel testing,

hydrodynamic simulations, and the in-water validation of the modeled values using prototype structures, are described in detail in **Section 6** of **Appendix 1**. The results from the modeling and in-water testing of the “Shell” Arks design are shown here. Two structures of each design were then deployed at Caribbean field sites in Puerto Rico and Curaçao (four total Arks structures installed), and corals were translocated to the structures. Water quality, microbial community, and coral survival metrics associated with the “Shell” Arks design and two seafloor control sites were collected at several time points spanning 6 months to characterize and determine the changes in the environmental parameters and coral health associated with the Arks structures following natural recruitment and the addition of seeded ARMS.

Drag characteristics of Coral Arks

It is important to understand the drag characteristics of Coral Arks in order to design a structure and mooring that will survive the target environment. From a structural perspective, the hydrodynamic drag, in combination with the net buoyancy, imposes loadings within the structure, particularly on the mooring and its anchoring system. We conducted modeling and experimental measurements to estimate the drag characteristics of the Arks structures. The results of these tests for the “Shell” design of Arks structures are detailed below. Modeling was carried out by estimating the drag of the individual elements of the structure, summing these, and then combining the result into an effective drag coefficient as shown in equation (**1**) and equation (**2**):

$$D_{total} = \sum_{i=0}^{n} D_i \qquad (\mathbf{1})$$

$$C_D = \frac{D_{total}}{\frac{1}{2}\rho U^2 A} \qquad (\mathbf{2})$$

where D_{total} is the total drag of the structure estimated from the sum of the D_i element drags, C_D is the overall structure drag coefficient, ρ is the fluid density, U is the flow speed of the object relative to the fluid, and A is the frontal area of the structure. In these calculations, the elements were all assumed to be cylinders, with their orientation to the flow dictated by the upright geometry of the Ark structure. The modeling was performed for the same prototype “Shell” system (a 2V geodesic sphere) that was used for tow testing (described below) prior to the construction of the final field systems. The prototype had a total frontal area of approximately 2.10 m^2, and the modeling results indicated an effective drag coefficient for the entire structure of approximately 0.12. The model-predicted drag of the structure as a function of velocity is shown in **Figure 2.4**.

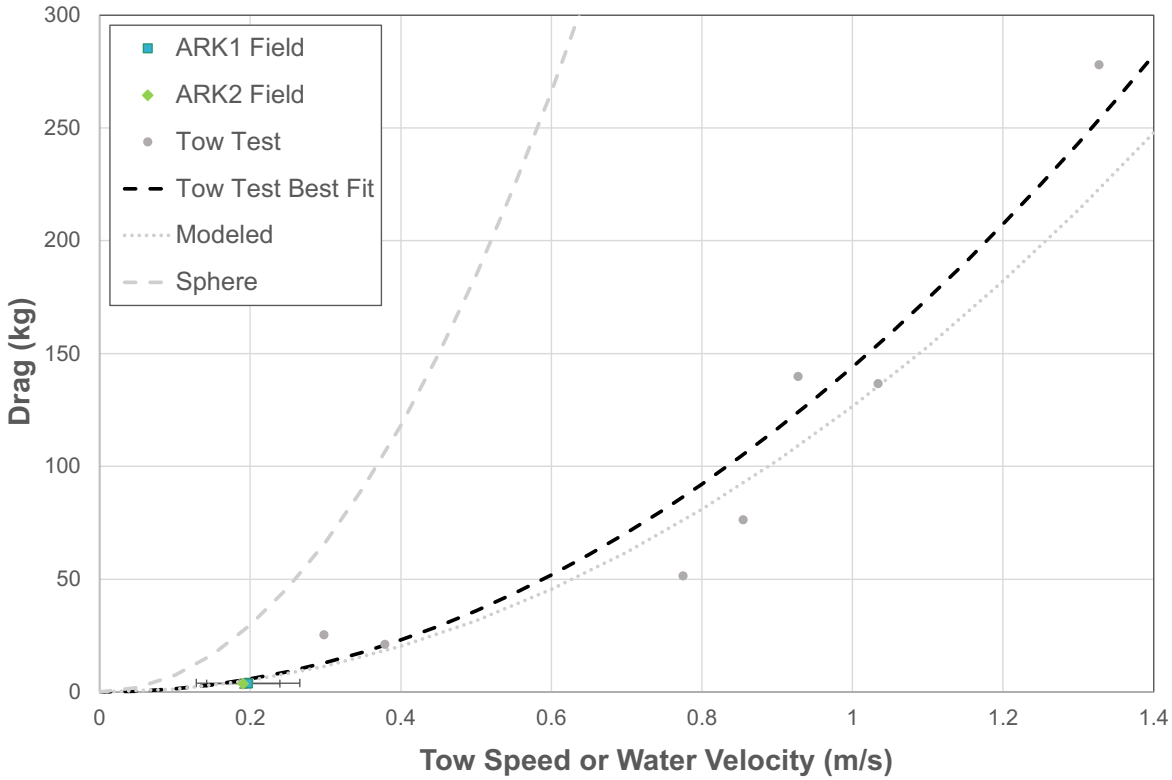


Figure 2.4 Drag characteristics of the “Shell” Ark structures based on modeling, experimental tow testing, and field validation relative to the drag of a sphere of the same approximate scale. “ARK1” and “ARK2” are identical “Shell” Ark structures installed at the same site in Vieques, Puerto Rico.

Experimental estimates of the drag force of the structure that would be experienced under different flow velocities were obtained by towing the Ark structure behind a vessel with a load cell spliced in-line with the towing line and a tilt sensor to record the changes in the Ark’s orientation relative to the vertical axis at a range of tow speeds. Prior to towing, the in-water weight of the structure was determined, and sufficient additional weight was added to the structure to simulate a net buoyancy of approximately 200 kg (an initial target for the system). Based on the tension in the tow

cable and the inclination angle of the Ark, the drag (D_{tow}) at each speed was determined using equation (**3**):

$$D_{tow} = T \times \sin\theta \qquad (3)$$

where T is the measured tension from the load cell, and θ is the tilt angle relative to the vertical axis. The resulting drag versus speed relationship is shown in **Figure 2.4**. A best fit drag curve (of the form $D_{tow} \propto U^2$; see **Figure 2.4**), combined with estimates of the frontal area and the water density, was then used to determine the empirical drag coefficient of 0.13.

The Reynolds number during the tow testing (and the range used for the modeling) was in the range of 10^5–10^6, generally in the turbulent flow regimes. Typical values of the drag coefficient for a sphere in this Reynolds number range are between 0.2 and 0.4. For comparison purposes, a plot of the drag curve for a sphere with a drag coefficient of 0.3 is shown in **Figure 2.4**. Thus, the modeled and experimental estimates of the drag coefficient are in the order of two to three times smaller than for a sphere, which is consistent with the more open character of the structure.

To validate these modeled results, we also conducted field measurements of the response of two “Shell” Arks structures to flow. To achieve this, the same load cell was installed temporarily in line with the Ark main mooring line, a tilt sensor was installed on the Ark, and a current meter was installed at the site to simultaneously monitor the water speed. The buoyancy and drag components of the tension were then calculated from the tilt angle and the load cell measurements (**Figure 2.5**). The current speeds during the measurement period were relatively stable at about 20 cm/s, and the data set was relatively short; hence, the data were averaged over the period and used to

compare the field drag and velocity response to the modeled and experimental towing estimates. These results show that under expected conditions at the deployment site (flow speeds up to 1.3 m/s during a typical storm event), the drag force on the system is expected to be less than 300 kg.

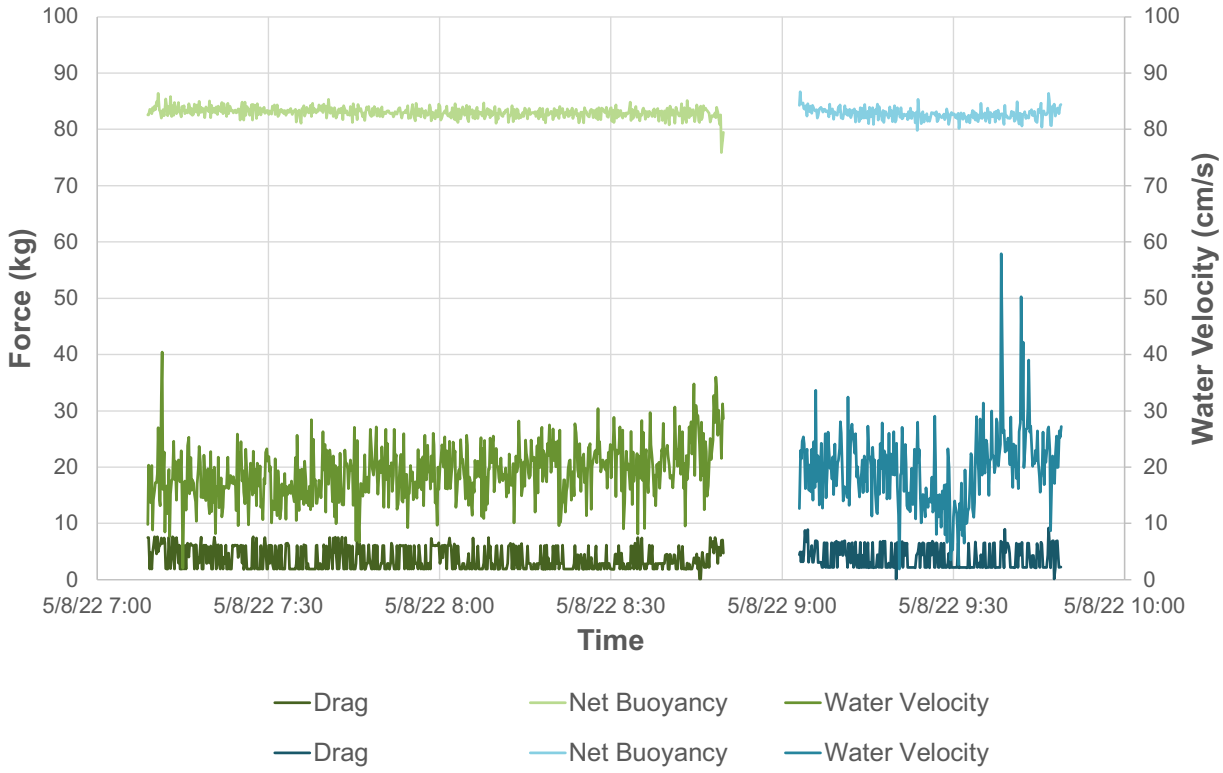


Figure 2.5 Measured net buoyancy values for two “Shell” Arks in Vieques, Puerto Rico. Shown are the water velocity (right axis, medium colors), net buoyancy (left axis, light colors), and calculated drag/tension on the mooring line (left axis, dark colors) for “Shell” Ark 1 (blue) and “Shell” Ark 2 (green).

Both “Shell” structures in Vieques, Puerto Rico, survived a direct hit from the Category 1 Hurricane Fiona in September 2022 with no apparent damage to the structures, mooring, or anchoring system, providing an *in situ* test that supports the design. A nearby buoy (CARICOOS) recorded current speeds of 1.05 m/s at a 10 m depth at the deployment site, corresponding to a drag force of approximately 160 kg on

the mooring systems. The systems were designed to withstand 1,600 kg of force (considering the anchor capacity and component breaking strength) and, therefore, are not expected to fail under ambient or typical storm conditions.

Net buoyancy monitoring for Coral Arks

The same approach described for validating the drag characteristics of the Ark structures was also used to develop a method for monitoring the net buoyancy of the Arks. As long as the physical structure of the Ark remains constant, the net buoyancy provides a rough proxy for monitoring the overall community calcification and, thus, the coral growth, as well as a maintenance metric to determine if the system has sufficient positive buoyancy to compensate for biological growth over time. The buoyancy component (*B*) of the mooring tension was calculated using the strain gauge and tilt sensor data in equation (**4**):

$$B = T \times \cos\theta \qquad (4)$$

where *T* is the measured tension from the load cell, and θ is the tilt angle. The resulting time series of the net buoyancy is shown in **Figure 2.5**. Under the relatively stable current conditions present during the field monitoring events, we found the two "Shell" Arks structures deployed in Vieques, Puerto Rico, to have similar net buoyancies of 82.7 kg ± 1.0 kg (Ark 1) and 83.0 kg ± 0.9 kg (Ark 2) when averaged over the monitoring period (± one standard deviation) after all the corals and seeded ARMS units were translocated to the structures 6 months after the initial structure deployment. The results show that short-term monitoring during relatively stable periods of water flow can be used to determine the net buoyancy in the field to within ~1 kg, which should prove useful over the long term for monitoring changes in biomass.

Water quality and microbial community dynamics

Metrics associated with water quality and water column-associated microbial communities were measured on two midwater “Shell” Arks, which were anchored in 55 ft of water with the top of the Arks at a 25 ft depth, offshore of Isla Vieques, Puerto Rico (**Figure 2.6C**). The water quality metrics, microbial and viral abundances, and average microbe size from two Arks were compared to the same metrics from two nearby seafloor “control” sites, which were also at a 25 ft depth but much closer to shore (**Figure 2.6D**). The measurements shown were collected immediately after the installation of the Arks with an initial batch of translocated corals (November 2021) and 6 months later after a second batch of corals and seeded ARMS were translocated to the Arks (May 2022); they were then averaged across both sites (Arks and Control sites) for comparison. As the seeded ARMS were transferred to the Arks at 6 months post-deployment, the accumulation of biological communities on the structures during the first 6-month period was associated with biofouling and natural recruitment.

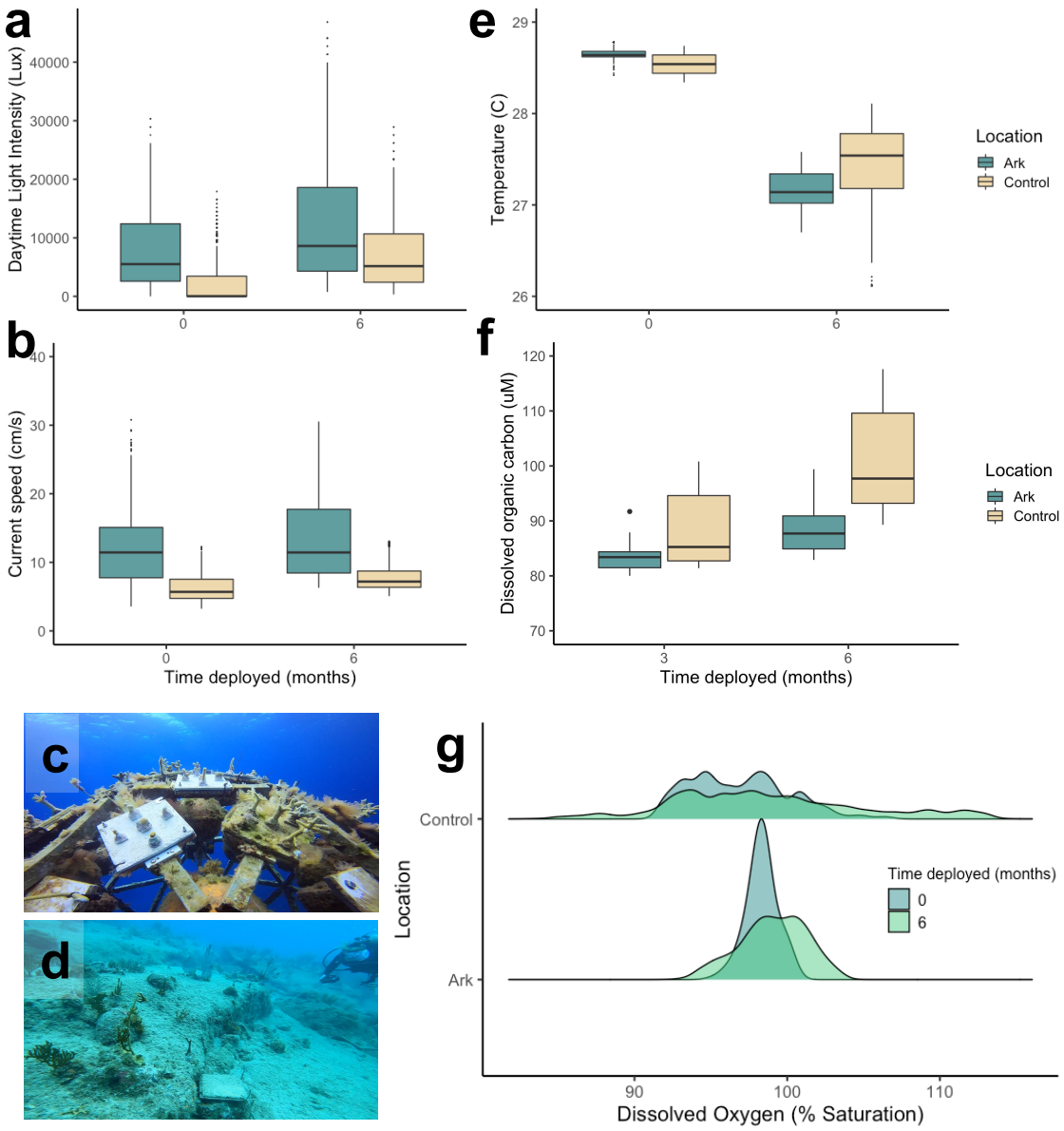


Figure 2.6 Water quality metrics associated with the “Shell” Arks and seafloor control sites in Vieques, Puerto Rico, immediately following the installation and 6 months afterward. (A) Daytime light intensity, (B) current speed, (C,D) photos taken 6 months post installation, (E) temperature, (F) dissolved organic carbon, (G) changes in dissolved oxygen levels in the Arks versus control sites over 6 months.

The Arks environment exhibited higher average daytime light intensities (**Figure 2.6A**), higher average flow speeds (**Figure 2.6C**), lower dissolved organic carbon concentrations (**Figure 2.6F**), and lower diel fluctuations in dissolved oxygen

concentrations (**Figure 2.6G**) than the benthic control sites. The Arks also displayed microbial communities with higher virus-to-microbe ratios than the control sites (**Figure 2.7A**), driven by a higher abundance of free viruses (**Figure 2.7C**) and a lower abundance of microbes (**Figure 2.7B**) in the midwater Arks environment. The microbial communities on the Arks were composed of, on average, physically smaller cells than the microbial communities at the seafloor sites (**Figure 2.7D**). Differences in temperature between the Arks and the control sites were not significant (**Figure 2.6E**). All of the above trends are consistent with better water quality and healthier microbial communities on the Arks than at the control sites. These conditions persisted through the initial 6 months of the deployment, during which a nascent biological community developed on the Arks through both the translocation of coral nubbins and natural recruitment from the water column and experienced successional changes, as well as through the addition of seeded ARMS onto the structures at month 6.

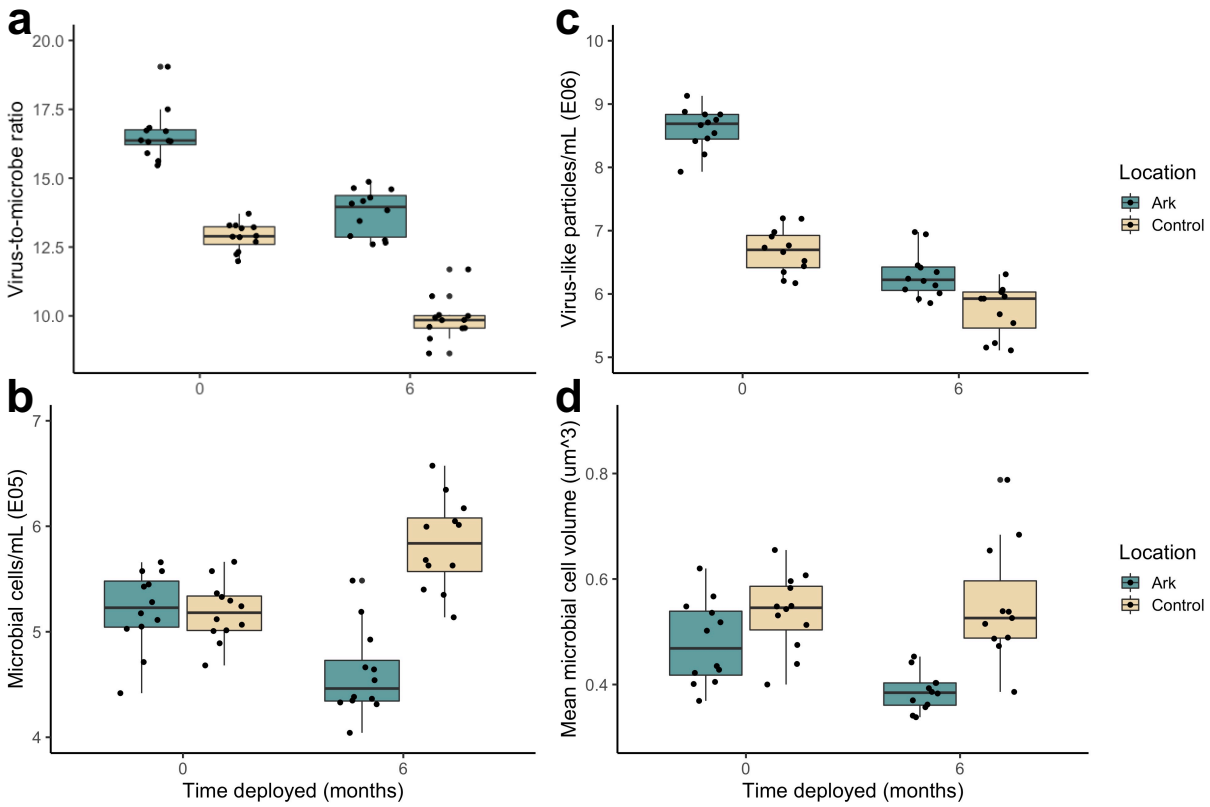


Figure 2.7 Metrics associated with the water column-associated microbial communities on the "Shell" Arks and seafloor control sites in Vieques, Puerto Rico immediately following installation and 6 months afterward. (A) Virus-to-microbe ratio, (B) bacterial cell abundance, (C) free virus abundance, and (D) average bacterial cell size.

Coral survival

A cohort of corals comprising eight species and various morphologies were distributed to the Arks and benthic control sites both following the installation of the Arks (month 0) and following the addition of the seeded ARMS at month 6. The original parent colonies of each species of coral were fragmented into nubbins (2–8 cm in a given dimension) and attached to limestone coral plates (four to five nubbins per 20 cm^2 plate) that were distributed equally at both the Arks and control sites, ensuring that the same species and genotypes were represented at both the midwater Arks sites and control sites. The survival of these translocated corals was assessed every 3 months at

the Arks and control sites. Nine months after the translocation of the first cohort of corals, more corals were still alive on the Arks (80%, **Figure 2.8**) compared to the control sites (42%, **Figure 2.8**).

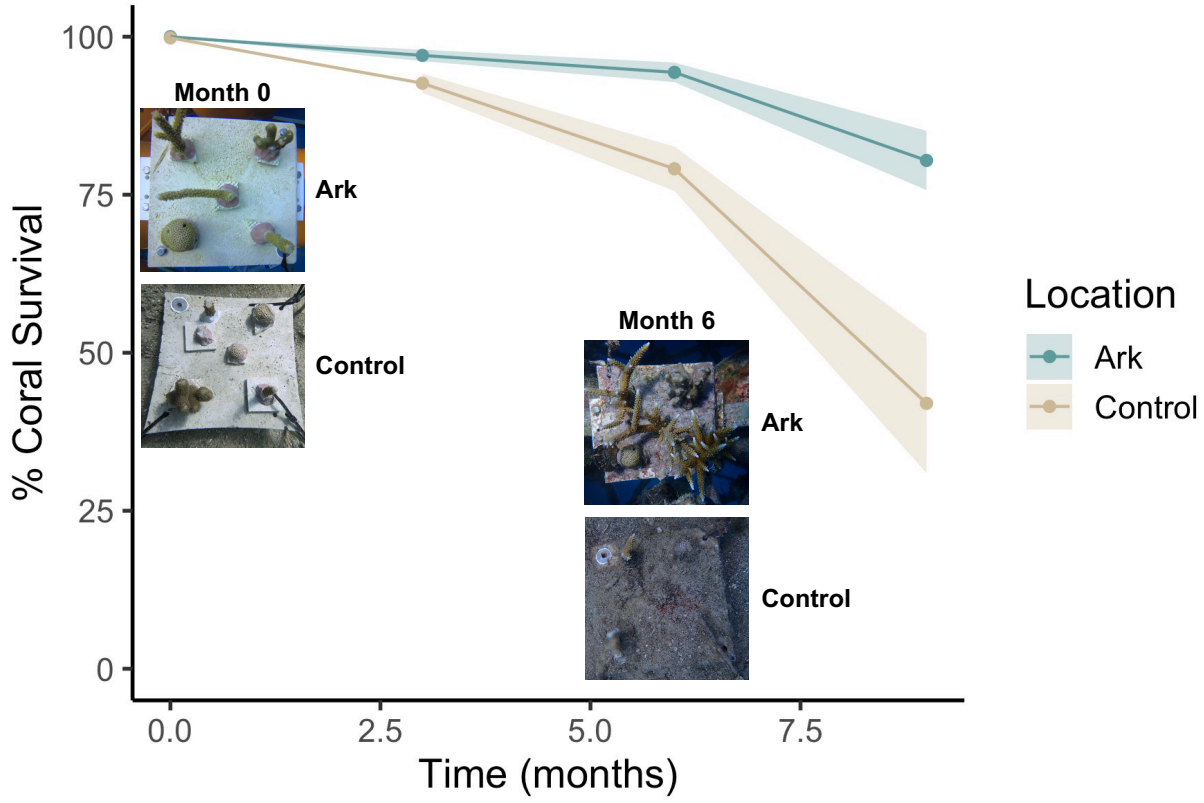


Figure 2.8 Proportion of surviving corals on the "Shell" Arks and seafloor control sites in Vieques, Puerto Rico during the first 9 months following translocation. The images represent the status of a single coral plate on the Arks (top) and on the benthic control sites (bottom) immediately following translocation (left) and 6 months after translocation (right).

DISCUSSION

The representative results presented above demonstrate that Coral Arks provide a habitat and improved water quality conditions for assembling reef communities on stable, *in situ* research platforms. Arks and seafloor control sites at the same depth displayed consistently different water quality profiles. Higher average current speeds

and further distance from the coast reduced sedimentation and turbidity in the midwater environment at the Arks sites (**Figure 2.6B**), likely contributing to the lower measured dissolved organic carbon concentrations on the Arks (**Figure 2.6F**). Further, these improvements in water clarity resulted in elevated daytime light intensities on the Arks relative to the control sites (**Figure 2.6A**). Lower diel fluctuations in dissolved oxygen indicate improved oxygen availability for corals on the Arks compared to the benthos, especially at night (**Figure 2.6G**). These metrics have all been associated with improvements in coral survival (Nakamura and Van Woesik 2001), growth (Dennison and Barnes 1988; Finelli et al., 2007; Mass et al., 2010), and recovery from stress (Nakamura et al., 2003; Nakamura and Yamasaki 2005) in past work and may be linked to enhanced survival outcomes of corals translocated to Arks as compared to benthic control sites (**Figure 2.8**). The fact that these conditions persist even after the accumulation of substantial biomass through biofouling indicates that natural recruitment processes do not diminish the improved water quality characteristics of the midwater environment. Arks were deployed 3 km offshore of the benthic control sites and likely benefitted from decreased inputs of terrestrially derived sediment, nutrients, and possibly fishing pressures that challenge nearshore sites. Siting Arks in areas with clean water and low human impact (such as offshore) may provide a better setting than heavily impacted coastal zones to propagate reef biodiversity for mesocosm-level experiments.

The preliminary findings also suggested that the midwater Arks experienced less microbialization, a central reef process associated with the degradation of benthic reef habitats (McDole et al., 2012; Haas et al., 2016). High nutrient inputs and overfishing

have been identified as drivers of reef-wide trophic feedback loops in which energetically destabilized microbial communities proliferate, resulting in the respiratory drawdown of metabolically available oxygen and the increased incidence of coral pathogens at the benthos (Haas et al., 2010, 2013; Zaneveld et al., 2016; Silveira et al., 2017). The reduced abundance of free viruses on microbialized reefs, which serve as a primary lytic control on microbial community growth, indicate a breakdown in the trophic structure that favors further microbial expansion (Knowles et al., 2016). Water column-associated microbes on the Arks were both less abundant (**Figure 2.7B**) and physically smaller (**Figure 2.7D**) than at the seafloor sites. The Arks also displayed higher virus-to-microbe ratios (**Figure 2.7A**), abundance of free viruses (**Figure 2.7C**), and dissolved oxygen availability, particularly at night (**Figure 2.6G**). Taken together, these findings indicate that the midwater environment displayed less potential for microbialization relative to the seafloor sites. Arks, as mesocosms on which environmental conditions can be altered simply by vertical adjustment in the water column, offer an opportunity to mitigate and further explore the microbial and molecular mechanisms of reef degradation.

Geodesic spheres of two different frequencies were selected for the design of the Coral Arks presented here (**Figure 2.1**). Geodesic frequency (1V, 2V, 3V) indicates the number of repeating sub-elements in a geodesic sphere, with higher frequencies corresponding with a higher number of triangular sub-elements. From a structural perspective, geodesic polyhedra distribute mechanical stress throughout the structure, resulting in a high innate strength for their size (Szmit 2017; Laila et al., 2021). These characteristics provide high durability and longevity but come at the cost of higher

hydrodynamic drag, which can result in higher loadings on the mooring system. From a habitat perspective, the drag generated by an Ark system represents an indicator of the diffusion of momentum within the structure and, thus, the degree to which the internal ambient flow is reduced. The modeled and experimentally validated results indicate a 40%–70% reduction in the flow speed inside of the “Shell” Arks relative to the surrounding flow field due to the generation of turbulent flow inside the structures (see **Section 6** of **Appendix 1**). While the optimal level of internal flow reduction is not clear (and differs with geodesic frequency), areas of reduced flow within the structure are important for creating niche habitats (Alldredge and King 1977; Graham and Nash 2013), remineralizing nutrients (Scheffers et al., 2004; Van Duyl et al., 2006), and promoting the retention and settlement of larvae (Reidenbach et al., 2009, 2021). In general, larger and higher frequency geodesic structures, particularly at more exposed installation sites, require anchoring systems with higher holding power and more redundancy incorporated into the structural design.

The results from the field-based measurements of the drag component of tension on the “Shell” Ark mooring system closely matched those results generated from the modeled and experimental towing estimates (**Figure 2.4**) and were well within the expected design ranges. These results indicate that the assumptions of the hydrodynamic model are valid and that the model can predict drag forces over the background current ranges. However, while the deviations in the modeled and experimental data were small, the range of flows during the testing period, which were typical of ambient, non-storm flow speeds at the site, did not enable a rigorous validation over the full modeling spectrum. In predicting the design requirements of

Coral Arks systems, modeling efforts should be combined with information on storm frequency and exposure at the planned deployment sites to design structures and mooring systems that can survive the anticipated hydrodynamic forces. The modeling work presented here can be used to design Ark systems at other sites with minimal inputs (desired Ark size, frequency, and average current speeds at the deployment site) by providing drag coefficients and maximum expected forces on the mooring and anchoring system.

Arks and ARMS systems are modular and may be built at different scales and with alternative materials than those described here. Although their ultimate longevity has not yet been determined, Coral Arks were designed to have an approximately 10-year life cycle. The material composition of the Arks and ARMS affects the longevity of the structures, the weight of the systems, and, therefore, the required buoyancy to offset the weight and may affect the response of early fouling communities (**Appendix 1—Figure S7**). For example, limestone provides a more natural substrate for biological colonization on the ARMS and is readily and inexpensively sourced on most carbonate reef islands, but it is more fragile and heavier than other materials such as PVC and fiberglass. These factors should be considered against site-specific characteristics to design ARMS, Arks, and mooring systems that best address the desired project outcomes.

The deployment sites for Coral Arks should also be selected based on the intended project goals (i.e., research, mitigation, or restoration). Factors to consider for site selection include the access to materials, reef state or condition, community investment/involvement, resource limitation, institutional support, and permit

requirements. Coral Arks may provide opportunities to meet specific needs at sites that (1) contain living coral reefs that are in relatively poor condition and would benefit from restoration activities to enhance the coral recruitment, coral cover, coastal protection, or human food resources; (2) have a need for the translocation of corals to another location, which may occur, for example, when there are legal requirements to move living corals off of debris items slated for removal (at these sites, Coral Arks can be used in collaboration with, or in support of, existing restoration and outplanting efforts to improve translocation outcomes); (3) require research into novel conservation and restoration technologies using Coral Arks to improve the success of local efforts; or (4) have sufficiently distinct local conditions (i.e., different magnitude of anthropogenic impact), meaning standardized mesocosms could yield meaningful comparisons about reef processes and interventions. The specific approaches for monitoring aspects of the Coral Arks ecosystem such as biological growth, diversity, and water chemistry will vary between projects based on the project goals and site-specific variables. A representative outline for the scientific monitoring of Coral Arks conducted to date is provided in **Section 5** of **Appendix 1**.

The design of Coral Arks structures can accommodate corals of nearly any species, size, and age and should provide improved conditions relative to those on a disturbed reef benthos. Depending on the growth and calcification rates observed on a given system, the addition of positive buoyancy to the Arks structures may be required to compensate for biological growth and to reduce the risk of sinking. Positively buoyant midwater structures can be weighed using a tension/compression load cell, or strain gauge, to determine if the in-water weight of the community is increasing (**Figure 2.5**).

Periodic or long-term measurements using the load cell can complement other finer-resolution coral growth metrics to generate a metric of community-level growth/calcification and have been included as a regular maintenance task to determine if the system has sufficient positive buoyancy to compensate for this biological growth over time. In the case that an installed Ark can no longer be monitored or maintained, it could be relocated and/or the buoyancy could be removed to allow the Ark to be firmly attached to the benthos.

CONCLUSIONS

The methods described here provide researchers with a versatile toolkit for assembling midwater reef communities that can be sited at locations with improved water quality. By altering the depth or location of the Arks structures, changes in water quality parameters can be experimentally linked to changes in reef community structure and successional trajectories. This design feature allows researchers to exploit the abundant and underutilized space in the midwater environment to assemble and study coral reef mesocosms. The use of seeded ARMS to translocate cryptic biodiversity and deliver a “boost” to the natural recruitment of mobile grazing invertebrates provides a functional solution for reducing algal biofouling and, thus, benthic competition for corals. Using established and standardized sampling structures as components of this system provides added value by enabling the long-term monitoring of cryptic communities on Arks and comparison to datasets generated using ARMS as a global biodiversity census tool.

Coral Arks can serve as a more holistic, integrated, and self-regulating platform for propagating coral and invertebrate biomass that can then be outplanted to nearby

degraded reefs and can provide a safe haven for corals to grow and reproduce in improved water quality conditions. As is currently being demonstrated in Puerto Rico, Arks can yield improved survival outcomes for mitigation projects involving the relocation of corals and reef biodiversity from debris items or degraded areas. Arks have relevance in long-term projects as a method to replace habitats for fish populations, test novel conservation strategies, and preserve native reef biodiversity. In the process, Arks provide versatile tools for conducting *in situ* studies of reef assemblies and ecological succession and may generate novel insights into reef connectivity.

ACKNOWLEDGEMENTS

We thank Mark Vermeij, Kristen Marhaver, and the CARMABI Research Foundation in Curaçao for providing resources, support, and insight for this project. We thank the NAVFAC Atlantic Vieques Restoration Program and the Jacobs Engineering team for their substantial logistical and technical support in installing, maintaining, and monitoring the Coral Arks in Vieques. We are also grateful to Mike Anghera, Toni Luque, Cynthia Silveira, Natascha Varona, Andres Sanchez-Quinto, Lars ter Horst, and Ben Darby for their help and constructive input in the field. This research was funded by the Gordon and Betty Moore Foundation and the Department of Defense Environmental Security Technology Certification Program (RC20-5175).

Chapter 2, in full, is a reprint of the material as it appears in the Journal of Visualized Experiments (JoVE). Jason L Baer, Jessica Carilli, Bart Chadwick, Mark Hatay, Anneke van der Geer, Yun Scholten, Will Barnes, Jenna Marie Cruz Aquino, Ashton Ballard, Mark Little, Jared Brzenski, Xiaofeng Liu, Gunther Rosen, PF Wang, Jose Castillo, Andreas Haas, Aaron Hartmann, and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

DISCLOSURES

The authors have no competing financial interests or other conflicts of interest.

REFERENCES

Alldredge, A. L., & King, J. M. (1977). Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Marine Biology*. https://doi.org/10.1007/BF00389098

Altieri, A. H., Harrison, S. B., Seemann, J., Collin, R., Diaz, R. J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1621517114

Bartley, R., Bainbridge, Z. T., Lewis, S. E., Kroon, F. J., Wilkinson, S. N., Brodie, J. E., & Silburn, D. M. (2014). Relating sediment impacts on coral reefs to watershed sources, processes and management: A review. *Science of the Total Environment*, *468–469*, 1138–1153. https://doi.org/10.1016/j.scitotenv.2013.09.030

Bianchi, D., Carozza, D. A., Galbraith, E. D., Guiet, J., & DeVries, T. (2021). Estimating global biomass and biogeochemical cycling of marine fish with and without fishing. *Science Advances*, *7*(41). https://doi.org/10.1126/sciadv.abd7554

Cárdenas, A., Neave, M. J., Haroon, M. F., Pogoreutz, C., Rädecker, N., Wild, C., Gärdes, A., & Voolstra, C. R. (2018). Excess labile carbon promotes the expression of virulence factors in coral reef bacterioplankton. *ISME Journal*. https://doi.org/10.1038/ismej.2017.142

Carvalho, S., Aylagas, E., Villalobos, R., Kattan, Y., Berumen, M., & Pearman, J. K. (2019). Beyond the visual: Using metabarcoding to characterize the hidden reef cryptobiome. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2018.2697

De Goeij, J. M., Van Oevelen, D., Vermeij, M. J. A., Osinga, R., Middelburg, J. J., De Goeij, A. F. P. M., & Admiraal, W. (2013). Surviving in a marine desert: The sponge loop retains resources within coral reefs. *Science*. https://doi.org/10.1126/science.1241981

Dennison, W. C., & Barnes, D. J. (1988). Effect of water motion on coral photosynthesis and calcification. *Journal of Experimental Marine Biology and Ecology*. https://doi.org/10.1016/0022-0981(88)90190-6

Enochs, I. C., Manzello, D. P., Donham, E. M., Kolodziej, G., Okano, R., Johnston, L., Young, C., Iguel, J., Edwards, C. B., Fox, M. D., Valentino, L., Johnson, S., Benavente, D., Clark, S. J., Carlton, R., Burton, T., Eynaud, Y., & Price, N. N. (2015). Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nature Climate Change*, *5*(12), 1083–1088. https://doi.org/10.1038/nclimate2758

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*(2), 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Finelli, C. M., Helmuth, B. S., Pentcheff, N. D., & Wethey, D. S. (2007). Intracolony variability in photosynthesis by corals is affected by water flow: Role of oxygen flux. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps07101

Francis, F. T., Filbee-Dexter, K., Yan, H. F., & Côté, I. M. (2019). Invertebrate herbivores: Overlooked allies in the recovery of degraded coral reefs? *Global Ecology and Conservation*, *17*, 1–11. https://doi.org/10.1016/j.gecco.2019.e00593

Goergen, E. A., Schopmeyer, S., Moulding, A. L., Moura, A., Kramer, P., & Viehman, T. S. (2020). Coral reef restoration monitoring guide: Methods to evaluate restoration success from local to ecosystem scales*. NOAA Technical Memorandum NOS NCCOS 279. Silver Spring, MD. September*, 145. https://doi.org/10.25923/xndz-h538

Graham, N. A. J., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*. https://doi.org/10.1007/s00338-012-0984-y

Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y. W., Maughan, H., Pantos, O., Roach, T. N. F., Sanchez, S. E., Silveira, C. B., Sandin, S., Smith, J. E., & Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2016.42

Haas, A. F., Jantzen, C., Naumann, M. S., Iglesias-Prieto, R., & Wild, C. (2010). Organic matter release by the dominant primary producers in a Caribbean reef lagoon: Implication for *in situ* O2 availability. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps08631

Haas, A. F., Nelson, C. E., Kelly, L. W., Carlson, C. A., Rohwer, F., Leichter, J. J., Wyatt, A., & Smith, J. E. (2011). Effects of coral reef benthic primary producers on dissolved organic carbon and microbial activity. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0027973

Haas, A. F., Nelson, C. E., Rohwer, F., Wegley-Kelly, L., Quistad, S. D., Carlson, C. A., Leichter, J. J., Hatay, M., & Smith, J. E. (2013). Influence of coral and algal exudates on microbially mediated reef metabolism. *PeerJ*. https://doi.org/10.7717/peerj.108

Häder, D. P., Banaszak, A. T., Villafañe, V. E., Narvarte, M. A., González, R. A., & Helbling, E. W. (2020). Anthropogenic pollution of aquatic ecosystems: Emerging problems with global implications. *Science of the Total Environment*, *713*, 136586. https://doi.org/10.1016/j.scitotenv.2020.136586

Hartmann, A. C., Petras, D., Quinn, R. A., Protsyuk, I., Archer, F. I., Ransome, E., Williams, G. J., Bailey, B. A., Vermeij, M. J. A., Alexandrov, T., Dorrestein, P. C., & Rohwer, F. L. (2017). Meta-mass shift chemical profiling of metabolomes from coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1710248114

Higgins, E., Metaxas, A., & Scheibling, R. E. (2022). A systematic review of artificial reefs as platforms for coral reef research and conservation. *PLoS ONE*, *17*(1 January), 1–23. https://doi.org/10.1371/journal.pone.0261964

Johnson, M. D., Scott, J. J., Leray, M., Lucey, N., Bravo, L. M. R., Wied, W. L., & Altieri, A. H. (2021). Rapid ecosystem-scale consequences of acute deoxygenation on a Caribbean coral reef. *Nature Communications*, *12*(1), 1–12. https://doi.org/10.1038/s41467-021-24777-3

Knowles, B., Silveira, C. B., Bailey, B. A., Barott, K., Cantu, V. A., Cobian-Guëmes, A. G., Coutinho, F. H., Dinsdale, E. A., Felts, B., Furby, K. A., George, E. E., Green, K. T., Gregoracci, G. B., Haas, A. F., Haggerty, J. M., Hester, E. R., Hisakawa, N., Kelly, L. W., Lim, Y. W., … Rohwer, F. (2016). Lytic to temperate switching of viral communities. *Nature*. https://doi.org/10.1038/nature17193

Laila, T., Arruda, A., Barbosa, J., & Moura, E. (2021). Advances in Ergonomics in Design. *Lecture Notes in Networks and Systems*, *955*(July). https://doi.org/10.1007/978-3-319-60582-1

Leray, M., & Knowlton, N. (2015). DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1424997112

Lirman, D., Thyberg, T., Herlan, J., Hill, C., Young-Lahiff, C., Schopmeyer, S., Huntington, B., Santos, R., & Drury, C. (2010). Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs*, *29*(3), 729–735.

Littler, M. M., Littler, D. S., & Brooks, B. L. (2006). Harmful algae on tropical coral reefs: Bottom-up eutrophication and top-down herbivory. *Harmful Algae*, *5*(5), 565–585. https://doi.org/10.1016/j.hal.2005.11.003

Mass, T., Genin, A., Shavit, U., Grinstein, M., & Tchernov, D. (2010). Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.0912348107

McDole, T., Nulton, J., Barott, K. L., Felts, B., Hand, C., Hatay, M., Lee, H., Nadon, M. O., Nosrat, B., Salamon, P., Bailey, B., Sandin, S. A., Vargas-Angel, B., Youle, M., Zgliczynski, B. J., Brainard, R. E., & Rohwer, F. (2012). Assessing coral reefs on a Pacific-wide scale using the microbialization score. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0043233

Nakamura, T., & Van Woesik, R. (2001). Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps212301

Nakamura, T., & Yamasaki, H. (2005). Requirement of water-flow for sustainable growth of Pocilloporid corals during high temperature periods. *Marine Pollution Bulletin*. https://doi.org/10.1016/j.marpolbul.2005.06.025

Nakamura, T., Yamasaki, H., & Van Woesik, R. (2003). Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps256287

Nedimyer, K., Gaines, K., & Roach, S. (2011). Coral Tree Nursery©: An innovative approach to growing corals in an ocean-based field nursery. *AACL Bioflux*, *4*(4), 442–446.

Nelson, H. R., & Altieri, A. H. (2019). Oxygen: the universal currency on coral reefs. In *Coral Reefs*. https://doi.org/10.1007/s00338-019-01765-0

Padi. (2005). *Mooring Buoy Planning Guide*. 92.

Pearman, J. K., Anlauf, H., Irigoien, X., & Carvalho, S. (2016). Please mind the gap - Visual census and cryptic biodiversity assessment at central Red Sea coral reefs. *Marine Environmental Research*. https://doi.org/10.1016/j.marenvres.2016.04.011

Pearman, J. K., Aylagas, E., Voolstra, C. R., Anlauf, H., Villalobos, R., & Carvalho, S. (2019). Disentangling the complex microbial community of coral reefs using standardized Autonomous Reef Monitoring Structures (ARMS). *Molecular Ecology*. https://doi.org/10.1111/mec.15167

Pearman, J. K., Leray, M., Villalobos, R., Machida, R. J., Berumen, M. L., Knowlton, N., & Carvalho, S. (2018). Cross-shelf investigation of coral reef cryptic benthic organisms reveals diversity patterns of the hidden majority. *Scientific Reports*. https://doi.org/10.1038/s41598-018-26332-5

Pennesi, C., & Danovaro, R. (2017). Assessing marine environmental status through microphytobenthos assemblages colonizing the Autonomous Reef Monitoring Structures (ARMS) and their potential in coastal marine restoration. *Marine Pollution Bulletin*. https://doi.org/10.1016/j.marpolbul.2017.08.001

Plaisance, L., Caley, M. J., Brainard, R. E., & Knowlton, N. (2011). The diversity of coral reefs: What are we missing? *PLoS ONE*. https://doi.org/10.1371/journal.pone.0025026
Ransome, E., Geller, J. B., Timmers, M., Leray, M., Mahardini, A., Sembiring, A., Collins, A. G., & Meyer, C. P. (2017). The importance of standardization for biodiversity comparisons: A case study using autonomous reef monitoring structures (ARMS) and metabarcoding to measure cryptic diversity on Mo'orea coral reefs, French Polynesia. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0175066

Reidenbach, M. A., Koseff, J. R., & Koehl, M. A. R. (2009). Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave-driven flow. *Limnology and Oceanography*, *54*(1), 318–330. https://doi.org/10.4319/lo.2009.54.1.0318

Reidenbach, M. A., Stocking, J. B., Szczyrba, L., & Wendelken, C. (2021). Hydrodynamic interactions with coral topography and its impact on larval settlement. *Coral Reefs*, *40*(2), 505–519. https://doi.org/10.1007/s00338-021-02069-y

Rinkevich, B. (2005). Conservation of coral reefs through active restoration measures: Recent approaches and last decade progress. In *Environmental Science and Technology*. https://doi.org/10.1021/es0482583

Rinkevich, B. (2019). The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. *Journal of Marine Science and Engineering*, *7*(7). https://doi.org/10.3390/jmse7070201

Rix, L., de Goeij, J. M., van Oevelen, D., Struck, U., Al-Horani, F. A., Wild, C., & Naumann, M. S. (2017). Differential recycling of coral and algal dissolved organic matter via the sponge loop. *Functional Ecology*. https://doi.org/10.1111/1365-2435.12758

Rogers, C. S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, *62*, 185–202. https://doi.org/10.3354/meps062185

Scheffers, S. R., Nieuwland, G., Bak, R. P. M., & Van Duyl, F. C. (2004). Removal of bacteria and nutrient dynamics within the coral reef framework of Curaçao (Netherlands Antilles). *Coral Reefs*, *23*(3), 413–422. https://doi.org/10.1007/s00338-004-0400-3

Scofield, V., Jacques, S. M. S., Guimarães, J. R. D., & Farjalla, V. F. (2015). Potential changes in bacterial metabolism associated with increased water temperature and nutrient inputs in tropical humic lagoons. *Frontiers in Microbiology*, *6*(MAR), 1–10. https://doi.org/10.3389/fmicb.2015.00310

Shafir, S., Van Rijn, J., & Rinkevich, B. (2006). A mid water coral nursery. *Proceedings of the 10th International Coral Reef Symposium*.

Silveira, C. B., Cavalcanti, G. S., Walter, J. M., Silva-Lima, A. W., Dinsdale, E. A., Bourne, D. G., Thompson, C. C., & Thompson, F. L. (2017). Microbial processes driving coral reef organic carbon flow. *FEMS Microbiology Reviews*. https://doi.org/10.1093/femsre/fux018

Stella, J. S., Pratchett, M. S., Hutchings, P. A., & Jones, G. P. (2011). Coral-associated invertebrates: Diversity, ecological importance and vulnerability to disturbance. In *Oceanography and Marine Biology: An Annual Review*.

Stewart, H. L., Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2006). Symbiotic crabs maintain coral health by clearing sediments. *Coral Reefs*, *25*(4), 609–615. https://doi.org/10.1007/s00338-006-0132-7

Szmit, R. (2017). Geometry design and structural analysis of steel single-layer geodesic domes. *Proceedings - 2017 Baltic Geodetic Congress (Geomatics), BGC Geomatics 2017*, *1*, 205–209. https://doi.org/10.1109/BGC.Geomatics.2017.9

Timmers, M. A., Jury, C. P., Vicente, J., Bahr, K. D., Webb, M. K., & Toonen, R. J. (2021). Biodiversity of coral reef cryptobiota shuffles but does not decline under the combined stressors of ocean warming and acidification. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(39). https://doi.org/10.1073/pnas.2103275118

Van Duyl, F. C., Scheffers, S. R., Thomas, F. I. M., & Driscoll, M. (2006). The effect of water exchange on bacterioplankton depletion and inorganic nutrient dynamics in coral reef cavities. *Coral Reefs*. https://doi.org/10.1007/s00338-005-0066-5

Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., & Gobler, C. J. (2014). Coastal ocean acidification: The other eutrophication problem. *Estuarine, Coastal and Shelf Science*, *148*, 1–13. https://doi.org/10.1016/j.ecss.2014.05.027

Williams, S. M. (2022). The reduction of harmful algae on Caribbean coral reefs through the reintroduction of a keystone herbivore, the long-spined sea urchin Diadema antillarum. *Restoration Ecology*, *30*(1), e13475. https://doi.org/https://doi.org/10.1111/rec.13475

Zaneveld, J. R., Burkepile, D. E., Shantz, A. A., Pritchard, C. E., McMinds, R., Payet, J. P., Welsh, R., Correa, A. M. S., Lemoine, N. P., Rosales, S., Fuchs, C., Maynard, J. A., & Thurber, R. V. (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature Communications*. https://doi.org/10.1038/ncomms11833

APPENDIX 1

PVC ARMS MANUFACTURE & ASSEMBLY

PVC ARMS are made of plates of dark PVC and stainless-steel rods, nuts, and bolts. They are comprised of between seven and nine PVC plates that are approximately one foot squared and one quarter inch thick. The plates are stacked with gaps that separate them by approximately one inch using PVC crossbars or circular plugs. The bottom of the ARMS is a rectangular PVC baseplate that is 18 x 14 inches and half an inch thick. The stack of foot-square plates is connected to the baseplate by stainless steel rods at all four corners of the plates that bolt into the baseplate. The baseplate is attached to the reef, most commonly by driving rebar posts through gaps on either side of the baseplate.

ARMS were designed to census cryptic reef diversity on benthic marine and freshwater ecosystems (Moews-Asher et al., 2018). To carry out a census with ARMS, a unit is secured to the sea-, lake-, or river-floor for a set period of time— usually one to three years—during which time the ARMS unit passively aggregates organisms. On coral reefs, our research group has found that 1 year is sufficient to collect most local taxa. It is important to note that qualitative accounts suggest long deployments (e.g., 4 years) lead to lower diversity of organisms and overgrowth of the ARMS unit by a few taxa.

Table S2.1 Manufacturing and assembly of PVC ARMS.

Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per ARMS	Total time to complete task (min)	Refer to drawing #
PVC ARMS	1	Cut PVC baseplate	Cut 0.5" thick PVC sheet on Waterjet to match ARMS baseplate drawing	Waterjet	10	1	10	Figure SI 1
PVC ARMS	2	Cut PVC long cross spacers	Cut 0.5" thick PVC sheet on Waterjet to match ARMS long cross spacer drawing	Waterjet	2	4	8	Figure SI 2
PVC ARMS	3	Cut PVC short cross spacers	Cut 0.5" thick PVC sheet on Waterjet to match ARMS short cross spacer drawing	Waterjet	2	8	16	Figure SI 3
PVC ARMS	4	Cut PVC layering plates	Cut 0.25" thick PVC sheet on Waterjet to match ARMS layering plate drawing	Waterjet	5	9	45	Figure SI 4

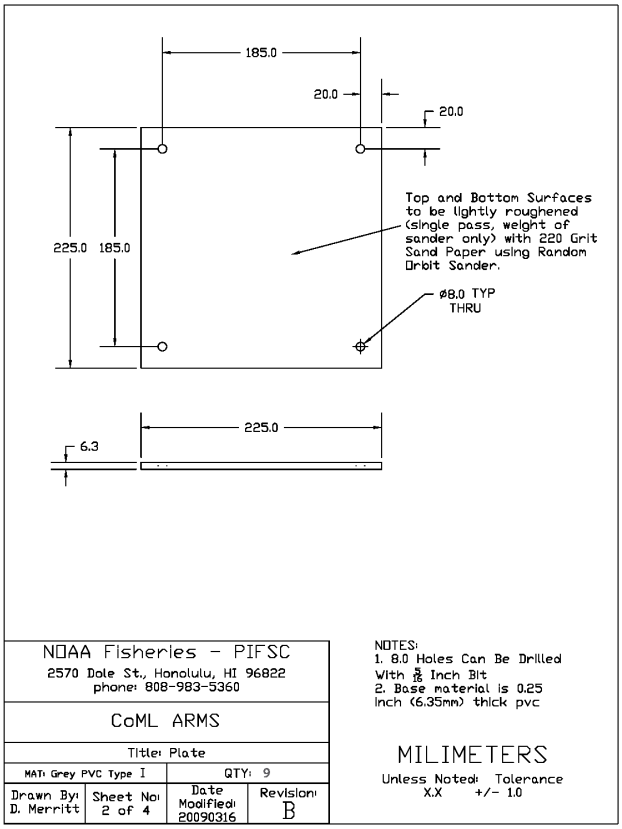


Figure S2.1 Technical drawing for manufacture of PVC baseplates.

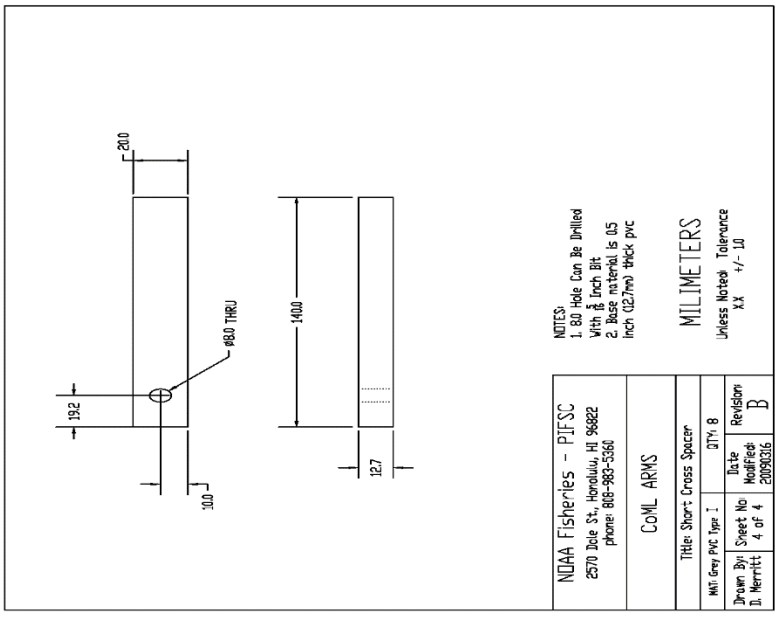


Figure S2.2 Technical drawing for manufacture of PVC long cross spacers

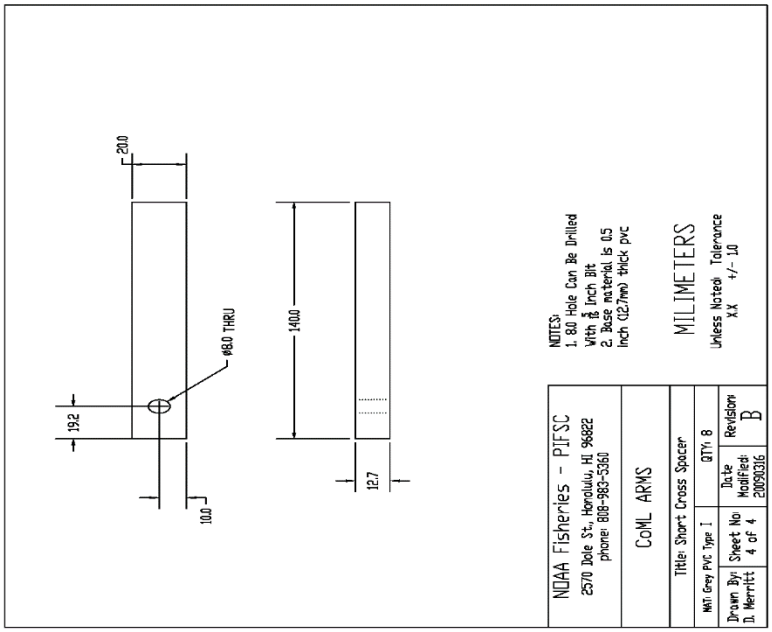


Figure S2.3 Technical drawing for manufacture of PVC short cross spacers

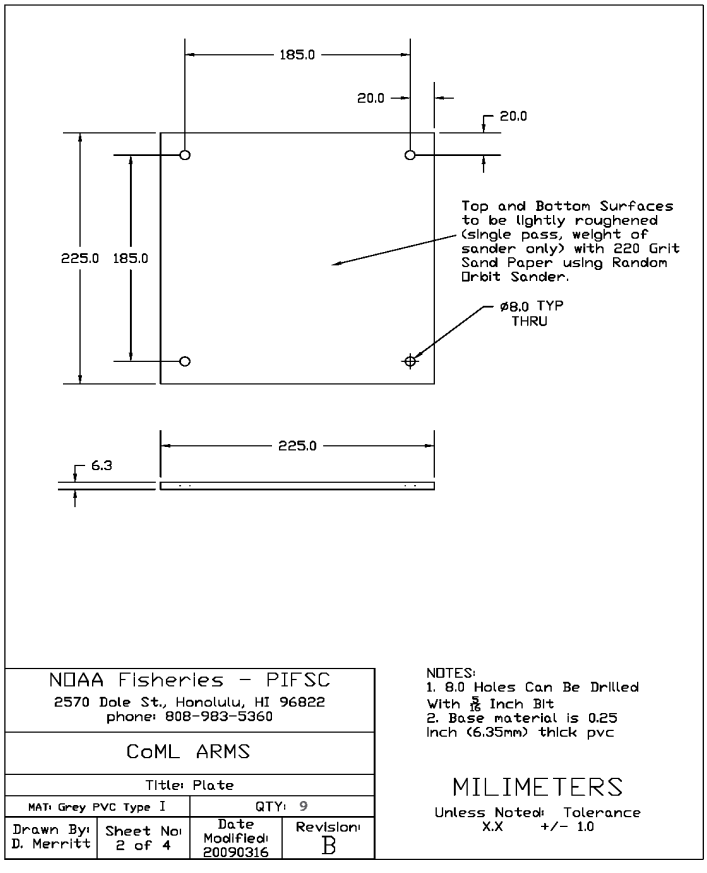


Figure S2.4 Technical drawing for manufacture of PVC layering plates.

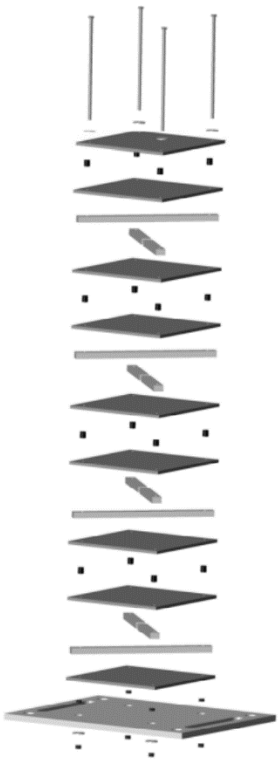


Figure S2.5 Exploded diagram of ARMS units and instructions for assembly.

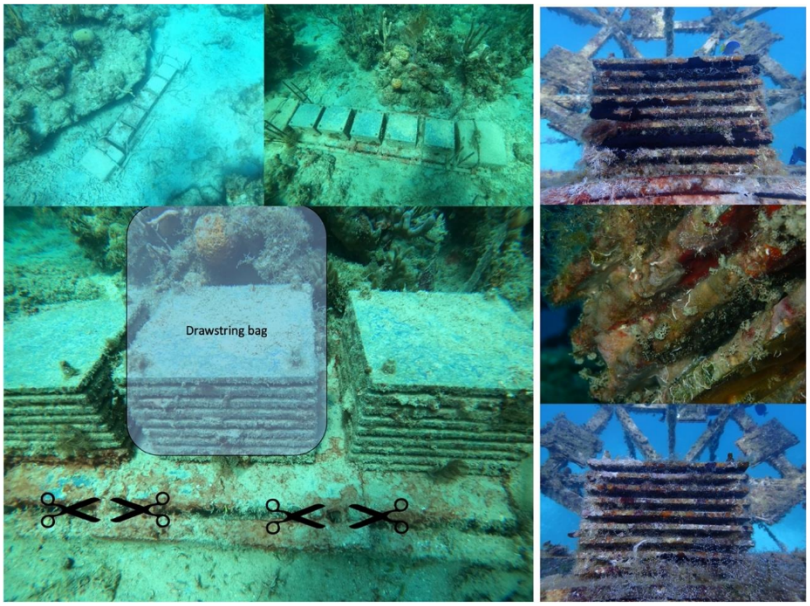


Figure S2.6 Alternative methods for ARMS deployment. (Top) Chains of ARMS are connected using heavy duty cable ties and the ends of these chains are anchored with hardened concrete bags. (Bottom) Seeded ARMS should be covered temporarily with 100µm mesh bags to transfer from seafloor sites to Arks without losing small mobile invertebrates.(Right) Seeded ARMS after transfer to Shell Arks.

Limestone ARMS Manufacture & Assembly

Limestone ARMS are constructed from unfinished limestone or travertine tiles and a two-part, quick- setting marine grade epoxy. A single limestone ARMS unit may consist of 5–6 tile layers separated by tile spacers, cut using a tile saw from the same limestone tiles. These spacers may be different sizes of rectangular and square pieces and are organized on ARMS layers in configurations that mimic the three- dimensional complexity of hardbottom substrates. Some layers may be stacked higher (2 cm) or lower (1 cm) than others to create crevices while leaving space for organisms to colonize the interior of the structure. Approximately 10 one-foot squared limestone tiles (1 cm thick) are used for the construction of one limestone ARMS. The quick-setting epoxy is used to glue the tile to the material below it. Limestone ARMS are not fastened to a baseplate.

Limestone tiles provide a cryptic environment made of the same material as hardbottom substrates found on coral reefs, and therefore, better replicate the natural habitat of the organisms that they are passively aggregating.

Table S2.2 Manufacture and assembly of Limestone ARMS.

Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per ARMS	Total time to complete task (min)	Refer to drawing #
Limestone ARMS	1	Cut limestone tile	Use tile saw to cut limestone tile into appropriate sized pieces for assembling limestone ARMS with desired internal complexity. Let dry.	Wet tile saw	5	10	50	Figure SI 7 & 8
Limestone ARMS	2	Assemble ARMS	Glue smaller travertine pieces to a larger travertine layering plate along a pre-drawn grid pattern. Allow to cure based on manufacturer recommendation.	Two-part marine epoxy putty	10	5	50	Figure SI 7 & 8

Figure S2.7 Limestone ARMS deployed on reefs passively aggregate sessile and mobile invertebrate communities. Mobile invertebrates tend to take refuge in ARMS whose internal complexity most closely matches their body size.

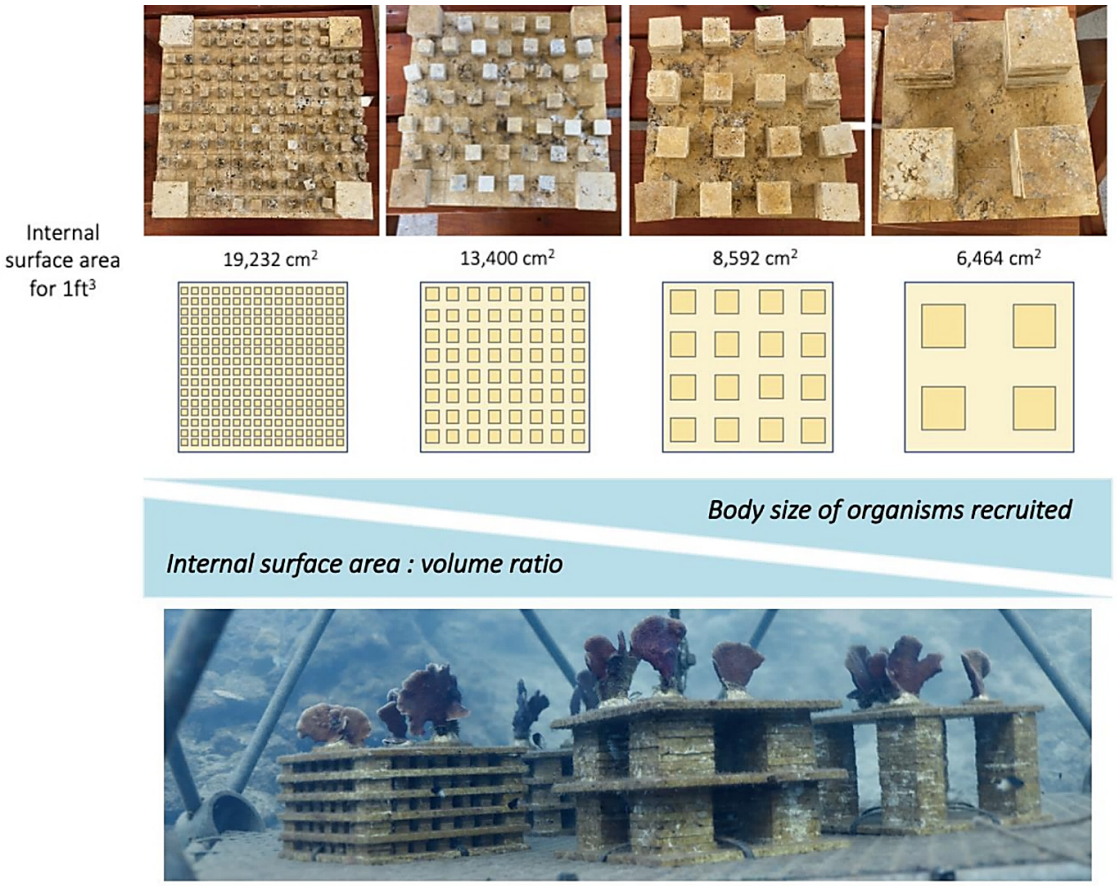


Figure S2.8 Limestone ARMS can be built with differing internal complexities. Smaller, more numerous internal components yield higher internal surface area, with implications on fouling (biofilms and sessile invertebrate communities) and a correspondingly lower internal surface area to volume ratio. ARMS complexities can be designed based on desired recruitment patterns, with higher complexity ARMS recruiting smaller mobile organisms.

Shell Ark Manufacture & Assembly

“Shell” Coral Arks are 2V frequency, geodesic, buoyant, submerged structures attached to an anchoring system to provide a midwater artificial reef structure. The structures deployed in Vieques, Puerto Rico, are 8’ in diameter and primarily comprised of 2” diameter foam-filled fiberglass struts, connected to one another with stainless steel hardware. Buoyancy is provided by 14” diameter plastic trawl floats. The Shell Arks have five mooring attachment points around their base and are attached to three previously installed sand anchors using a mooring system comprised of lines, chain, shackles, and swivels made of stainless steel and galvanized components. They also include HDPE baseplates that are designed to receive limestone plates onto which corals requiring translocation have been secured and seeded ARMS (autonomous reef monitoring structures) that are used to translocate non-coral reef biodiversity to the Arks. See below for detailed manufacture and assembly instructions.

In air, each Shell Ark weighs 700 lbs fully constructed, and is top-heavy because the buoyant trawl floats are concentrated at the top of the structure. Ten of the trawl floats can be removed, bringing the weight in air down to 500 lbs, to allow for potentially easier transport to the installation site.

Table S2.3 Manufacture and assembly of components for Shell Arks frame.

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Shell	Struts	1	Cut struts (S1)	Cut to 20.905" long (531 mm) on miter saw	Miter saw, saw blades	2	55	110	Figure SI 9
Shell	Struts	2	Cut struts (S2)	Cut to 24.331" long (618 mm) on miter saw	Miter saw, saw blades	2	60	120	Figure SI 9
Shell	Struts	3	Cut struts (stainless)	Cut to 20.905" long (531 mm) on miter saw	Miter saw, saw blades	10	5	50	Figure SI 9
Shell	Struts	4	Drill bolt holes in struts (fiberglass)	Drill two 7/32" holes at the end of each strut (thru entire rod). Center of first hole dilled at 0.98" from end of strut (25 mm). Distance from the center of the first hole to the center of the second hole is 1.06" (27 mm). The distance between the two inside holes on S1 struts is 16.81" (427 mm) and for S2 struts is 20.24" (514 mm).	Drill press, drill bit (7/32")	2	115	230	Figure SI 9
Shell	Struts	5	Drill bolt holes in struts (stainless)	Hole dimensions same for both S1 and S2 struts. Drill template stainless strut and set up vertically in vice, with non-drilled stainless strut behind it. Use template screw holes (7/32") as a guide to drill the remaining stainless struts (both sides).	Drill press, drill bit (7/32")	10	5	50	Figure SI 9

Table S2.3 Manufacture and assembly of components for Shell Arks frame. (Continued)

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Shell	Struts	6	Cut foam into strips for struts	Rip to 1.5" wide and thick on table saw, and to 15.5" long for S1 and 19" long for S2 struts	Table saw, exacto blade	1	115	115	
Shell	Struts	7	Add foam into struts	Push into strut until flush using a firm tap against a table; then use a marked piece of wood and mallet to insert so that the foam sits in the middle of the strut	Mallet	1	115	115	
Shell	Struts	8	Epoxy to seal foam in struts	Stand foam-filled struts on end, mix epoxy and hardener in small batches, pour about 5 ml (~0.3-0.4 cm depth) into one side of each strut. Leave to harden overnight, then flip struts and repeat	Two-part epoxy	1	115	115	

Table S2.3 Manufacture and assembly of components for Shell Arks frame. (Continued)

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Shell	Stars	1	Prepare 5x N2 stars for stainless connections	Drill larger bolt hole on outer hole of one arm for Padeye connector	Drill bit (1/4")	3	5	15	Figure SI 10
Shell	Stars	2	Prepare 10x N2 stars for floats	Drill out larger central hole to accommodate 1" threaded fiberglass rod	Use 2x step bits: first High-Speed Steel Multidiameter Drill Bit, 10 Inch Sizes (part 89315A42 from McMaster) and then 12 Inch Sizes (part 89315A42 from McMaster)	15	10	150	Figure SI 10
Shell	Stars	3	Prepare 2x N1 stars for top/bottom connections	Machine/weld connections to insert top and bottom of central unthreaded fiberglass structural rod	*Outsourced*	*Out-sourced*	*Out-sourced*	*Out-sourced*	Figure SI 10

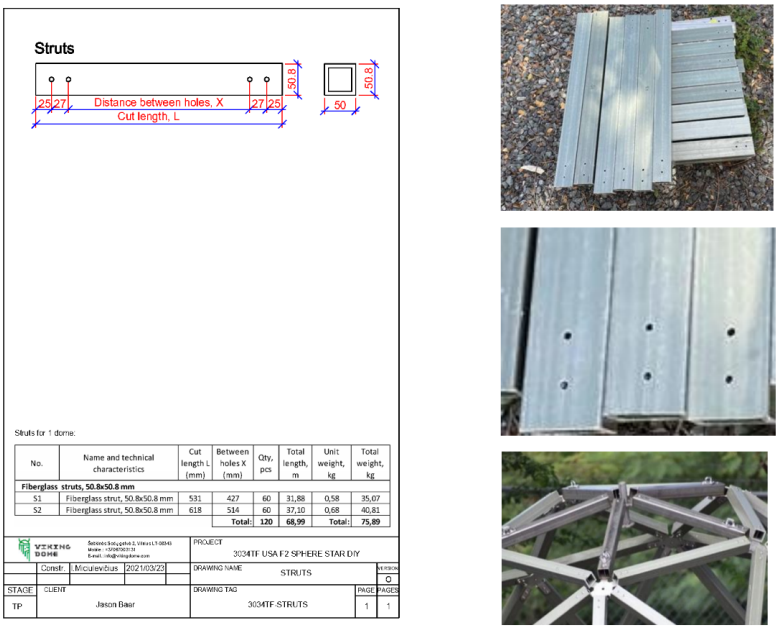


Figure S2.9 Types of struts. (Left) Technical drawing for manufacture of fiberglass square struts (adapted from Viking Dome assembly materials). (Right) Images of cut and drilled fiberglass and stainless steel struts.

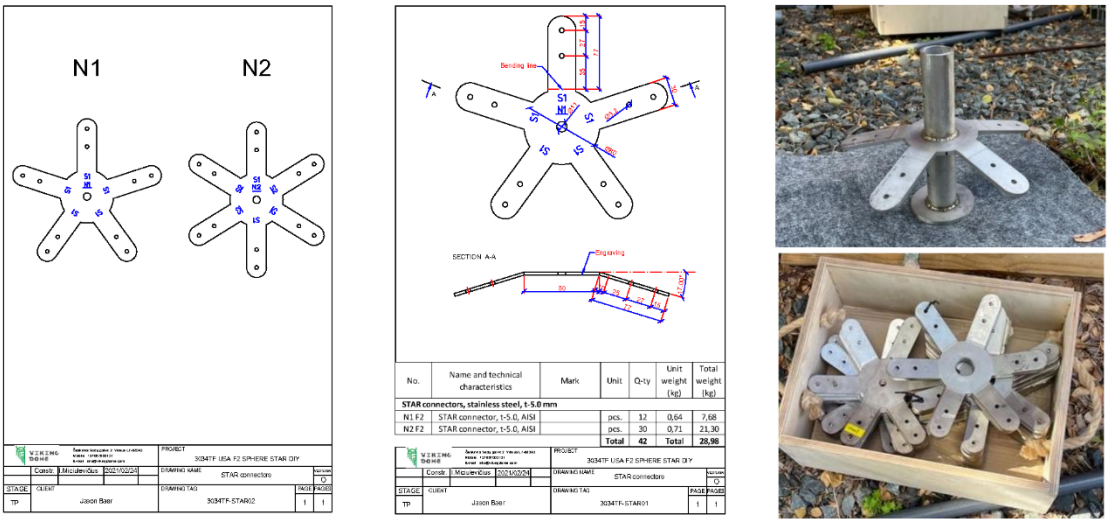


Figure S2.10 **(**Left and middle) Technical drawing for manufacture of STAR connectors (adapted from Viking Dome assembly materials). (Right) Images of STAR connectors modified for top/bottom of Arks and for float attachments**.**

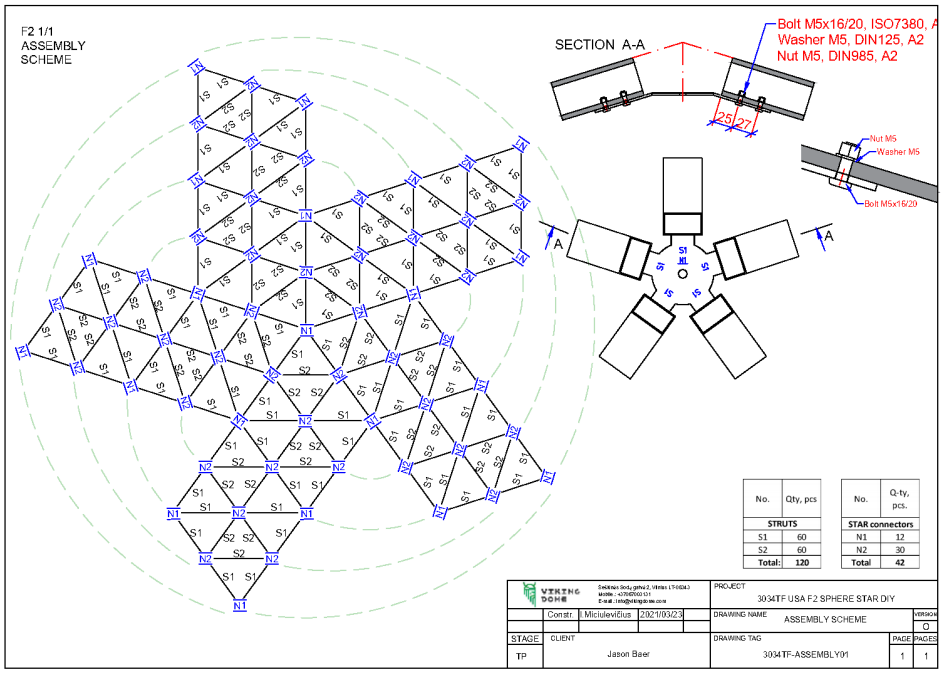


Figure S2.11 Assembly of Struts and STAR connectors in geodesic spheres. Technical drawing for assembly of struts and STAR connectors into 2V geodesic sphere (adapted from Viking Dome assembly materials).

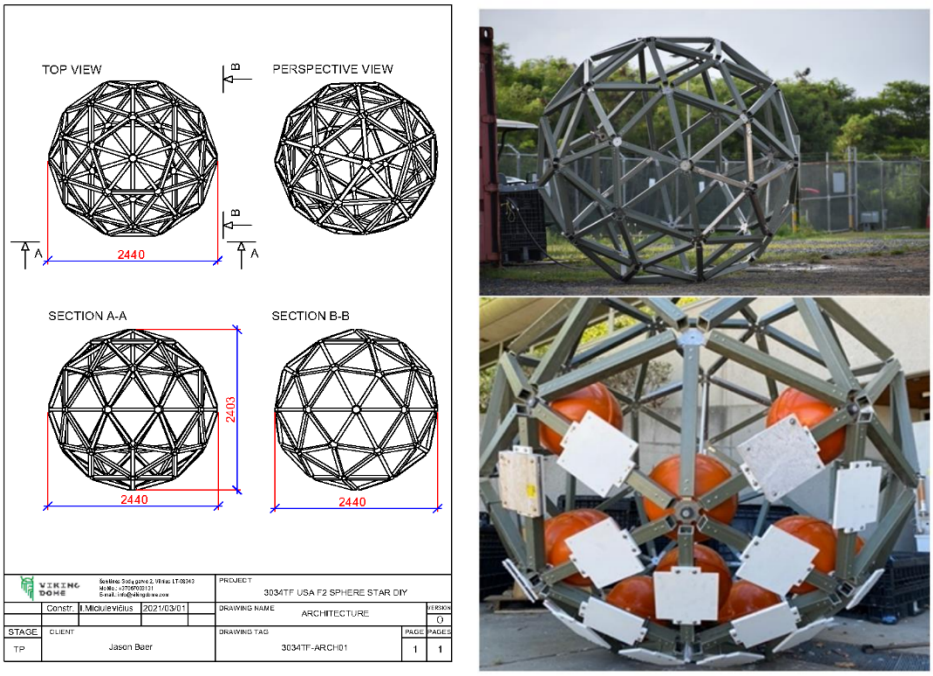


Figure S2.12 Assembly of a 2V geodesic sphere. (Left) Technical drawing for complete assembly of 2V geodesic sphere (adapted from Viking Dome assembly materials). (Right) Images of a fully assembled sphere.

Table S2.4 Manufacture and assembly of components for ARMS and coral plates and attachment to Shell Ark frame.

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Shell	ARMS and Coral Plate Baseplates	1	Waterjet baseplates	For each 48"x48" sheet of HDPE, 6x ARMS and 5x coral aseplates can be cut. Each sheet takes ~1 hour of waterjet time.	Waterjet	10	20	200	Figure SI 13 & 14
Shell	ARMS and Coral Plate Baseplates	2	Heat shrink connector plates	Cut 0.5" thick heat-shrink tubing into 1.5" lengths. Slide heat shrink over a stainless steel u-bolt bracket and use heat gun to tighten heat shrink onto bracket.	Scissors, heat gun	1	60	60	Figure SI 15
Shell	ARMS and Coral Plate Baseplates	3	Cut PVC standoffs	Cut 1/4" pipe into 1.75" long sections.	Miter saw	0.5	10	5	
Shell	Coral plates	1	Waterjet PVC baseplates	For each 48"x48" sheet of 0.25" thick PVC, 25x coralbaseplates can be cut.	Waterjet	10	20	200	Figure SI 4

Table S2.4 Manufacture and assembly of components for ARMS and coral plates and attachment to Shell Ark frame. (Continued)

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Shell	Coral plates	2	Cut travertine tiles to size	Cut on a wet tile saw to match size of coral baseplates (9" x 9") and let dry.	Wet Tile Saw	3	20	60	Figure SI 15
Shell	Coral plates	3	Mount tiles onto coral baseplates	Add liberal amount of 3M 5200 sealant to a coral baseplate and press the limestone tile down onto it.Add weight while setting.	3M 5200, weights	5	20	100	Figure SI 15
Shell	Coral plates	4	Drill out corners of coral plates	Use 1/4" masonry bit to drill out all four corners of each coral plate, through limestone and PVC plate.	Drill press, masonry bit (1/4")	2	20	40	Figure SI 15
Shell	Coral plates	5	Prepare numbered tags for coral plates	Stamp stainless steel washers with numbered stamps for desired numbers. Glue to one corner of coral plate, over corner hole.	Hammer, vice, numbered stamps	1	20	20	Figure SI 15

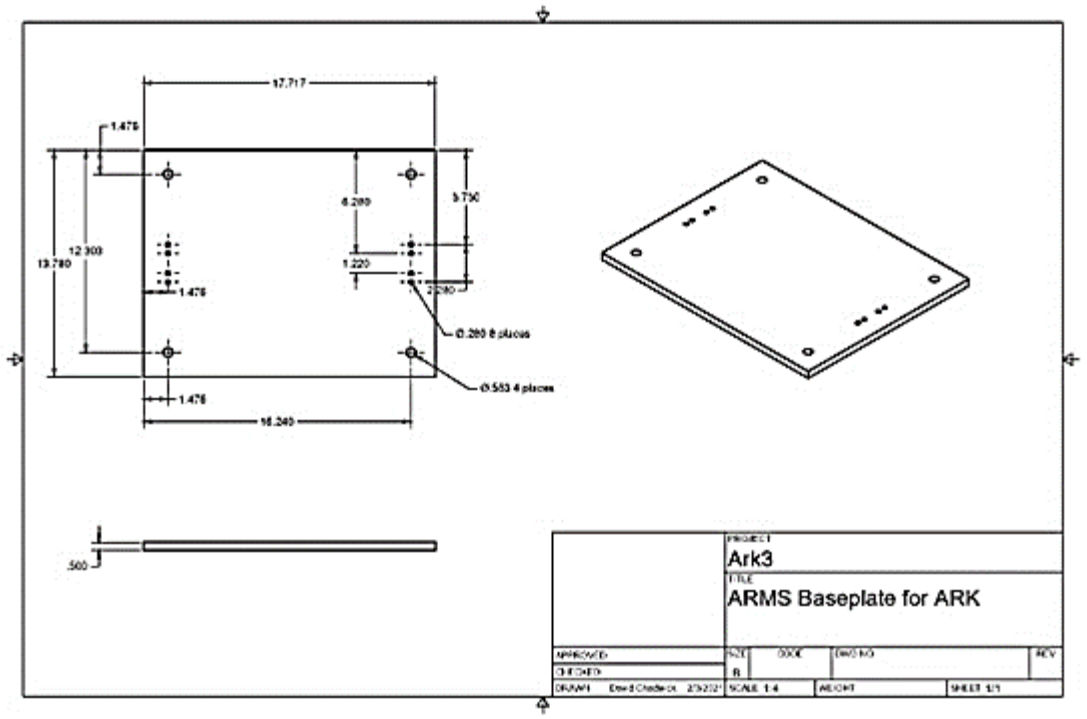


Figure S2.13 Technical drawing for manufacture of baseplates for mounting ARMS to Ark frame.

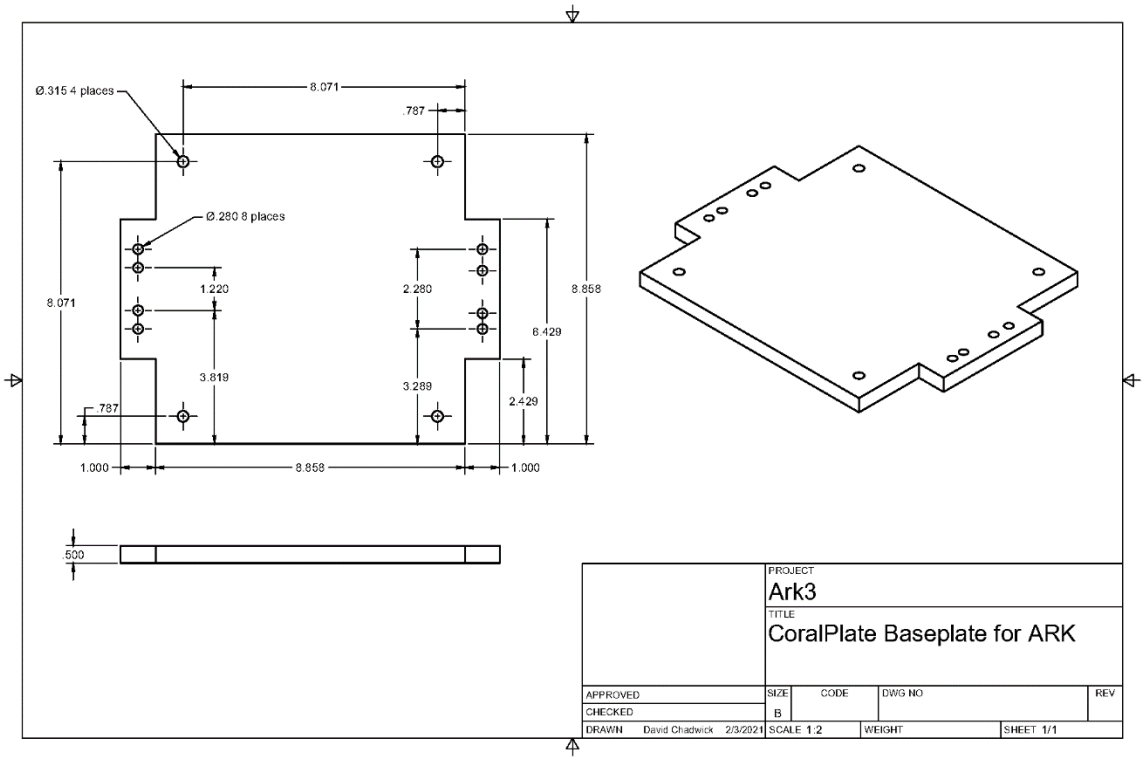


Figure S2.14 Technical drawing for manufacture of baseplates for mounting coral plates to Ark frame

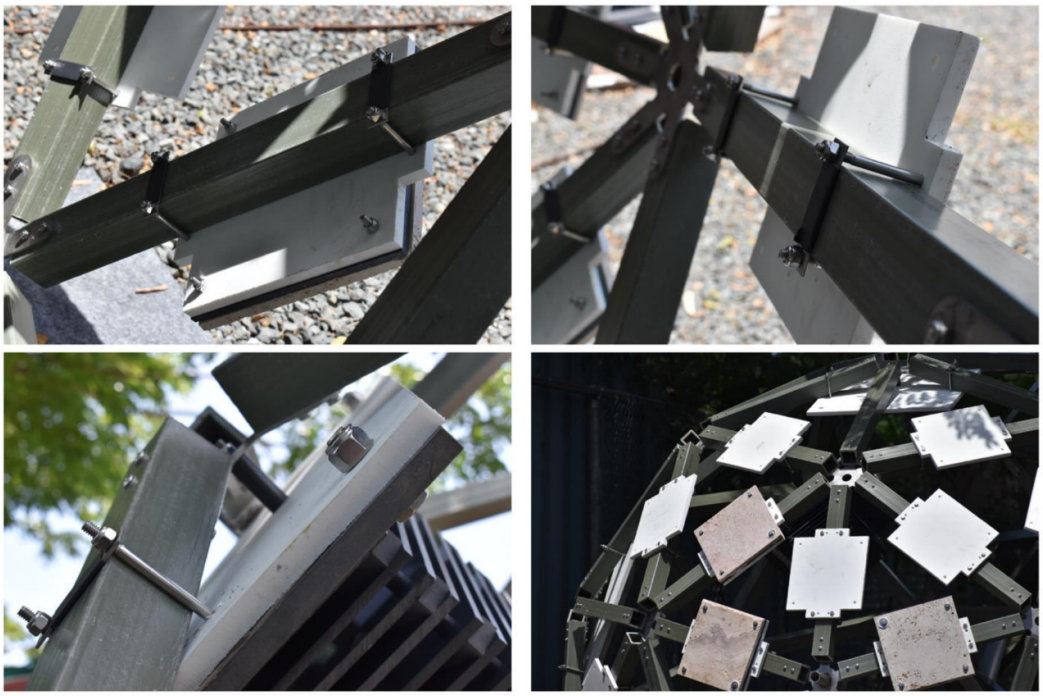


Figure S2.15 Images of coral plate and ARMS baseplates mounted to Shell Ark fiberglass struts using hardware and “non-slip” U-bolt brackets wrapped in heat-shrink tubing.

Table S2.5 Manufacture and assembly of components for buoyancy and mooring system design of Shell Arks.

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Shell	Floats	1	Cut fiberglass unthreaded rod	Cut to Ark diameter. Drill two holes at either end to match holes on machined top and bottom Stars.	Miter saw, drill bit (1/4")	5	1	5	Figure SI 16
Shell	Floats	2	Cut fiberglass threaded rods	Cut to 17-1/4" on miter saw	Miter saw, saw blades	1	10	10	Figure SI 16
Shell	Floats	3	Add heat shrink to rods	Cut 2" thick heat shrink tubing into 14" lengths. Slide onto fiberglass rods with 1" exposed on one end and 2-1/4" exposed on the other. Use a heat gun to shrink until snug.	Scissors, heat gun	3	10	30	Figure SI 16
Shell	Floats	4	Mount and seal rods into trawl floats	Slide fiberglass rod with heat shrink through trawl float. Add stainless washer and fiberglass hex nut on both sides. Before tightening, add a generous amount of 3M 5200 sealant on the inside of the washers. Tighten nuts down.	3M 5200, wrench	5	10	50	Figure SI 16
Shell	Mooring system	1	Make double-spliced Spectra lengths for Ark mooring bridle	Splice a 1/2" stainless steel sailmaker thimble into one end of a length of 5/8" Spectra rope. Splice another 1/2" stainless steel sailmaker thimble into the other end. Repeat for 5 total lines of equal length.	Outsourced	Outsourced	Outsourced	Outsourced	Figure SI 17
Shell	Mooring system	2	Make double-spliced Nylon length for Ark downline	Splice a 1" stainless steel sailmaker thimble into one end of a length of 1" nylon rope. Splice a 1" heavy duty galvanized thimble into the other end. Total length will depend on anchoring depth.	Outsourced	Outsourced	Outsourced	Outsourced	Figure SI 17

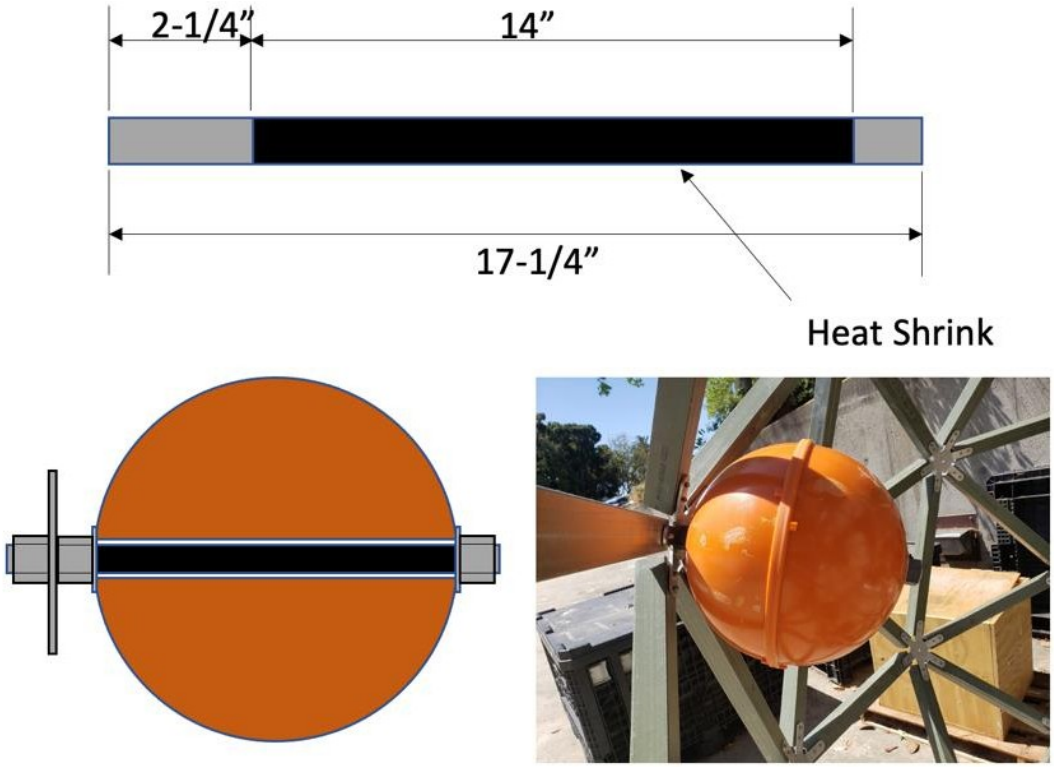


Figure S2.16 Technical drawing for manufacture of trawl floats (fixed buoyancy) and attachment to Ark frame.

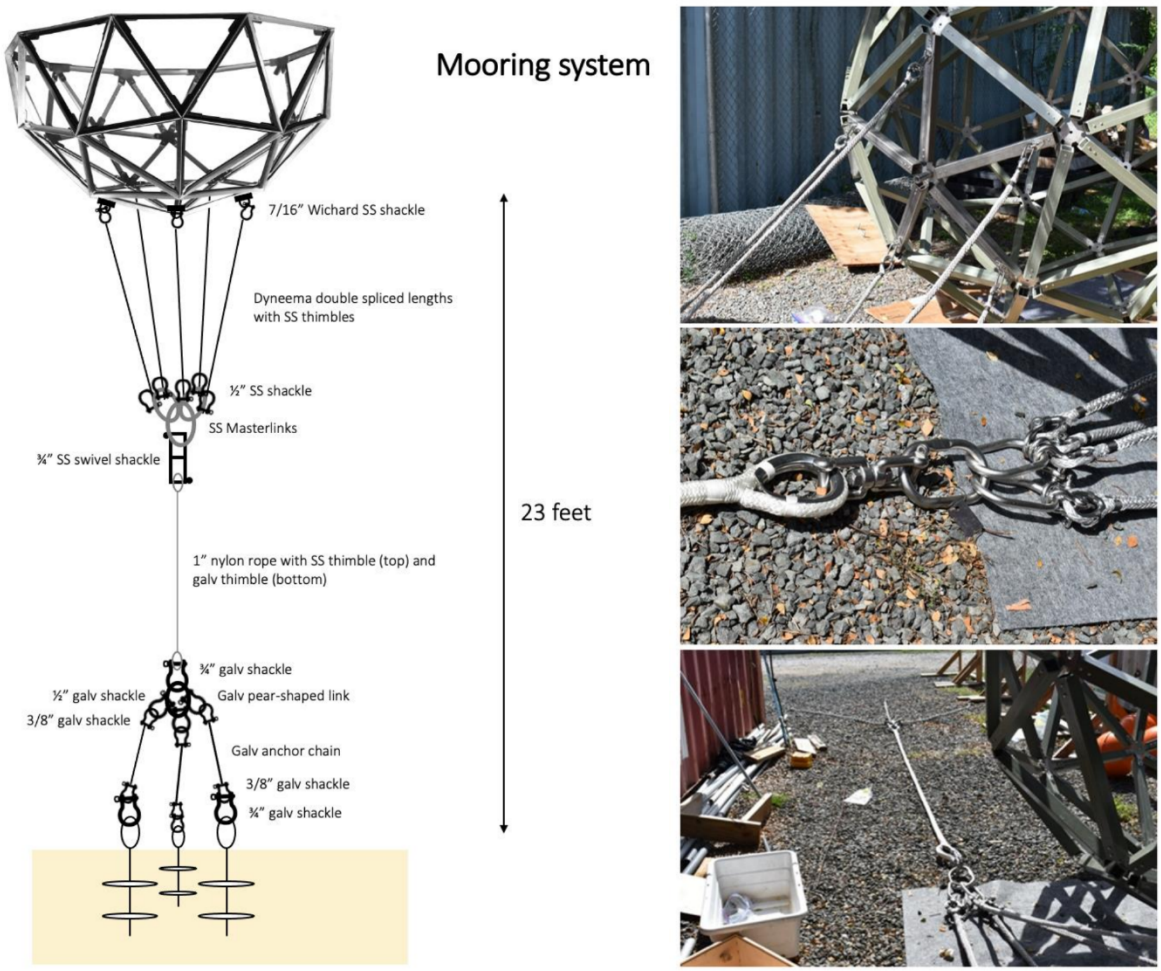


Figure S2.17 Ark Mooring system. (Left) Diagram of Ark mooring system. (Top right) Bottom of Coral Ark structure showing 5-point mooring bridle (3/4" Dyneema lines) connected to the 5 pad eyes at the base of the Ark. (Mid right) The lower portion of the Ark mooring bridle, showing 3 of the Dyneema mooring bridle lines connected to the left link, and 2 of the Dyneema mooring bridle lines connected to the right link, at the top of the stainless Masterlink using ½" stainless shackles. Also shown is the stainless swivel connecting the bottom of the stainless Masterlink to the top of the 1" nylon downline. (Bottom right) The1" nylon downline connects the mooring bridle to a chain anchor bridle, consisting of 3 lengths of chain that meet at a single galvanized pear-shaped link and are each attached to their own sand anchor eye at the opposite end using 3/8" galvanized shackles.

Location	Component	Condition - Good	Condition - Worn	Condition - Corrosion	Condition - Angled load	Condition - Fouling invasion	Comments
Ark	Orange trawl floats (11)						
	Fiberglass struts						
	SS Stars						
Ark Base	Pad eye 1						
	7/16" Wichard shackle 1						
	Pad eye 2						
	7/16" Wichard shackle 2						
	Pad eye 3						
	7/16" Wichard shackle 3						
	Pad eye 4						
	7/16" Wichard shackle 4						
	Pad eye 5						
	7/16" Wichard shackle 5						
	Zinc hull anode 1						
	Zinc hull anode 2						
	Zinc hull anode 3						
Mooring bridle	Dyneema bridle length 1						
	1/2" SS screw pin shackle 1						
	Dyneema bridle length 2						
	1/2" SS screw pin shackle 2						
	Dyneema bridle length 3						
	1/2" SS screw pin shackle 3						
	Dyneema bridle length 4						
	1/2" SS screw pin shackle 4						
	Dyneema bridle length 5						
	1/2" SS screw pin shackle 5						
	MasterLink (2-shackle)						
	MasterLink (3-shackle)						
	MasterLink - base						
	Zinc collar anode						
Down line	3/4" swivel shackle						
	1" Megebreid down line						
	SS thimble (top)						
	Galv thimble (bottom)						
Anchor bridle	3/4" galv shackle						
	Pear shaped link						
	1/2" galv shackle 1						
	3/8" galv shackle 1						
	1/2" galv chain 1						
	1/2" galv shackle 2						
	3/8" galv shackle 2						
	1/2" galv chain 2						
	1/2" galv shackle 3						
	3/8" galv shackle 3						
	1/2" galv chain 3						
Anchor	Skrew Anchor 1						
	3/4" galv shackle 1						
	3/8" galv shackle 1						
	Skrew Anchor 2						
	3/4" galv shackle 2						
	3/8" galv shackle 2						
	Skrew Anchor 3						
	3/4" galv shackle 3						
	3/8" galv shackle 3						

Figure S2.18 Ark maintenance. (Left) Ark maintenance checklist for assessing long term integrity of components and (Right) images of zinc hull anodes attached to stainless steel struts. Ark base and zinc collar anodes attached to the stainless steel Masterlink in the mooring system. Anodes should be removed and replaced as necessary to protect the stainless-steel components from degradation.

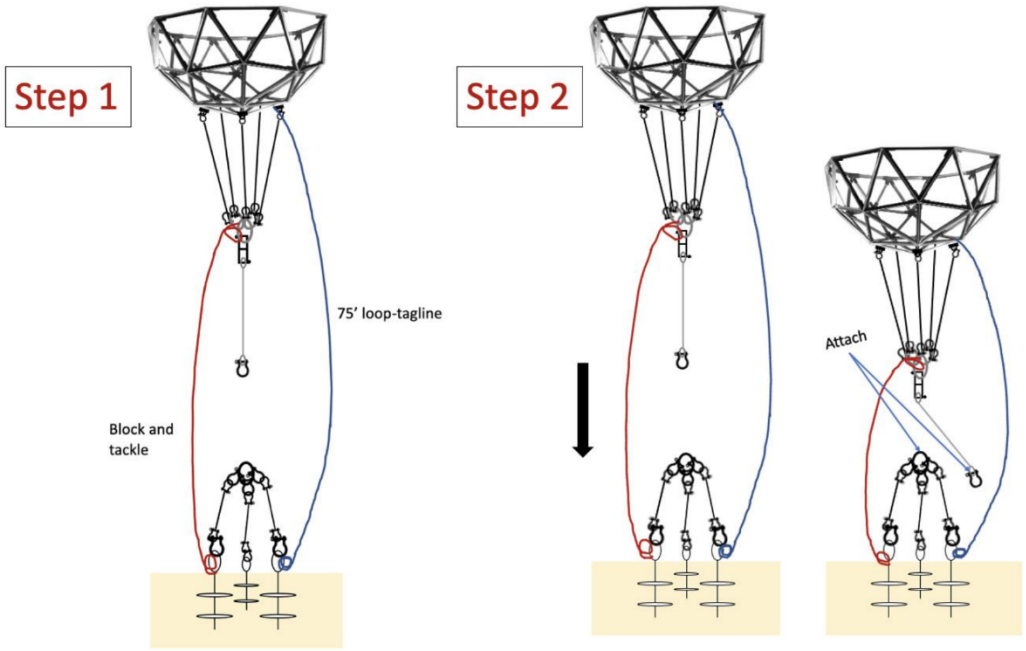


Figure S2.19 Attachment of the Arks to their mooring system. The positively buoyant Ark structures is pulled to depth using a block and tackle in order to attach the downline to the mooring system. In Step 1,the block and tackle is unspooled in order to attach one side (the end with the becket and cam) to the anchor point, and the other end to the base of the Ark mooring bridle. A safety "loop-tagline "that is attached to the Ark base and a single anchor point may be used for security in case of block and tackle failure. In Step 2, the block and tackle is engaged to pull the structure to depth. The structure is 300 lbs. positively buoyant and the block and tackle has a 6:1 purchase; thus, the force required to pull the Ark to depth is approximately 50 lbs. At the end of Step 2, the shackle at the base of the downline should be fastened to the galvanized pear-shaped link at the top of the anchor bridle, then the tension can be transferred to the mooring system and the strain gauge removed. Note: Divers should maintain continuous observation of the sand anchors to make sure they are not failing under the various loading scenarios of the installation.

Figure S2.20 Three sand anchors are installed in a triangular arrangement to provide redundancy in holding power. To install the anchors, the lower disk of the sand anchor is first buried in the sand and then a long turning bar placed through the anchor eye is used to twist the anchor into the substrate until only the eye remains above the sand.

Figure S2.21 Shell Arks may be attached to a pallet and lifted via a forklift to load them onto vessels or transport them as needed.

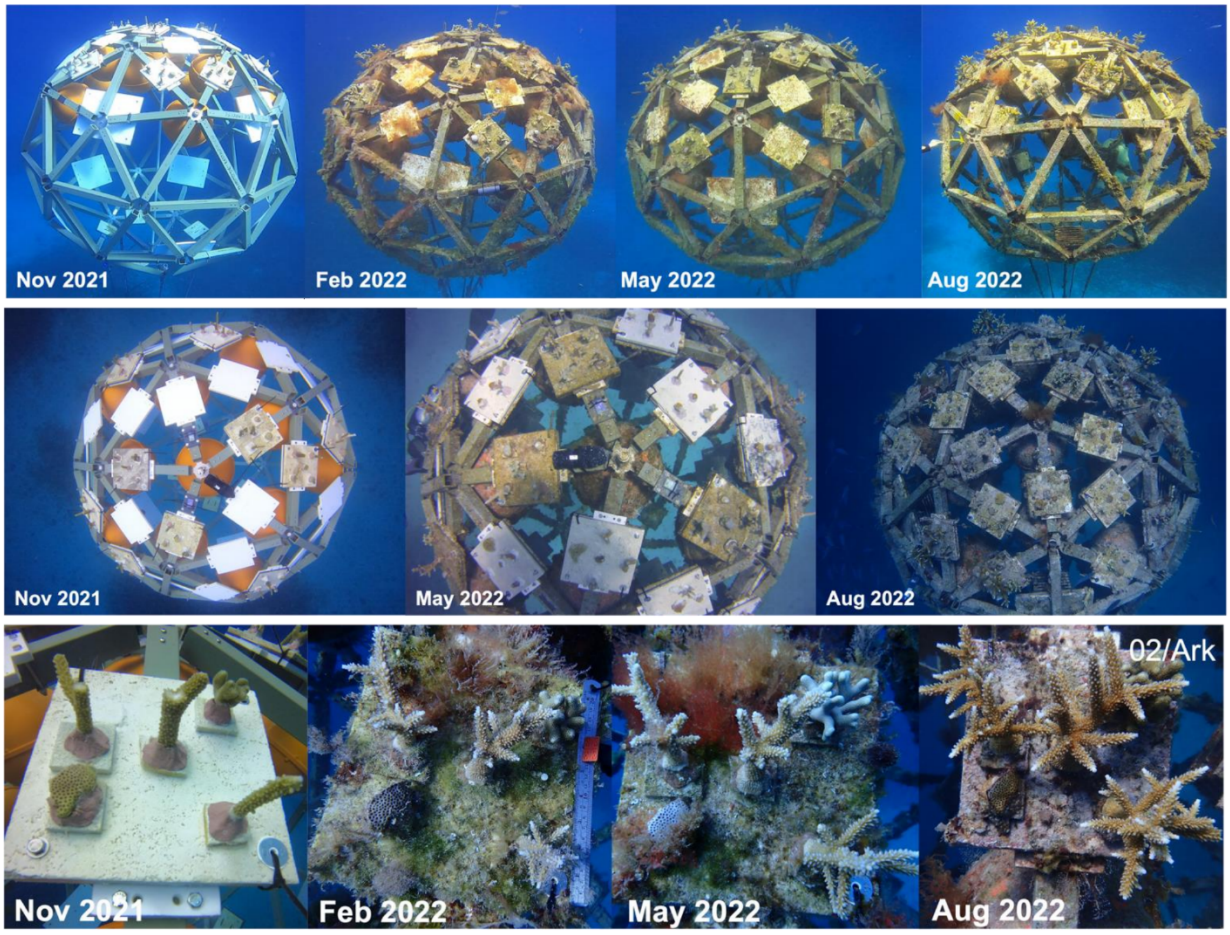


Figure S2.22 Time series of Shell Arks. (Top and Middle) Successional time series of biofouling on Shell Arks over 9 months. (Bottom) Time series of one coral plate (with 5 coral nubbins attached) on a Shell Ark over 9 months.

Two Platform Ark Manufacture & Assembly

Coral Arks are 1V frequency polyhedral structures (also called “icosahedra”) constructed from “struts” and “hubs,” with struts used to assemble the polyhedral frame and hubs used to secure these struts in place at each vertex. Arks can be built using various polyhedral geometries and frequencies and can be built as a dome (half-polyhedron) or a full polyhedron. Higher frequency polyhedrons provide more mounting locations and enhanced strength but have a higher material cost.

Arks are assembled by inserting the struts into the holes in the connectors and angling the strut downwards until they “lock” in place in the connector. This process is repeated until the half-dome or full polyhedron is constructed. Assembled polyhedrons can then be transported to the deployment site for anchoring.

Table S2.6 Manufacture and assembly of components for Two-Platform Arks frame.

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Two Plat-form	Struts	1	Cut struts	Cut 1" pipe to 4 ft lengths	Ratcheting PVC cutter or miter saw	1	30	30	
Two Plat-form	Struts	2	Drill four holes in each strut	Drill a 1/4" hole through both walls of the PVC 1.5" from the end of the strut. Drill another 1/4" hole 2 inches away from the first hole, towards the center of the strut. Repeat for the other side of the strut, ensuring all holes are along the same plane.	Drill bit (1/4")	3	30	90	
Two Plat-form	Hubs	1	Cut hubs	Cut 6" pipe to 4" lengths.	Band saw	2	12	24	

Table S2.6 Manufacture and assembly of components for Two-Platform Arks frame. (Continued)

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Two Platform	Hubs	2	Drill five equidistant holes in each hub	Mark the center line of each hub at 2". Mark the location of five equidistant points on the hub that intersect the center line. Using a 1.5" hole saw, drill five holes in each hub symmetrically around the midline.	Drill press, 1.5" hole saw and arbor	15	12	180	Figure SI 22
Two Platform	Hubs	3	Cut hub end caps	Cut 6" PVC endcaps to remove the bottom 2-3 inches (shortening to ~4"). Drill a 3/8" hole through the center of each endcap.	Band saw, drill bit (3/8")	5	2	10	
Two Platform	Platform	1	Cut molded fiberglass grating	Use waterjet to cut molded fiberglass grating platform into mirrored half pentagon shapes.	Waterjet	60	4	240	Figure SI 23
Two Platform	Platform	2	Cut fiberglass I-beam	Cut 5 ft length of structural fiberglass I-beam into 5,1 ft long segments.	Miter saw, sawblades	1	5	5	
Two Platform	Platform	3	Drill four holes in each fiberglass I-beam	Drill a 1/4" hole 2 inches from the end of each fiberglass I-beam length. Drill another 1/4" hole 2.25 inches away from the first hole towards the center of the I-beam. Repeat for the other end of the I-beam (4holes total per length).	Drill bit (1/4")	3	5	15	

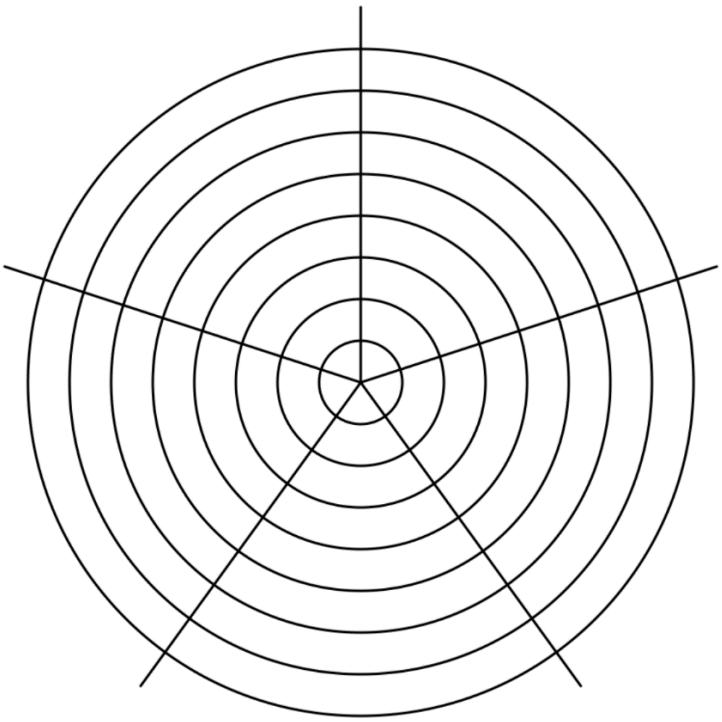


Figure S2.23 Template for marking and drilling equidistant holes in 6” PVC to form hubs.

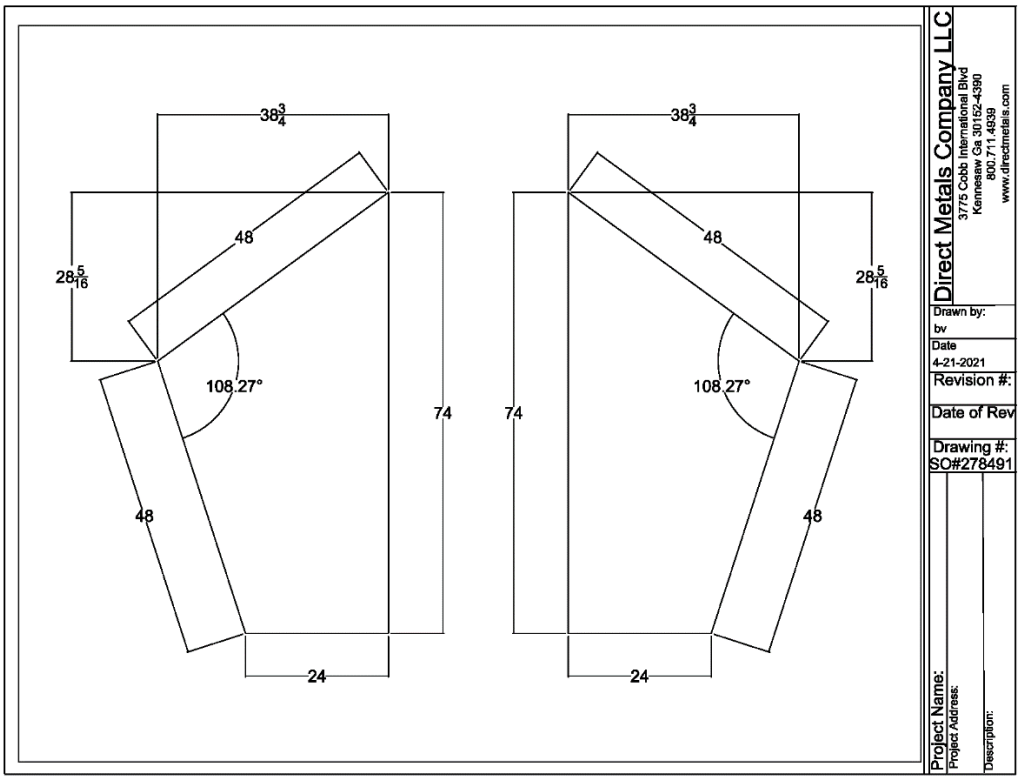


Figure S2.24 Technical drawing for manufacture of Ark platforms from molded fiberglass grating.

Figure S2.25 Assembly of Two-Platform Ark framework. Struts are inserted into hubs and locked into place via bolts and locknuts, and then a stainless-steel wire rope is passed through the finished structure to increase the strength. Two platforms are then added, bisecting the Ark horizontally.

Table S2.7 Manufacture and assembly of components for Two-Platform Ark mooring system.

Ark	Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Two Platform	Mooring system	1	Make double-spliced Spectra lengths for buoys and Ark base	Splice a 1/2" stainless steel sailmaker thimble into one end of a length of 1/2" Spectra rope. Splice another 1/2" stainless steel sailmaker thimble into the other end. Total length should be ~5 ft.	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	
Two Platform	Mooring system	2	Make double-spliced Nylon length for Ark downline	Splice a 1" stainless steel sailmaker thimble into one end of a length of 1" nylon rope. Splice a 1" heavy duty galvanized thimble into the other end. Total length will depend on anchoring depth.	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	
Two Platform	Mooring system	3	Swage thimbles into both ends of two cable systems	Hydraulically swage a 3/8" stainless steel thimble into one end of a 3/8" stainless steel cable. Add one 6" PVC end cap onto this cable through the center hole on the end cap. Swage another thimble onto the other end of the cable (cable has swaged eyes at both ends). Repeat for a second cable.	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	
Two Platform	Mooring system	4	Add turnbuckle and attach both ends of cabling system	Use Jaw-Jaw turnbuckle system to connect the inner ends of the two cabling systems. Total length should be approximately the distance from Ark top to bottom.	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	*Out-Sourced*	

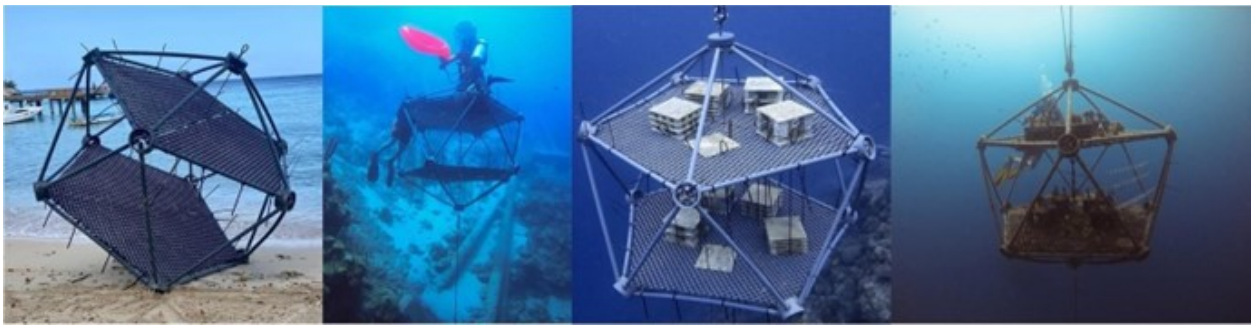


Figure S2.26 Two-Platform Arks. (Left) Two-Platform Ark prior to beach deployment. (Middle left) Two-Platform Ark shortly after attaching to the mooring system. Lift bags at the top of the Arks are used to provide temporary buoyancy prior to the addition of mooring buoys. (Middle right) Two-Platform Ark after the addition of limestone ARMS.(Right) Two-Platform Ark system after 1 year of deployment.

Sample and Data Collection

Physical parameters

1. Dissolved Oxygen

1.1. Calibrate DO sensors following manufacturer recommendation. Verify probe readings in the same water prior to use to account for slight differences in temperature/DO measurements.

1.2. Deploy reef DO sensors on the reef with the optode placed within 5 cm of the benthos and deploy Ark DO sensors on the Ark mounting framework. DO sensors may also be placed in the Ark interior or replicate sensors may be added.

1.3. DO sensors should be deployed throughout the water sampling window (ideally, several days) to (1) match molecular and microbial metrics to oxygen saturation values and (2) to determine diel fluctuations associated with each site.

1.4. For long term deployments, sensors should be checked periodically for fouling and sensor drift.

2. ***Energy dynamics*** – HOBO light & temperature pendants are a reliable and cost-effective method to capture long term fluctuations in temperature and light intensity.

2.1. Mount HOBO pendants to the top of the Ark and to an adjacent spot on the reef, facing vertically towards the surface.

2.2. Sensors may require periodic monitoring to clean fouling from the light sensor.

3. ***Water characters*** – Multiprobes provide reliable and simultaneous measurements of pH, salinity, dissolved oxygen, temperature, and redox state (among other potential sensor additions).

3.1. Calibrate sensors following manufacturer recommendations.

3.2. Deploy on Arks and reef sequentially or simultaneously during water sampling period.

4. ***Flow dynamics*** – Acoustic dopplers such as Acoustic doppler current profilers (ADCP) and Acoustic doppler velocimeters (ADV) collect current magnitude and directional data throughout the water column or at a single point, respectively, and can describe turbulent flows surrounding and within the Arks framework.

4.1. Deploy ADCP on the seafloor to collect current measurements throughout water sampling period or for long term current assessment.

4.2. Deploy ADV in the Ark interior, facing the center of the structure, to characterize turbulent flows in the interior of the structures, which have implications on water chemistry transformations and recruitment of mobile organisms.

5. ***Ark Physics*** – HOBO 'G' pendants are a reliable and cost-effective method to capture long term data on Ark physics, including tilt and acceleration, and can be used as a proxy for long-term flow patterns.

    5.1. Deploy HOBO G pendants on the Ark exterior, facing up. Sequential uses of these loggers should maintain the same attachment orientation.

6. ***In-water weight*** – Floating structures can be weighed using a tension/compression load cell, or strain gauge, to determine if the in-water weight of the community is increasing. This may serve as a rough proxy for community calcification, and thus coral growth, in restoration and conservation projects. Submersible load cells may be deployed long term or periodically to capture buoyant weight.

    6.1. Attach the submersible load cell to a block and tackle pulley system which can be used to temporarily transfer tension on the mooring line to the strain gauge system.
    6.2. Attach the base of the block and tackle to a secure location on the Ark mooring system, such as an intermediate shackle point or to the seafloor anchor. Attach the top of the load cell to a secure location on the Ark mounting framework.
    6.3. Without removing or altering mooring components on the Ark, pull line through the block and tackle pulley system such that tension is transferred from the Ark mooring system to the pulley system, cleating the line with each pull.
    6.4. Ensure mooring line is completely slacked to allow strain gauge to collect in-water weight measurements.
    6.5. Slowly transfer tension from block and tackle pulley system to Ark mooring line, checking to ensure shackles and other mooring components are properly seated and secure.
    6.6. For long term data collection, load cell can be integrated into the mooring system as an "in-line" component. Dataloggers can be periodically switched out to collect data from long term sensors.

Macro Ecology

1. ***Fish abundance & biomass –*** For either of the below-described methods, surveys should be performed at the desired frequency on (1) the Ark, (2) the surrounding reef benthos, and (3) for a parcel of empty water column approximately equivalent to the volume of the Ark, as a control for pelagic and transient water column fish communities. Fish biomass and abundance should be normalized to this volume.

    1.1. **Stationary point counts** – see Bohnsack & Bannerot, 1986 and Hylkema et al., 2020 for procedure. Briefly:
        1.1.1. Two divers identify their target site for data collection and remain 10m+ from site. One diver (the recorder) collects video footage while the other (the counter) counts and records fish data.

1.1.2. The counter records the species, abundance, and size (to the nearest 5 cm) of fish inside the designated volume of water for 10 min.

1.1.3. The divers swim closer to the target site and record species, abundance, and size of smaller, cryptobenthic fish within the sampling volume.

1.1.4. Divers repeat for the next site.

1.2. **Video-based fish biomass estimates** – see Letessier et al., 2015 and Neuswanger et al., 2016 for procedures. Briefly:

1.2.1. Assemble a stereo video system using two GoPros mounted at 18-degree angle inwards, and properly calibrate using a calibration frame 5.

1.2.2. Position stereo video system underwater with the target site in full view. Divers should exit the water and allow Go Pros to record video for at least 30 min to capture natural fish communities associated with each site.

1.2.3. Recommended GoPro settings are to film in Wide View, 60 frames/s, in 2.5K or 1,080 resolution. Automatic stabilization is also recommended.

2. ***Benthic cover*** – Benthic communities dominated by non-calcifying organisms, such as turf and fleshy macroalgae, can drive microbial and biogeochemical processes in opposition of calcifying organisms such as crustose coralline algae and scleractinian corals. We recommend quantifying percent cover of benthic organisms on Arks and seafloor control plots monthly during early successional stages, and later quarterly, as a metric for ecosystem health. See Roelfsema, Phinn & Joyce, 2006 and Wilson, Graham & Polunin, 2007 for procedures. Briefly:

2.1. Divers capture top-down photos of coral plates, ARMS plates, Ark mounting framework, or equivalent surface area on reef benthos using camera equipped with flash.

2.2. Alternatively, pre-trained divers can generate percent cover estimates from underwater surveys using a dive slate and a quadrat.

3. ***Coral growth –*** Coral growth and calcification are commonly used metrics to quantify reef success and determine changes in a reef structural complexity over time. We recommend quantifying coral growth on Arks via a combination of the following methods at the desired frequency. Briefly:

3.1. **Total linear extension –** see Johnson et al., 2011 and Lirman et al., 2014

3.1.1. Divers manually measure coral fragment dimensions using a ruler and record measurements on a dive slate.

3.1.2. We recommend measuring (a) maximum vertical height (measured from the base of the coral fragment), (b) maximum horizontal extension (measured between the two furthest points of the coral fragment, and (c) 90 degrees to maximum horizontal extension (measured along the axis rotated 90 degrees from maximum horizontal extension).

3.2. **3D Photogrammetry –** see protocols detailed in Lange & Perry, 2020 and Million et al., 2021

3.2.1. Diver places a ruler scale adjacent to the target object (individual corals or coral plates).

3.2.2. Diver collects a set of overlapping images of target object using an "umbrella"-shaped flight path. This process commonly requires 70–200 photos, depending on the size of the object— smaller and less complex objects require fewer photos.

3.2.3. Diver records the number of coral plate or other identifier on a slate, photographing it before or after each image set for later identification of photo sets.

3.3. **In-water weight** – This is a modification of the technique described in Jokiel, Maragos & Franzisket, 1978. Measurements using the load cell (described in detail above) can complement other finer-resolution coral growth metrics to generate a metric of community level growth/calcification.

3.3.1. Follow procedure described in main protocol or above (Section 5)

4. ***Coral health –*** We recommend complementing diver-based assessments of coral health and survival with physiological proxies for coral health, such as Pulse Amplitude Modulated (PAM) Fluorometry to determine maximum photosynthetic quantum yield (Fv/Fm) of the endosymbiotic zooxanthellae.

4.1. **Diver-based coral health assessment**

4.1.1. Health assessments can be conducted in conjunction with total linear extension measurements described above.

4.1.2. Diver visually assesses status (alive or dead) and general condition (bleached, damaged, healthy, diseased) of each coral fragment. Percent descriptors should be added for finer resolution health data.

4.1.3. Health of corals can also be assessed post-dive using photos taken of corals or coral plates at multiple angles.

4.2. **PAM Fluorometry –** Fv/Fm ratio generated from this measurement can be used as a proxy for photosystem health and photosynthetic capacity of the endosymbiotic dinoflagellates within coral tissues. See Beer et al., 1998 and Ralph et al., 1999 for detailed procedures. Briefly:

4.2.1. Diver transports underwater DIVING-PAM to Ark or seafloor site.

4.2.2. Following manufacturer recommendations, diver collects 3–5 readings at different locations across coral surface, then averages these readings to generate an average maximum photosynthetic quantum yield (Fv/Fm) value.

4.3. ***Invertebrate diversity –*** DNA-based surveys of the COI gene can generate high-resolution assessments of cryptic diversity (Carvalho et al., 2019; Stat et al., 2017; West et al., 2020), which can be difficult to perform using traditional diver- based visual surveys.

4.3.1. Divers collect water sample from desired sampling location (i.e., ARMS unit interior, Arks, or reef) using 2 L Hatay-Niskin bottle (described in detail below)
4.3.2. Filter at least 1 L of sample seawater through a 0.22 µm PES Sterivex filter and dry the filter using a syringe.
4.3.3. Freeze filter at -20°C until DNA extraction and sequencing.

Microbiology and Biogeochemistry

1. ***Water sample collection*** – Collect 2 L of seawater from each sampling location at desired frequency to complete the below analyses following procedure outlined in Haas et al., 2014. Briefly:
   1.1. Collect water sample in 2 L polycarbonate Hatay-Niskin bottle from Ark or reef sites by passing the open sampling cylinder back and forth in the target sampling location to flush with sample seawater, and then cap the ends.
   1.2. For reef samples, we recommend collecting water from within 0.5 m from the benthos. Depending on project-specific questions, Arks samples may be collected from the Ark interior, exterior, upstream, or downstream of the structures. Duplicate or triplicate samples are recommended.
   1.3. Collect samples moving from downstream of the structures to upstream to avoid contamination associated with sampling downstream of boat or divers
   1.4. During transport, store water samples in a cool, shaded area (at 4°C if possible). Process sample water within 4 h of collection.

2. ***Inorganic nutrients*** – For sample collection and analysis of inorganic nutrients (PO_4, NO_x, and NH_4) in seawater, follow procedure outlined in Haas et al., 2014. Briefly:
   2.1. Flush ~100 mL of sample water from Hatay-Niskin bottle through attached tubing and discard.
   2.2. Attach 0.22 µm Sterivex filter and flush with another 100 mL, discarding flow through.
   2.3. Rinse a clean, 20 mL HDPE plastic vial with sample water three times, then fill the bottle to the shoulder.
   2.4. Freeze vial immediately at -20°C. Keep frozen until analysis.

3. ***Bulk dissolved organic carbon (DOC)*** – For sample collection and analysis of bulk DOC in seawater, follow procedure outlined in Haas et al., 2014. Briefly:
   3.1. Ensure all glassware and tubing has been washed in 10% HCl to prevent contamination.
   3.2. Filter sample seawater through a same 0.22 µm Sterivex filter as in previous section into a clean, pre-combusted, 40 mL amber borosilicate glass vial. Rinse vial three times with sample water, then fill the bottle to the shoulder.
   3.3. Add 3 drops of full strength, molecular grade HCl, then cap with a PTFE-lined silicone septa (with the PTFE septa facing into the vial).
   3.4. Store at 4°C until analysis.

3.5. After 1 L of seawater has passed through the 0.22 µm Sterivex filter, remove filter from the line, dry by pushing air through with a syringe, and freeze at -20°C for eDNA extraction.

4. ***Viral and microbial abundances*** – To enumerate virus-like particles and microbial cells in seawater, follow procedure outlined in Haas et al., 2014. Briefly:

   4.1. Add 1 mL of unfiltered sample water to an Eppendorf tube. Add 66 µL of 32% paraformaldehyde and allow to fix in the dark for 15 min.

5. ***Microbial biomass*** – To determine total microbial biomass and mean cell volume in seawater, follow procedure outlined in Haas et al., 2014. Briefly:

   5.1. Add 1 mL of unfiltered sample water to an Eppendorf tube. Add 20 µL of 25% glutaraldehyde and allow to fix in the dark for 15 min.

6. ***Viral and microbial metagenomics –*** Thurber et al., 2009 provided a procedure to extract viral DNA from seawater using PEG-precipitation and CsCl density centrifugation. The following protocol is modified from Thurber et al., 2009 to isolate total DNA from viral and microbial communities in seawater.

   6.1. Add 500 mL unfiltered sample water to a 500 mL HDPE bottle. Add 50 g of polyethylene glycol (PEG) and 15 g of NaCl, cap the bottle, and shake vigorously.
   6.2. Allow sample to rest at 4°C for at least 2 h, mixing intermittently by inversion.
   6.3. Using a peristaltic pump system, pass 500 mL sample through a 0.22 µm PES Sterivex filter. Maintain low flow rate to avoid damaging the sample through excess hydrostatic pressure.
   6.4. Store Sterivex filter at -20°C until DNA extraction and sequencing.

7. ***Flow cytometry*** – For sample collection and analysis of microbial community autotroph: heterotroph ratios, follow procedure outlined in Haas et al., 2014. Briefly:

   7.1. Add 1 mL unfiltered sample seawater to a 2 mL cryovial.
   7.2. Add 5 µL of 25% glutaraldehyde and invert to mix. Allow samples to fix in the dark at room temperature for 15–30 min.
   7.3. Flash freeze cryovials in liquid nitrogen and maintain frozen at -80°C until analysis via flow cytometry as in McDole et al., 2012.

8. ***Metabolomics*** – For sample processing and analysis of untargeted metabolomics, follow procedure outlined in Dittmar et al., 2008 and Petras et al., 2017. Briefly:

   8.1. Collect remaining filtrate from the 0.22 µm Sterivex (between 0.8 and 1 L) into a HCL-rinsed polycarbonate bottle for untargeted metabolomics. Note: volume should be kept the same for all samples.
   8.2. Acidify the filtrate samples with concentrated HCl until the pH of the sample reaches 2.0 (typically 0.12% acid for seawater). Check pH with pH strips to confirm.
   8.3. Activate PPL resin as follows without letting them run dry:

8.3.1. Three times the column volume with 100% LC-MS grade MeOH
8.3.2. Three times the column volume with acidified H_2O (1 mL of 37% HCl into 1 L of LC-MS grade H_2O; pH 2.0).
8.3.3. Three times the column volume 100% LC-MS grade MeOH again.
8.3.4. Three times the column volume of acidified H_2O again.

8.4. Place pipette tip of tubing into the sample bottle and turn on the vacuum pump.
8.4.1. Adjust the vacuum pump to a flow rate between 8 and 16 mL/min

8.5. After all the filtrate sample is loaded, rinse it with two column volumes of pH 2 H_2O to remove salts from the resin.

8.6. Dry the resin with nitrogen gas until the color of the cartridge changes to a light yellow.
8.6.1. Skip this step if you are in the field and do not have access to nitrogen. You may dry them later.

8.7. Freeze the cartridges, ideally at -80°C but alright in -20°C for a short period.

Sample Processing & Analysis

1. **Microscopy**

1.1. ***Viral and microbial abundances –*** see Haas et al., 2014
1.1.1. Place a 0.02 µm pore size Whatman Anodisc filter onto the glass filter stand of the vacuum- filtration rig. Cover with a glass filter tower and use a metal tower clamp to secure.
1.1.2. Add 3 mL of molecular grade, DNA-free water to the filter tower. Add 1 mL of paraformaldehyde-fixed sample. Pipet up and down to evenly distribute sample across filter.
1.1.3. Turn on vacuum to pull sample water through filter until dry.
1.1.4. Place dried filter, face-up, on a 100 µL drop of 10x SYBR Gold solution in a Petri dish and allow to stain for 20 min in the dark.
1.1.5. Rinse filter in a 100 µL drop of molecular grade water, dab excess water from the bottom of the filter with a kim wipe, and mount on a microscope slide using a slide mount solution (a 0.02 µm-filtered solution of 10% ascorbic acid, 1x PBS, and 100% glycerol). Add cover slip.
1.1.6. Enumerate viruses (small white dots) and microbes (larger white circles) on an epifluorescence microscope (excitation/emission: 325–375/537 nm). Determine abundances manually or using image processing software such as ImageJ. A minimum of 200 cells should be counted per sample.
1.1.7. Calculate virus-to-microbe ratio based on resulting viral and microbial abundances.
1.1.8. Store prepared slide in a slide box at -20°C.

1.2. ***Microbial biomass –*** see McDole et al., 2012 and Haas et al., 2014
1.2.1. Place a 0.2 µm pore size Whatman Anodisc filter onto the glass filter stand of the vacuum- filtration rig. Cover with a glass filter tower and use a metal tower clamp to secure.

1.2.2. Add 3 mL of molecular grade, DNA-free water to the filter tower, then add 1 mL of glutaraldehyde-fixed sample. Pipet up and down to evenly distribute sample across filter.
1.2.3. Turn on vacuum to pull sample water through filter until dry.
1.2.4. Place dried filter, face-up, on a 100 µL drop of 25 ng/mL DAPI solution in a Petri dish and allow to stain for 20 min in the dark.
1.2.5. Rinse filter in a 100 µL drop of molecular grade water, dab excess water from the bottom of the filter with a kim wipe, and mount on a microscope slide using a slide mount solution (a 0.02 µm-filtered solution of 10% ascorbic acid, 1x PBS, and 100% glycerol). Add cover slip.
1.2.6. Capture 10+ photos of microbial cells (or at least 200 cells total) on an epifluorescence microscope (excitation/emission: 358/461 nm).
1.2.7. Use image processing software such as ImagePro or ImageJ to determine abundances and dimensions (length and width) of each cell.
1.2.8. Cell volumes (μm^3) is calculated from length and width measurements by assuming each cell has the shape of a cylinder with hemispherical endcaps. See McDole et al., 2012 and Haas et al., 2014 for calculations and bacterial size-dependent relationships, which can be used to generate estimates of total biomass (g/10 m^3).

2. **Water chemistry**

2.1. ***Bulk Dissolved Organic Carbon (DOC)***

2.1.1. Analyze bulk DOC via high-temperature catalytic oxidation as described by Carlson et al., 2010.

2.2. ***Inorganic Nutrients***

2.2.1. Analyze nutrient concentrations using flow injection analysis as described by Guildford & Hecky, 2000.

2.3. ***Untargeted Metabolomics***

2.3.1. The sample is eluted from the resin in 2 mL of LC-MS grade MeOH
2.3.1.1. Pipette the methanol into the LC vial using 1 mL pipette.
2.3.1.2. Force the resin through using a 50 mL plastic syringe
2.3.1.3. Dry the sample down in a Centrivap (typically overnight) at room temperature.
2.3.2. Once the sample is dry, store it at -80°C or -20°C or resuspend the dried extract for LC-MS analysis.
2.3.3. For LC-MS analysis, resuspend the sample in 100 µL of 80% LC-MS grade MeOH + 0.1% FA by pipetting the solvent up and down over the DOM pellet.
2.3.4. Transfer the resuspended sample to a micro glass insert inside of a 1.5 mL HPLC vial.
2.3.5. The sample is now ready for LC-MS/MS analysis.

2.3.5.1. After the sample has been analyzed, store it at -80°C.

3. **Image-based measurements**

3.1. ***Benthic cover – see Roelfsema, Phinn & Joyce, 2006 for full procedure.*** Briefly:

3.1.1. Import photos into ImageJ or similar software. Overlay each photo with a grid of dots (ideally, 100 dots per image).

3.1.2. Visually identify the substrate under each dot to the highest taxonomic resolution possible. Examples include: (1) turf algae, (2) benthic cyanobacterial mat, (3) macroalgae (*Dictyota* spp), (4) coral (*Pseudodiploria strigosa*), (5) crustose coralline algae, (6) sponge, and (7) sand.

3.1.3. Sum identities to generate a benthic percent cover for each image.

3.2. ***3D Photogrammetry – see Lange & Perry, 2020 and Million et al., 2021 for*** full procedure. Briefly:

3.2.1. Upload photo sets for a target object (coral plate or individual coral colonies) to Agisoft Metashape software. Exclude blurry or poor-quality photos from analysis.

3.2.2. Use Metashape software to align photos using settings described in Lange & Perry, 2020

3.2.3. Perform error reduction on photo set.

3.2.4. Use Metashape to generate dense point-cloud reconstructions of the target object.

3.3. ***Fish biomass – see Neuswanger et al., 2016 for full procedure. Briefly:***

3.3.1. Upload fish monitoring videos into VidSync software and synchronize footage time between videos from each camera

3.3.2. Use VidSync software to perform calibration and correct for distortion from still images of calibration frame in situ

3.3.3. VidSync will use 3-D positioning and triangulation to calculate fish biomass and abundance from fish monitoring videos.

Results from Hydrodynamic Modeling and Arks Prototype Testing

A series of modeling and experimental tests were conducted in order to select a geometry with the desired strength and physical characteristics to serve as a midwater platform for propagating reef biodiversity.

Scale models of 1V frequency solid and hollow Arks structures (frequency describes the number of triangles that comprise the structure, with higher frequencies containing larger numbers of triangles) were subjected to wind tunnel tests to investigate their hydrodynamic characteristics and test their structural stability under hydrodynamic loading (Abassi et al., 2021). The motion of fluid across an object creates vibrations that can compromise structural integrity over the long term. It is therefore advantageous to build a structure that does not “resonate” on its own. Solid and hollow models were subjected to a pinging test to determine natural frequencies of the structures. Both models were also tested in a wind tunnel at velocities that correspond to environmentally relevant water current speeds to determine the drag coefficient of each structure as it interacts with a fluid medium. Hollow Arks models exhibited lower natural resonance and produced less drag, and thus were selected for further testing.

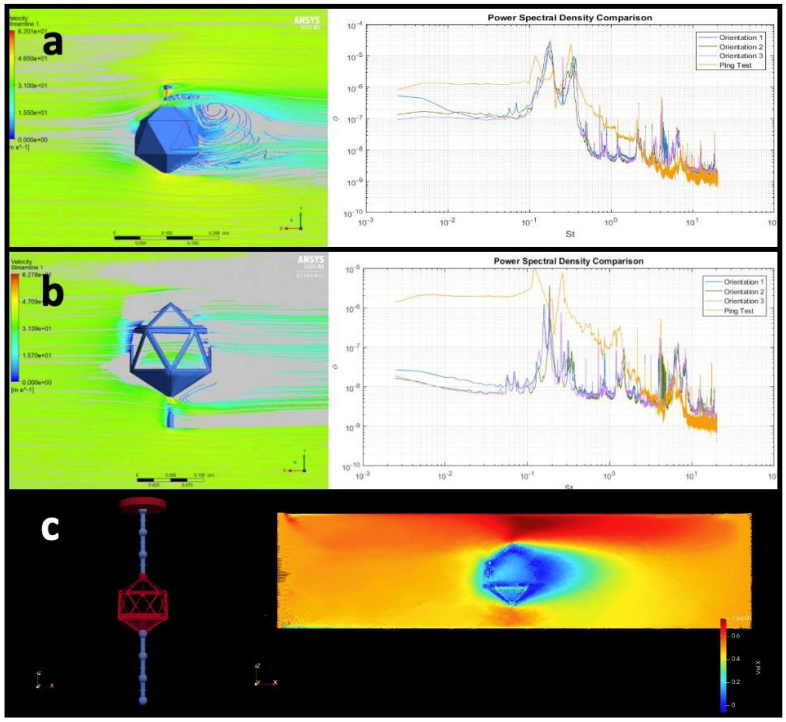


Figure S2.27 Wind tunnel tests were conducted to assess the hydrodynamic characteristics of Ark models.(a) solid and (b) hollow scale models of Arks. Accompanying plots represent power spectral density analyses and dominant Strouhal numbers, indicating frequencies induced by flow. The hollow Ark model was then simulated using flow regimes from Curacao to predict the magnitude of reduction in interna flow speed as water passes through the structure (c).

Hollow models of Arks structures were then modeled in natural flow scenarios using detailed computational models of the currents and bathymetry surrounding the Caribbean island of Curacao, a site at which two Two-Platform Arks were later deployed. Small-scale flow was simulated around a basic model of a hollow, 1V Arks structure at 10 cm resolution using Smooth Particle Hydrodynamics (SPH) for current speeds up to 5 m/s. These models predict a 50% reduction in flow speed in the interior of the Arks structures relative to the surrounding water.

Next, multiple-element hydrodynamic models were developed for both Two-Platform and Shell (1V and 2V frequency polyhedra) structures to design Coral Arks systems that can withstand hydrodynamic forces expected in both typical flow conditions and extreme, hurricane-level scenarios. These models incorporated

hydrodynamic forces on the Arks structure driven by currents (ambient and storm-associated), by waves (ambient and storm-associated), and forces on the mooring/anchoring system (cable stress, drag, and required strength of cables and anchor). The basic approach was to project the elements on the side of the structure facing the current into a plane projection, and to do the same for the opposite side of the structure. Based on the SPH results, it was assumed that the water current inside the structure would be reduced by half (therefore, the current acting on the planar projection on the opposite side of the structure would be half the strength of that acting on the side of the structure facing the current).

Figure S28b shows the resulting initial calculated forces on the Shell Ark that would be expected from ambient currents ranging up to 6 knots (~3 m/s; hydrodynamic model element 1). Also shown is the modelled tilt of the structure relative to the seafloor under these flow conditions. Figure S29 shows the resulting initial calculated forces on the 2V Coral Ark that would be expected from ambient waves based on wave dispersion calculations in 10 m water depth, with the top an Ark at 5 m depth, wavelength of 11.1 m and amplitude of 0.35 m (hydrodynamic model element 2). Current speeds and wave conditions during both ambient (non-storm) and hurricane conditions were obtained from buoy data in the vicinity of Isla Vieques (Caribbean Regional Association for Coastal Ocean Observing [CARICOOS], www.caricoos.org), a site at which two Shell Arks were later deployed. Note that under ambient (non- storm) conditions, current speeds typically top out at approximately 2 knots (1 m/s).

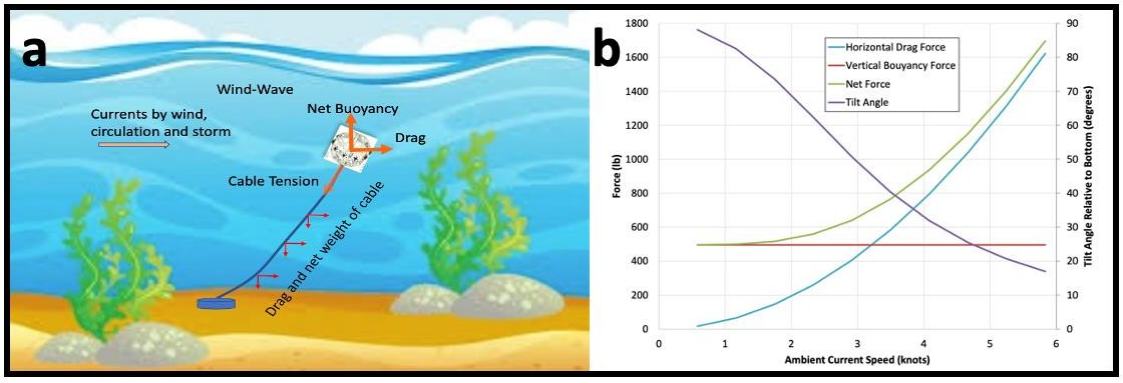


Figure S2.28 (Left) Generalized schematic of hydrodynamics modelling approach used. Models integrate hydrodynamic forces due to (1) currents, (2) waves, and (3) the combined effect of tension and drag forces on the mooring/anchoring system. (Right) Estimated horizontal drag force (blue), net hydrodynamic force (green), and fixed buoyant force (red) in pounds (lb) on a Shell Coral Ark based on ambient current speeds up to 6 knots (~3m/s) and assumptions described above. Also shown is the estimated tilt angle of the structure (purple), which increases as currents increase in speed.

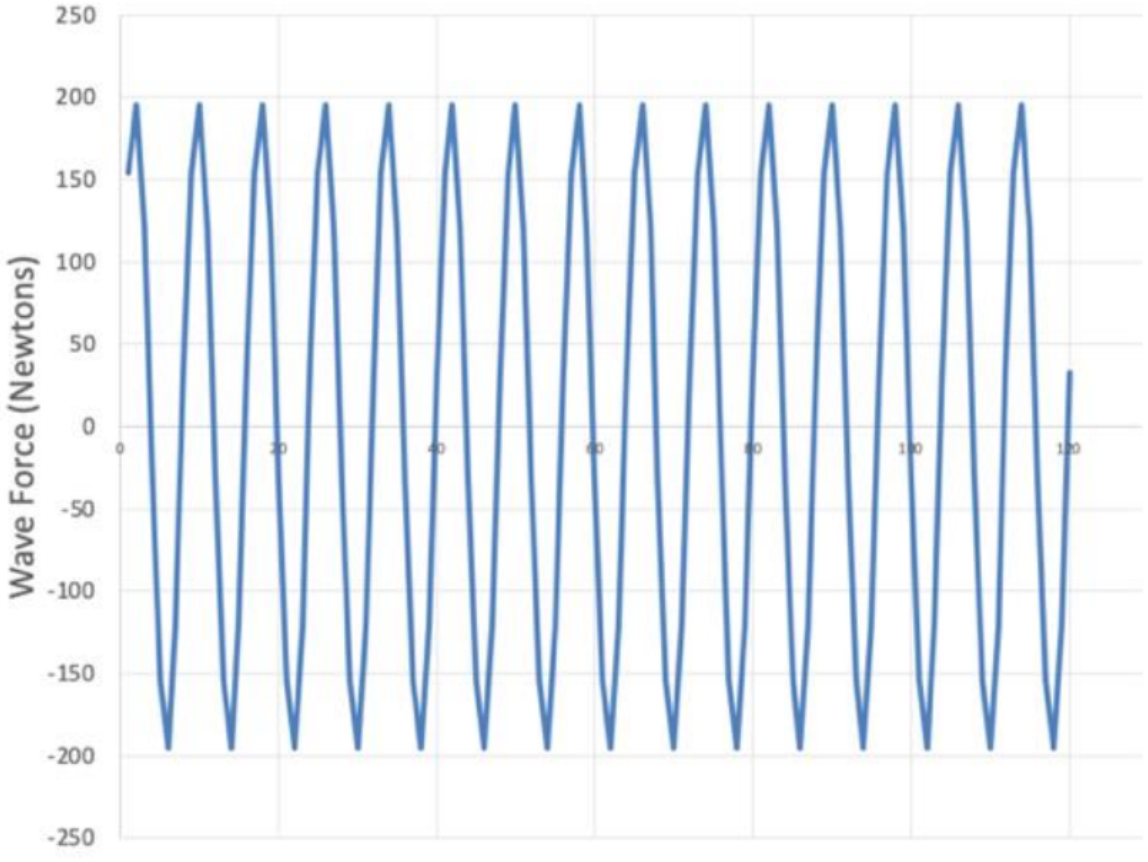


Figure S2.29 Estimated hydrodynamic force (in Newtons; 200 Newtons ~45 lbs) on a Shell Coral Ark at 5 m depth in 10 m of water based on ambient typical wave conditions and assumptions described above.

Prototypes of the Two-Platform (1V, 1.25 m radius) and Shell (2V, 1.5 m radius) Arks structures were then constructed in San Diego for in-water testing. Testing was focused on validating and refining several criteria contained in the models: (1) the drag coefficients on the Arks systems, (2) the reduction in current strength that occurs within Coral Arks structures of different geometries as water passes through the structures, and (3) overall hydrodynamic model validation (i.e., does the model accurately predict the measured force on the structure during testing).

We used a fixed-testing approach (a mooring test) to determine the internal reduction in flow and a mobile-testing approach (a towing test) to simulate stronger currents that the Coral Ark may experience during storm events. These tests used an acoustic doppler current profiler (ADCP) to measure currents in the vicinity of the testing, an acoustic doppler velocimeter (ADV) to measure currents within the Arks system, and a submersible load cell to refine drag coefficients originally obtained in wind tunnel testing. Drag coefficients for each Arks structure were calculated by towing the Arks structures behind a vessel with the load cell spliced in-line with the towing line and a tilt sensor to record changes in the Ark's orientation relative to the vertical axis. These coefficients were then integrated into the tension/drag component of the hydrodynamic models.

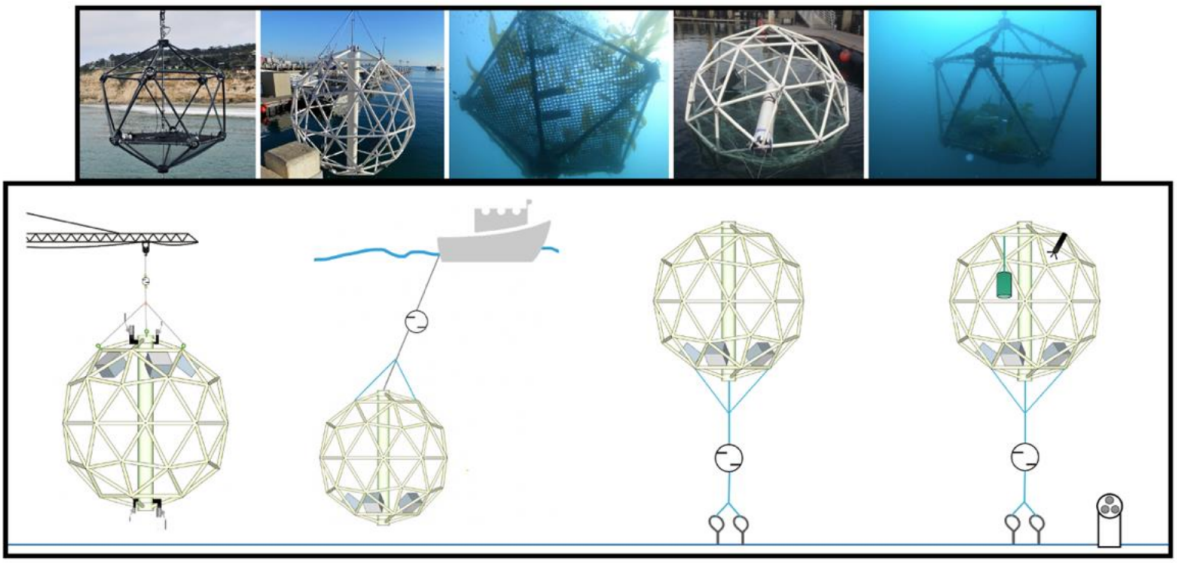


Figure S2.30 1V and 2V prototype Arks structures were subjected to crane tests, towing tests, and mooring tests in San Diego to validate and refine values contained in hydrodynamic models.

Overall, data collected during testing of both Arks prototypes demonstrate that the hydrodynamic models developed can be used to accurately simulate and predict the drag, the tension, and the tilt angles resulting from hydrodynamic forces on the structures under varying water current speeds. Based on the calculated forces from these models, mooring systems for the Arks later deployed in Vieques were designed with all individual components capable of withstanding 3,500 lbs (1,600 kg) of breakout force.

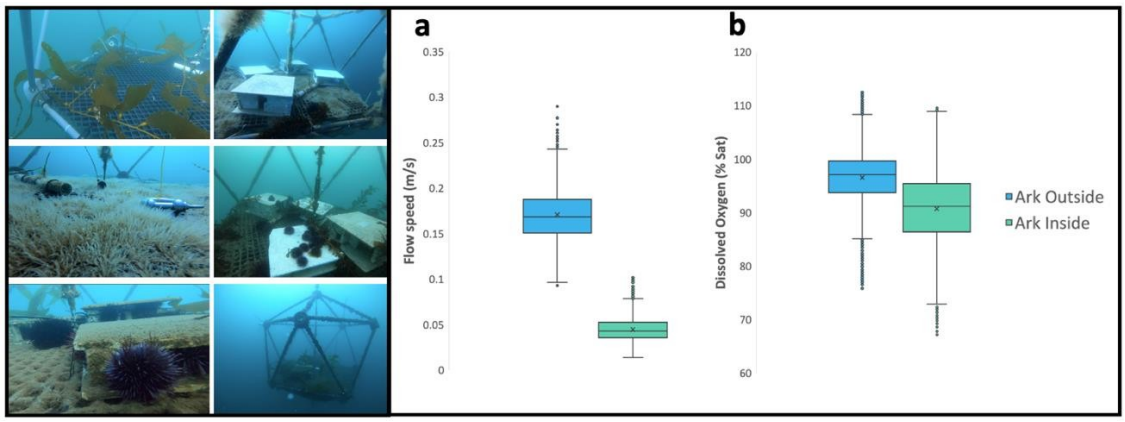


Figure S2.31 A Two Platform Ark was deployed for 6 months off the coast of San Diego. During this time, measurements were collected for (a) flow speeds and (b) dissolved oxygen concentrations both inside and outside the structures.

Analysis of flow speeds on the inside and outside of Arks using acoustic dopplers demonstrated that the flow passing through the Arks becomes turbulent, resulting in a significant reduction (40–70%) in current speed within the Arks interior relative to the surrounding water. Dissolved oxygen concentrations on Arks were found to be lower within the Arks interior relative to the surrounding water, possibly linked to reduced flow inside the structures. We predicted that the local differences in flow magnitude and direction across Arks would result in local differences in other water characters as well, such as dissolved oxygen and pH. To test this, we measured physical parameters (flow speed, dissolved oxygen, pH, and temperature) at several locations inside and outside Arks structures to develop “maps” of physical conditions associated with Arks structures. These results were used to identify optimal locations to translocate corals and seeded ARMS to the Arks. For example, high flow and dissolved oxygen concentrations at the top of Arks provides an enhanced environment for coral growth, while the turbulent internal environment provides conditions more similar to those experienced by cryptic communities inside the reef matrix. Shell Arks in Vieques were

therefore designed with coral plates attached to the top of the structures and ARMS attached in the interior.

Projects using Coral Arks as coral mitigation tools are currently underway in the Caribbean. One of these projects, funded as a demonstration through the Environmental Security Technology Certification Program (ESTCP) within the Department of Defense (DoD), is using Coral Arks to support the ongoing munitions cleanup effort at the Vieques Naval Training Range (VNTR) by housing and maintaining corals translocated from seafloor munitions. Coral Arks offer a new technology for coral mitigation that is expected to result in higher success rates, additional ecosystem benefits, and lower overall costs associated with coral mitigation, compared to traditional approaches. The testing described above informed and supported the development of two Coral Arks structures that were deployed in Vieques, Puerto Rico in November 2021 with logistical and in-kind support from the Naval Facilities Engineering Command (NAVFAC) Vieques Restoration Program team.

Table S2.8 Manufacture and assembly of components for submersible strain gauge system to measure in-water weight of Coral Arks.

Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Strain Gauge	1	Install eyebolts into load cell	Screw a M16 x 2, 27 mm thread length eyebolt into either side of a STA-8-1T tension/compression load cell, using Loctite 262 threadlocker to seal.	Thread-locker, torque wrench	1	1	1	
Strain Gauge	2	Cut and machine datalogger housing	Cut 1-1/2 clear PVC pipe and machine one end to integrate the datalogger housing cap (see drawing). To the other end, attach a 1-1/2 PVC cap using PVC primer and glue.	Miter saw, lathe	15	1	15	Figure SI 31
Strain Gauge	3	Cut and machine datalogger housing cap	Cut 2" PVC rod to drawing.	Miter saw, lathe	Out-Sourced	Out-Sourced	Out-Sourced	Figure SI 32
Strain Gauge	4	Splice male connector to load cell wires	Use wire strippers to expose wires in the load cell cable and on the male SubConn connector lead. Splice these two cables together by soldering the wires (black to black, red to red, green to yellow, white to white) and seal with heat shrink.	Soldering iron, wire strippers, solder, heat gun	10	1	10	
Strain Gauge	5	Waterproof splice	Using a rubber mold, fill mold with a polyurethane potting compound to fully encapsulate the spliced wires. Let dry before removing carefully.	Polyurethane resin and hardener	60	1	60	

Table S2.8 Manufacture and assembly of components for submersible strain gauge system to measure in-water weight of Coral Arks. (Continued)

Component	Task #	Basic description	Detailed description	Tools required	Time estimate per unit (min)	Total number needed per Ark	Total time to complete task (min)	Refer to drawing #
Strain Gauge	6	Install female connector into datalogger housing cap	Using PTFE tape, install female SubConn connector into the threaded hole at the top of the datalogger housing cap until snug.	PTFE tape, crescent wrench	5	1	5	Figure SI 33
Strain Gauge	7	Attach datalogger housing to load cell.	Attach datalogger to a cut piece of fiberglass sheeting using a vibration-damping routing clamp, secured around the clear PVC pipe on the housing. Attach this assembly to the load cell via a clamping U- bolt placed around the waterproof strain relief located at the middle edge of the load cell.	Table saw, wrench, screwdriver	60	1	60	Figure SI 33
Strain Gauge	8	Install Datalogger	Install Bridge101A 30mV Datalogger into the housing by wiring the leads from the female SubConn connector to the datalogger.	Jewelers screwdriver	2	1	2	Figure SI 33
Strain Gauge	9	Waterproof datalogger housing	Install a greased O-ring into the O-ring groove on the datalogger housing cap. Install two screws through both the clear PVC wall and the datalogger housing cap.	O-ring grease, hex key	2	1	2	Figure SI 33

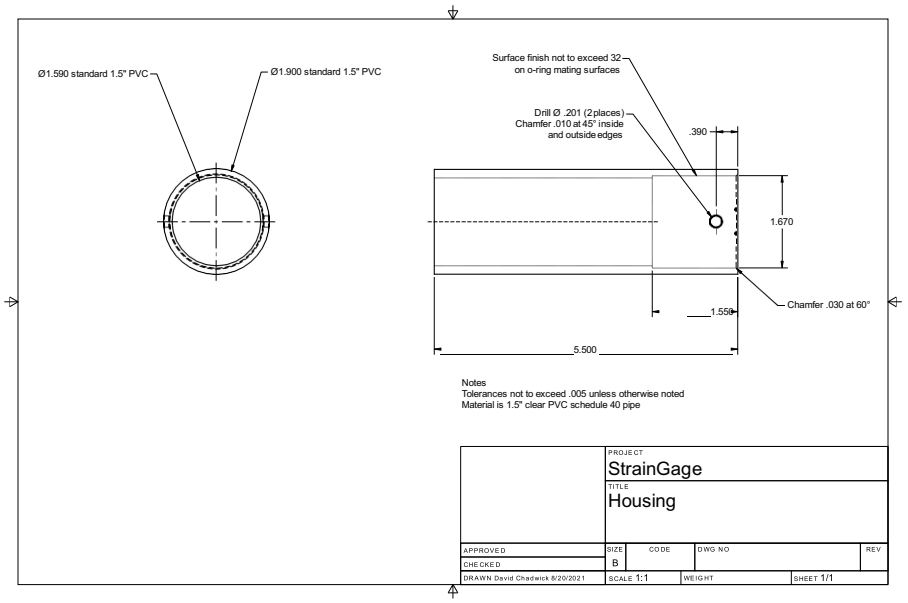


Figure S2.32 Technical drawing for the Bridge101A 30mV datalogger submersible housing.

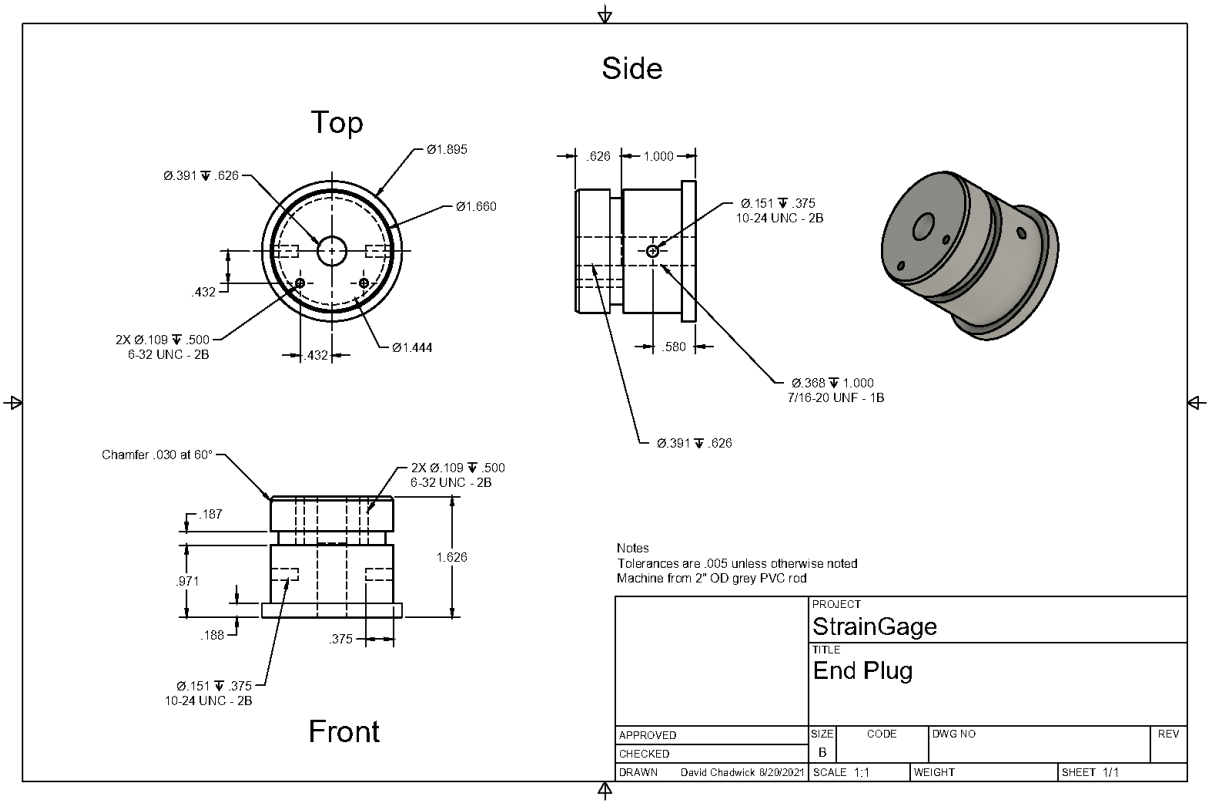


Figure S2.33 Technical drawing for the Bridge101A datalogger submersible housing end cap.

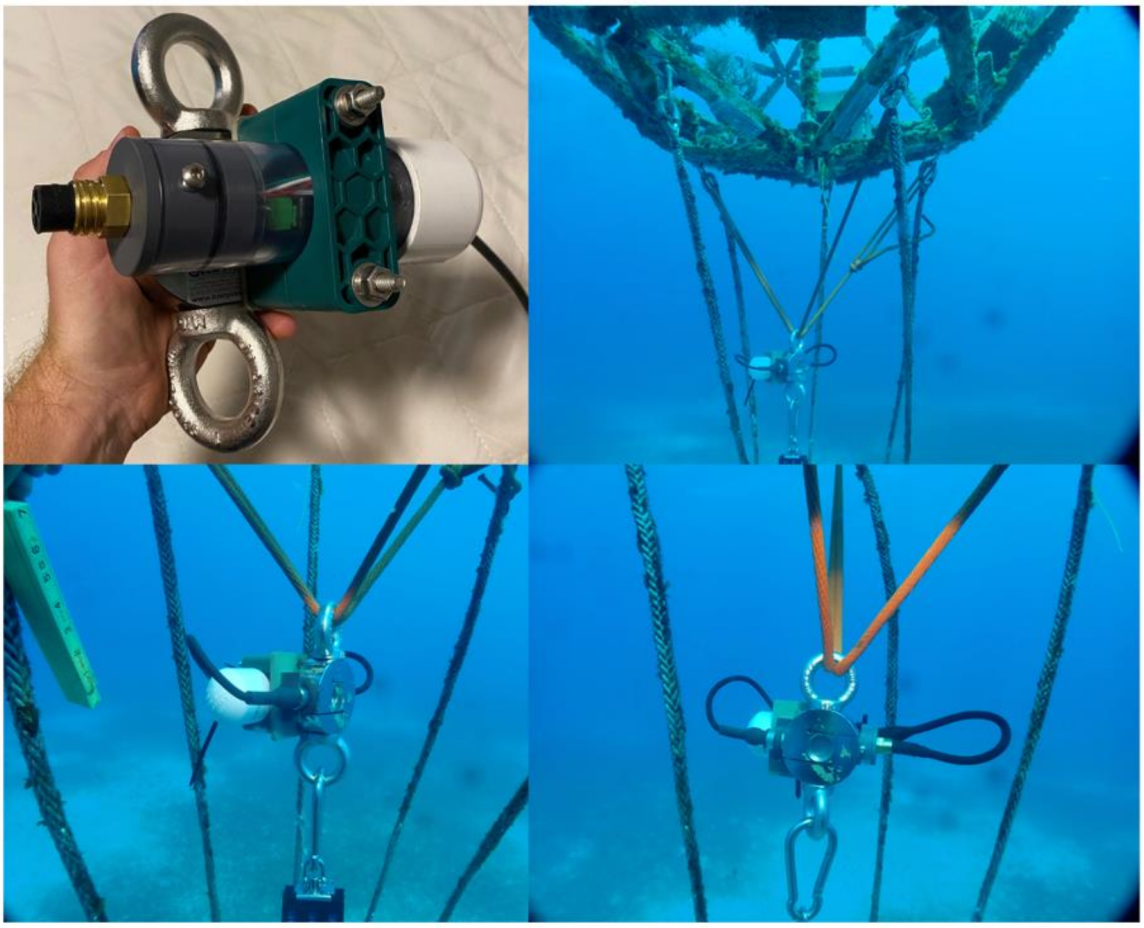


Figure S2.34 Strain gauge. (Top left) Fully assembled strain gauge and submersible datalogger housing. (Top right, bottom left and right) Use of strain gauge to measure in-water weight of Coral Arks. A block and tackle is used to transfer tension from the mooring line to the strain gauge system.

References

Abassi, M., Gayon, C., Liu, X., Rohwer, F., & Castillo, J. (2021). Wind tunnel testing for hydrodynamic load characterization of icosahedron-shaped coral reef arks. In *AIAA Scitech 2021 Forum* (p. 0133).

Beer, S., Ilan, M., Eshel, A., Weil, A., & Brickner, I. (1998). Use of pulse amplitude modulated (PAM) fluorometry for *in situ* measurements of photosynthesis in two Red Sea faviid corals. *Marine Biology*, *131*, 607-612.

Bohnsack, J. A., & Bannerot, S. P. (1986). A stationary visual census technique for quantitatively assessing community structure of coral reef fishes.

Carlson, C. A., Hansell, D. A., Nelson, N. B., Siegel, D. A., Smethie, W. M., Khatiwala, S., ... & Halewood, E. (2010). Dissolved organic carbon export and subsequent remineralization in the mesopelagic and bathypelagic realms of the North Atlantic basin. *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*(16), 1433-1445.

Carvalho, S., Aylagas, E., Villalobos, R., Kattan, Y., Berumen, M., & Pearman, J. K. (2019). Beyond the visual: using metabarcoding to characterize the hidden reef cryptobiome. *Proceedings of the Royal Society B*, *286*(1896), 20182697.

Chris, M. R., Phinn, S. R., & Joice, K. E. (2006). Evaluating benthic survey technique for validating maps of coral reef derived from remotely sensed images. In *Proceeding of 10 th International Coral reef Symposium*

Dittmar, T., Koch, B., Hertkorn, N., & Kattner, G. (2008). A simple and efficient method for the solid-phase extraction of dissolved organic matter (SPE-DOM) from seawater. *Limnology and Oceanography: Methods*, *6*(6), 230-235.

Guildford, S. J., & Hecky, R. E. (2000). Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? *Limnology and oceanography*, *45*(6), 1213-1223.

Haas, A. F., Knowles, B., Lim, Y. W., Somera, T. M., Kelly, L. W., Hatay, M., & Rohwer, F. (2014). Unraveling the unseen players in the ocean-a field guide to water chemistry and marine microbiology. *JoVE (Journal of Visualized Experiments)*, (93), e52131.

Hylkema, A., Debrot, A. O., Osinga, R., Bron, P. S., Heesink, D. B., Izioka, A. K., ... & Murk, A. J. (2020). Fish assemblages of three common artificial reef designs during early colonization. *Ecological Engineering*, *157*, 105994.

Johnson, M. E., Lustic, C., Bartels, E., Baums, I. B., Gilliam, D. S., Larson, E. A., ... & Schopmeyer, S. (2011). Caribbean *Acropora* restoration guide: best practices for propagation and population enhancement.

Jokiel, P. L., & Maragos, J. E. (1978). Coral growth: buoyant weight technique. *Coral reefs: research methods* (1978).

Lange, I. D., & Perry, C. T. (2020). A quick, easy and non-invasive method to quantify coral growth rates using photogrammetry and 3D model comparisons. *Methods in Ecology and Evolution*, *11*(6), 714-726.

Letessier, T. B., Juhel, J. B., Vigliola, L., & Meeuwig, J. J. (2015). Low-cost small action cameras in stereo generates accurate underwater measurements of fish. *Journal of Experimental Marine Biology and Ecology*, *466*, 120-126.

Lirman, D., Schopmeyer, S., Galvan, V., Drury, C., Baker, A. C., & Baums, I. B. (2014). Growth dynamics of the threatened Caribbean staghorn coral *Acropora cervicornis*: influence of host genotype, symbiont identity, colony size, and environmental setting. *PloS one*, *9*(9), e107253.

McDole, T., Nulton, J., Barott, K. L., Felts, B., Hand, C., Hatay, M., ... & Rohwer, F. (2012). Assessing coral reefs on a Pacific-wide scale using the microbialization score.

Million, W. C., O'Donnell, S., Bartels, E., & Kenkel, C. D. (2021). Colony-level 3D photogrammetry reveals that total linear extension and initial growth do not scale with complex morphological growth in the branching coral, *Acropora cervicornis*. *Frontiers in Marine Science*, *8*, 384.

Moews-Asher, M., Castor, C. B., Reardon, K., & Timmers, M. A. (2018). Field guide to cryptic marine invertebrates of the Philippines: a sample of biodiversity from Autonomous Reef Monitoring Structures.

Neuswanger, J. R., Wipfli, M. S., Rosenberger, A. E., & Hughes, N. F. (2016). Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(12), 1861-1873.

Petras, D., Koester, I., Da Silva, R., Stephens, B. M., Haas, A. F., Nelson, C. E., ... & Dorrestein, P. C. (2017). High-resolution liquid chromatography tandem mass spectrometry enables large scale molecular characterization of dissolved organic matter. *Frontiers in Marine Science*, *4*, 405.

Ralph, P. J., Gademann, R., Larkum, A. W. D., & Schreiber, U. (1999). *In situ* underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. *Marine Ecology Progress Series*, *180*, 139-147.

Stat, M., Huggett, M. J., Bernasconi, R., DiBattista, J. D., Berry, T. E., Newman, S. J., ... & Bunce, M. (2017). Ecosystem biomonitoring with eDNA: metabarcoding across the tree of life in a tropical marine environment. *Scientific reports*, *7*(1), 12240.

Thurber, R. V., Haynes, M., Breitbart, M., Wegley, L., & Rohwer, F. (2009). Laboratory procedures to generate viral metagenomes. *Nature protocols*, *4*(4), 470-483.

West, K. M., Stat, M., Harvey, E. S., Skepper, C. L., DiBattista, J. D., Richards, Z. T., ... & Bunce, M. (2020). eDNA metabarcoding survey reveals fine-scale coral reef community variation across a remote, tropical island ecosystem. *Molecular ecology*, *29*(6), 1069-1086.

Wilson, S. K., Graham, N. A. J., & Polunin, N. V. (2007). Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, *151*(3), 1069-1076.

Table S2.9 Materials for PVC ARMS

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
	316 Stainless Steel Hex Head Bolt, Partially Threaded, 8" length, 1/4"-20 Thread Size	McMaster Carr	92186A569	Bolts for PVC ARMS assembly	4x	
	316 Stainless Steel Hex Nut, Super-Corrosion-Resistant, 1/4"-20 Thread Size	McMaster Carr	94805A029	Nuts for PVC ARMS assembly	8x	
	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 1/4"-20 Thread Size	McMaster Carr	90715A125	Locknuts for PVC ARMS assembly	4x	
	316 Stainless Steel Washer for 1/4" Screw Size, 0.281" ID, 0.625" OD	McMaster Carr	90107A029	Washers for PVC ARMS assembly	8x	
	Nylon Unthreaded Spacers - 1/2" Long, 1/2" OD, Black	McMaster Carr	90176A159	Nylon spacers for PVC ARMS assembly	20x	
	PVC Sheet Type 1, 0.25" Thick, Gray	McMaster Carr	8747K215	PVC for ARMS stacking plates. See Figure SI 4.	9x	Yes
	PVC Sheet Type 1, 0.5" Thick, Gray	McMaster Carr	8747K217	PVC for ARMS baseplates. See Figure SI 1.	1x	Yes
	PVC Sheet Type 1, 0.5" Thick, Gray	McMaster Carr	8747K217	PVC for ARMS long cross spacers. See Figure SI 2.	4x	Yes

Table S2.9 Materials for PVC ARMS (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
	PVC Sheet Type 1, 0.5" Thick, Gray	McMaster Carr	8747K217	PVC for ARMS short cross spacers. See Figure SI 3.	8x	Yes
	Ratcheting Combination Wrench, 7/16"	McMaster Carr	5163A15	Wrenches to secure PVC ARMS hardware	2x	
	Rebar, 3-ft Lengths, 1/2" Thick	McMaster Carr	7480N115	Rebar stakes to secure PVC ARMS to benthos. Mallet required.	4x	
	Sequentially Numbered Metal Tags	McMaster Carr	2208N349	Numbered tags for ARMS ID	1x	

Table S2.10 Materials for Limestone ARMS

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
	DeWalt Wet Tile Saw	Home Depot	D24000S	Cut limestone tile into stackable pieces	1x	
	Lift Bag, 50 lb Capacity	Amazon	B07GCNGRDR	Lift bag for transport of Limestone ARMS to benthos	1x	
	Milk Crate, Heavy Duty, 13" x 19" x 11"	Amazon	B06XGBDJMD	Crate for transport of Limestone ARMS to benthos	1x	
	Natural Limestone or Travertine Tile (Unfilled) - 12" x 12"	Bedrosians Tile & Stone	TRVSIENA1212T	Base material for Limestone ARMS layers and stacking pieces. See Figure SI 7 & 8.	10x	Yes
	PC-11 Epoxy Adhesive Paste, Two-Part Marine Grade	Amazon	B008DZ1864	Two-part epoxy for Limestone ARMS assembly		

Table S2.11 Materials for Shell ARK

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Downline	1" Nylon, 6' length thimble-to-thimble with stainless sailmaker thimble at top, heavy duty galvanized thimble at bottom	West Marine	Custom	Nylon mooring line for attaching Ark mooring bridle to anchor system.	1	
Main structure	105-B Epoxy	West Marine (made by West System)	318352	Epoxy to seal foam in struts.		
Main structure	205-B Hardener	West Marine (made by West System)	318378	Epoxy to seal foam in struts.		
Mooring bridle	3-1/8" X 2" small diamond base padeye with 7/8" bail	West Marine (Made by Harken)	130560	Padeyes for attaching mooring system to Ark base.	5	
Main structure	3/4" H-80 Divinycell Closed-Cell Foam, Plain Sheet 48" x 96"	Fiberglass Supply	L18-1110	Buoyant foam for struts. Cut foam into 1.5" wide strips, 15.5" long for S1 struts and 19" long for S2 struts, add to struts.	120	
Downline	3/4" Stainless Masterlink	Lift-It (Made by Suncor)	S0652-0020	Masterlink, connects top of swivel to lower portion of 5-point mooring bridle.	1	
Mooring bridle	3/8" Stainless Long D Shackles with Captive Self-Locking Pin	West Marine (Made by Wichard)	116293	High-strength shackles to connect pad eyes to mooring system.	5	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Main structure	316 SS, Pan Head Phillips Screw, 1/4-20, 3" Long	McMaster Carr	91735A385	Bolts to attach hull anodes to stainless struts	2	
ARMS attachments	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 1/2"-13 Thread Size	McMaster	90715A165	Locknuts for attaching ARMS to ARMS mounting baseplates (8 per unit)	80	
ARMS Baseplates	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 1/4"-20 Thread Size	McMaster	90715A125	Locknuts for ARMS mounting baseplates (struts and Stars)	600	
Coral plate baseplates	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 1/4"-20 Thread Size	McMaster	90715A125	Locknuts for attaching coral plate baseplates to struts	600	
Coral plate attach	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 1/4"-20 Thread Size	McMaster	90715A125	Locknuts to attach coral plates to baseplates	80	
Mooring bridle	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 1/4"-20 Thread Size	McMaster	90715A125	Padeye locknuts for attaching pad eyes to struts.	20	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Main structure	316 Stainless Steel Nylon-Insert Locknut, Super-Corrosion-Resistant, 10-32 Thread Size	McMaster	90715A115	Locknuts for star-strut connections	475	
Main structure	316 Stainless Steel Pan Head Phillips Screw, 10-32 Thread, 2-1/2" Long	McMaster	91735A368	Bolts for star-strut connections	475	
Mooring bridle	316 Stainless Steel Phillips Flat Head Screws, 1/4"-20 Thread Size, 2-3/4" Long	McMaster	91500A341	Padeye bolts for attaching pad eyes to struts.	15	
ARMS Baseplates	316 Stainless Steel Phillips Flat Head Screws, 1/4"-20 Thread Size, 3" Long	McMaster	91500A554	Bolts for attaching ARMS mounting baseplates to Stars	475	
Mooring bridle	316 Stainless Steel Phillips Flat Head Screws, 1/4"-20 Thread Size, 3" Long	McMaster	91500A554	Padeye bolts for attaching pad eyes through struts & Stars.	5	
Mooring bridle	316 Stainless Steel Screw-Pin Shackle - for Lifting, 1/2" Thick	McMaster	3583T15	Shackles to connect lower bridle thimbles to small links on Masterlink.	5	
ARMS attachments	316 Stainless Steel Split Lock Washer for 1/2" Screw Size, 0.512" ID, 0.869" OD	McMaster	92147A033	Lock washers for attaching ARMS to ARMS mounting baseplates (4 per unit)	40	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
ARMS attachments	316 Stainless Steel Washer for 1/2" Screw Size, 0.531" ID, 1.25" OD	McMaster	90107A033	Backing washers for attaching ARMS to ARMS mounting baseplates (4 per unit)	40	
ARMS Baseplates	316 Stainless Steel Washer for 1/4" Screw Size, 0.281" ID, 0.625" OD	McMaster	90107A029	Washers for attaching ARMS mounting baseplates to struts	40	
Coral plate baseplates	316 Stainless Steel Washer for 1/4" Screw Size, 0.281" ID, 0.625" OD	McMaster	90107A029	Washers for attaching coral plate baseplates to struts	40	
Coral plate attach	316 Stainless Steel Washer for 1/4" Screw Size, 0.281" ID, 0.625" OD	McMaster	90107A029	Washers to attach coral plates to baseplates	160	
Main structure	316 Stainless Steel Washer for Number 10 Screw Size, 0.203" ID, 0.438" OD	McMaster	90107A011	Washers for star-strut connections	475	
Buoyancy	316 Stainless Steel Washer, 1" Screw Size, 2" OD	McMaster	90107A038	Large washers for central rod (2 per float)	22	
ARMS attachments	316 Stainless Steel Washer, Oversized, 1/2" Screw, 1.5" OD, 0.052"- 0.072" Thickness	McMaster	91525A145	Oversized washers for attaching ARMS to ARMS mounting baseplates (4 per unit)	40	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Coral plates	3M Marine Adhesive Sealant - Fast Cure 5200	McMaster	67015A44	Adhesive to glue limestone tiles to PVC coral baseplates. Drill out corners with masonry bit.		
Buoyancy	3M Marine Adhesive Sealant - Fast Cure 5200	McMaster	67015A44	Adhesive for securing fiberglass threaded rods into trawl floats	2	
Mooring bridle	5/8" Dyneema with Stainless Sailmakers Thimbles at Top and Bottom	West Marine	Custom	5-leg mooring bridle for attaching Ark to downline.	5	
Downline	Clevis-to-Clevis Swivel - Not for Lifting, 316 Stainless Steel, 6-7/32" Long	McMaster	37405T29	Swivel, bottom connects to top of downline, top connects to large link in Masterlink.	1	
Buoyancy	Fiberglass Hex Nut, 1"-8 Thread Size	McMaster	91395A038	Fiberglass hex nuts for securing fiberglass threaded rods into trawl floats	30	
Buoyancy	Fiberglass Threaded Rod, 1"-8 Thread Size, 8 Feet Long	McMaster	91315A238	Fiberglass threaded rod to attach float to Ark. See Figure SI 16.	10	Yes
Anchor system	Galvanized Alloy Steel Shackle with Screw Pin - for Lifting, 1/2" Thick	McMaster	3663T42	Middle shackle from chain to pear link.	3	
Anchor system	Galvanized Alloy Steel Shackle with Screw Pin - for Lifting, 3/4" Thick	McMaster	3663T44	Upper large shackle to connect pear link to lower downline thimble.	1	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Anchor system	Galvanized Alloy Steel Shackle with Screw Pin - for Lifting, 3/4" Thick	McMaster	3663T44	Anchor shackle.	3	
Anchor system	Galvanized Alloy Steel Shackle with Screw Pin - for Lifting, 3/8" Thick	McMaster	3663T51	Shackle to connect chain to upper middle hackle.	3	
Anchor system	Galvanized Alloy Steel Shackle with Screw Pin - for Lifting, 3/8" Thick	McMaster	3663T51	Lower small shackle to connect chain and anchor shackle.	3	
Install & Tools	HARKEN–57mm Carbo Air® Triple Block	West Marine	200076	Top of block and tackle	1	
Install & Tools	HARKEN–57mm Carbo Air® Triple Block with Becket and Cam	West Marine	1171644	Base of block and tackle	1	
ARMS Baseplates	Heat-Shrink Tubing, 0.50" ID Before Shrinking	McMaster	7856K47	Heatshrink for non-slip. Cut into 1.5" lengths, slide over a SS u-bolt bracket and use heat gun to tighten onto bracket.	20	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Coral plate baseplates	Heat-Shrink Tubing, 0.50" ID Before Shrinking	McMaster	7856K47	Heatshrink for non-slip. Cut into 1.5" lengths, slide over a SS u-bolt bracket and use heat gun to tighten onto bracket.	40	
Buoyancy	Heatshrink for covering threaded rods before mounting in floats, 14" sections	McMaster	7856K66	Heatshrink for non-slip. Cut into 14" lengths. Slide onto fiberglass rods with 1" exposed on one end and 2-1/4" exposed on the other. Use heat gun to shrink until snug.	11	
Anchor system	High-Strength Grade 40/43 Chain-Not for Lifting, Galvanized Steel, 5/16 Trade Size	McMaster	3588T23	Chain to connect anchors and downline.	3	
Install & Tools	LOW-STRETCH ROPE, 7/16" DIAMETER	McMaster	3789T25	Rope for block and tackle	250	
ARMS Baseplates	Marine-Grade Moisture-Resistant HDPE, 48" x 48", 1/2" Thick	McMaster	9785T82	Sheeting for ARMS mounting baseplates. See Figure SI 13.	10	Yes
Coral plate baseplates	Marine-Grade Moisture-Resistant HDPE, 48" x 48", 1/2" Thick	McMaster	9785T82	Sheeting for coral plate baseplates. See Figure SI 14.	20	Yes
Mooring bridle	Martyr Collar Anode Zinc 3/4" x 2 1/8" x 2 1/8"	West Marine	5538715	Sacrificial anodes for Masterlinks on mooring lines	2	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Main structure	Martyr Hull Anode Zinc 6 1/4" x 2 3/4" x 5/8"	West Marine	484998	Sacrificial anodes for stainless struts at Ark base	3	
ARMS Baseplates	Mounting Plate for 1/4"-20 Thread Size, 2" ID 304 Stainless Steel U-Bolt	McMaster	8896T156	Bracket plate w/heatshrink, for attaching ARMS mounting baseplates to struts	6	
Coral plate baseplates	Mounting Plate for 1/4"-20 Thread Size, 2" ID 304 Stainless Steel U-Bolt	McMaster	8896T156	Bracket plate w/heatshrink, for attaching coral plate baseplates to struts	40	
Main structure	N1 Stars, 316 SS, 5mm Thick Connectors for DIY VikingDome F2 Sphere, modified	Viking Dome	ICO2-AISI	N1 Stars modified for central rod. Machine/weld connections to insert top and bottom of unthreaded fiberglass structural rod. See Figure SI 10.	2	
Main structure	N1 Stars, 316 SS, 5mm Thick Connectors for DIY VikingDome F2 Sphere, unmodified	Viking Dome	ICO2-AISI	Unmodified N1 Stars for Ark assembly. See Figure SI 10	10	Yes
Main structure	N2 Stars, 316 SS, 5mm Thick Connectors for DIY VikingDome F2 Sphere, modified	Viking Dome	ICO2-AISI	N2 Stars modified for floats. Drill larger center hole to accommodate 1" threaded fiberglass rod.	10	
Main structure	N2 Stars, 316 SS, 5mm Thick Connectors for DIY VikingDome F2 Sphere, modified	Viking Dome	ICO2-AISI	N2 Stars modified for pad eyes. Drill larger bolt hole (bit - 1/4") on outer hole of one arm for Padeye connector.	5	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Main structure	N2 Stars, 316 SS, 5mm Thick Connectors for DIY VikingDome F2 Sphere, unmodified	Viking Dome	ICO2-AISI	Unmodified N2 Stars for Ark assembly	15	
Anchor system	Pear-Shaped Link - Not for Lifting, Galvanized Steel, 3/4" Thick	McMaster	3567T34	Link to connect 3x 1/2" shackles to upper large shackle.	1	
Install & Tools	Phillips Screwdriver, Size No. 2	McMaster Carr	5682A28	Tighten down locknuts on star-strut bolts	1	
Coral plates	PVC Sheet Type 1, Gray, 48" x 48", 1/4" Thick	McMaster	8747K194	PVC baseplates for coral plates. See Figure SI 4.	20	Yes
Install & Tools	Ratcheting Combination Wrench, 3/4"	McMaster Carr	5163A21	Attach ARMS to ARMS mounting baseplates	2	
Install & Tools	Ratcheting Combination Wrench, 3/8"	McMaster Carr	5163A14	Tighten down locknuts on star-strut bolts	2	
Install & Tools	Ratcheting Combination Wrench, 7/16"	McMaster Carr	5163A15	Attach coral plates to coral plate baseplates	2	
Install & Tools	Round Bend-and-Stay Multipurpose Stainless Steel Wire, 0.012" diameter, 645 feet	McMaster	9882K35	Wire for mousing stainless shackles	1	
Main structure	S1 Struts - Structural FRP Fiberglass Square Tube, 2" Wide x 2" High Outside, 1/4" Wall Thickness	McMaster	8548K34	Fiberglass S1 Struts. Cut to 20.905" long (531 mm), drill bolt holes (bit - 7/32"), fill w/ divinycell foam & epoxy. See Figure SI 9	55	Yes
Main structure	S1 Struts (SS) - Corrosion-Resistant	McMaster	2937K17	Stainless S1 Struts. Cut to 20.905" long (531	5	Yes

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
	316/316L Stainless Steel Rectangular Tube, 0.12" Wall Thickness, 2" x 2" Outside			mm), drill bolt holes (bit - 1/4"). See Figure SI 9.		
Main structure	S2 Struts - Structural FRP Fiberglass Square Tube, 2" Wide x 2" High Outside, 1/4" Wall Thickness	McMaster	8548K34	Fiberglass S2 Struts. Cut to 24.331" long (618 mm), drill bolt holes (bit - 7/32"), fill w/ divinycell foam & epoxy. See Figure SI 9.	60	Yes
Anchor system	Skrew SK2500	Spade Anchor USA	SK2500	Two-plate sand screw anchors	3	
Coral plates	Stainless Steel Washers for 1/4" Screw Size, 0.281" ID, 0.625" OD	McMaster	90107A029	Numbered tags for coral plates. Stamp SS washers with numbered stamps and glue to coral plate for later ID.	100	
Main structure	Structural FRP Fiberglass Rod, 10 Feet Long, 1" Diameter	McMaster	8543K26	Central fiberglass rod, cut to Ark diameter	1	
ARMS attachments	Super-Corrosion-Resistant 316 Stainless Steel Hex Head Screw, 1/2"-13 Thread Size, 1-3/4" Long	McMaster	93190A718	Bolts for attaching ARMS to ARMS mounting baseplates (4 per unit)	40	

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Coral plate attach	Super-Corrosion-Resistant 316 Stainless Steel Hex Head Screw, 1/4"-20 Thread Size, 2" Long, Fully Threaded	McMaster	93190A550	Bolts to attach coral plates to baseplates	80	
ARMS Baseplates	Super-Corrosion-Resistant 316 Stainless Steel Hex Head Screw, 1/4"-20 Thread Size, 3-1/2" Long	McMaster	92186A556	Bolts for attaching ARMS mounting baseplates to struts	40	
Coral plate baseplates	Super-Corrosion-Resistant 316 Stainless Steel Hex Head Screw, 1/4"-20 Thread Size, 3" Long, Partially Threaded	McMaster	92186A554	Bolts for attaching coral plate baseplates to struts	160	
Buoyancy	TFLOAT 14" CENTERHOLE OR 437FM, modified	Seattle Marine	YUN12B-8	14" trawl floats for mounting to Stars. Slide fiberglass rod with heat shrink through trawl float. Add stainless washer and fiberglass hex nut on both sides. Seal washers with 3M 5200. Tighten nuts down. See Figure SI 16.	11	Yes

Table S2.11 Materials for Shell ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Buoyancy	TFLOAT 14" CENTERHOLE OR 437FM, unmodified	Seattle Marine	YUN12B-8	14" trawl float	2	
ARMS Baseplates	Thick-Wall Dark Gray PVC Pipe for Water, Unthreaded, 1/4 Pipe Size, 5 Feet Long	McMaster	48855K41	Star standoffs for attaching ARMS mounting baseplates to Stars. Cut to 1.75" long sections.	40	
Coral plates	Unfilled, Natural Travertine Flooring Tile, 16" x 16"	Home Depot	304540080	Limestone tiles for coral plates. Cut to 9" x 9" tiles using wet tile saw.	20	
Buoyancy	Vibration-Damping Routing Clamp, Weld mount, Polypropylene with Stainless Steel Plates, 1" ID	McMaster	3015T47	Attachment for central rod and float	1	
Buoyancy	Water- and Steam-Resistant Fiberglass Washer for 1" Screw Size, 1.015" ID, 1.755" OD	McMaster	93493A110	Fiberglass washers for securing fiberglass threaded rods into trawl floats	20	
Install & Tools	Zinc-Galvanized Steel Wire, 0.014" diameter, 475 feet long	McMaster	8872K19	Wire for mousing galvanized shackles	1	

Table S2.12 Materials for Two Platform ARK

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Downline	1" Nylon, 15' length thimble-to-thimble with SS Sailmaker Thimble spliced at top, galvanized thimble spliced at bottom	West Marine	Custom	Runs from bottom of swivel shackle (SS) to top of anchor system (galvanized)	1x	
Downline	1/2" Spectra Rope with SS316 Sailmakers Thimbles Spliced at Top and Bottom	West Marine	Custom	Runs from bottom of Ark to top of swivel shackle.	2x	
Buoyancy	1/2" Spectra Rope with SS316 Sailmakers Thimbles Spliced at Top and Bottom	West Marine	Custom	Connects mooring buoy to top eye on Ark	2x	
Main structure	3/8 x 36 Inch SS Thimble Eye Swages and 5/8 Jaw-Jaw Turnbuckle Cable Assembly	Pacific Rigging & Loft	Custom	Custom rigging system with turnbuckle, 3/8" SS wire rope swaged into PVC end caps	1x	
Main structure	304 SS U-Bolt with Mounting Plate, 1/4"-20, 2" ID	McMaster Carr	8896T123	For joining fiberglass platforms using I-beams	10x	
Main structure	316 SS Hex Nut, 1/4"-20	McMaster Carr	94804A029	For locking struts in hubs	120x	
Main structure	316 SS Nylon-Insert Locknut, 1/4"-20	McMaster Carr	90715A125	For locking struts in hubs	240x	
Main structure	316 SS Pan Head Phillips Screw, 1/4"-20 Thread, 2.5" Long	McMaster Carr	91735A384	For locking struts in hubs	120x	

Table S2.12 Materials for Two Platform ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Downline	316 SS Safety-Pin Shackle, 1/2" Thick	McMaster Carr	3860T25	Connect Ark bottom eye to 1/2" Spectra rope.	1x	
Buoyancy	316 SS Safety-Pin Shackle, 1/2" Thick	McMaster Carr	3860T25	Connects bottom of 1/2" rope to top Ark eye	2x	
Buoyancy	316 SS Safety-Pin Shackle, 7/16" Thick	McMaster Carr	3860T24	Connects mooring buoy to 1/2" rope	2x	
Install & Tools	Arbor with 7/16" Hex for 1-1/2" Diameter Hole Saw	McMaster Carr	4066A63	Drill holes in 6" PVC (Hubs)	1x	
Main structure	Clamping U-bolt, 304 SS, 1/4"-20 Thread Size, 9/16" ID	McMaster Carr	3042T149	For clamping SS wire rope at Ark vertices	15x	
Downline	Clevis-to-Clevis Swivel, 316 SS, 5-7/16" Long	McMaster Carr	37405T28	Swivel shackle between 1/2" spectra rope and 1" nylon downline	1x	
Main structure	Corrosion-Resistant Wire Rope, 316 SS, 1/8" Thick	McMaster Carr	8908T44	String through assembled Ark and clamp at vertices	250 ft	
Main structure	Fiberglass Molded Grating, Square Grid, 1" Grid Height, 1-1/2" x 1-1/2" Square Grid, Grit Surface, 70% Open Area	McNichols	MS-S-100	Cut to half pentagon shape, mirror images. See Figure SI 23.	2x	Yes
Anchor system	Galvanized Alloy Steel Screw-Pin Shackle, 1/2" Thick	McMaster Carr	3663T42	Connects base of 1" nylon downline to anchor chain	1x	
Anchor system	Galvanized Alloy Steel Screw-Pin Shackle, 3/8" Thick	McMaster Carr	3663T51	Connects anchor chain together	1x	

Table S2.12 Materials for Two Platform ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Anchor system	Grade 30 Chain, Galvanized Steel, 1/4 Trade Size	McMaster Carr	3592T45	Anchor chain		
Install & Tools	HARKEN–57mm Carbo Air® Triple Block	West Marine	200076	Top of block and tackle	1x	
Install & Tools	HARKEN–57mm Carbo Air® Triple Block with Becket and Cam	West Marine	1171644	Base of block and tackle	1x	
Install & Tools	Hole Saw, 1-15/16" Cutting Depth, 1-1/2" Diameter	McMaster Carr	4066A27	Drill holes in 6" PVC (Hubs)	1x	
Install & Tools	Low Pressure Inflator Nozzle	Amazon (Made by Trident)	B00KAI940E	Inflate mooring buoys underwater	1x	
Main structure	Nylon Cable Ties, UV Resistant Heavy Duty, 19" long, 250 lb strength	CableTies AndMore	CT19BK	Use to secure platforms to Ark framework	30x	Main structure
Install & Tools	Phillips Screwdriver, Size No. 3	McMaster Carr	5682A29	For locking struts in hubs	1x	Install & Tools
Buoyancy	Polyform Buoy, A-5 Series All-Purpose Buoy, 27"	West Marine (Made by PolyformUS)	11630142	Mooring buoy for buoyancy.	2x	Buoyancy
Main structure	PVC Pipe, Schedule 80, 1" diameter	McMaster Carr	48855K13	Struts. Cut to 1.2 m (4 ft) lengths, drill to accommodate bolts	30x	Main structure
Main structure	PVC Pipe, Schedule 80, 6" diameter	McMaster Carr	48855K42	Hubs. Cut into 4" lengths, drill 5 holes symmetrically around midline using 1-1/2" hole saw. See Figure SI 22.	12x	Main structure

Table S2.12 Materials for Two Platform ARK (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
Main structure	PVC Thick Wall Pipe Fitting, End Cap, Schedule 80, 6 " diameter, Female	PRMFiltration (Made by ERA)	PVC80CAP 600X	End caps for top and bottom of Ark. Cut off bottom 2 inches.	2x	Main structure
Install & Tools	Ratcheting Combination Wrench, 7/16"	McMaster Carr	5163A15	For locking struts in hubs	1x	Install & Tools
Install & Tools	Ratcheting PVC Cutter, 1-1/4"	McMaster Carr	8336A11	Cut 1" PVC into struts	1x	Install & Tools
Main structure	Ring, 18-8 SS, for 5/32 Chain Trade Size, 3/4" Inside Length	McMaster Carr	3769T71	Substitute for 1/2" SS wire rope clamps.	12x	Main structure
Install & Tools	Round Bend-and-Stay Multipurpose Stainless Steel Wire, 0.012" diameter, 645 feet	McMaster	9882K35	Wire for mousing stainless shackles	1	Install & Tools
Main structure	Structural FRP Fiberglass I-Beam, 1/4" Wall Thickness, 1-1/2" Wide x 3" High, 5 ft long	McMaster Carr	9468T41	Cut to 5 1-ft long sections.	1x	
Install & Tools	Underwater Lift Bag, 220 lbs Lift Capacity	Subsalve Commercial	C-200	Transport Ark to deployment site	1x	Install & Tools
Install & Tools	Zinc-Galvanized Steel Wire, 0.014" diameter, 475 feet long	McMaster	8872K19	Wire for mousing galvanized shackles	1	Install & Tools

Table S2.13 Materials for Strain Gauge

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
	316 Stainless Steel Eyebolt, for Lifting, M16 x 2 Thread Size, 27 mm Thread Length	McMaster Carr	3130T14	For strain gauge eyebolts	2x	
	Bridge101A Data Logger, 30 mV	MadgeTech	Bridge101A-30	Collect voltage data from load cell.	1x	
	Chemical-Resistant PVC Rod, 2" Diameter	McMaster Carr	8745K26	For datalogger housing endcap. See Figure SI 32.	1x	Yes
	Clamping U-Bolt, 304 SS, 5/16"-18 Thread Size, 1-3/8" ID	McMaster Carr	3042T154	For attachment of datalogger housing to strain gauge.	1x	
	Dow Corning Molykote 44 Medium Grease Lubricant	Amazon (Made by Dow Corning)	B001VY1EL8	For mating male and female underwater connectors.	1x	
	STA-8 Stainless Steel S Type Tension and Compression Load Cell	LCM Systems	STA-8-1T-SUB	Load cell instrument for assessment of in-water weight.	1x	
	Standard-Wall Clear Blue Rigid PVC Pipe for Water, Unthreaded, 1-1/2 Pipe Size, 2 ft	McMaster Carr	49035K47	For datalogger housing. See Figure SI 31.	1x	Yes
	Standard-Wall PVC Pipe Fitting for Water, Cap, White, 1-1/2 Pipe Size Socket Female	McMaster Carr	4880K55	For datalogger housing.	2x	

Table S2.13 Materials for Strain Gauge (Continued)

Component	Name of Material/ Equipment	Company	Catalog Number	Comments/ Description	Per unit	Refers to drawing
	Structural FRP Fiberglass Sheet, 12" Wide x 12" Long, 3/16" Thick	McMaster Carr	8537K24	For attachment of datalogger housing to strain gauge.	1x	
	SubConn Micro Circular Connector, Female, 4-port	McCartney (Made by SubConn)	MCBH4F	Install into machined housing endcap.	1x	
	SubConn Micro Circular Connector, Male, 4-contact	McCartney (Made by SubConn)	MCIL4M	Splice to load cell wiring and waterproof connection.	1x	
	Threadlocker, Loctite® 262, 0.34 FL. oz Bottle	McMaster Carr	91458A170	For strain gauge eyebolts	1x	
	Vibration-Damping Routing Clamp, Weld-Mount, Polypropylene with Zinc-Plated Steel Top Plate, 1-7/8" ID	McMaster Carr	3015T39	For attachment of datalogger housing to strain gauge.	1x	

Chapter 3

ESCAPING THE MICROBIALIZED BENTHOS WITH CORAL REEF ARKS: EFFECTS ON MICROBIAL ECOLOGY AND BIOGEOCHEMISTRY

ABSTRACT

Microbes on coral reefs drive biogeochemical cycles by remineralizing organic matter and drawing down dissolved oxygen, impacting the health of reef macroorganisms. Increased dissolved organic matter (DOM) on reefs enhances the growth and abundance of microbial heterotrophs and pathogens, which create deoxygenated benthic conditions hostile to corals and reef macrobiota. Increases in nearshore DOM occur directly due to land-based runoff and indirectly by fertilizing the growth of fleshy and turf algae that produce DOM in excess. These shifted conditions create so-called *microbialized* reefs and pose a major challenge to coral restoration efforts, especially in the global practice of transplanting corals from nurseries to the benthos. This work characterized viral and microbial ecology and the physicochemical environment associated with two coral transplantation approaches: (1) traditional benthic transplantation (“control”) sites, and (2) midwater reef mesocosm systems called Coral Arks off the benthos. Over 18 months, the seafloor control sites displayed hallmarks of microbialization, with low virus-to-microbe ratios, larger and more abundant microbes, and nighttime reductions in dissolved oxygen, conditions which were observed concurrently with poor coral survival. The Arks environment had higher viral abundances and virus-to-microbe ratios, smaller and less abundant microbes, and consistently higher dissolved oxygen, water flow speeds, and light availability than the control sites. Reduced microbialization on the midwater Coral Arks was linked to

enhanced viral predatory control on seawater microbial communities, enhanced oxygen, and reduced DOM, creating conditions that facilitate success of corals and other foundational reef macrobiota. These results suggest microbialization plays a large role in coral restoration outcomes and will be critical to consider in the design and monitoring of restoration projects.

INTRODUCTION

Coral reefs support some of the highest levels of biodiversity on the planet, with an estimated 1.5 million species living within or around the carbonate reef framework built by corals (Fisher et al., 2015; Galand et al., 2023). Microbes account for at least a third of this diversity (Galand et al., 2023) and maintain essential ecosystem processes, including nutrient cycling, organic matter processing, trophic interactions, and energy provisioning, all of which are integral to community stability and resilience (Hatcher 1997; Nelson et al., 2023). A combination of global and local human impacts have resulted in dysregulation among reef microbial communities (Haas et al., 2016), driving widespread declines in stony coral cover and biodiversity and subsequently spurring efforts to restore coral reefs and preserve the $400 billion in annual ecosystem services they provide (Costanza et al., 2014; Woodhead et al., 2019). Coral restoration efforts have been challenged by a changing climate, local impacts of overfishing and pollution, and microbialization and disease (Boström-Einarsson et al., 2020; Hein et al., 2020), which persistently reshape coral reef communities and diminish their resilience. Understanding the shifting environment of the degraded reefscape is crucial to supporting coral survival, but the specific role of microbial and environmental drivers in influencing coral restoration outcomes remains poorly understood.

Microbes are the invisible agents of energy transfers on coral reefs: through a process known as the microbial loop, free-living microbial communities consume forms of dissolved organic material (DOM) that are inaccessible to other organisms and then are consumed themselves, returning organic carbon and nutrients to the traditional food web and contributing to high productivity in nutrient poor waters (Azam et al., 1983; reviewed in Nelson et al., 2023). Microbes are also essential symbiotic partners in coral reef wholobionts (Knowlton and Rohwer 2003), shaping host physiology and function through the acquisition of nutrients, metabolic recycling, protection against pathogens, and increasing host stress tolerance (Thurber et al., 2008; Rädecker et al., 2015; Bourne et al., 2016; Glasl et al., 2016; Peixoto et al., 2020; Roach et al., 2020; Gardner et al., 2022). Both free-living and host-associated microbes are actively regulated on reefs: free-living microbes are kept under trophic control by viral lysis and protist grazing (Wilcox and Fuhrman 1994; Wilhelm and Suttle 1999; Suttle 2007, Silveira et al., 2023), while coral and other wholobiont hosts control their microbiome through chemical signaling, immune responses, and niche partitioning. Coral reef degradation has been widely linked to a breakdown of these regulatory controls on free-living and host-associated microbes in a process known as microbialization (Haas et al., 2016, Knowles et al., 2016), in which microbial communities on reefs shift towards opportunistic and pathogenic states which drive disease and host mortality (Cárdenas et al., 2018; Little et al., 2020; Silveira et al., 2017, 2020). At the reef scale, overfishing and eutrophication initiate this process by releasing top down (grazing) and bottom up (growth) controls on reef macroalgae, whose labile photosynthetic exudates stimulate the growth of copiotrophic and pathogenic microbial communities (Kline et al., 2006; Kuntz et al.,

2005; Barott and Rohwer 2012). Increasing microbial biomass and energetic demands on reefs and in wholobionts cause deoxygenation (Altieri et al., 2017; Silveira et al., 2019) and disease (Dinsdale et al., 2008; Silveira et al., 2020; Little et al., 2020), killing macroorganisms and reinforcing transitions to low diversity, trophically simplified reef states. These microbial feedback loops alter reef biogeochemistry and hamper coral restoration efforts, potentially explaining the high variability and low success rates of coral survival even among the many restoration methods used in different reef locations (Bayraktarov et al., 2016; Boström-Einarsson et al., 2020; Hein et al., 2020).

The coral microbiome is dynamic, shifting in response to the host and the external environment (Bourne et al., 2016; van Oppen and Blackall 2019; Lima et al., 2023). Recent evidence suggests shifts in the coral microbiome may be a primary reason for coral mortality and disease when corals are outplanted to reef habitat (Casey et al., 2015; Moriarty et al., 2020). Shifts in coral microbiomes towards a diseased state have also been associated with nutrient enrichment (Zaneveld et al., 2016; Shaver et al., 2017), predation (Shaver et al., 2017), alterations in fish behavior (Casey et al., 2014), thermal stress (Thurber et al., 2009), and poor water quality (Bourne 2005; Haapkylä et al., 2011). For example, host microbiomes can become dominated by one or more putatively pathogenic bacterial taxa (such as *Rickettsia* and *Vibrionales*). However, the structure and composition of coral microbiomes tend to be habitat-, species-, and even genotype- specific (Glasl et al., 2019; Miller et al., 2020), and microbiomes of different coral species and genotypes exhibit variable responses to translocation (Miller et al., 2020; Strudwick et al., 2022). There is evidence suggesting microbiome reorganization can facilitate coral adaptation to changing environmental

conditions (Röthig et al., 2016; Zaneveld et al., 2016; Maher et al., 2020; Santoro et al., 2021), underscoring the importance of considering not just corals, but the entire coral wholobiont, in reef restoration.

Less is known about the role of free-living, seawater microbes on coral survivorship in restoration projects. Free-living microbial communities have been well documented on coral reefs across a gradient of anthropogenic pressure, with pristine, coral-dominated reefs supporting microbial communities dominated by autotrophs (SAR11 and *Alphaproteobacteria*) and highly impacted, algae-dominated reefs supporting a higher abundance of heterotrophs (*Gammaproteobacteria*, *Vibrionaceae*, *Pseudoalteromonadacaea*, *Bacteroidetes*) and pathogens (Dinsdale et al., 2008; Bruce et al., 2012; Haas et al., 2016). Algae-stimulated bacterial communities are less diverse (Dinsdale et al., 2008; Knowles et al., 2016), more pathogenic (Nelson et al., 2013; Silveira et al., 2020), have elevated metabolic rates (Haas et al., 2016; Roach et al., 2017a), and higher per-cell biomass (McDole et al., 2012; Silveira et al., 2019), contributing to a reef-wide reallocation of metabolic energy to the microbes (Somera et al., 2016). These shifts in seawater microbial communities, largely driven by dissolved organic carbon supply by the benthos (Nelson et al., 2013; Cárdenas et al., 2018), can cause rapid and long-lasting changes to reef benthic communities through disease and deoxygenation (Silveira et al., 2019; Johnson et al., 2021). Yet, seawater microbial communities are highly responsive to their external environment (Glasl et al., 2019; Kelly et al., 2019) and community shifts are often short-lived (Johnson et al., 2021). The genetic functions encoded by seawater microbes are strongly correlated with abiotic factors (Kelly et al., 2014), and microbial communities have been used to accurately

infer changes in reef environmental factors such as eutrophication state, water quality, and temperature (Glasl et al., 2019). Seawater microbes influence all aspects of reef function and are likely to influence coral transplantation efforts, but the impact of these communities on the survival of transplanted corals has not yet been assessed.

This work evaluated the microbial, physical, and chemical environment associated with two coral transplantation scenarios: a midwater system called Coral Reef Arks (Baer et al., 2023) and a benthic “control” site replicating the traditional coral restoration approach (Rinkevich 2005; Lirman et al., 2010). Water quality was a defining difference between these two translocation sites: Arks were installed offshore and elevated above the benthos (at a depth of 25 feet in 55 feet of water), with water quality conditions more similar to open-ocean environments than the coastal control sites, which are subject to terrestrial inputs and benthic-associated reductions in water quality. Abiotic and biotic metrics associated with the Arks and control sites were tracked at multiple timepoints over approximately 18 months (Figure 3.1). This work hypothesized that improved physical and chemical conditions on midwater Arks would support microbial communities with lower per-cell biomass and a higher proportion of free viruses (predators of the microbes), and that these communities would enhance survival of translocated corals. In contrast, microbial communities associated with corals translocated to seafloor sites were expected to display hallmarks of microbialization, with fewer viral predators and microbes with higher per-cell biomass, leading to poor survivorship of translocated corals.

METHODS

Site design

Two midwater Coral Reef Arks structures were installed off the west coast of Vieques, Puerto Rico in the northeastern Caribbean. Corals were outplanted to the Arks as well as to two seafloor “control” sites used to emulate a traditional benthic restoration method.

Arks

Coral Reef Arks (hereafter “Arks”) are positively buoyant, midwater structures tethered to a seafloor anchoring system. Each Ark is a geodesic sphere measuring 2.4 m (8 ft) in diameter and constructed from stainless steel and fiberglass base materials following methods described in Baer et al. (2023). In November 2021, two Arks were installed approximately 2 miles offshore of the west coast of Vieques Island, Puerto Rico (Figure 3.1) within part of the U.S. Navy’s unexploded ordnance remediation site 16 (UXO 16). The installation site was characterized by sandy bottom at approximately 17 m depth (56 ft) with patches of seagrass and macroalgae (primarily *Padina spp.* and *Halimeda spp.*). Once installed, the midline of the positively buoyant Arks was located at approximately 8.8 m depth (29 ft) and the top of the Arks was located at approximately 7.6 m depth (25 ft).

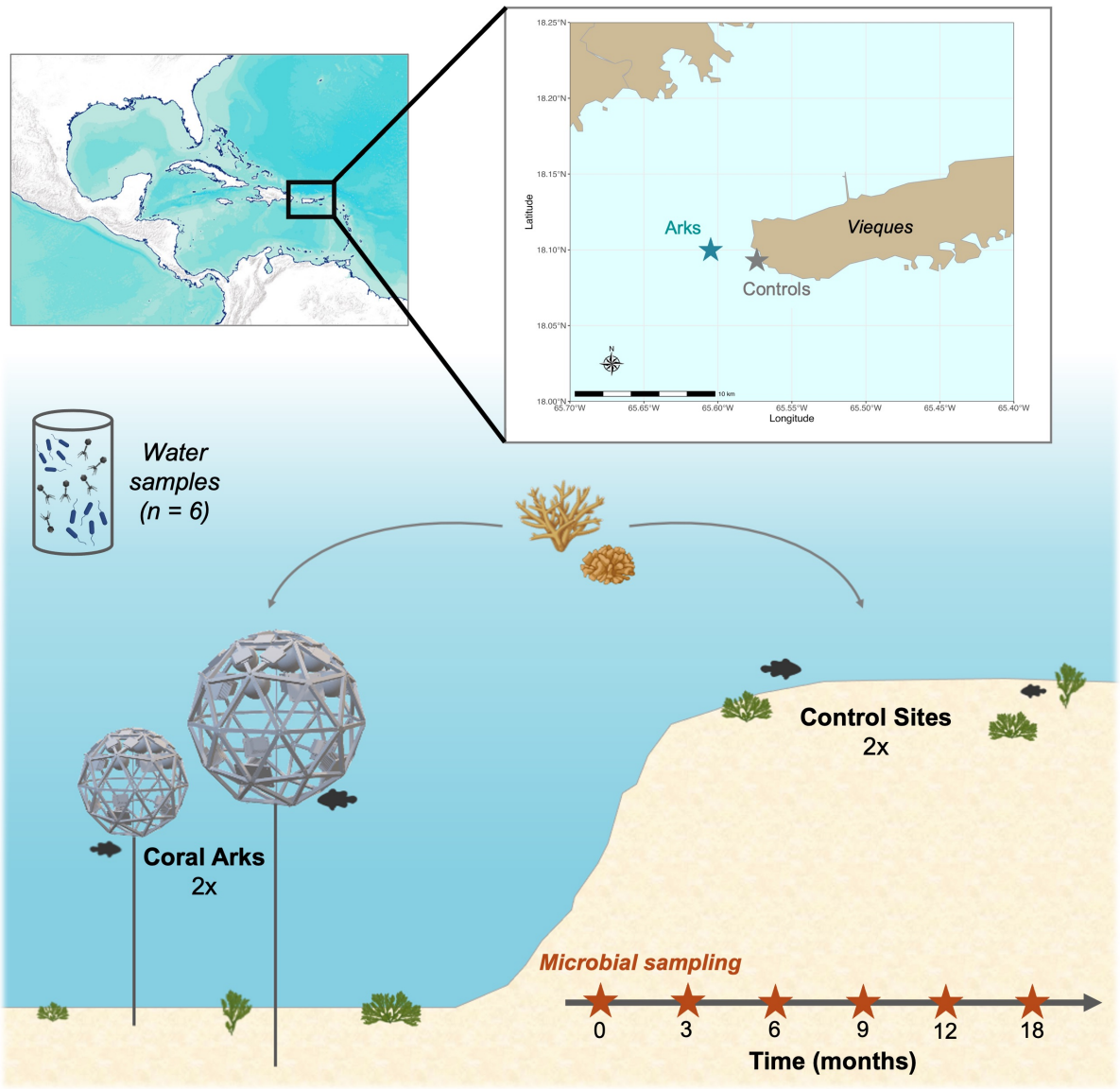


Figure 3.1 Experimental design and water sampling scheme. The experiment was conducted offshore of Isla Vieques, Puerto Rico, located within the eastern Caribbean Sea (top left map). Two Coral Arks were deployed approximately 2 miles offshore of Isla Vieques and two control sites were installed at the same depth as the Arks, but closer to shore (top right map). Coral fragments were distributed equally across both Arks and control sites at the beginning of the experiment (0 months on the timeline). 6 water samples were collected from both Arks and control sites during each of 6 monitoring events, for a total of 144 samples, for microbial community and chemical analysis.

Control Sites

Two seafloor control sites were selected off the west coast of Vieques at similar depths as the tops of the Arks structures to compare the Arks approach to the traditional

method of outplanting corals to the seafloor. The two sites were located within another nearshore zone of UXO16 at 7.6 m (25 ft) and 6.4 m (21 ft) depth, respectively, and separated by approximately 25 m (Figure 3.1). Control sites were broadly characterized as reef hardbottom and included colonized pavement, linear reef, and aggregated patch reef habitats (Bauer and Kendall 2010). Several genera of stony corals, including *Orbicella, Siderastrea, Diploria,* and *Porites* are present at the site, as well as abundant fire corals, soft corals, sponges, and a high benthic cover of turf and macroalgae. Similar to other reefs around Vieques, the control sites are in relatively poor condition, with sparse living coral cover. Patches of sand and seagrass can be found at the edges of the sites.

Corals

A total of 400 coral fragments comprising 8 species were distributed equally across two Arks and two control sites in two distinct translocation events, or “phases,” for a total of 100 corals moved to each site. Phase 1 occurred concurrently with the installation of the Arks and control sites (November 2021) and initiated the experiment. Phase 1 corals were sourced from a NOAA coral nursery on the northeast of Puerto Rico and from a sunken barge near Guayama on Puerto Rico’s south coast. Phase 2 occurred six months later (May 2022) and used corals sourced from the same coral nursery as well as corals of opportunity located on a spalling concrete boat ramp at Mosquito Pier on Vieques’ north coast. Further details on coral species, attachment methods, and coral monitoring can be found in Carilli and Baer et al., 2024.

ARMS

Autonomous Reef Monitoring Structures (ARMS) are standardized settlement structures that passively recruit reef cryptic biodiversity (Pearman et al., 2016). In May 2021, ARMS units were installed on a patch reef approximately 500 m from the control sites off the west coast of Vieques and left to accumulate cryptobiota for one year. In May 2022, ten “seeded” ARMS were translocated to each midwater Ark to transfer native reef cryptobiota alongside the Phase 2 cohort of corals. Seeded ARMS contained fouling communities composed of primarily sponges, ascidians, algae, and mobile invertebrates.

Monitoring

Water samples were collected from the two Arks and two control sites at three-month intervals over the course of a year for a total of 6 sampling events (November 2021, February 2022, May 2022, August 2022, December 2022, June 2023). Six water samples (n = 6) were collected from each site during each sampling event for a total of 144 water samples and were processed to analyze water chemistry (dissolved organic carbon, inorganic nutrients), viral and microbial abundances, and microbial cell size. Sensors were used to collect physical time series data (temperature, dissolved oxygen, flow speed, and light intensity) for each site at every monitoring event.

Water sample collection

Water samples were collected on SCUBA using 2 L polycarbonate Hatay-Niskin bottles as described in Haas et al., 2014 and Baer et al., 2023. Briefly, Hatay-Niskin bottles were rinsed prior to sampling with 5% hydrochloric acid solution (HCl) to remove

organic carbon contamination, brought in an open configuration via SCUBA to the sampling site, passed back and forth to flush the interior of the cylinder with sample water, and sealed using end caps. At the control sites, all water samples were collected from within 20 cm of the benthos, in close proximity to the translocated corals. Arks water samples were similarly collected in close proximity to the translocated corals, however half of the samples (n = 3) were collected from inside the Arks (below the corals) and half of the samples (n = 3) were collected from outside (above the corals) at each site. Water sampling occurred between the hours of 0900 and 1200 daily at all sites. Following sample collection, water samples were stored in the dark in a cooler until sample processing.

Sample processing

Water samples were processed within 6 hours of collection to prepare for analysis of dissolved organic carbon (DOC); inorganic nutrients including nitrate + nitrite (NO_3^- + NO_2^-), ammonia (NH_3), and phosphate (PO_4^{3-}); enumeration of viral and microbial abundances; and microbial cell size and biomass. Methods are described in detail in Haas et al., (2014) and summarized below.

Viral and microbial abundances and virus-to-microbe ratio (VMR)

1 mL of unfiltered sample water was fixed using paraformaldehyde (*Electron Microscopy Sciences*) to a final concentration of 2%, passed through a 0.02 µm Anodisc filter (*Whatman*), and stained with 5X SYBR Gold (*Invitrogen*). The filter was then mounted on a microscope slide using a mountant solution (glycerol, 1X PBS, ascorbic acid) and stored at -20°C until analysis via epifluorescence microscopy

(excitation/emission: 325-375/537 nm). Direct counts were obtained using the ImagePro Software (*Media Cybernetics*) and used to determine viral and microbial abundances in each water sample (Noble and Fuhrman 1998). Viral and microbial abundances were used to calculate the virus-to-microbe ratio (VMR) per sample.

Microbial biomass and cell size

1 mL of unfiltered sample water was fixed with glutaraldehyde (*Electron Microscopy Sciences*) to a final concentration of 0.3% v/v, passed through a 0.2 µm Anodisc filter (*Whatman*), and stained with 25 µg/mL DAPI (*Molecular Probes, Invitrogen*). The filter was then mounted on a microscope slide using a mountant solution (glycerol, 1X PBS, ascorbic acid) and stored at -20°C until analysis via epifluorescence microscopy (excitation/emission: 358/461 nm). Microbial cell dimensions (length and width) were obtained using the ImagePro Software (*Media Cybernetics*). Cell volume (μm^3) was calculated from length and width measurements by assuming each cell has the shape of a cylinder with hemispherical endcaps, according to the following equation:

$$V = \pi / 4 \times w^2(L - w/3)$$

Where L is length and w is width (Bjørnsen 1986; McDole et al., 2012).

Dissolved organic carbon (DOC)

All glassware and tubing used was washed in 5% HCl to prevent organic carbon contamination. Sample seawater for bulk DOC analysis was filtered through a 0.22 µm Sterivex filter (*EMD Millipore*), discarding the first ~100 mL of filtered sample water. An acid-washed and pre-combusted 40 mL amber borosilicate glass vial was then rinsed

five times with sample water and filled to the shoulder (~35 mL). The sample was then poisoned with three drops of full strength, molecular grade HCl, capped with a PTFE-lined silicone septa, and stored at 4°C until analysis via high-temperature catalytic oxidation as described by Carlson et al., (2010).

Inorganic nutrients

Sample seawater for inorganic nutrient analysis was filtered through a 0.22 µm Sterivex filter, discarding the first ~100 mL of filtered sample water. A clean, 20 mL HDPE plastic vial was then rinsed three times with sample water, filled to the shoulder (~18 mL), and frozen immediately at -20°C until analysis via flow injection analysis as described by Guildford and Hecky (2000).

Physical variables

Measurements of current speed (cm/s) were collected by an acoustic doppler current profiler (ADCP; Aquadopp 1MHz, *Nortek*) placed at the Arks and control sites for approximately two days per site per sampling event at a five-minute reading interval. Dissolved oxygen data (mg/L, % saturation) at each Ark and control site were collected using HOBO (*Onset*) dissolved oxygen dataloggers at a one-minute reading interval and were corrected for salinity using a portable refractometer. Temperature/light HOBO pendant loggers (*Onset*) were deployed at each site to record measurements of temperature (°C) and light intensity (lux) at a five-minute reading interval.

Data processing and statistical analysis

All data analysis was conducted using R (Version 4.3.2) and RStudio statistical software (Version 2023.12.1+402).

Viral and microbial ecology

Statistical tests were performed on the variables VMR, viral-like-particle (VLP) abundance, microbial abundance, and mean microbial cell size to compare the two treatments (Ark and control) as well as differences within treatments through time. For each monitoring time point (0-, 3-, 6-, 9-, 12-, and 18-months following deployment), each of these variables were compared between treatments using non-parametric Mann Whitney U tests. The same test was used to evaluate differences between the two treatments over all timepoints. For each variable, non-parametric Kruskal-Wallis tests were used to test for differences through time within each treatment (Ark or control). Limited viral and microbial ecology data was also collected from the ARMS units directly and tested for significant differences from the Arks and control treatments using a non-parametric Kruskal-Wallis test. A Dunn Test with a Bonferroni correction for multiple comparisons was used to further test for specific differences between the ARMS, Arks, and control groups.

Physical variables

Dissolved oxygen, temperature, flow, and light intensity data were collected as time series. For the dissolved oxygen and light intensity variables, measurements were classified as “night” or “day” measurements based on the sensor timestamp (between 7 PM and 7 AM local time for “night,” and between 7 AM and 7 PM local time for “day”).

Only daytime measurements of light intensity were used in statistical analyses. Daytime Dissolved Oxygen (DDO) for each time point was calculated by averaging the top 5% of daytime dissolved oxygen (% saturation) measurements at each site. Similarly, Nighttime Dissolved Oxygen (NDO) for each time point was calculated by averaging the bottom 5% of nighttime dissolved oxygen (% saturation) measurements at each site, capturing the maximum range of DO experienced at each site and timepoint. The dissolved oxygen saturation ratio (DO Sat Ratio) was calculated for each site and time point by dividing DDO by NDO to generate a single value describing the diel variance in dissolved oxygen at each site.

All of the time series datasets were tested for normality using a Shapiro-Wilks test and for homogeneity of variance using a Levene's test. In all cases, data were normal but had significantly different variances. A Welch's Two Sample t-test (which does not assume equal variances) was used to test for differences in each of the variables between treatments at each time point. A Welch's ANOVA was used to test for differences in dissolved oxygen, temperature, flow, and light intensity between the Arks and control sites over all time.

Chemical variables

Similar statistical tests were performed on dissolved organic carbon, ammonia, nitrate + nitrite, and phosphate as for the viral and microbial ecology variables. For inorganic nutrients (nitrate + nitrite, phosphate, and ammonia), all data were used in statistical analysis, including those values below the laboratory method detection limit (Succop et al 2004). No chemical data were collected at the initial time point, but for each successive monitoring time point (3-, 6-, 9-, 12-, and 18-months following

deployment), the chemical variables were compared between treatments using non-parametric Mann Whitney U tests. The same test was used to test for differences between the two treatments over all timepoints. For each variable, non-parametric Kruskal-Wallis tests were used to test for differences through time within each treatment (Ark or control).

Variable relationships and multivariate analyses

All variables described above were averaged to a single value per site per time point to simplify between-metric comparisons. A Spearman's correlation matrix was used to test for significant correlations between the variables. Each correlation coefficient was interpreted to understand the strength and direction of the monotonic relationship between pairs of variables, where values close to ±1 indicate strong relationships, and values close to 0 indicate weak or no relationship. A heatmap of the correlation matrix was generated with a color gradient indicating the strength and sign of each correlation. Linear regression models were performed on several of the strongly correlated variables, including (1) mean microbial cell volume and microbial abundance, (2) VMR and mean microbial cell volume, (3) viral abundance and microbial abundance, (4) microbial abundance and DOC, (5) VMR and NDO and (6) VMR and DO Sat Ratio. T-tests were performed on the coefficients of each linear regression model to test for significance.

The same dataset was used in a supervised Random Forest analysis to identify the most significant predictors of whether samples were collected from Arks or control sites. Missing datapoints were imputed with the missForest package in *R* and a permuted Random Forest was used to identify statistically significant predictors. PCA

was then performed on the imputed dataset to identify patterns of variability and to reduce the dimensionality of the data. The PCA included all normalized variables from the collected datasets. The number of principal components retained was determined based on the Kaiser criterion, retaining only components with eigenvalues greater than 1, and this was further supported by examination of a scree plot showing a clear elbow. The resulting components were interpreted based on their loadings, with high absolute values indicating variables that contribute most to each component.

RESULTS

Viral and microbial ecology

Over the 18-month experiment, viral and microbial communities on the Arks differed significantly from the control sites at nearly all time points (Table 3.1). Arks supported microbial communities with significantly higher virus-to-microbe ratios (VMR, Figure 3.2a) and virus-like particle (VLP) abundances (Figure 3.2b), and significantly lower microbial cell abundances (Figure 3.2c) and mean microbial cell volumes (Figure 3.2d) relative to the control sites (Mann Whitney U test, all $p < 0.001$). Viral and microbial communities also differed through time within each Ark and control site, which may reflect seasonal changes or natural variability. These differences were significant for VMR (Figure 3.2e), VLP abundance (Figure 3.2f), microbial cell abundance (Figure 3.2g), and mean microbial cell volume (Figure 3.2h) for both Arks and control treatments (Kruskal-Wallis test, all $p < 0.001$).

Table 3.1 Results from a Mann Whitney U test comparing viral and microbial ecology and chemical variables at Arks and control sites at each monitoring time point. Values represent p-values from each test, with bolded values indicating significant differences at a significance threshold of $\alpha = 0.05$.

Variable/Time point	0	3	6	9	12	18
VMR	**3.64E-05**	**7.40E-07**	**7.40E-07**	**0.002**	**7.40E-07**	**2.84E-06**
VLPs/mL	**3.64E-05**	0.132	**0.004**	**0.004**	**5.96E-05**	**0.005**
Cells/mL	0.707	**1.00E-04**	**9.70E-05**	**0.005**	0.442	**1.00E-04**
Mean Cell Volume	**0.025**	0.094	**1.00E-04**	**0.026**	**4.68E-05**	**0.003**
DOC	NA	**0.002**	0.105	**0.004**	0.193	0.525
$NO_3^- + NO_2^-$	NA	0.236	0.212	0.297	**2.00E-04**	**0.005**
PO_4^{3-}	NA	0.459	0.232	0.490	0.860	0.109
NH_3	NA	**2.00E-04**	0.128	0.935	0.072	0.061

Viral and microbial communities within ARMS units exhibited distinct differences from those at the Arks and control sites. Specifically, ARMS units had significantly lower VMRs (Figure 3.3a) and significantly higher virus-like particle (VLP) abundances (Figure 3.3b), microbial cell abundances (Figure 3.3c), and mean microbial cell volumes (Figure 3.3d) compared to the other sites (Kruskal-Wallis test, all $p < 0.001$). Post-hoc analysis with Dunn's test and Bonferroni correction confirmed significant differences across all comparisons (Ark – ARMS, Ark – control, ARMS – control) for each metric ($p < 0.01$).

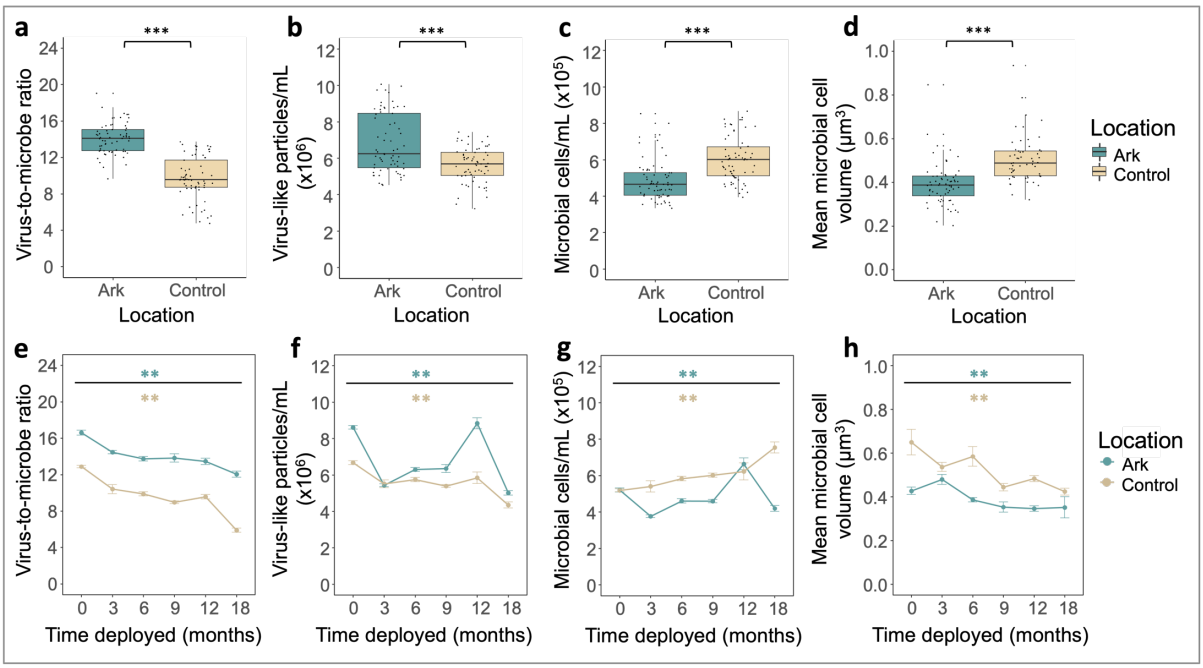


Figure 3.2 Viral and microbial ecology variables at Arks and control sites. (a-d) Boxplots showing virus-to-microbe ratio, viral-like particle (VLP) abundance, microbial abundance, and mean microbial cell volume of seawater microbial communities collected from the Arks and control sites. Asterisks denote significant differences between Ark and control treatments (Mann Whitney U test, $p < 0.001$). (e-h) Line plots showing the same variables as in (a-d) plotted over time. Colored asterisks denote significant differences within the Ark (teal) and control (tan) treatments over time (Kruskal-Wallis test, $p < 0.001$).

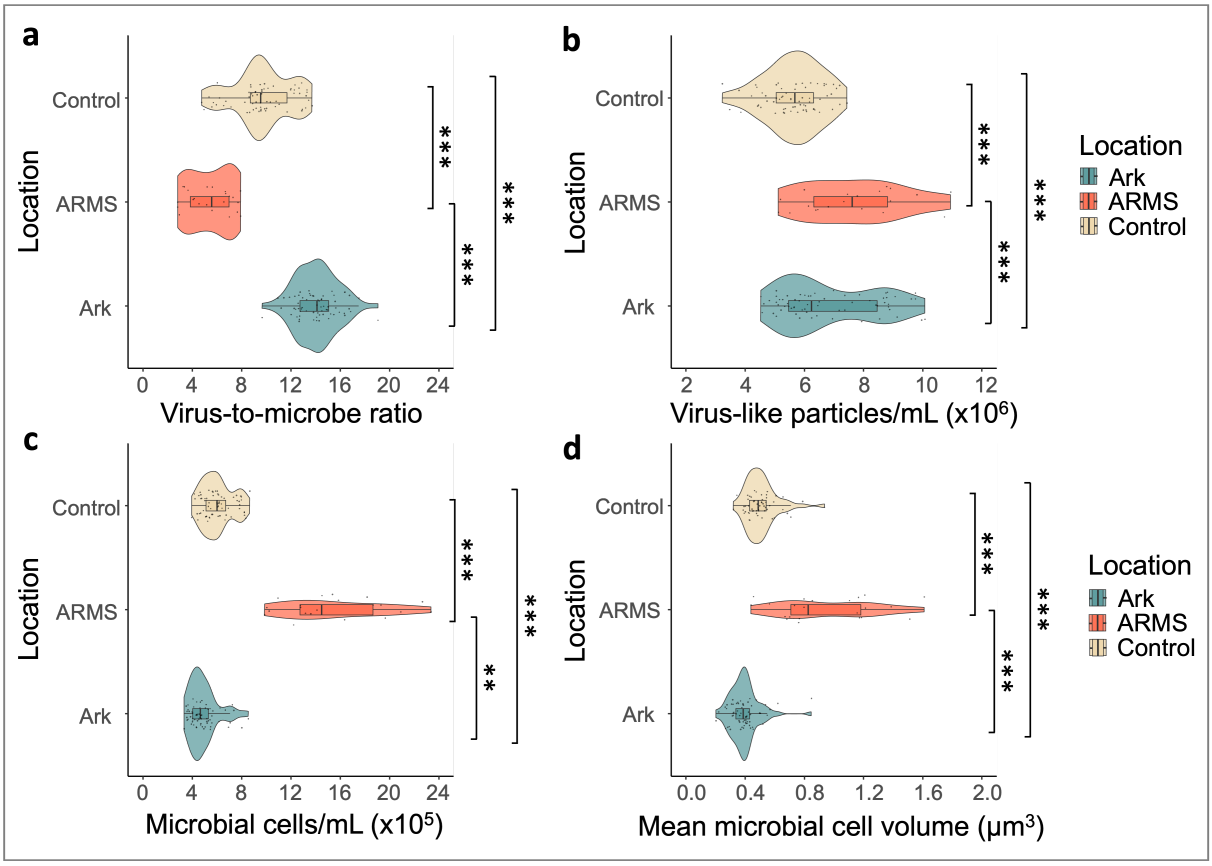


Figure 3.3 Viral and microbial ecology variables at Arks, control sites, and ARMS. (a-d) Violin plots showing virus-to-microbe ratio, viral-like particle (VLP) abundance, microbial abundance, and mean microbial cell volume of seawater microbial communities collected from the Arks, control sites, and ARMS units. Asterisks denote significant differences between the following comparisons: Arks – ARMS, Arks – control, and control – ARMS (post-hoc Dunn test with Bonferroni correction, ** = $p < 0.01$, *** = $p < 0.001$).

Physical variables

Arks and control sites displayed significant differences in physical variables both between sites and within sites over time. Overall, dissolved oxygen concentrations (Figure 3.4a), current speeds (Figure 3.4c), and daytime light intensities (Figure 3.4e) were significantly higher at the Arks than at the control sites (Welch's ANOVA, all $p < 0.001$). All three variables differed significantly between the two treatments at every monitoring time point (Welch's Two-Sample t-test, all $p < 0.001$). Temperature also differed significantly over all time between the two treatments (Figure 3.4b; Welch's

ANOVA, $p < 0.001$) as well as at every monitoring time point (Figure 3.4b; Welch's Two-Sample t-test, $p < 0.001$), although differences were less pronounced.

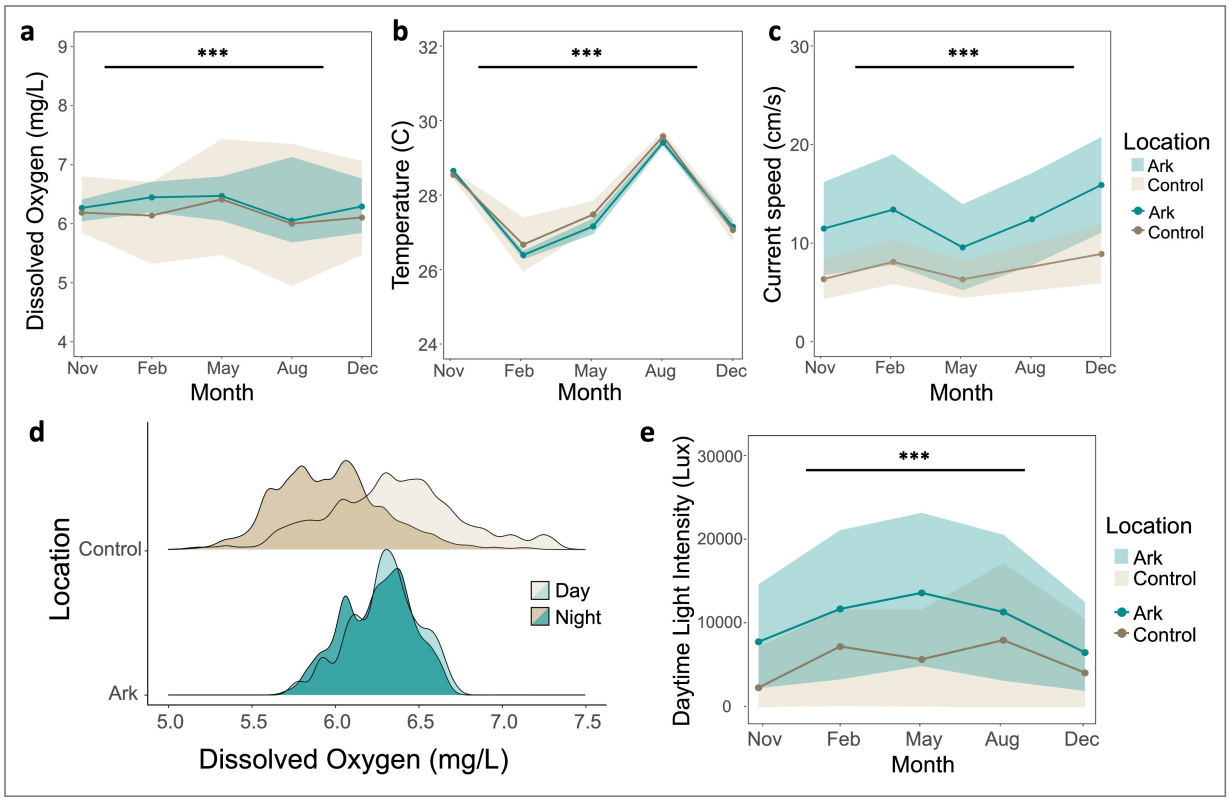


Figure 3.4 Physical variables at Arks and control sites. (a-c, e) Line plots showing dissolved oxygen, temperature, average current speed, and daytime light intensity measured at the Arks and control sites during each monitoring time point. The shaded regions around each line indicate the range of data. Asterisks denote significant differences between Ark and control treatments at each time point (Welch's Two Sample t-test, $p < 0.001$). (d) Ridgeline plot showing the diel range of dissolved oxygen measurements collected at Arks and control sites, with daytime measurements displayed in light colors and nighttime measurements displayed in darker colors.

Chemical variables

Significant differences between the Arks and control sites in chemical variables were not observed at most monitoring time points (Table 3.1), with the exceptions of dissolved organic carbon (DOC) concentrations at the 3 and 9 month monitoring time points (Figure 3.5e), nitrate + nitrite (NO_3^- + NO_2^-) concentrations at the 12 and 18 month monitoring time points (Figure 3.5f), and ammonia (NH_3) at the 3 month monitoring time point (Figure 3.5g) (Mann Whitney U test, all $p < 0.01$). Across all timepoints, Arks did not have significantly different dissolved organic carbon (DOC, Figure 3.5a), ammonia (NH_3, Figure 3.5c) or phosphate (PO_4^{3-}, Figure 3.5d) than the control sites, but did have significantly lower nitrate + nitrite (NO_3^- + NO_2^-, Figure 3.5b, $p < 0.001$) (Mann Whitney U test, $\alpha = 0.05$). However, all of these variables differed over time within each Ark and control site. These differences were significant for DOC (Figure 3.5e), NO_3^- + NO_2^- (Figure 3.5f), NH_3 (Figure 3.5g), and PO_4^{3-} (Figure 3.5h) for both Arks and control treatments (Kruskal-Wallis test, all $p < 0.001$).

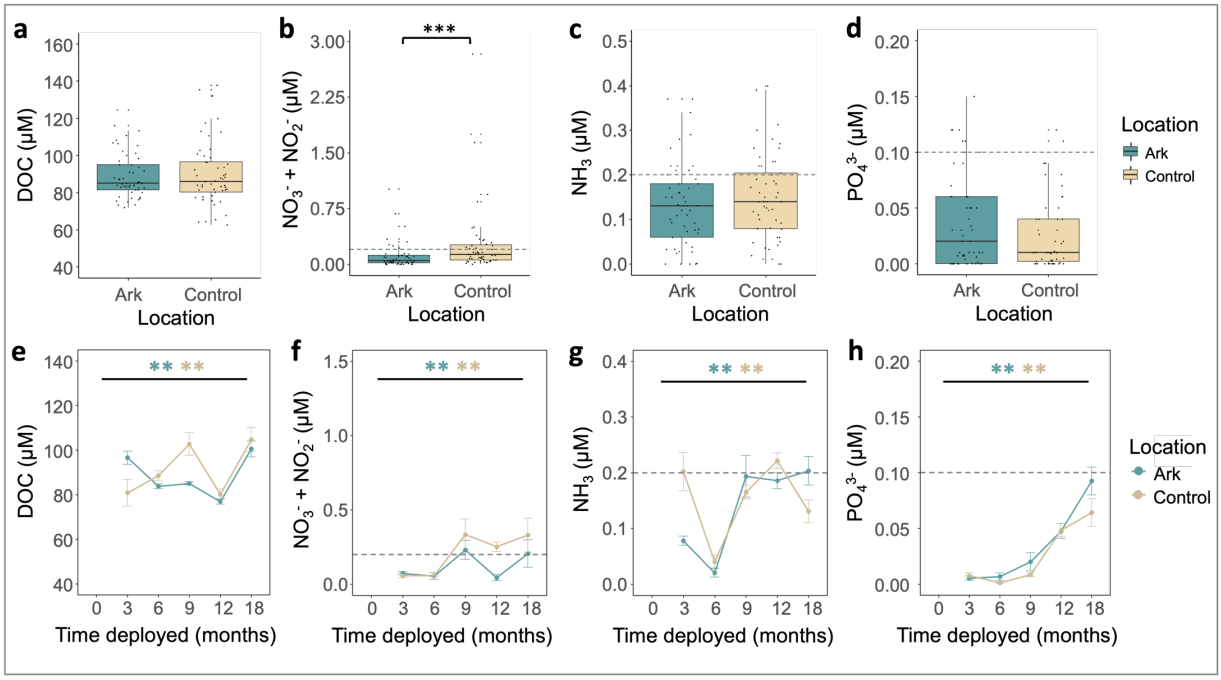


Figure 3.5 Chemical variables at Arks and control sites. (a-d) Boxplots showing dissolved organic carbon (DOC), nitrate + nitrite (NO_3^- + NO_2^-), ammonia (NH_3), and phosphate (PO_4^{3-}) concentrations in seawater collected from the Arks and control sites. Asterisks denote significant differences between Ark and control treatments (Mann Whitney U test, $p < 0.001$). Gray dashed line indicates the laboratory method detection limit for nutrient analysis. (e-h) Line plots showing the same variables as in (a-d) plotted over time. Colored asterisks denote significant differences within the Ark (teal) and control (tan) treatments over time (Kruskal-Wallis test, $p < 0.01$).

Variable relationships and multivariate analyses

Spearman's rank correlation coefficients were computed and plotted on a correlation matrix to assess the monotonic relationships between viral and microbial ecology, chemical, and physical variables (Figure 3.6a). Several significantly correlated variable pairs were extracted and assessed for the strength and directionality of the relationship using linear regression analysis. VMR and mean microbial cell volume were significantly negatively correlated (Figure 3.6b; $r^2 = 0.360$, $p < 0.001$). Mean microbial cell volume and microbial cell abundance were significantly positively correlated (Figure 3.6c; $r^2 = 0.546$, $p < 0.001$). At the Arks, VLP abundance and microbial cell abundance were significantly positively correlated (Figure 3.7a; $r^2 = 0.723$, $p < 0.001$), but the same

relationship at the control sites was absent (Figure 3.7a; r^2 = 8.82e-05, p = 0.94). At all sites, DOC was significantly, though weakly, correlated with microbial cell abundance (Figure 3.7b; r^2 = 0.069, p < 0.01). VMR was significantly positively correlated with average NDO concentration (Figure 3.7c; r^2 = 0.5457) and significantly negatively correlated with DO Sat Ratio (Figure 3.7d; r^2 = 0.5768, both p < 0.01).

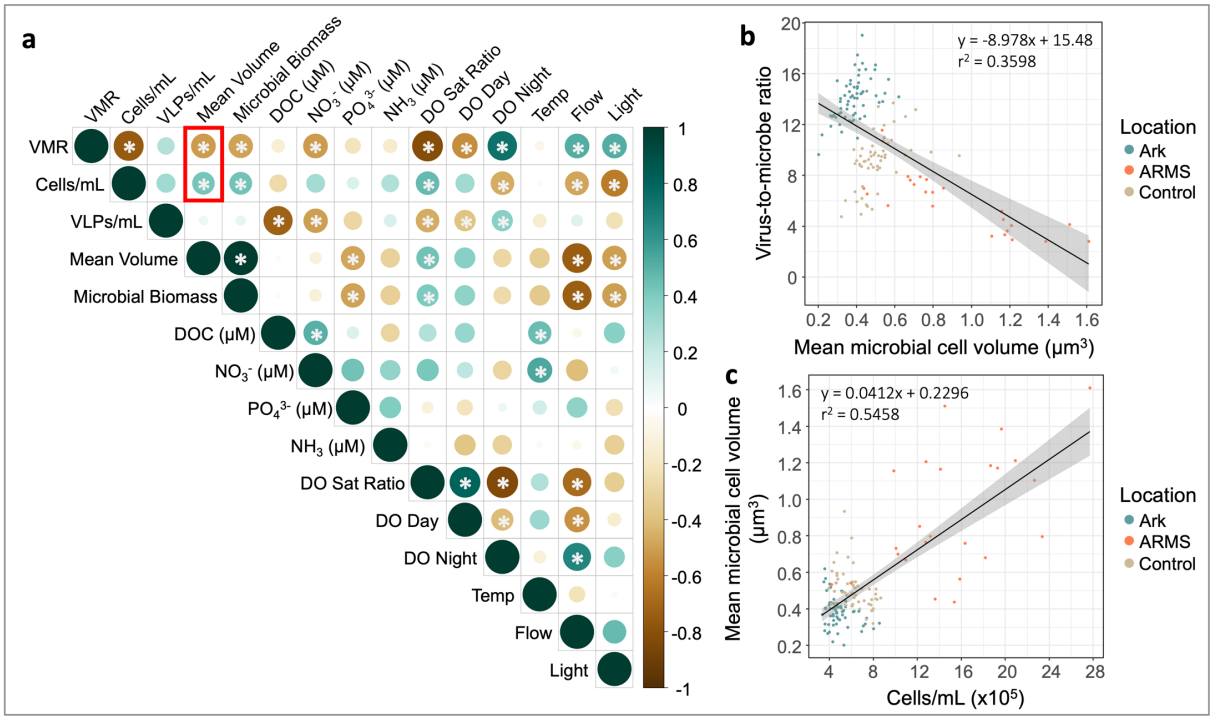


Figure 3.6 Relationships between viral and microbial, chemical, and physical variables. (a) Spearman's correlation matrix, with green colors indicating a positive correlation and brown colors indicating a negative correlation between the variable pair (darker color = stronger correlation). Circle size indicates significance of the correlation, with a "*" denoting a significance threshold of p < 0.05. Two of these significant correlations (red box) are plotted in (b) and (c). (b) Linear regression model of virus-to-microbe ratio (VMR) and mean microbial cell volume (μm^3), colored by treatment (Ark, ARMS, and control sites). (c) Linear regression model of mean microbial cell volume (μm^3) and microbial cell abundance, colored by treatment. Linear equation and r^2 value are displayed on both regression plots.

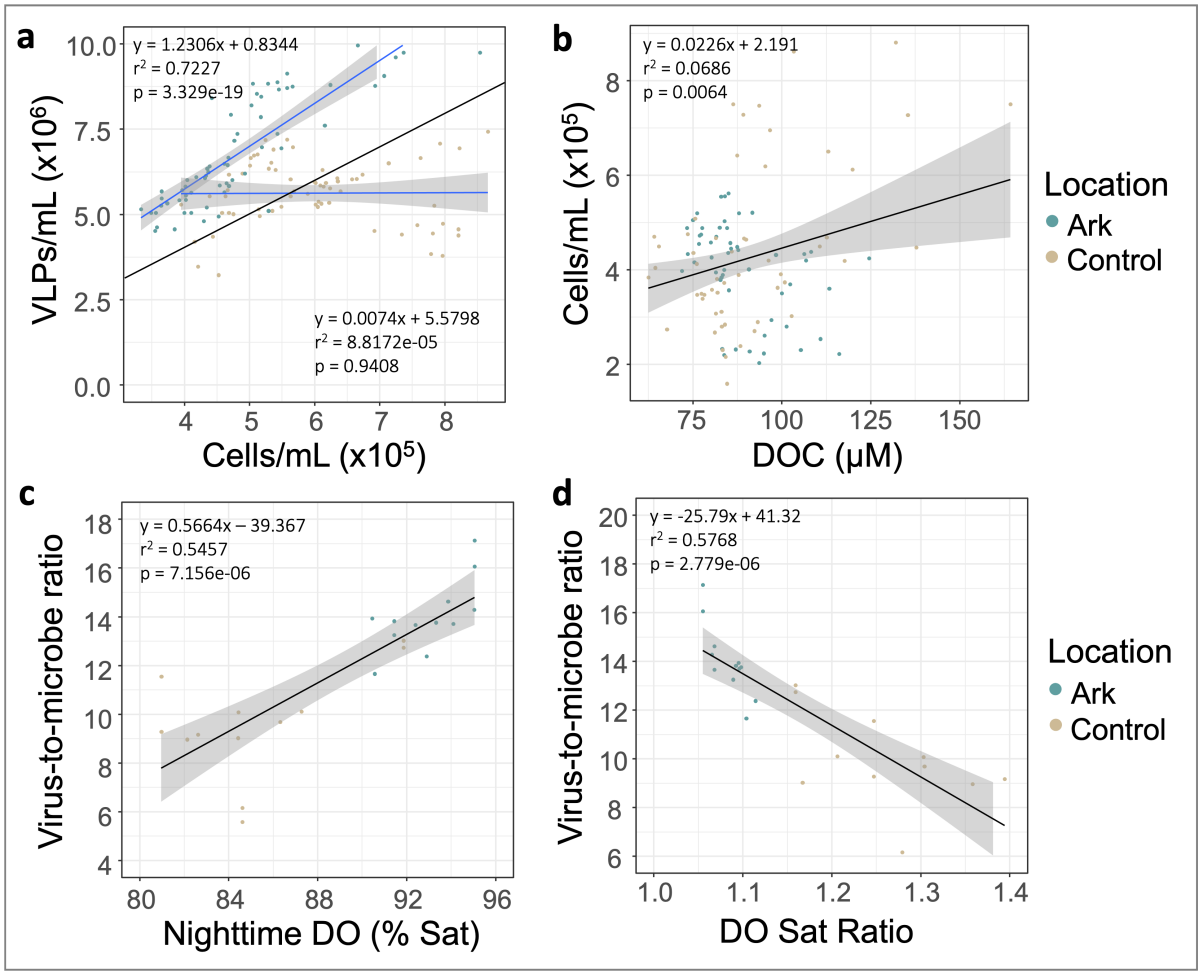


Figure 3.7 Linear regression models of viral and microbial, chemical, and physical variables at Arks and control sites. (a) Virus-like particle (VLPs) abundance vs microbial cell abundance, with linear regression models plotted separately for Arks and control sites. Linear equation, r^2, and p-value (t-test, $p < 0.05$) also plotted. Black solid line indicates 10:1 line. (b) Linear regression model of microbial cell abundance vs dissolved organic carbon (DOC) concentration with linear equation, r^2, and p-value (t-test, $p < 0.05$). (c) Linear regression model of virus-to-microbe ratio vs average nighttime dissolved oxygen with linear equation, r^2, and p-value (t-test, $p < 0.05$). (d) Linear regression model of virus-to-microbe ratio vs dissolved oxygen saturation ratio with linear equation, r^2, and p-value (t-test, $p < 0.05$).

The supervised Random Forest analysis used 4000 trees to construct the model identifying the variables that best predicted the Arks versus control site environments; the out-of-bag error (OOB) was 11.11% (Figure 3.8a). The permuted Random Forest identified DO Sat ratio as the most significant predictor, followed by flow speed, VMR, NDO, DDO, and daytime light intensity (Figure 3.8a, all $p < 0.05$).

The PCA revealed two principal components that cumulatively explain 54.3% of the variance within the dataset, with the first component (Dim1) accounting for 35.1% and the second (Dim2) for 19.2%. The PCA biplot (Figure 3.8b) illustrates the

distribution of the two experimental groups and the orientation of variables in the component space. The samples segregate into two distinct clusters along the first principal component axis, with Arks samples predominantly positioned towards the negative side of Dim 1 and significantly separated from control samples ($p < 0.05$), located towards the positive side.

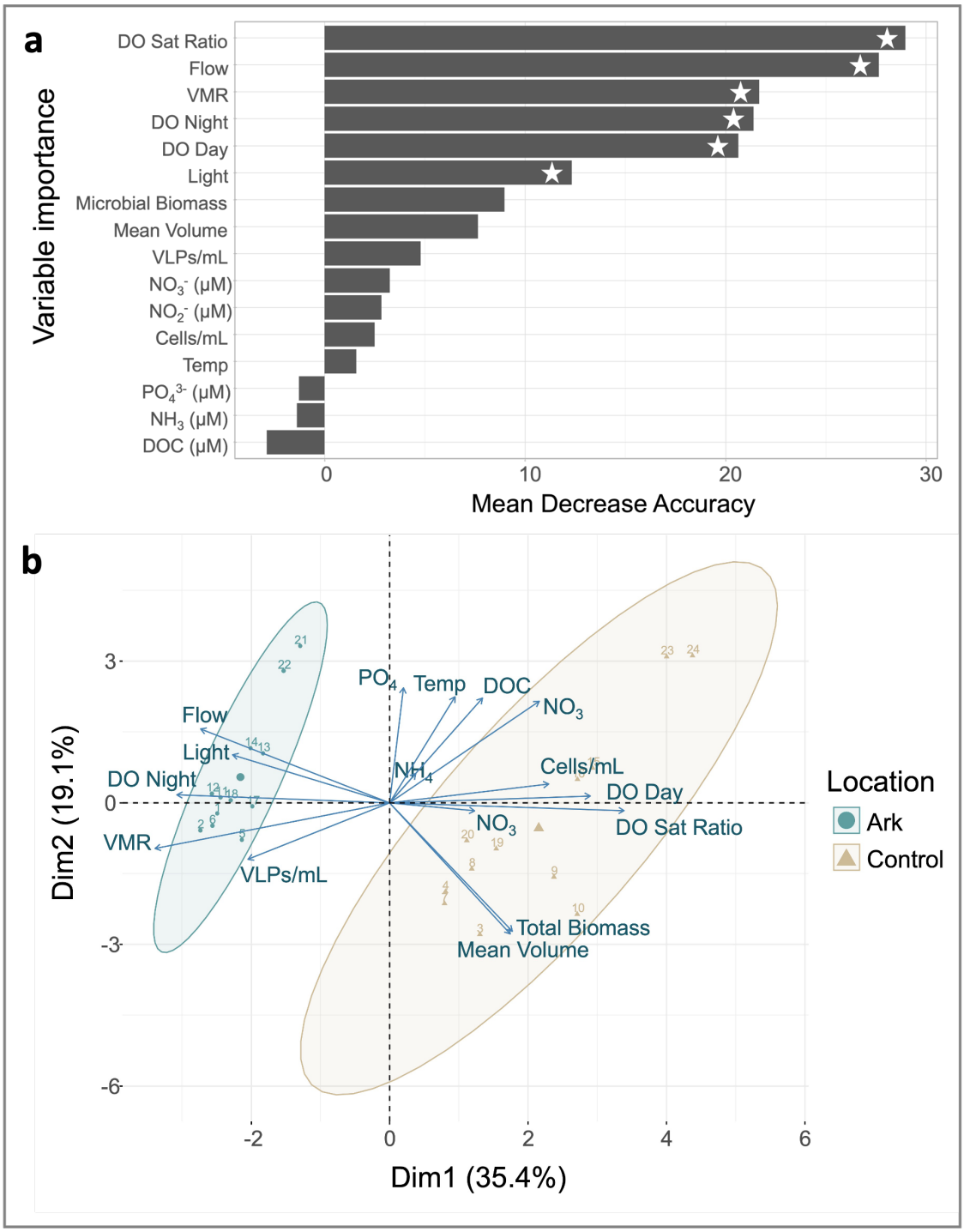


Figure 3.8 Multivariate analyses of viral and microbial, chemical, and physical variables on Arks and control sites. (a) Supervised Random Forest analysis showing variables most predictive of the Ark vs control treatments. White stars indicate significant variables as predicted by permuted Random Forest analysis. (b) Principal coordinate analysis (PCA) plot showing variables driving the variance between Ark and control treatments. Biplot shows the loadings of variables on the principal components and the distribution of samples from Ark and control sites along these components.

DISCUSSION

This study characterized the viral and microbial, chemical, and physical environment of two Coral Arks for 18 months, comparing the Arks' midwater environment to that of two seafloor sites at the same depth. Overall, viral and microbial communities at the Arks were more characteristic of healthy and stable coral reef environments, with higher VMR, more abundant free viruses (a major trophic control on bacteria), and physically smaller, less abundant microbes than the more microbialized control sites. The Arks and control site environments did not display major differences in inorganic nutrients, which is often cited as a strong predictor for microbialization (Kline et al., 2006; Dinsdale et al., 2008; Zaneveld et al., 2016). However, the Arks displayed significantly higher DO concentrations (especially at night), flow speeds, and light intensities relative to the seafloor sites, all of which are known to impact fundamental growth and metabolic processes in coral reef macroorganisms (Nakamura et al., 2003; Nelson and Altieri 2019). These differences were maintained during the 18-month experiment, even while substantial biological growth and ecological succession occurred on the Arks during this time period (Carilli and Baer et al., 2024).

Coral survival

The major hypothesis in this work predicted that improved physical and chemical conditions in the midwater would support healthier viral and microbial communities, which would in turn enhance survivorship of translocated corals relative to a traditional benthic restoration approach. Carilli and Baer et al. (2024) tracked coral growth and survival, fish community structure, and algae cover metrics at the Arks and control sites following the same sampling timeline as this experiment. To our knowledge, this is the

first coral restoration project to collect data integrating across ecosystem scales (microbial and macrobial ecology, chemical, and physical conditions). Translocated coral fragments from 8 coral species (n = 200 per site) survived and grew significantly better at Arks vs control sites, with 47% of corals on Arks still alive after 18 months compared to 24% coral survival at the control sites (Carilli and Baer et al., 2024). Limestone plates with coral fragments became rapidly and almost entirely fouled by highly competitive turf and macroalgae at the seafloor control sites, while coral plates at the Arks had much less algae cover and were instead colonized by more diverse benthic invertebrate communities including sponges, bryozoans, and hydrozoans (Carilli and Baer et al., 2024). Turf algae is recognized as a prominent driver of microbialization on coral reefs (Silveira et al., 2023) and is often associated with pathogenic microbial communities which cause coral disease and reduce outplant success in coral restoration projects (Casey et al., 2014, 2015). The Arks also attracted diverse fish communities, with fish community biomass and abundance at Arks exceeding that of the control sites after 9 months (Carilli and Baer et al., 2024).

Physical variables and water quality

Differences in seawater physical factors are likely to have been major contributors to the differences in coral growth, survival, and benthic succession on Arks and control sites. For example, higher flow speeds (as observed on the Arks, Figure 3.4c) are associated with increased coral growth rates (Nakamura and Yamasaki 2005; Finelli et al., 2006; Mass et al., 2011), increased resilience to bleaching (Nakamura et al., 2003), and decreased turf and macroalgae cover (Brown and Carpenter 2015). Improved water clarity offshore supplied the corals with abundant light for

photosynthesis and growth relative to the more turbid nearshore environment (Figure 3.4e), in which turf algae, requiring less light for photosynthesis, have the growth advantage (Mueller et al., 2016). Average DO concentrations on the Arks were marginally higher than the control sites, but the diel range of DO was substantially larger at the control sites (Figure 3.4a), with supersaturated DO during the daytime reflecting algal photosynthesis and a decrease in nighttime DO indicating respiratory drawdown (Haas et al., 2010; Wild et al., 2010). Local nighttime hypoxia is a well-documented feature of degraded reefs and can negatively impact growth and survival of corals, mobile invertebrates, and reef fish (Nelson and Altieri 2019) as well as cause shifts in viral and microbial communities towards opportunism and pathogenesis (Johnson et al., 2021). Differences in temperature between the Arks and control sites were statistically significant but minimal (Figure 3.4b) and are unlikely to have differentially caused thermal stress to the corals at either site.

Viral and microbial ecology

Seawater viral and microbial communities, which both shape and respond to the physical and chemical environment, are also likely to have contributed to the success of macrofauna on the Arks. Microbialization is an ecosystem-level shift in biomass and energy use from predominantly macroorganisms to the microbes (Baer et al., 2024, Haas et al., 2016) which is reinforced by changing benthic conditions (i.e., hypoxia) and a loss of predation pressure by viruses (Silveira et al., 2023). When microbial growth rates are high, viruses shift from using the lytic mode of replication that kills microbes to the latent strategy of lysogeny, in which viruses behave more like parasites and instead of killing their microbial hosts, protect them against predation by protist grazers

(Knowles et al., 2016b; Cárdenas et al., 2018; Silveira et al., 2020; Roughgarden et al., 2023). Higher VMR in the Arks environment (driven by more abundant free viruses and less abundant microbes, Figure 3.2a) suggest increased viral predatory control on seawater microbes in the so-called Kill-the-Winner model (Figure 3.7a, Thingstad 2000) or through prophage induction (Weinbauer and Suttle 1999), thus reducing microbial biomass accumulation and microbialization (Haas et al., 2016; Knowles et al., 2016). In contrast, free virus abundance at the control sites was reduced relative to microbes (Figure 3.7a), suggesting a shift among viruses to lysogeny at higher microbial densities in a manner consistent with the Piggyback-the-Winner infection model (Silveira and Rohwer 2016). A strong relationship was also observed between VMR and DO (Figure 3.7c-d), suggesting DO may play a role in the lysis-lysogeny decision. Both VMR and DO were among the strongest predictors of reef state identified by Random Forest analysis (Figure 3.8a), highlighting the key role of viral predation pressure and oxygen in structuring coral reef microbial communities (Silveira et al., 2019, 2023).

Chemical variables

Despite substantial differences between the abiotic and biotic environments of the midwater and seafloor, chemical variables did not significantly differ between Arks and control sites and were not significant predictors of reef state in either PCA or Random Forest analysis (Figure 3.8). Ammonia and nitrate + nitrite concentrations were generally higher at the control sites, but measurements were often below the laboratory method detection limit and, at such low concentrations, were unlikely to be primary drivers of microbial and macrobial trajectories (Figure 3.5f-g). An increase in ammonia concentrations on the Arks beginning at 6 months following deployment may be linked

to increased fish biomass and resulting nitrogen-rich wastes on the Arks (Villanueva et al., 2005), which increased substantially around that same time (Figure 3.5g). DOC concentrations are strongly linked to benthic cover (Haas et al., 2013, 2016a), as algae have higher release rates of labile DOC than corals, but significant differences between the Arks and control sites in DOC concentrations were only observed at two time points (Figure 3.5e). However, the labile fraction of seawater DOC is consumed by seawater microbes within minutes to hours after being released (Carlson and Ducklow 1996), with the remaining recalcitrant fraction of DOC degrading over annual to decadal timescales. Differences in labile organic carbon concentrations between the two sites may have been obscured by this rapid microbial consumption, leaving behind the more stable refractory DOC pool (Wegley Kelly et al., 2022).

Coral reef microbialization: Rise of the microbes

The relationships observed in this study are consistent with the predictions of microbialization and suggest the control sites and ARMS units were more microbialized than the Arks (Figure 3.3a-d). A positive relationship between dissolved organic carbon (DOC) and microbial abundance (Figure 3.7b) demonstrates the well-documented growth response of microbial communities to labile organic matter (Carlson et al., 2007; Nelson et al., 2011). The positive relationship observed between mean microbial cell volumes and microbial abundances (Figure 3.6c) is consistent with Silveira et al., 2019, which showed that shifts in primary carbon metabolism strategies among microbial communities exposed to algal DOC cause these microbes to accumulate surplus carbon as biomass, thus increasing average cell size in addition to abundance (Roach et al., 2017; Silveira et al., 2019). These trends are particularly significant in the ARMS

units, in which enclosed spaces and high cryptic diversity create a microenvironment that accumulates organic matter, representing an extreme end of the microbialization transition occurring at the control sites. Overall, these data indicate ARMS and control sites support more copiotrophic microbial communities, and that viruses respond to these microbial transitions by shifting primary infection strategies in favor of lysogeny.

CONCLUSIONS

Despite being a widespread phenomenon, microbialization has rarely been considered in coral reef restoration and may be a reason for limited success in restoration projects (Glasl et al., 2019). Here, we demonstrate that reducing microbialization leads to significantly improved outcomes for translocated corals and reef-associated biota. Water quality and microbial ecology were substantially more favorable for corals on midwater Arks than on seafloor sites at the same depth. Improved environmental conditions on the Arks facilitated the growth of diverse coral reef communities and enabled rapid ecological succession throughout the experiment, whereas the more microbialized control sites were rapidly outcompeted by turf and macroalgae. Reef restoration efforts will benefit from explicitly considering microbialization in project design, either by relocating portions of the reef community to the less-microbialized midwater on Coral Arks and floating nurseries, or by using microbes as diagnostic tools for selecting less microbialized sites where restoration efforts are more likely to succeed.

ACKNOWLEDGEMENTS

This project was supported by the Environmental Security Technology Certification Program (grant CR20-5175) and the Gordon and Betty Moore Foundation (grant GBMF9207) with in-kind support from the Vieques Restoration Program, Naval Facilities Engineering Command Southeast. We are grateful for the support received from John Martin, Lora Pride, Brett Doerr, Maria Danois, Ronny Fields, Kristin McClendon, Dan Waddill, Kevin Cloe, Daniel Hood, Nilda Jimenez Marrero, Michael Nemeth, Tali Vardi, Sarah Elise Field, Pedro Rodriguez, Pete Seufert, Tania Puell, and others who have supported this project.

Chapter 3 is currently being prepared for submission for publication of the material. Jason L Baer, Mark Little, Jenna Marie Cruz Aquino, Anneke van der Geer, Ashton Ballard, Andrés Sánchez-Quinto, Jessica Carilli, Aaron Hartmann, and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

REFERENCES

Altieri, A. H., Harrison, S. B., Seemann, J., Collin, R., Diaz, R. J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1621517114

Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L., & Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, *10*(3), 257–263. https://doi.org/10.3354/meps010257

Baer, J. L., Carilli, J., Chadwick, B., Hatay, M., van der Geer, A., Scholten, Y., Barnes, W., Aquino, J., Ballard, A., Little, M., Brzenski, J., Liu, X., Rosen, G., Wang, P. F., Castillo, J., Haas, A. F., Hartmann, A. C., & Rohwer, F. (2023). Coral Reef Arks: An *in situ* mesocosm and toolkit for assembling reef communities. *Journal of Visualized Experiments*, *2023*(191). https://doi.org/10.3791/64778

Bauer, L.J. and Kendall, M. S. (2010). An ecological characterization of the marine resources of Vieques, Puerto Rico Part II: Field studies of habitats, nutrients. *May*, 174.

Bayraktarov, E., Saunders, M. I., Abdullah, S., Mills, M., Beher, J., Possingham, H. P., Mumby, P. J., & Lovelock, C. E. (2016). The cost and feasibility of marine coastal restoration. *Ecological Applications*, *26*(4), 1055–1074.

Bjørnsen, P. K. (1986). Automatic determination of bacterioplankton biomass by image analysis. *Applied and Environmental Microbiology*, *51*(6), 1199–1204.

Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C. A., Hancock, B., Harrison, P., Hein, M., & Shaver, E. (2020). Coral restoration–A systematic review of current methods, successes, failures and future directions. *PloS One*, *15*(1), e0226631.

Bourne, D. G. (2005). Microbiological assessment of a disease outbreak on corals from Magnetic Island (Great Barrier Reef, Australia). *Coral Reefs*, *24*, 304–312.

Bourne, D. G., Morrow, K. M., & Webster, N. S. (2016). Insights into the coral microbiome: underpinning the health and resilience of reef ecosystems. *Annual Review of Microbiology*, *70*, 317–340.

Bruce, T., Meirelles, P. M., Garcia, G., Paranhos, R., Rezende, C. E., de Moura, R. L., Filho, R. F., Coni, E. O. C., Vasconcelos, A. T., Filho, G., Hatay, M., Schmieder, R., Edwards, R., Dinsdale, E., & Thompson, F. L. (2012). Abrolhos bank reef health evaluated by means of water quality, microbial diversity, benthic cover, and fish biomass data. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0036687

Cárdenas, A., Neave, M. J., Haroon, M. F., Pogoreutz, C., Rädecker, N., Wild, C., Gärdes, A., & Voolstra, C. R. (2018). Excess labile carbon promotes the expression of virulence factors in coral reef bacterioplankton. *ISME Journal*. https://doi.org/10.1038/ismej.2017.142

Casey, J. M., Ainsworth, T. D., Choat, J. H., & Connolly, S. R. (2014). Farming behaviour of reef fishes increases the prevalence of coral disease associated microbes and black band disease. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788), 20141032.

Casey, J. M., Connolly, S. R., & Ainsworth, T. D. (2015). Coral transplantation triggers shift in microbiome and promotion of coral disease associated potential pathogens. *Scientific Reports*. https://doi.org/10.1038/srep11903

Costanza, R., De Groot, R., Sutton, P., Van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., & Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, *26*, 152–158.

Cyronak, T., & Eyre, B. D. (2016). The synergistic effects of ocean acidification and organic metabolism on calcium carbonate (CaCO3) dissolution in coral reef sediments. *Marine Chemistry*, *183*, 1–12. https://doi.org/10.1016/j.marchem.2016.05.001

Dinsdale, E. A., Pantos, O., Smriga, S., Edwards, R. A., Angly, F., Wegley, L., Hatay, M., Hall, D., Brown, E., Haynes, M., Krause, L., Sala, E., Sandin, S. A., Thurber, R. V., Willis, B. L., Azam, F., Knowlton, N., & Rohwer, F. (2008). Microbial ecology of four coral atolls in the Northern Line Islands. *PLoS ONE*.

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, *4*(9), 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016

Egan, S., & Gardiner, M. (2016). Microbial dysbiosis: rethinking disease in marine ecosystems. *Frontiers in Microbiology*, *7*, 991.

Fisher, R., O'Leary, R. A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R. E., & Caley, M. J. (2015). Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology*, *25*(4), 500–505. https://doi.org/10.1016/j.cub.2014.12.022

Galand, P. E., Ruscheweyh, H. J., Salazar, G., Hochart, C., Henry, N., Hume, B. C. C., Oliveira, P. H., Perdereau, A., Labadie, K., Belser, C., Boissin, E., Romac, S., Poulain, J., Bourdin, G., Iwankow, G., Moulin, C., Armstrong, E. J., Paz-García, D. A., Ziegler, M., … Planes, S. (2023). Diversity of the Pacific Ocean coral reef microbiome. *Nature Communications*, *14*(1), 1–13. https://doi.org/10.1038/s41467-023-38500-x

Gardner, S. G., Nitschke, M. R., O'Brien, J., Motti, C. A., Seymour, J. R., Ralph, P. J., Petrou, K., & Raina, J.-B. (2022). Increased DMSP availability during thermal stress influences DMSP-degrading bacteria in coral mucus. *Frontiers in Marine Science*, *9*, 912862.

Glasl, B., Bourne, D. G., Frade, P. R., Thomas, T., Schaffelke, B., & Webster, N. S. (2019). Microbial indicators of environmental perturbations in coral reef ecosystems. *Microbiome*, *7*(1), 1–13. https://doi.org/10.1186/s40168-019-0705-7

Glasl, B., Herndl, G. J., & Frade, P. R. (2016). The microbiome of coral surface mucus has a key role in mediating holobiont health and survival upon disturbance. *The ISME Journal*, *10*(9), 2280–2292.

Haapkylä, J., Unsworth, R. K. F., Flavell, M., Bourne, D. G., Schaffelke, B., & Willis, B. L. (2011). Seasonal rainfall and runoff promote coral disease on an inshore reef. *PloS One*, *6*(2), e16893.

Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y. W., Maughan, H., Pantos, O., Roach, T. N. F., Sanchez, S. E., Silveira, C. B., Sandin, S., Smith, J. E., & Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2016.42

Haas, A. F., Knowles, B., Lim, Y. W., Somera, T. M. D., Kelly, L. W., Hatay, M., & Rohwer, F. (2014). Unraveling the unseen players in the ocean - A field guide to water chemistry and marine microbiology. *Journal of Visualized Experiments*. https://doi.org/10.3791/52131

Hatcher, B. G. (1997). Coral reef ecosystems: How much greater is the whole than the sum of the parts? *Coral Reefs*. https://doi.org/10.1007/s003380050244

Hein, M. Y., Beeden, R., Birtles, A., Gardiner, N. M., Le Berre, T., Levy, J., Marshall, N., Scott, C. M., Terry, L., & Willis, B. L. (2020). Coral restoration effectiveness: Multiregional snapshots of the long-term responses of coral assemblages to restoration. *Diversity*, *12*(4), 1–22. https://doi.org/10.3390/D12040153

Johnson, M. D., Scott, J. J., Leray, M., Lucey, N., Bravo, L. M. R., Wied, W. L., & Altieri, A. H. (2021). Rapid ecosystem-scale consequences of acute deoxygenation on a Caribbean coral reef. *Nature Communications*, *12*(1), 1–12. https://doi.org/10.1038/s41467-021-24777-3

Kelly, L. W., Nelson, C. E., Haas, A. F., Naliboff, D. S., Calhoun, S., Carlson, C. A., Edwards, R. A., Fox, M. D., Hatay, M., Johnson, M. D., Kelly, E. L. A., Lim, Y. W., Macherla, S., Quinlan, Z. A., Silva, G. G. Z., Vermeij, M. J. A., Zgliczynski, B., Sandin, S. A., Smith, J. E., & Rohwer, F. (2019). Diel population and functional synchrony of microbial communities on coral reefs. *Nature Communications*.

Kelly, L. W., Williams, G. J., Barott, K. L., Carlson, C. A., Dinsdale, E. A., Edwards, R. A., Haas, A. F., Haynes, M., Lim, Y. W., McDole, T., Nelson, C. E., Sala, E., Sandin, S. A., Smith, J. E., Vermeij, M. J. A., Youle, M., & Rohwer, F. (2014). Local genomic adaptation of coral reef-associated microbiomes to gradients of natural variability and anthropogenic stressors. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1403319111

Knowles, B., Silveira, C. B., Bailey, B. A., Barott, K., Cantu, V. A., Cobian-Guëmes, A. G., Coutinho, F. H., Dinsdale, E. A., Felts, B., Furby, K. A., George, E. E., Green, K. T., Gregoracci, G. B., Haas, A. F., Haggerty, J. M., Hester, E. R., Hisakawa, N., Kelly, L. W., Lim, Y. W., … Rohwer, F. (2016). Lytic to temperate switching of viral communities. *Nature*. https://doi.org/10.1038/nature17193

Knowlton, N., & Rohwer, F. (2003). Multispecies microbial mutualisms on coral reefs: The host as a habitat. *American Naturalist*. https://doi.org/10.1086/378684

Lima, L. F. O., Alker, A. T., Papudeshi, B., Morris, M. M., Edwards, R. A., de Putron, S. J., & Dinsdale, E. A. (2023). Coral and seawater metagenomes reveal key microbial functions to coral health and ecosystem functioning shaped at reef scale. *Microbial Ecology*, *86*(1), 392–407. https://doi.org/10.1007/s00248-022-02094-6

Lirman, D., Thyberg, T., Herlan, J., Hill, C., Young-Lahiff, C., Schopmeyer, S., Huntington, B., Santos, R., & Drury, C. (2010). Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs*, *29*(3), 729–735.

Maher, R. L., Schmeltzer, E. R., Meiling, S., McMinds, R., Ezzat, L., Shantz, A. A., Adam, T. C., Schmitt, R. J., Holbrook, S. J., & Burkepile, D. E. (2020). Coral microbiomes demonstrate flexibility and resilience through a reduction in community diversity following a thermal stress event. *Frontiers in Ecology and Evolution*, *8*, 555698.

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*, *18*(4), 357–367. https://doi.org/10.1007/s003380050213

McDole, T., Nulton, J., Barott, K. L., Felts, B., Hand, C., Hatay, M., Lee, H., Nadon, M. O., Nosrat, B., Salamon, P., Bailey, B., Sandin, S. A., Vargas-Angel, B., Youle, M., Zgliczynski, B. J., Brainard, R. E., & Rohwer, F. (2012). Assessing coral reefs on a Pacific-wide scale using the microbialization score. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0043233

Miller, N., Maneval, P., Manfrino, C., Frazer, T. K., & Meyer, J. L. (2020). Spatial distribution of microbial communities among colonies and genotypes in nursery-reared *Acropora cervicornis*. *PeerJ*, *8*, 1–20. https://doi.org/10.7717/peerj.9635

Moree, W. J., McConnell, O. J., Nguyen, D. D., Sanchez, L. M., Yang, Y.-L., Zhao, X., Liu, W.-T., Boudreau, P. D., Srinivasan, J., & Atencio, L. (2014). Microbiota of healthy corals are active against fungi in a light-dependent manner. *ACS Chemical Biology*, *9*(10), 2300–2308.

Moriarty, T., Leggat, W., Huggett, M. J., & Ainsworth, T. D. (2020). Coral disease causes, consequences, and risk within coral restoration. *Trends in Microbiology*, *28*(10), 793–807. https://doi.org/10.1016/j.tim.2020.06.002

Nelson, C. E., Goldberg, S. J., Wegley Kelly, L., Haas, A. F., Smith, J. E., Rohwer, F., & Carlson, C. A. (2013). Coral and macroalgal exudates vary in neutral sugar composition and differentially enrich reef bacterioplankton lineages. *ISME Journal*. https://doi.org/10.1038/ismej.2012.161

Nelson, C. E., Wegley Kelly, L., & Haas, A. F. (2023). Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. *Annual Review of Marine Science*, *15*, 431–460. https://doi.org/10.1146/annurev-marine-042121-080917

Noble, R. T., & Fuhrman, J. A. (1998). Use of SYBR Green I for rapid epifluorescence counts of marine viruses and bacteria. *Aquatic Microbial Ecology*, *14*(2), 113–118.

Pearman, J. K., Anlauf, H., Irigoien, X., & Carvalho, S. (2016). Please mind the gap - Visual census and cryptic biodiversity assessment at central Red Sea coral reefs. *Marine Environmental Research*. https://doi.org/10.1016/j.marenvres.2016.04.011

Peixoto, R. S., Sweet, M., Villela, H. D. M., Cardoso, P., Thomas, T., Voolstra, C. R., Høj, L., & Bourne, D. G. (2020). Coral probiotics: premise, promise, prospects. 1–24.

Rädecker, N., Pogoreutz, C., Voolstra, C. R., Wiedenmann, J., & Wild, C. (2015). Nitrogen cycling in corals: the key to understanding holobiont functioning? *Trends in Microbiology*, *23*(8), 490–497.

Rinkevich, B. (2005). Conservation of coral reefs through active restoration measures: Recent approaches and last decade progress. In *Environmental Science and Technology*. https://doi.org/10.1021/es0482583

Roach, T. N. F., Abieri, M. L., George, E. E., Knowles, B., Naliboff, D. S., Smurthwaite, C. A., Kelly, L. W., Haas, A. F., & Rohwer, F. L. (2017). Microbial bioenergetics of coral-algal interactions. *PeerJ*. https://doi.org/10.7717/peerj.3423

Röthig, T., Ochsenkühn, M. A., Roik, A., Van Der Merwe, R., & Voolstra, C. R. (2016). Long-term salinity tolerance is accompanied by major restructuring of the coral bacterial microbiome. *Molecular Ecology*, *25*(6), 1308–1323.

Santoro, E. P., Borges, R. M., Espinoza, J. L., Freire, M., Messias, C. S. M. A., Villela, H. D. M., Pereira, L. M., Vilela, C. L. S., Rosado, J. G., & Cardoso, P. M. (2021). Coral microbiome manipulation elicits metabolic and genetic restructuring to mitigate heat stress and evade mortality. *Science Advances*, *7*(33), eabg3088.

Shaver, E. C., Shantz, A. A., McMinds, R., Burkepile, D. E., Thurber, R. L. V., & Silliman, B. R. (2017). Effects of predation and nutrient enrichment on the success and microbiome of a foundational coral. *Ecology*, *98*(3), 830–839. https://doi.org/10.1002/ecy.1709

Silveira, C. B., Cavalcanti, G. S., Walter, J. M., Silva-Lima, A. W., Dinsdale, E. A., Bourne, D. G., Thompson, C. C., & Thompson, F. L. (2017). Microbial processes driving coral reef organic carbon flow. *FEMS Microbiology Reviews*. https://doi.org/10.1093/femsre/fux018

Silveira, C. B., Coutinho, F. H., Cavalcanti, G. S., Benler, S., Doane, M. P., Dinsdale, E. A., Edwards, R. A., Francini-Filho, R. B., Thompson, C. C., Luque, A., Rohwer, F. L., & Thompson, F. (2020). Genomic and ecological attributes of marine bacteriophages encoding bacterial virulence genes. *BMC Genomics*. https://doi.org/10.1186/s12864-020-6523-2

Silveira, C. B., Luque, A., Roach, T. N., Villela, H., Barno, A., Green, K., Reyes, B., Rubio-Portillo, E., Le, T., Mead, S., Hatay, M., Vermeij, M. J., Takeshita, Y., Haas, A., Bailey, B., & Rohwer, F. (2019). Biophysical and physiological processes causing oxygen loss from coral reefs. *ELife*. https://doi.org/10.7554/eLife.49114

Somera, T. M. D., Bailey, B., Barott, K., Grasis, J., Hatay, M., Hilton, B. J., Hisakawa, N., Nosrat, B., Nulton, J., Silveira, C. B., Sullivan, C., Brainard, R. E., & Rohwer, F. (2016). Energetic differences between bacterioplankton trophic groups and coral reef resistance. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2016.0467

Strudwick, P., Seymour, J., Camp, E. F., Edmondson, J., Haydon, T., Howlett, L., Le Reun, N., Siboni, N., & Suggett, D. J. (2022). Impacts of nursery-based propagation and out-planting on coral-associated bacterial communities. *Coral Reefs*, *41*(1), 95–112. https://doi.org/10.1007/s00338-021-02207-6

Suttle, C. A. (2007). Marine viruses - Major players in the global ecosystem. *Nature Reviews Microbiology*. https://doi.org/10.1038/nrmicro1750

Thurber, R. V., Willner-Hall, D., Rodriguez-Mueller, B., Desnues, C., Edwards, R. A., Angly, F., Dinsdale, E., Kelly, L., & Rohwer, F. (2009). Metagenomic analysis of stressed coral holobionts. *Environmental Microbiology*. https://doi.org/10.1111/j.1462-2920.2009.01935.x

van Oppen, M. J. H., & Blackall, L. L. (2019). Coral microbiome dynamics, functions and design in a changing world. *Nature Reviews Microbiology*, *17*(9), 557–567.

Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., & Gobler, C. J. (2014). Coastal ocean acidification: The other eutrophication problem. *Estuarine, Coastal and Shelf Science*, *148*, 1–13. https://doi.org/10.1016/j.ecss.2014.05.027

Wilhelm, S. W., & Suttle, C. A. (1999). Viruses and nutrient cycles in the sea. *BioScience*. https://doi.org/10.2307/1313569

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

Zaneveld, J. R., Burkepile, D. E., Shantz, A. A., Pritchard, C. E., McMinds, R., Payet, J. P., Welsh, R., Correa, A. M. S., Lemoine, N. P., Rosales, S., Fuchs, C., Maynard, J. A., & Thurber, R. V. (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature Communications*. https://doi.org/10.1038/ncomms11833

Chapter 4

ESCAPING THE MICROBIALIZED BENTHOS WITH CORAL REEF ARKS: EFFECTS ON CORAL TRANSLOCATION AND FISH BIOMASS

ABSTRACT

Anthropogenic stressors like overfishing, eutrophication, and increasing temperatures directly and indirectly increase microbial loads on coral reefs. This process, called microbialization, decreases benthic oxygen levels and increases coral disease and death. To test the hypothesis that corals would be healthier by moving them off the microbialized benthos, a common garden experiment was used and corals were translocated to floating geodesic spheres (hereafter called Coral Reef Arks or Arks). Coral fragments translocated to the Arks survived significantly longer than equivalent coral fragments translocated to the Control sites (i.e., microbialized benthos at the same depth). Average living coral surface area and volume were higher on the Arks than the Control sites. The abundance and biomass of fish was also higher on the Arks compared to the Control sites. Addition of Autonomous Reef Monitoring Structures (ARMS), which served as habitat for sessile and motile reef-associated organisms, increased the fish biomass. Overall, the Arks increased translocated coral survivorship and growth and enhanced the local fishery.

INTRODUCTION

Coral reef ecosystems are declining globally due to local and global stressors including overfishing, pollution, and climate change (Eddy et al., 2021). Most reef mitigation and restoration efforts have focused on protecting and rebuilding coral

communities, due to the role of corals as ecosystem engineers. Such projects traditionally rely on some form of coral translocation; for example, corals are moved off of piers to natural reef sites to mitigated damage (Dickenson et al., 2022). Corals are also fragmented and grown in nurseries, then out planted to natural or artificial reef sites for restoration (Bayraktarov et al., 2020). These projects have varying success (Boström-Einarsson et al., 2020, Hein et al., 2020), in part because transplanting corals to sites with poor environmental conditions is likely to fail unless the source of the poor conditions are addressed (Ferse et al., 2021).

Given that many environmental stressors causing coral reef decline are large-scale and unlikely to be remediated in the near future (e.g., ocean warming), the Coral Reef Arks approach was designed to provide an interim solution to enhance the survival of corals, study the successional patterns of reef communities, and determine whether Arks may help surrounding areas recover ecosystem functions (Baer et al., 2023). The midwater Arks create suitable habitat in a location with better abiotic conditions, including higher light availability, flow speeds, and dissolved oxygen (Baer et al., 2023) than the microbialized benthos (Webb et al., 2021), and provide corals translocated to this habitat with reef-associated biota to support ecosystem services necessary to promote coral and reef survival. These services include grazing to reduce competition with algae, nutrient remineralization, water filtering, and defense against corallivores (Stella et al., 2011, Ladd and Shantz 2020, Nelson et al., 2023). Reef-associated species are translocated to the Arks using Autonomous Reef Monitoring Structures (ARMS) units, which provide habitat and passively collect a significant fraction of reef

diversity from natural reef sites (e.g. Ransome et al., 2016, Hartmann and Rohwer 2019) before being transferred to the Arks.

During the nursery stage for coral gardening projects, corals are often elevated off the benthos with tables or ropes and nets suspended by buoys, providing corals with improved water quality and resulting in improved survival and growth rates compared to benthic nurseries (e.g. Shafir et al., 2006, Nedimyer et al., 2011). These nurseries are intended as a temporary holding site for corals prior to affixing them to the benthos, often require significant maintenance, and do not create a complex reef system, which is the ultimate goal of restoration. In contrast, Arks are intended to provide the same beneficial water quality conditions as nurseries, while creating an artificial reef for corals to permanently reside. Furthermore, Arks include cryptic biodiversity to support coral health and replace human maintenance (e.g., algae and corallivore removal) with nature-based solutions (e.g., herbivores and predators). As such, Arks are designed to meet the Coral Restoration Consortium priorities to “Support a holistic approach to coral reef ecosystem restoration” and to “Increase restoration efficiency,” by outplanting a range of coral species and genotypes as well as non-coral species (Vardi et al., 2021).

Here we describe two Arks structures that were deployed in Vieques, Puerto Rico. Stony corals were translocated to the Arks in two stages about six months apart, first without, and then with an accompanying transfer of seeded ARMS units. Corals were also translocated to two benthic Control sites akin to traditional coral outplanting approaches during each stage. Biotic and abiotic metrics were subsequently tracked at multiple monitoring timepoints. This paper presents results from the first five monitoring timepoints, spanning approximately 19 months on the Arks and Control sites to address

three related hypotheses: 1) Corals translocated to the Arks will survive longer and have greater tissue growth than corals translocated to the benthic Control sites, 2) turf and macroalgae cover around corals on the Arks will be lower than at the benthic Control sites, and 3) fish abundance and biomass associated with the Arks will be greater than fish associated with the benthic Control sites.

METHODS

Site design: Coral Reef Arks

Arks are midwater, positively buoyant, 2.4 m (8 ft) diameter geodesic spheres tethered to the seafloor. In November 2021, two Arks were deployed offshore approximately 2 miles to the west of Vieques Island, Puerto Rico (Figure 4.1A-B), within part of the Navy's unexploded ordnance remediation site 16 (UXO16). The seafloor in this area is 16.7 m (55 feet) deep and consists of sand with patches of rubble and macroalgae such as *Padina* spp. and *Halimeda* spp. in the immediate area. A mapping survey of Vieques underwater habitat classified the Arks deployment area as sand, with coral reef and hardbottom/pavement habitat located approximately 100 m south of the Arks site (Bauer et al., 2010). Arks were installed using a set of three helical sand anchors and a multipoint bridle system described in Baer et al., (2023), following specific guidelines for work within a UXO site. Once installed, the top of Ark 1 and Ark 2 was located at approximately 7.6 m (25 ft) and 7.3 m (24 ft) below the water surface, respectively. The two Arks were separated by approximately 50 m. Additional details regarding building and deploying Arks can be found in Baer et al., (2023).

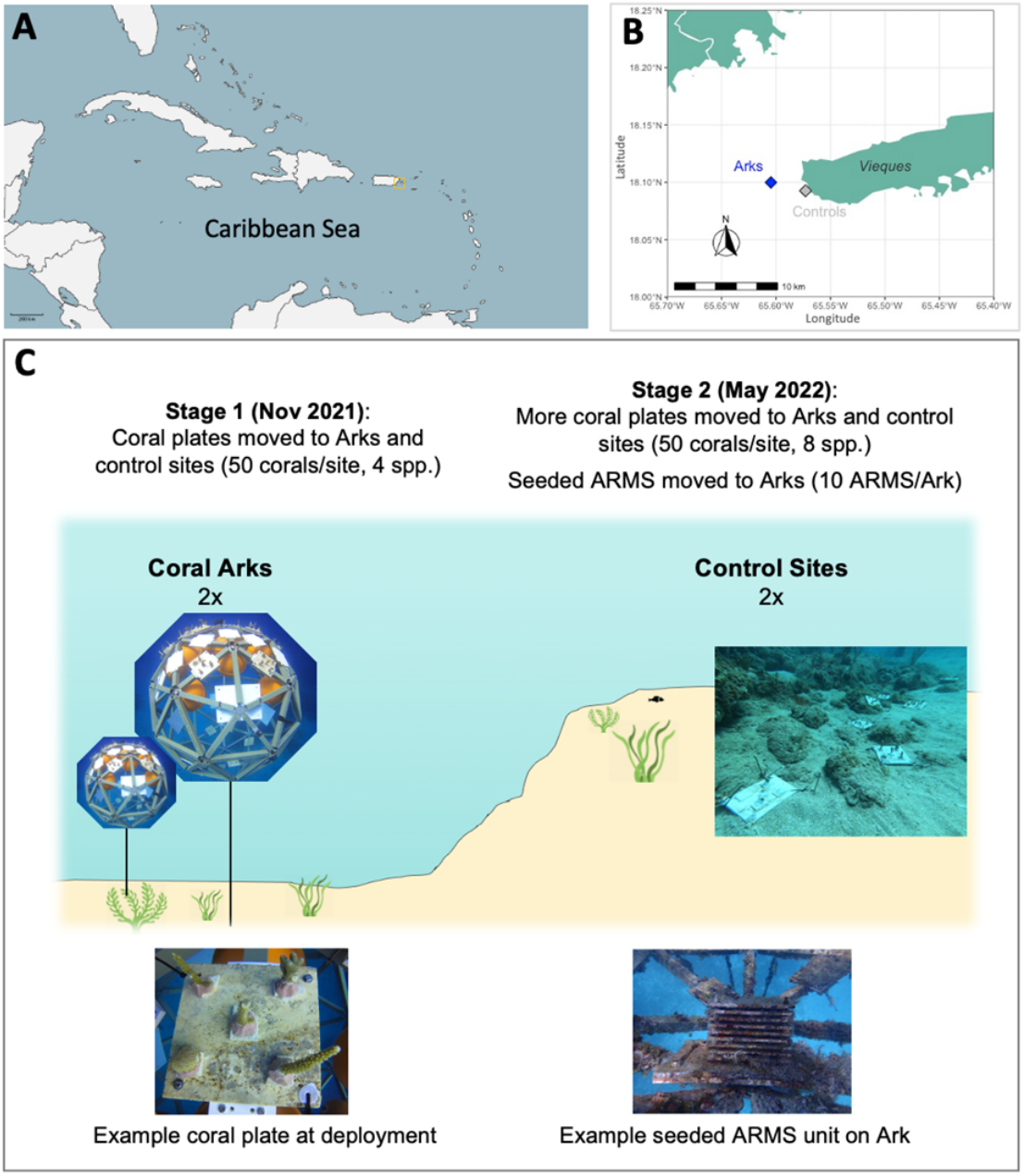


Figure 4.1 Maps of (A) regional setting, and (B) treatment sites for Arks and Control sites, and (C) schematic representation of experimental design.

Site design: Control sites

Two Control sites were established at similar depths as the tops of the Arks (7.6 m/25 ft and 6.4 m/21 ft water depth, respectively), to compare the Arks approach to the traditional approach of translocating corals to the benthos. The two Control sites were also located off the west coast of Vieques Island within another portion of UXO16, closer to shore to achieve similar depths (Figure 4.1B). The two Control sites were separated by approximately 25 m. The habitat in this area was classified as reef hardbottom characterized by colonized pavement, linear reef, and aggregated patch reef habitats (Bauer et al., 2010). Qualitatively, the sites are dominated primarily by carbonate rock colonized by turf and macroalgae, stony corals (mainly in the genera *Orbicella*, *Siderastrea*, *Porites*, and *Diploria*), gorgonians, fire corals, and other sessile invertebrates, with scattered patches of sand and seagrass found at the deeper fringes of the sites.

Site design: ARMS seeding

ARMS units are three-dimensional structures made of PVC plates and stainless-steel hardware that create a standardized area of substrate to passively collect reef communities via natural recruitment and growth (<www.oceanARMS.org>). Thirty ARMS were placed on the benthos in the vicinity of the Control sites off the west coast of Vieques, located at depths between 8 and 14 ft and close to living coral assemblages. ARMS were secured to the benthos in sets of five using rebar stakes and cable ties to link the ARMS and concrete bags as weighted anchors (Baer et al., 2023). ARMS were left to accumulate coral reef cryptic biodiversity for a one-year “seeding” period before they were moved to the Arks.

Coral sourcing and translocation

Corals were translocated to the Arks and Control sites in two cohorts six months apart (November 2021 and May 2022). Approximately half of the corals were sourced from a NOAA coral nursery called Palominos, off the east coast of the main island of Puerto Rico during both time periods, and from metal debris (a barge and pipes) in Bahía de Jobos, Puerto Rico, slated for removal by Puerto Rico's Department of Natural and Environmental Resources (DNER) in November 2021. Additional corals of opportunity were obtained from rubble fields and a spalling concrete boat ramp on the south side of Mosquito Pier, Vieques, in May 2022. After collection, all corals were held in plastic bins with seawater (refreshed intermittently) or placed in plastic milkcrates suspended underwater beneath a small boat dock at Mosquito Pier. Corals were then fragmented and attached to numbered, unfinished limestone tiles (termed "coral plates") with a mixture of epoxy (Aquastik Coralline Red, Two Little Fishies) and superglue (Seachem). This attachment method was selected based on literature review and lab-based trials of different attachment methods.

Coral fragments were distributed such that fragments from the same parent colony were placed on different coral plates and would be deployed to both the Arks and Control sites, providing an even balance of coral genets between the two treatments. The following data were recorded for each coral fragment on each coral plate: species, source site, date collected, approximate depth collected, date attached to coral plate, height, maximum horizontal dimension, horizontal dimension 90 degrees to maximum, number of branches if applicable (including number of branches with intact apical tips for *Acropora cervicornis* corals), and general health of the fragment (healthy, pale,

bleached). Fewer than five collected corals had lesions consistent with Stony Coral Tissue Loss Disease (SCTLD). Though SCTLD infection was not confirmed, these corals were not used on coral plates out of an abundance of caution.

Coral plates were attached with cable ties at a temporary holding site established in a rubble field on the south side of Mosquito Pier comprised of upside down plastic milkcrates, weights, and cinderblocks until plates were deployed to either an Ark or Control site. Corals remained on coral plates in the temporary holding location off Mosquito pier for variable time periods ranging from 0-9 days. While at the temporary holding location, corals were visually checked daily, and any accumulated fine sediment on the plates was fanned off. Attachment panels for coral plates were built into the Arks design and structure. At the Control sites, locations for coral plates were selected by a certified scientific diver to cluster coral plates relatively closely, as on the Arks structures, while avoiding areas that would impact living corals, native seagrass beds, or critical habitat for corals, and avoiding deep sand that might smother or scour the corals on the tiles. Divers then installed 2-4 stainless steel anchor points (camping spikes or lag bolts) into the benthos to which the coral plates were later attached.

Coral plates were deployed to either an Ark or a Control site by transferring them to the deployment site in bins of seawater on the shaded deck of a dive boat, and to the deployment site in milk crates. Coral plates were secured to either one of the Arks or to the benthos at one of the Control sites using stainless steel hardware and/or cable ties (Figure 4.1C). The site, date, angle of deployment from horizontal, and condition of corals on the plates were recorded for each coral plate deployed.

ARMS translocation

The Arks were monitored for the six months following coral translocation (stage 1), without the presence of seeded ARMS. In May 2022, ARMS units were transferred to Arks (10 to each Ark) to seed the Arks with reef biodiversity (stage 2). ARMS were covered in a fine mesh to retain motile organisms, removed from the benthos, and brought to the surface. Each ARMS was individually placed in seawater-filled bins on the boat and kept in the shade during transit from the ARMS seeding site to the Arks (Baer et al., 2023). At the Arks, each ARMS was hand-carried from the boat to the Arks on SCUBA and attached to a pre-installed attachment plate built into the Arks. The ARMS were secured to the Arks with stainless steel hardware and zip ties, then the mesh bag was removed (Figure 4.1C).

Monitoring

Coral survival and growth

Data were collected at the Arks and Control sites at preplanned monitoring timepoints, immediately following the installation of the Arks (time 0), then approximately every 3 months for the first year, then another 7 months to span a total of about 19 months. At each monitoring timepoint, the following data were recorded *in situ* for each coral fragment: height, maximum horizontal dimension, horizontal dimension 90 degrees to maximum, number of branches if applicable, and general health (percent of living tissue that appeared healthy, pale, bleached, or diseased). If applicable, the percent of the entire fragment that had suffered partial mortality was also recorded. This data collection approach follows guidance from the NOAA Coral Reef Restoration

Monitoring Guide (Goergen et al., 2020), with the addition of three-dimensional measurements to allow estimates of both living coral volume and surface area.

Fish abundance, biomass, and diversity

Fish associated with the Arks and Control sites were observed and recorded from GoPro video footage and/or direct observations in the field (Table 4.1). In both cases, observations were based on approximately 10-15 minutes of video or direct observations at each site. All fish captured in a given video were identified to species, binned into various estimated size classes, and the number of fish in each estimated size class were counted. For *in situ* observations, stationary size estimates and counts were made to capture larger pelagic-associated fish, followed by closer-up mobile observations to record smaller and/or cryptic fish. The video approach proved more time intensive to accurately identify fish species, so this approach was replaced entirely with direct observations starting in August 2022. However, qualitatively, the methods produced comparable results, so the data collected at all timepoints are included here and considered representative of the site fish conditions at the monitoring timepoints. The focus of this effort was to capture the abundance and biomass of fish that were ecologically associated with either the Arks or the Control sites; therefore, although some large schools (100-300 individuals) of forage fish (such as sardines) were observed passing near the Arks, these were not enumerated. Similarly, nurse sharks that were observed around the Arks anchoring system were also not enumerated.

Table 4.1 Summary of fish surveys completed

Treatment	Rep.	Nov 2021		Feb 2022		May 2022		Aug 2022		Dec 2022		Jun 2023	
		#	Method	#	Method	#	Method	#	Method	#	Method	#	Method
Ark	1	1	GoPro	1	GoPro	1	In Situ	2	In Situ	1	In Situ	2	In Situ
	2	1	GoPro	1	GoPro	1	In Situ	2	In Situ	1	In Situ	2	In Situ
Control	1	0	--	0	--	0	--	1	In Situ	1	In Situ	2	In Situ
	2	1	GoPro	1	GoPro	1	GoPro	2	In Situ	1	In Situ	1	In Situ

The trophic role of each species of fish observed was categorized based on literature references, in particular Sandin and Williams (2010). Fish biomass was estimated using length-weight relationships published in Fishbase (Froese and Pauly 2023), using the formula $W = a * L^b$, where W is weight in grams, L is length in cm (calculated as the midpoint of bins used for size estimates), and a and b are coefficients describing the relationship between length and weight for different fish species. Coefficients were mostly obtained using the R package rfishbase or were manually retrieved from Fishbase if they were not included in the Fishbase length-weight table but were estimated using Bayesian analysis of all length-weight measurements for fishes with similar body shapes (Froese et al., 2014).

Turf and macroalgae on coral plates

At each monitoring timepoint, top-down photographs were collected of each coral plate. These images were used to visually estimate percent cover of turf algae and/or macroalgae for the portion of the coral plates not occupied by living corals. In cases where algae cover on the Control site plates accumulated sediment, this turf-consolidated sediment was also counted as turf/macroalgal cover. This metric was the

strongest predictor of overall coral reef ecological function in a large-scale meta-analysis by Silveira et al., (2023).

Data analysis

All data analysis was conducted using R (Version 4.3.1) and RStudio statistical software (Version 2023.06.1+524; R Core Team 2023). Because coral plates were deployed in two stages, time-since-deployment was used for coral analyses instead of calendar-time. To allow comparisons between stage 1 and stage 2 corals, time-since-deployment was approximated as 3 months (stage 1: November 2021 to February 2022, stage 2: May 2022 to August 2022), 6 months (stage 1: November 2021 to May 2022, stage 2: May 2022 to December 2022), 9 months (stage 1: November 2021 to August 2022), 12 months (stage 1: November 2021 to December 2022, stage 2: May 2022 to June 2023), and 19 months (stage 1: November 2021 to June 2023).

Coral survival and growth

Coral survival was tracked and assessed using survival analysis methods to compare the length of time corals survived between treatments (Arks vs. Control sites). Here, loss of corals via death was considered the main event of interest and was scored categorically at each timepoint, with each coral nubbin assigned a 0 if at least part of the coral colony was alive (death had not occurred), or a 1 if the coral was completely dead. A separate categorical variable was used for missing corals that had broken off the plates between monitoring timepoints and for which the status (live or dead) at that timepoint was unknown. A coral could have been missing due to the epoxy failing or due to physical contact with the fragment which caused it to break off. Coral survival (in

weeks since deployment) was visualized using a Kaplan-Meier survival plot, where missing corals and those that were still alive at the last monitoring timepoint are 'censored', indicating that the event (death) did not occur for the time period the subject was tracked, but it is unknown after that time whether or not the event occurred. In addition, a competing risks analysis was conducted, in which survival was coded as 0, and the events "death" and "missingness" were coded as 1 and 2, respectively, allowing assessment of the relative cumulative risk to coral survival based on the likelihood of dying or falling off coral plates. Differences in survival outcomes between treatments was statistically compared using log-rank tests conducted in R software using the survival package.

To quantify the living volume and surface area of massive and encrusting corals, formulas for the volume and surface area of a dome were used, while for branching corals, the volume of an ellipse (Kiel et al., 2012) and the surface area of a cylinder with a top with an adjustment factor from Naumann et al., (2009) was used (Table 4.2). These calculated values were then multiplied by the proportion of coral tissue recorded as "living" to account for partial mortality. This approach is conceptually similar to the methods suggested by Goergen et al., (2020) for coral restoration monitoring.

Table 4.2 Equations used to estimate living surface area and volume of corals

Coral morphology	Volume formula	Surface area formula
Massive and encrusting	Dome: $\frac{1}{6}\pi h(3r^2 + h^2)$	Dome: $\pi(h^2 + r^2)$
Branching	Ellipse: $\frac{4}{3}\pi(\frac{h}{2} * \frac{x}{2} * \frac{y}{2})$ Kiel et al., 2012	Cylinder with top: $2\pi rh + \pi r^2$ Multiplied by adjustment factor of 0.44 Naumann et al., 2009

Note: h is measured colony height and r was calculated as half the average of both measured horizontal dimensions, x and y.

To assess overall coral growth and survival related to treatment, the total living coral surface area and volume was summed on each coral plate for each monitoring timepoint to provide sufficient statistical replicates. For each approximate time-since-deployment period (3, 6, 9, 12, and 19 months), the average living coral surface area and volume per coral plate was compared between treatments using non-parametric Wilcox tests.

Fish abundance, biomass, and diversity

Statistical tests to assess change in fish communities were applied following methods in Aburto-Oropeza et al., (2011), which evaluated changes in fish communities after establishment of a marine protected area. Changes in fish biomass, abundance, species richness, and species evenness over time (for each survey conducted at each timepoint and/or treatment replicate) were assessed at the Arks and Control sites, separately, using ANOVA. For two monitoring timepoints (August 2022, June 2023), at least three surveys were conducted for each treatment (Ark vs. Control), therefore providing the minimum sample size required to statistically compare differences in total biomass as well as biomass of each trophic guild between treatments using t-tests. Other timepoints had fewer surveys, precluding statistical comparison between treatments.

Turf and macroalgae growth on coral plates

The initial deployment timepoint was excluded from statistical analysis, as the coral plates were comprised of bare limestone with no growth other than translocated corals. Turf and macroalgae coverage on coral plates at other timepoints were

compared using non-parametric Wilcox tests to assess whether the coverage was significantly different based on treatment (Ark vs. Control for all plates deployed for the same approximate lengths of time). To test whether ARMS units affected the amount of turf and macroalgae cover on coral plates, Wilcox tests were also used to evaluate turf and macroalgae coverage after 3 or 6 months of deployment between coral plates that were deployed with (stage 2) or without ARMS (stage 1).

RESULTS

Coral survival and growth

After about 19 months, average survival on the Arks was about 58% compared to 34% at the Control sites, with approximately 42% of corals at the Control sites dead and 24% of corals having fallen off plates; in contrast, 22% of corals had died and 20% had fallen off plates on the Arks (Figure 4.2A-B). Corals were significantly more likely to survive to a given timepoint on the Arks relative to the Control sites (Figure 4.2A; Chi-squared = 42.2, p=8e-11). When death vs. falling off was considered, corals were significantly more likely to die at a Control site compared to an Ark after a given amount of time (Figure 4.2A-B; Gray's test = 24.8, $p<0.001$), but there was no difference in the likelihood of falling off of coral plates over time between the Arks and Control sites (Figure 2A-B; Gray's test = 2.77, p=0.10).

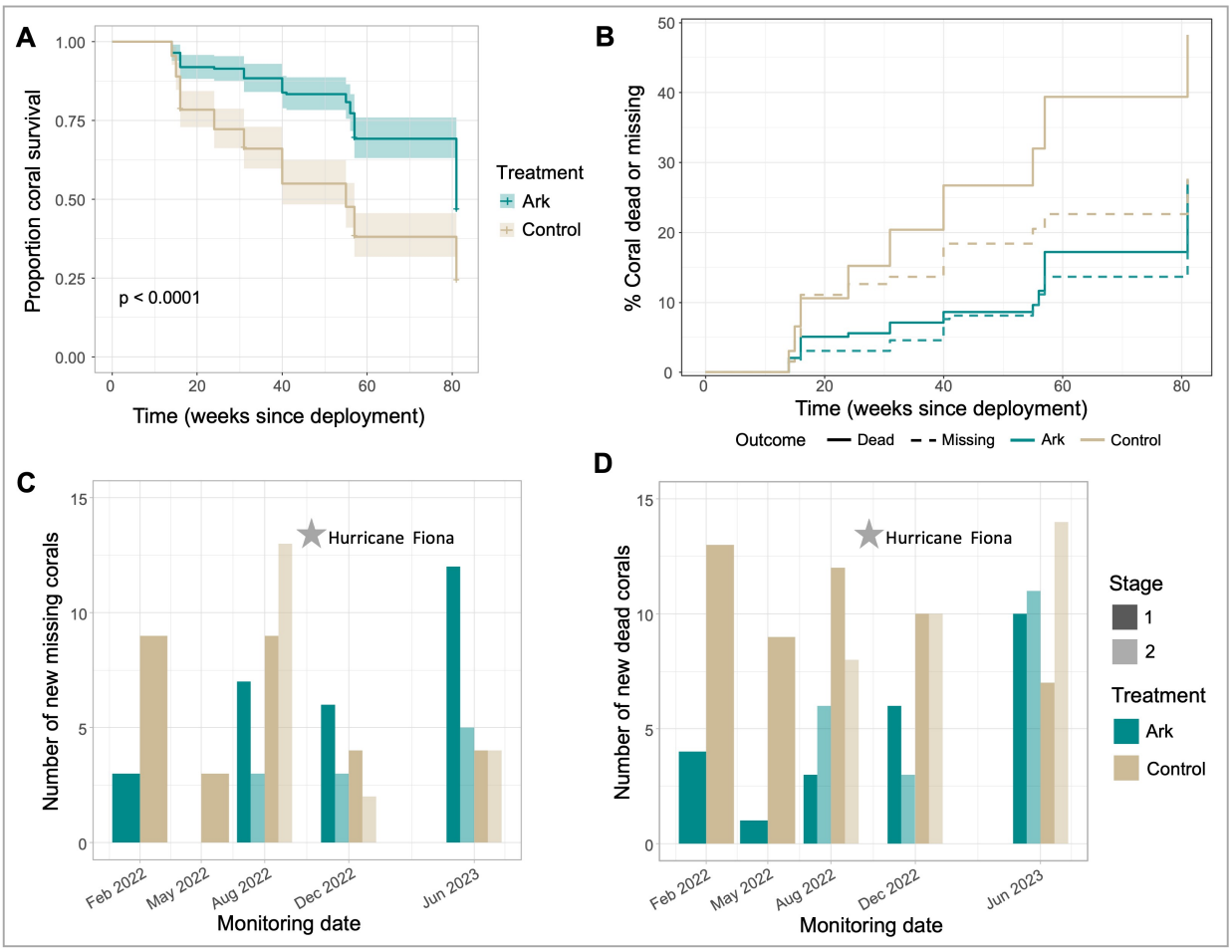


Figure 4.2 (Top) Coral survival with time shown as (A) Kaplan-Meier survival curves based on treatment and (B) cumulative risk of either death or falling off coral plates with time based on treatment. (Bottom) Number of new (C) missing and (D) dead corals observed at each monitoring period, colored by Treatment and shaded by deployment stage (stage 1 corals deployed November 2021, stage 2 deployed May 2022).

For corals deployed at the same time, fewer corals died on the Arks compared to the Control sites at all monitoring timepoints (except in December 2022, where 6 of the stage 1 corals initially deployed November 2021 died on both the Arks and the Control sites; Figure 4.2D). Corals at the Control sites tended to fall off plates early after deployment, while corals tended to fall off of the Arks after longer periods of time (Figure 2C). There was no obvious impact on loss or death of corals related to the passage of Hurricane Fiona in September 2022 (Figure 4.2C-D).

Considering both coral survival and tissue growth, the average living volume and surface area of coral on each coral plate was significantly higher on Arks compared to Control sites at all timepoints, with a spike in growth observed between the 6- and 9-month time point, coinciding with the addition of the ARMS units (Figure 2.3A-B).

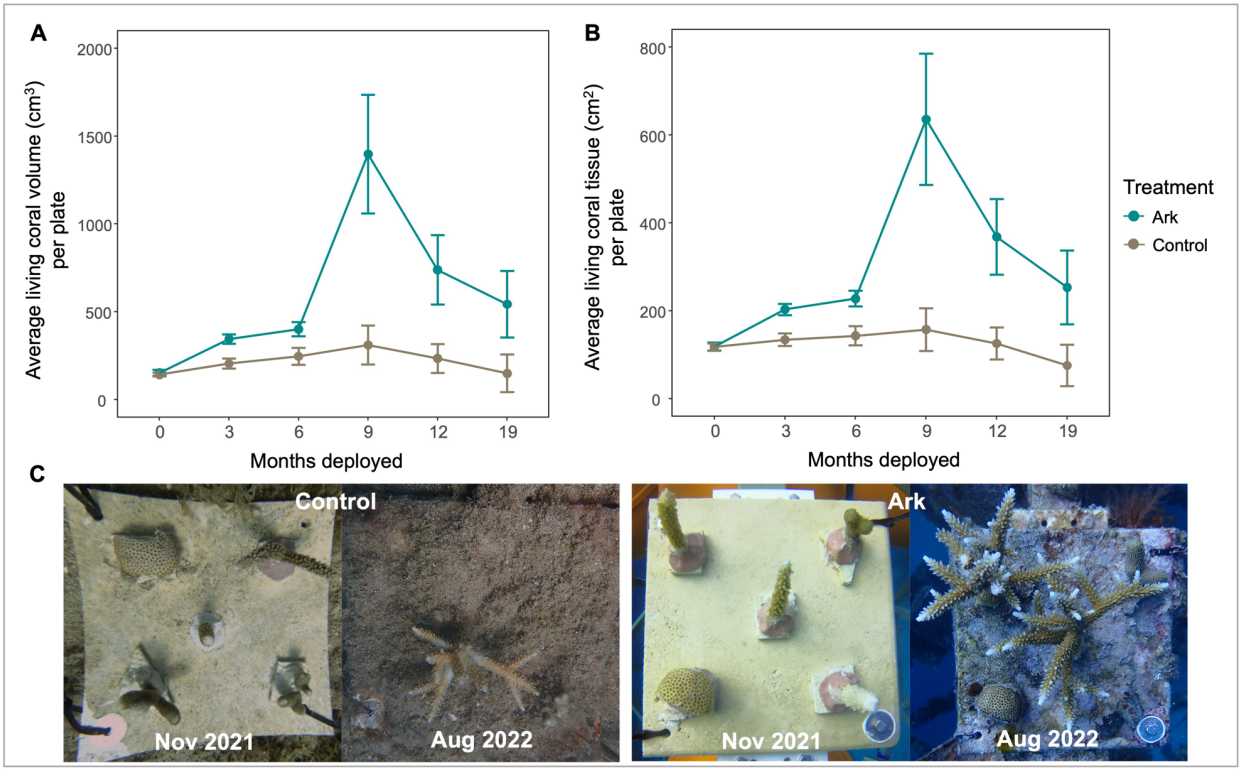


Figure 4.3 Average living coral volume (A) and surface area (B) per coral plate, based on the Treatment and number of months each plate had been deployed. After month 0, all differences between treatments are significant. (C) Representative photos from a coral plate at a Control site (left) and an Ark (right) at the start of the experiment in Nov 2021 and 9 months later in Aug 2022.

Fish abundance, biomass, and diversity

At the initial timepoint, no fish had yet discovered the Arks structures, and at the second monitoring timepoint (February 2022), only a few small fish had begun to associate with the Arks (mostly wrasses and juvenile blue tangs). Total fish numbers and biomass significantly increased over time at both Arks ($p=0.0002$ and $p=0.02$,

Figure 4.4A), while at the Control sites, fish biomass did not significantly change with time (p=0.47), but abundance slightly but significantly increased over time (p=0.02; Figure 4.4B-C). Differences in fish biomass and abundance could only be statistically compared in August 2022 and June 2023; biomass was not significantly different between treatments, but there were significantly higher numbers of fish associated with the Arks compared with the Control site in August 2022 (p<0.0001; Figure 4.4C).

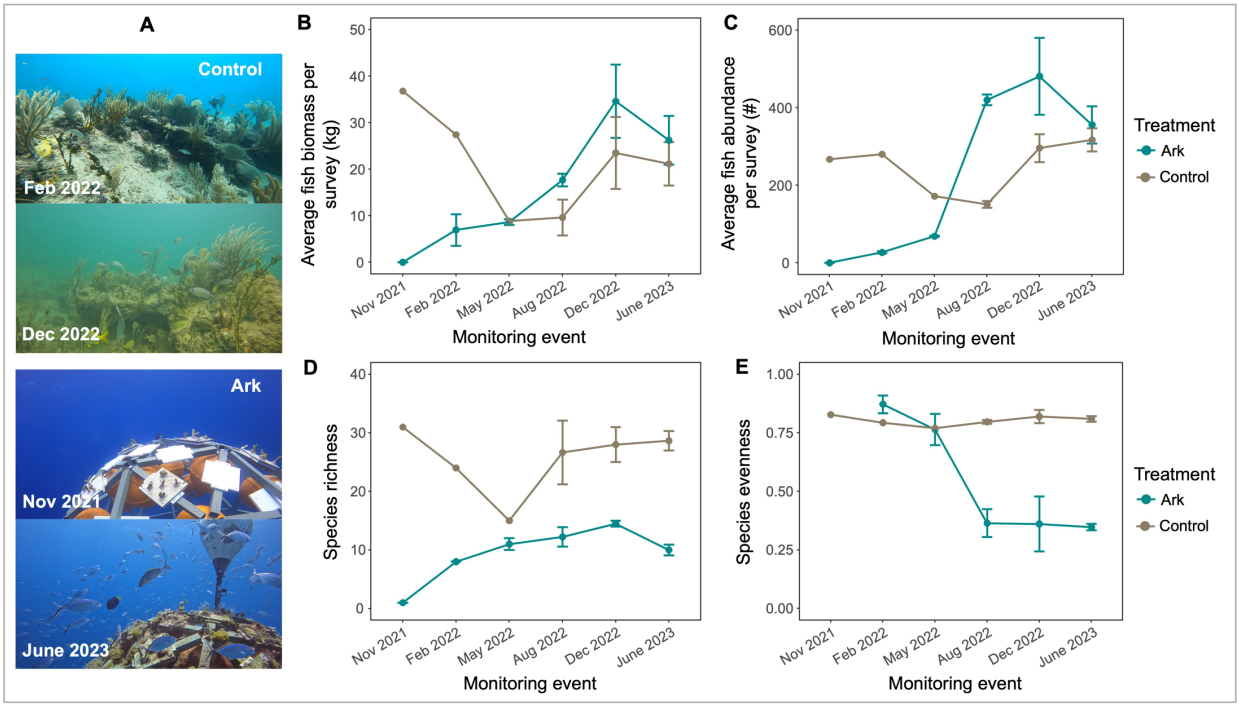


Figure 4.4 Fish communities at the Arks and Control sites, with (A) representative photos at two time points. Fish (B) biomass and (C) abundance associated with each treatment at each monitoring timepoint. Fish (D) species richness and (E) evenness associated with each treatment at each monitoring timepoint.

Fish communities associated with the Arks had lower species richness than the Control sites at all timepoints, but species richness increased over time at the Arks (p=0.008), with no significant temporal change at the Control sites (p=0.1; Figure 4.4D).

Fish species evenness increased slightly over time at the Control sites ($p=0.01$) and decreased over time at the Arks (excluding timepoint 0, $p=0.02$; Figure 4.4E).

The trophic roles of fish associated with the Arks and Control sites changed through time and differed between treatments (Figure 4.5A-B). In August 2022, 9 months after the Arks were deployed, there was significantly higher biomass and numbers of piscivores at the Arks ($p<0.001$ for both), and higher numbers and biomass of planktivores at the Control sites ($p=0.01$ and $p<0.001$, respectively), with no significant differences in other trophic guilds (Figure 4.5A-B). In June 2023, about 19 months after the Arks were deployed, there were significantly more piscivores ($p=0.004$) and significantly fewer planktivores ($p=0.02$), primary consumers ($p<0.001$), and secondary consumers ($p=0.036$), as well as lower biomass of primary consumers and secondary consumers at the Arks compared to the Control sites ($p=0.02$ and $p=0.008$, respectively; Figure 4.5C-D). As shown by these results, as well as reduced species diversity and evenness values, the fish community at the Arks is heavily skewed towards piscivorous fishes, with high abundances of bar jacks (*Carangoides ruber*) and almaco jacks (*Seriola rivoliana*) observed associating with the Arks. The numbers and biomass of piscivores associating with the Arks were significantly enhanced after ARMS units were added in May 2022 ($p=0.002$ and $p=0.001$, respectively), and persisted for the duration of the experiment (Figure 4.5). There were no significant differences in biomass or numbers of piscivores associated with the Control sites between these time periods.

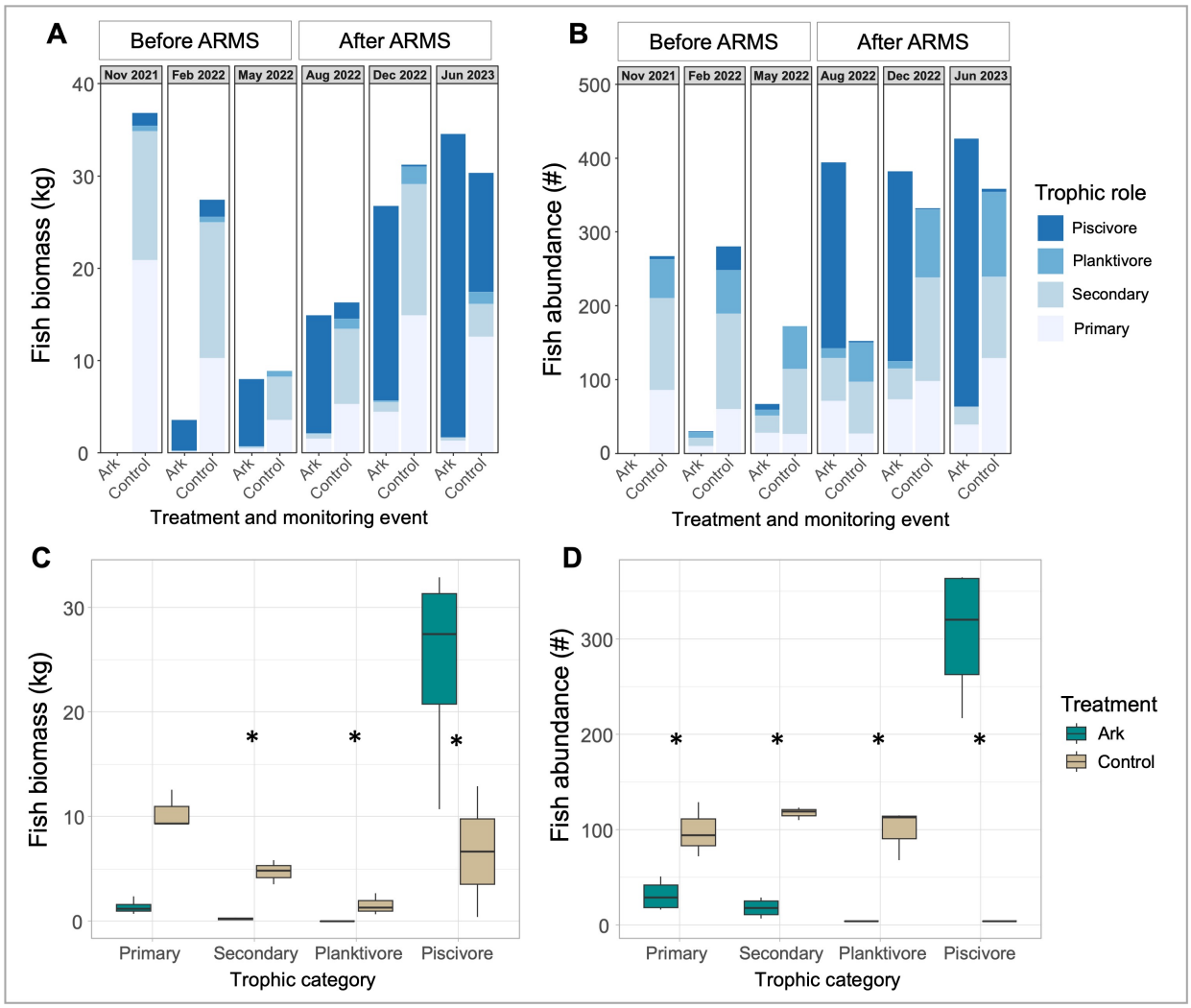


Figure 4.5 Fish (A) biomass and (B) abundance from a representative survey from each Treatment for each monitoring timepoint, separated by trophic role.(C) Biomass and (D) number of fish recorded in each trophic category within each treatment, from June 2023 monitoring data. Significant differences between treatments indicated with an asterisk.

Turf and macroalgae on coral plates

Combined turf and macroalgae cover was significantly higher on coral plates at the Control site compared to the Arks at all timepoints after time 0 ($p < 2.2e-16$ for all comparisons; Figure 4.6A). After initial increases 3-6 months after deployment, turf and macroalgae cover significantly decreased over time on both the Arks and Control site

coral plates ($p<0.001$ for both treatments), though with much smaller reductions at the Control sites.

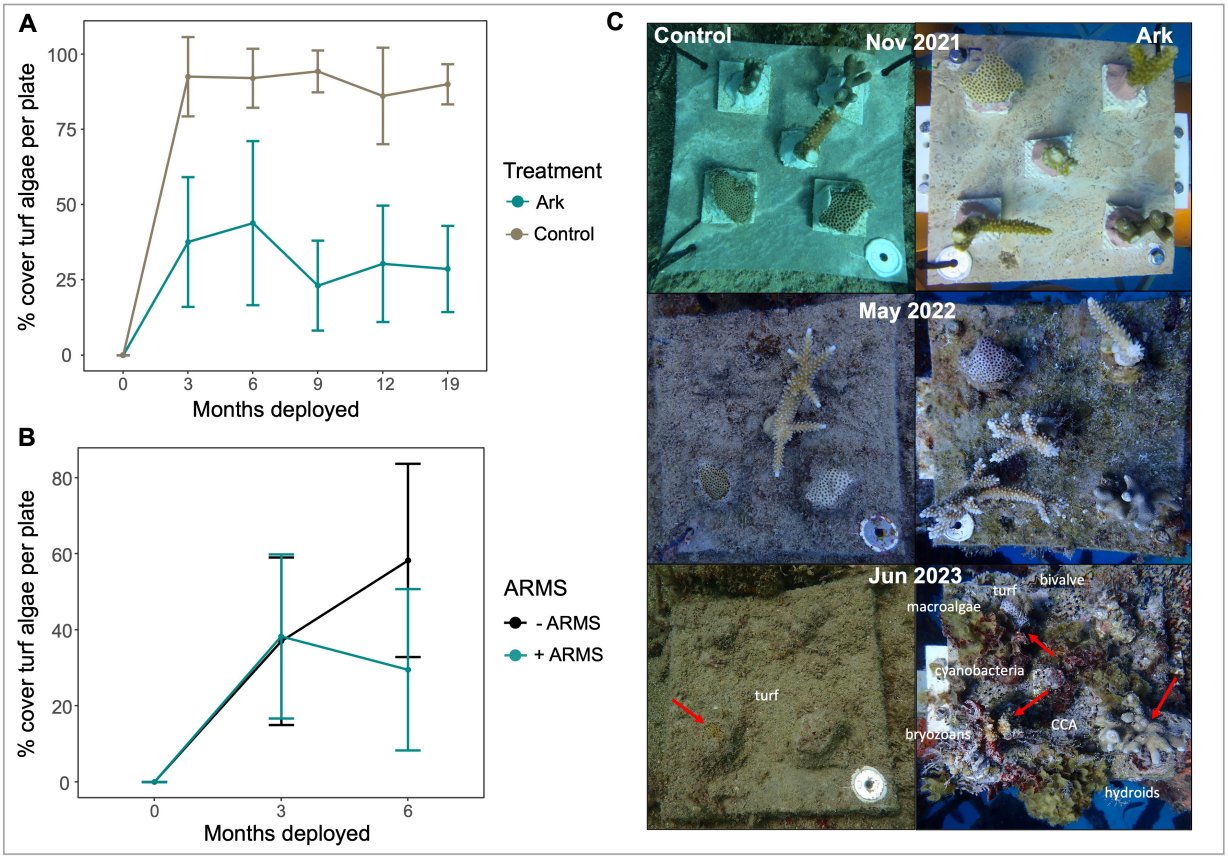


Figure 4.6 (A) Average turf and macroalgae coverage on coral plates at each monitoring timepoint, separated by treatment. After month 0, all differences between treatments are significant. (B) Average turf and macroalgae cover per coral plate after the initial 3 and 6 months of deployment for coral plates deployed in the first project stage without ARMS units (- ARMS) and in the second project stage with ARMS units (+ ARMS). (C) Side-by-side comparison of the biofouling coommunities developed over 19 months on a representative (left) Control site coral plate and (right) Ark coral plate. In the bottom (June 2023) panels, remaining living corals are indicated with red arrows. Labels are also included on the Ark coral plate (bottom right), indicating some of the non-coral organisms visible on the coral plate.

Some of the reduction in turf and macroalgae cover with time at the Control sites was probably driven by sand scouring, while at the Arks, it may have been grazed down and/or overgrown or outcompeted by other organisms such as sponges, fire coral,

crustose coralline algae, and bryozoans. These other competing organisms were also observed to overgrow living corals on coral plates on the Arks (Figure 4.6C).

Turf and macroalgae coverage on the Arks coral plates was not significantly different for those plates deployed with or without ARMS after about 3 months of deployment (means of 37% and 38% cover, respectively), but was significantly higher for coral plates deployed without ARMS units (mean of 58% cover) than with ARMS units (mean of 30% cover) after about 6 months of deployment ($p = 0.001$; Figure 4.6B). These results may be influenced by seasonal changes, as the 6-month timepoint for coral plates deployed without ARMS was May 2022 and with ARMS was December 2022. However, at the Control sites, coral plates deployed at the same times as on the Arks displayed the opposite pattern, with slightly but significantly lower turf and macroalgae cover 6 months after deployment for those plates deployed in stage 1 (mean of 89% cover in May 2022) vs. stage 2 (mean of 95% cover in December 2022; $p= 5.388e-05$), suggesting the differences in turf and macroalgae cover on coral plates after 6 months on the Arks was associated with the addition of ARMS (Figure 4.6B).

DISCUSSION

Stony corals had better survival and growth on the midwater Arks systems relative to the seafloor at the same depth, demonstrating that environmental conditions on Arks were better for stony corals than conditions on the benthos near Vieques. More broadly, the Arks system outperformed benthic transplantation approaches typically used in coral mitigation and coral outplanting, analogous to the improved performance of corals grown in nurseries on structures off the benthos (Shafir et al., 2006). Yet, unlike coral nurseries and compared to the Control sites, the Arks also had more

predatory fish, lower levels of turf and macroalgae overgrowth, and qualitatively higher biodiversity. Higher levels of coral survival may be related to favorable environmental conditions such as higher dissolved oxygen, fewer bacteria and more viruses, higher water flow speeds, higher light intensity (Baer et al., 2023), and/or improved ecological function at the Arks sites. These characteristics indicate that the Arks developed a self-sustained reef ecosystem, favor coral over macroalgae, and generate enhanced ecosystem services compared to the natural reefs from which they were seeded.

A meta-analysis of coral restoration projects worldwide found an average survival rate of 66% for translocated corals, though this rate does not consider differing lengths of time that various projects were monitored (Boström-Einarsson et al., 2020). At the Control sites, 66% of corals survived for about 8 months (31 weeks; Figure 4.2), but after that time, survival continued to decline, with just 34% of corals still alive after about 19 months (Figure 4.2). On the Arks, about 69% of corals were still alive after more than a year, indicating about 50% longer survival compared to the Control sites, and 58% of corals were still alive after about 19 months (Figure 4.2). These data show that assessments of coral transplantation projects should establish a “local background” survival rate for translocated corals, as in the Control sites used here, to fully assess the efficacy of a given approach. Survival of corals on the Arks was somewhat similar to survival in a 2007-2009 study in Vieques which also translocated corals to artificial reef structures (73% survival to 19 months; Dial Cordy and Associates Inc., 2013). That study used larger colonies rather than fragments (i.e., more robust stock) and took place more than 15 years ago, during which time there have been multiple mass coral bleaching events and the emergence of new coral diseases in the Caribbean.

Coral transplantation creates the potential for coral loss through detachment (epoxy attachment and entire fragment falls off) or breakage (portion of coral fragment breaks off) as well as coral loss due to mortality. The rate of detachment was not statistically different between the Arks and Controls and was similar to rates of detachment reported elsewhere (i.e. Dizon et al., 2008). Incidental grazing disturbance by herbivorous fishes can cause detachment of experimental coral nubbins (Quimpo et al., 2020), and this effect may explain the larger loss of corals from Control site plates within the first ~3 months of deployment, given that very few fish were observed at the Arks during this time period. Interestingly, relatively few corals (9) fell off the Arks during the time period that Hurricane Fiona passed almost directly over the Arks (September 2022), suggesting coral loss was not strongly tied to storm events. The rate of corals falling off of the Arks generally increased over time, possibly because as corals grew larger, they became top-heavier and detached more easily, or their increased size created stronger horizontal drag forces that allowed currents to dislodge the corals (Madin and Connolly 2006). However, breakage of corals off of Arks structures is not necessarily problematic; breakage can facilitate reef substrate accumulation and carbon sequestration on the benthos below an Ark in deep water and/or aid in asexual reproduction of corals from Arks in water shallow enough for coral survival.

The superior performance of corals translocated to the Arks relative to the Control sites was likely the result of direct effects of algal competition and indirect effects of fish communities and microbial processes. Previous benthic artificial reefs built in Vieques found, over a similar period of time, that the reef became covered in turf algae that surrounded the corals (Dial Cordy and Associates Inc., 2013). A similar

successional trajectory was observed here: Control site coral plates became fouled almost exclusively by turf and macroalgae (as well as sediment bound to these substrates) that surrounded the coral fragments and remained this way throughout the study. In contrast, fouling communities surrounding coral fragments on Arks plates were more diverse, with higher proportions of other invertebrates and lower coverage of turf and macroalgae (Figure 4.6). Competition is high on coral reef benthos and turf algae are one of the strongest competitors of corals, explaining why coral nurseries routinely manually remove algae to support coral growth (Shafir et al., 2006). No algal removal was completed on the Arks, though, allowing the system to develop relatively naturally into a complex midwater reef system instead of a maintained nursery. Instead, higher diversity reef communities formed, enhanced by the addition of ARMS, which was associated with decreases in turf algal cover and increases in species diversity with time.

The Arks developed a piscivore-dominated fish community with numbers and biomass of fish associated with the Arks similar to or greater than the Control sites (Figure 4.4), particularly for fishery target species such as jacks. Top-heavy, piscivore-dominated coral reef food webs, as observed on the Arks, are typically associated with low standing stock of algae and herbivores, as trophic efficiency is high (Sandin et al., 2008). Higher cover of turf and macroalgae are strong predictors of poor reef health and “microbialization” (Haas et al., 2016, Silveira et al., 2023), likely due to algae releasing dissolved organic matter that bacteria feed upon and draw down dissolved oxygen (Mueller et al., 2022). The Control sites had lower dissolved oxygen, more bacteria and fewer viruses, lower water flow speeds, and lower light intensity despite similar depths

than the Arks (Baer et al., 2023), demonstrating an additional indirect effect pushing the Arks system towards corals winning over algae.

CONCLUSIONS

Arks provide numerous ecological benefits and ecosystem services. Arks increased survival and growth of translocated corals, suggesting these systems could be used for mitigation and to enhance restoration projects. Specifically, higher coral survival and the presence of multiple coral recruits on the Arks suggests they could act as a source of larvae to nearby reefs (Amar and Rinkevich 2007). Top-heavy fish communities, particularly after addition of seeded ARMS units, highlight that Arks can enhance fisheries productivity. The addition of seeded ARMS was associated with lower turf abundance. While not quantified during limited monitoring events for this project, many juvenile fishery target invertebrates including scallops, lobster, and crabs were also observed on the Arks, further enhancing fisheries. Arks can therefore act as *in situ* mesocosms for scientific studies (Baer et al., 2023), “house reefs” for divers, snorkelers, and education, and can contribute to coral reef mitigation and restoration.

ACKNOWLEDGEMENTS

This project was supported by the Environmental Security Technology Certification Program, grant CR20-5175, with in-kind support from the Vieques Restoration Program, Naval Facilities Engineering Command Southeast. We are grateful for the support received from Gunther Rosen, P.F. Wang, Adam Candy, John Martin, Lora Pride, Brett Doerr, Maria Danois, Ronny Fields, Kristin McClendon, Dan Waddill, Kevin Cloe, Daniel Hood, Nilda Jimenez Marrero, Michael Nemeth, Tali Vardi, Sarah Elise Field, Pedro Rodriguez, Pete Seufert and Tania Puell. Corals of opportunity were collected under Puerto Rico Department of Natural and Environmental Resources permit number O-VS-PVS15-SJ-01233-20092021.

Chapter 4, in full, has been accepted for publication of the material by the journal PeerJ. Jessica Carilli*, Jason L Baer*, Jenna Marie Cruz Aquino, Mark Little, Bart Chadwick, Forest Rohwer, Gunther Rosen, Anneke van der Geer, Andrés Sánchez-Quinto, Ashton Ballard, and Aaron Hartmann. The dissertation author was the co-primary investigator and co-first author of this paper.

REFERENCES

Aburto-Oropeza, O., Erisman, B., Galland, G.R., Mascarenas-Osorio, I., Sala, E. and Ezcurra, E., 2011. Large recovery of fish biomass in a no-take marine reserve. Plos one, 6(8), p.e23601.

Amar, K.O. and Rinkevich, B., 2007. A floating mid-water coral nursery as larval dispersion hub: testing an idea. Marine Biology, 151, pp.713-718.

Baer, J.L., Carilli, J., Chadwick, B., Hatay, M., van der Geer, A., Scholten, Y., Barnes, W., Aquino, J., Ballard, A., Little, M. and Brzenski, J., 2023. Coral Reef Arks: An *in situ* mesocosm and toolkit for assembling reef communities. JoVE (Journal of Visualized Experiments), (191), p.e64778.

Bauer, Laurie J. and Kendall, Matthew S. (eds.). 2010. An ecological characterization of the marine resources of Vieques, Puerto Rico Part II: Field studies of habitats, nutrients, contaminants, fish, and benthic communities. NOAA Technical Memorandum NOS NCCOS, 110. pp. 9-46.

Boström-Einarsson, L., Babcock, R.C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S.C., Hancock, B., Harrison, P., Hein, M., Shaver, E. and Smith, A., 2020. Coral restoration–A systematic review of current methods, successes, failures and future directions. PloS one, 15(1), p.e0226631.

Dickenson, N.C., McNeilly, F.J. and Marx, D., 2022. Coral mitigation for pier construction at the Atlantic undersea test and evaluation center. Available at https://apps.dtic.mil/sti/pdfs/AD1180372.pdf

Dizon, R.M., Edwards, A.J. and Gomez, E.D., 2008. Comparison of three types of adhesives in attaching coral transplants to clam shell substrates. Aquatic Conservation: Marine and Freshwater Ecosystems, 18(7), pp.1140-1148.

Eddy, T.D., Lam, V.W., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., Bruno, J.F., Ota, Y. and Cheung, W.W., 2021. Global decline in capacity of coral reefs to provide ecosystem services. One Earth, 4(9), pp.1278-1285.

Ferse, S.C., Hein, M.Y. and Rölfer, L., 2021. A survey of current trends and suggested future directions in coral transplantation for reef restoration. PloS one, 16(5), p.e0249966.

Froese, R. and D. Pauly. Editors. 2023. FishBase. World Wide Web electronic publication. www.fishbase.org (02/2023)

Froese, R., J. Thorson and R.B. Reyes Jr., 2014. A Bayesian approach for estimating length-weight relationships in fishes. Journal of Applied Ichthyology 30(1):78-85.

Goergen, E.A., Schopmeyer, S., Moulding, A.L., Moura, A., Kramer, P., and Viehman, T.S. 2020. Coral reef restoration monitoring guide: Methods to evaluate restoration success from local to ecosystem scales. NOAA Technical Memorandum NOS NCCOS 279. Silver Spring, MD. 158 pp. https://doi.org/10.25923/xndz-h538

Haas, A.F., Fairoz, M.F., Kelly, L.W., Nelson, C.E., Dinsdale, E.A., Edwards, R.A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B. and Lim, Y.W., 2016. Global microbialization of coral reefs. Nature microbiology, 1(6), pp.1-7.

Hein, M.Y., Beeden, R., Birtles, A., Gardiner, N.M., Le Berre, T., Levy, J., Marshall, N., Scott, C.M., Terry, L. and Willis, B.L., 2020. Coral restoration effectiveness: multiregional snapshots of the long-term responses of coral assemblages to restoration. Diversity, 12(4), p.153.

Higgins, E., Metaxas, A. and Scheibling, R.E., 2022. A systematic review of artificial reefs as platforms for coral reef research and conservation. PLoS One, 17(1), p.e0261964.

Kiel, C., Huntington, B.E. and Miller, M.W., 2012. Tractable field metrics for restoration and recovery monitoring of staghorn coral *Acropora cervicornis*. Endangered Species Research, 19(2), pp.171-176.

Ladd, M.C. and Shantz, A.A., 2020. Trophic interactions in coral reef restoration: A review. Food Webs, 24, p.e00149.

Madin, J. S., & Connolly, S. R. (2006). Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature, 444(7118), 477-480.

Mueller, B., Brocke, H.J., Rohwer, F.L., Dittmar, T., Huisman, J., Vermeij, M.J. and de Goeij, J.M., 2022. Nocturnal dissolved organic matter release by turf algae and its role in the microbialization of reefs. Functional Ecology, 36(8), pp.2104-2118.

Naumann, M.S., Niggl, W., Laforsch, C., Glaser, C. and Wild, C., 2009. Coral surface area quantification–evaluation of established techniques by comparison with computer tomography. Coral reefs, 28, pp.109-117.

Nedimyer, K., Gaines, K., and Roach, S., 2011. Coral Tree Nursery: An innovative approach to growing corals in an ocean-based field nursery. AACL Bioflux 4(4):442-446.

Nelson, C.E., Wegley Kelly, L. and Haas, A.F., 2023. Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. Annual Review of Marine Science, 15, pp.431-460.

Quimpo, T.J., Cabaitan, P.C. and Hoey, A.S., 2020. Detachment of *Porites cylindrica* nubbins by herbivorous fishes. Restoration Ecology, 28(2), pp.418-426.

R Core Team (2023). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://www.R-project.org/>.

Ransome, E.J., Timmers, M., Hartmann, A., Collins, A. and Meyer, C., 2016. Cryptic coral reef diversity across the Pacific assessed using Autonomous Reef Monitoring Structures and multi-omic methods. American Geophysical Union, 2016, pp.OD34B-2512.

Sandin, S.A. and Williams, I., 2010. Trophic classifications of reef fishes from the tropical US Pacific (version 1.0). University of California San Diego, Scripps Institution of Oceanography Technical Report, 8/25/2010.

Shafir, S., Van Rijn, J. and Rinkevich, B., 2006, June. A mid-water coral nursery. In Proceedings of the 10th International Coral Reef Symposium (Vol. 10, pp. 1974-1979).

Silveira, C.B., Luque, A., Haas, A.F., Roach, T.N., George, E.E., Knowles, B., Little, M., Sullivan, C.J., Varona, N.S., Wegley Kelly, L. and Brainard, R., 2023. Viral predation pressure on coral reefs. BMC Biology, 21(1), p.77.

Stella, J.S., Pratchett, M.S., Hutchings, P.A. and Jones, G.P., 2011. Coral-associated invertebrates: diversity, ecology importance and vulnerability to disturbance. Oceanography and Marine Biology: an annual review, 49, pp.43-104.

Webb, A.E., de Bakker, D.M., Soetaert, K., da Costa, T., van Heuven, S.M.A.C., van Duyl, F.C., Reichart, G.J. and de Nooijer, L.J., 2021. Functional consequences of Caribbean coral reef habitat degradation. Biogeosciences, 18, pp.6501-6516.

Chapter 5

A CONTROL THEORETIC FRAMEWORK AND IN SITU EXPERIMENTAL PLATFORM FOR ACTIVE RESTORATION OF CORAL REEFS

ABSTRACT

Coral reefs provide crucial ecosystem services to over 1 billion people globally and this intense pressure is causing their decline. Despite substantial investments in coral restoration, current methods are proving ineffective for restoring these ecosystems. This work demonstrates how to apply control theory to coral reef restoration, leveraging the framework's proven effectiveness for optimizing the growth of crops and expanding it to a complex ecosystem. An *in situ* mesocosm called Coral Reef Arks is used as a platform to test control interventions and refine the approach. The results from four field experiments using Coral Reef Arks demonstrate how control interventions are used to alter ecological and environmental conditions and push reef state factors towards their target values. The results from these tests identify maximally effective control interventions that can be scaled to natural reefs. This control-based restoration framework advances coral reef management by providing a path to identify precise, adaptable interventions based on real-time ecological feedback. This framework contrasts with static conservation strategies, offering a dynamic approach to maintain and enhance reef function in the face of ongoing environmental changes.

INTRODUCTION

Each year, coral reefs generate an estimated $400 billion globally through ecosystem services such as coastline protection, tourism, fisheries, and new

pharmaceuticals and biotechnologies (Moberg and Folke 1999; Costanza et al., 2014). Yet coral reefs are in decline: global coral cover has declined by half since the 1950s due to the cumulative effects of overfishing, pollution, habitat destruction, and climate change, with corresponding losses in the capacity of coral reefs to provide ecosystem services (Eddy et al., 2021). Common conservation and restoration efforts centered primarily on passive habitat protections, such as the establishment of marine protected areas, have largely failed to re-establish functioning reef ecosystems, mitigate population declines, and enhance ecosystem services (Graham et al., 2011; Mouillot et al., 2016; Bates et al., 2019; Bruno et al., 2019), and estimates suggest up to 90% of global coral reefs will face collapse by 2055 (Setter et al., 2022). In this Perspective, we propose a control framework for restoring coral reefs using an engineered, *in situ* midwater mesocosm system—an active management approach to restoration built deliberately around human intervention and aimed at addressing key shortcomings of past restoration approaches.

Substantial restoration investments over the past decade ($258 million USD across 56 countries, Hein et al., 2021) have struggled to stem coral reef decline through reef flattening, declining fish stocks and biodiversity, and microbialization (Alvarez-Filip et al., 2009; Haas et al., 2016a; Ladd et al., 2019). Despite some successes with coral propagation (Hein et al., 2020), interventions have failed to preserve key ecosystem attributes such as accretion, biodiversity, and water quality that enable coral reefs to provide ecosystem services (Hatcher 1997; Silbiger et al., 2014; Woodhead et al., 2019; Hein et al., 2021b). Four main problems have plagued efforts to restore reefs. First is poor project design: a lack of clear objectives, poorly defined projects in relation to the

stated objectives, and a lack of holistic, standardized metrics used to assess success (Boström-Einarsson et al., 2020; Hein et al., 2020). Second is the lack of interventions tailored to specific conditions on the reef. With limited methods for coral restoration, most practitioners have adopted generic, coarse practices instead of precise, site-specific interventions that consider local conditions (Hein et al., 2021b). Third, most restoration efforts overlook the fundamental ecological processes that shape coral reef ecosystem function (Shaver and Silliman 2017; Brandl et al., 2019; Ladd and Shantz 2020). Restoration monitoring tends to focus on survival and growth metrics of outplanted coral fragments rather than trophic interactions which indicate whether key ecosystem functions are recovered. Fourth, restoration goals tend to be oriented towards historic baselines (Rogers et al., 2015), which may no longer be achievable, rather than adopting new goals which place essential coral reef functions and services in the context of future conditions. Coral restoration will greatly benefit from a change in approach to a control-based framework that sets clear, quantifiable objectives and measures of success, emphasizes core ecosystem processes, centers its goals on engineering reefs highly integrated with human systems, and supports the testing and integration of new methods for controlling key reef variables.

Active control of ecosystems is common in and critical to success in agriculture (Zhang et al., 2002; Ding et al., 2018), forestry (Farnum 2001; Nocentini et al., 2017), and fisheries (Meza and Bhaya 2010) but has not been applied to coral reefs. Control approaches are goal-oriented, require intervention, and apply interventions based on the current state of the system: farmers control the amount of fertilizer, pesticide, and water delivered to a field to maximize crop yield; fishers harvest a fish species only if its

population exceeds a certain density threshold. Control of entire ecosystems (beyond individual target species) is theoretically possible (Hill and Durham 1978; Walters and Hilborn 1978; Holland 2006; Loehle 2006; Heinimann 2010), but only certain aspects of the theory have been applied in ecosystem restoration. On the Pacific coast of North America, the decline of kelp beds due to grazing by sea urchins was successfully managed by increasing hunting enforcement on sea otters, leading to effective control of kelp forest densities (Estes and Palmisano 1974; Smith et al., 2021). Reducing organic matter inputs from sewage treatment plants and land-based sources of pollution has successfully reduced local hypoxia on coral reefs (Kemp et al., 2009), resulting in shifts in benthic community composition that favor corals over macroalgae (Weijerman et al., 2016). Coral cover almost doubled on reefs in which the densities of herbivorous fish were artificially enhanced (Hughes et al., 2007), and macroalgal cover increased by up to 10-fold when herbivorous fish were excluded (Shantz et al., 2020). These and other previous restoration efforts have included elements of control but have not been integrated into broadly effective intervention strategies and fail in the face of environmental uncertainty and sampling difficulties (Loehle 2006).

Control approaches define key state factors, or quantifiable indicators of the state of the ecosystem, and then measure, control, and guide them to preferred states. Here we provide a control framework for active restoration of coral reefs using an *in situ*, midwater mesocosm system called Coral Reef Arks (Baer et al., 2023). We propose six state factors: calcification rate, fish biomass, aesthetic score, virus-to-microbe ratio (VMR), biodiversity, and chemical diversity, which are key to maintaining a calcifier-dominated reef system (Table 5.1). We set achievable restoration goals for each

variable and report the results from four field experiments that demonstrate how control interventions are used to move towards these goals. Using several applied examples, we show that using Coral Reef Arks increase controllability and reduce environmental noise, two main reasons that prior attempts at ecological control have failed (Loehle 2006; Heinimann 2010). Coral Reef Arks link theory to practice by providing an experimental platform to (1) identify the most effective control interventions, (2) determine the response of the key state variables to these interventions, and (3) develop a site-specific control strategy that can be applied beyond Coral Reef Arks on natural reefs.

ACTIVE RESTORATION OF REEF ECOSYSTEMS USING CONTROL THEORY

Control frameworks define a system's *state* and identify methods for pushing that state to a desired point. This requires three main components to be defined: (1) state factors, (2) set points, and (3) controllers.

State factors

State factors are measured variables that describe the system's *state* at a point in time in relation to desired *outputs*. States indicate the extent to which the system under control is behaving optimally. In agriculture, for example, the system under control is cultivated land, the desired output is yield, and states, such as accumulated biomass of corn, indicate whether the cultivated land is generating yield. The desired outputs of a coral reef, known as ecosystem services, include coastal protection through dissipation of wave energy, food provisioning through fisheries, tourism revenue, habitat for biodiversity, and drug discovery (Table 5.1, Rogers et al., 2015; Woodhead et al., 2019).

A state factor selected for each ecosystem service should (1) quantify the extent to which the service is being provided, (2) represent ecosystem attributes essential to reef function (i.e., calcium carbonate accretion, biological production, and biogeochemical cycling, Hatcher 1997), (3) focus on dynamic processes operating over time instead of static structures (Heinimann 2010), and (4) together with the other state factors, generate sufficient information about overall ecosystem state and economic value to ensure restoration objectives are being met. For example, *calcification rate* is a stronger state factor than *rugosity* or *turbulent kinetic energy dissipation* to describe the coastal protection capacity of reefs because it describes a growth process that is directly linked to reef persistence and the continued delivery of coastal protection (Table 5.1, Hatcher 1997; Brandl et al., 2019).

We selected six state factors to capture the ecologically essential and economically valuable aspects of reef function: (1) calcification rate, (2) fish biomass, (3) aesthetic score, (4) virus-to-microbe ratio (VMR), (5) biodiversity, and (6) chemical diversity (Table 1). Fish biomass and biodiversity are well-described in the literature and already integrated into many reef monitoring plans (Shaver and Silliman 2017; Hein et al., 2020; Seraphim et al., 2020). In a recent meta-analysis, VMR and fish biomass emerged as among the strongest predictors of reef health (Silveira et al., 2023) and shifts in both aesthetic scores (Haas et al., 2015) and chemical diversity (Wegley Kelly et al., 2022) have been correlated with coral reef transitions to degraded, macroalgae-dominated states. These state factors together provide a holistic assessment of reef function, which are not captured by common restoration metrics such as coral cover or growth and survival of individual coral fragments.

Table 5.1 Six variables, or state factors, representing coral reef ecosystem attributes essential to reef function and to an integrated human-reef system. These measured variables describe a coral reef's state, with the set points representing target values for outcomes of reef interventions. When the measured values of all state factors meet or exceed the set points, the reef is considered to be "healthy" and capable of delivering essential ecosystem services.

State factor	Measurement	Set point	Rationale	References
Calcification rate ($g/m^2/year$)	Buoyant weight Calcification accretion units (CAUs)	>500 $g/m^2/year$	Shoreline protection & habitat complexity. Is system accreting or dissolving? ***Ecosystem attribute*** – accretion	Price et al., 2012; Vargas-Angel et al., 2015; Reis et al., 2016; Januchowski-Hartley et al., 2017; Estrada-Saldívar et al., 2019; Lange et al., 2020; Davis et al., 2021; Randi et al., 2021; Johnson et al., 2022
Fish biomass (g/m^2)	Visual surveys	<50 g/m^2	Food provisioning. Positively impact reefs through herbivory and trophic structuring. ***Ecosystem attribute*** - secondary production & predation	Newman et al., 2006; Sandin et al., 2008b, a; Williams et al., 2011; Edwards et al., 2014; Ladd et al., 2019; Robinson et al., 2019
Aesthetic score	Photos & machine learning algorithm	<20	Generates tourism revenue. Visual index of structural complexity and community composition. ***Ecosystem attributes*** - accretion, biodiversity	Uyarra et al., 2009; Haas et al., 2015; Grafeld et al., 2016; Marshall et al., 2019
Virus-to-microbe ratio (VMR)	Epifluorescence microscopy	>10	Index of microbial community stability. Viral control over microbes directs microbial carbon up the trophic web. ***Ecosystem attributes*** – organic matter recycling & decomposition, microbialization	Haas et al., 2016b; Knowles et al., 2016b; Silveira et al., 2019, 2020, 2023; Nelson et al., 2023
Biodiversity (H')	Sequencing	>4.5	Generates ecosystem resilience. Ensures efficient recycling of reef resources. ***Ecosystem attributes*** – biodiversity & resilience	Bellwood et al., 2006; Plaisance et al., 2011b; Díaz-Pérez et al., 2016; Ransome et al., 2017; Pearman et al., 2018; Duffy 2019; Wee et al., 2019; Galand et al., 2023
Chemical diversity (H')	LC-MS/MS	>5.5	Discovery of natural products and therapeutics. ***Ecosystem attribute*** - biogeochemical cycling	Hartmann et al., 2017; Wegley Kelly et al., 2021, 2022; Nelson et al., 2023

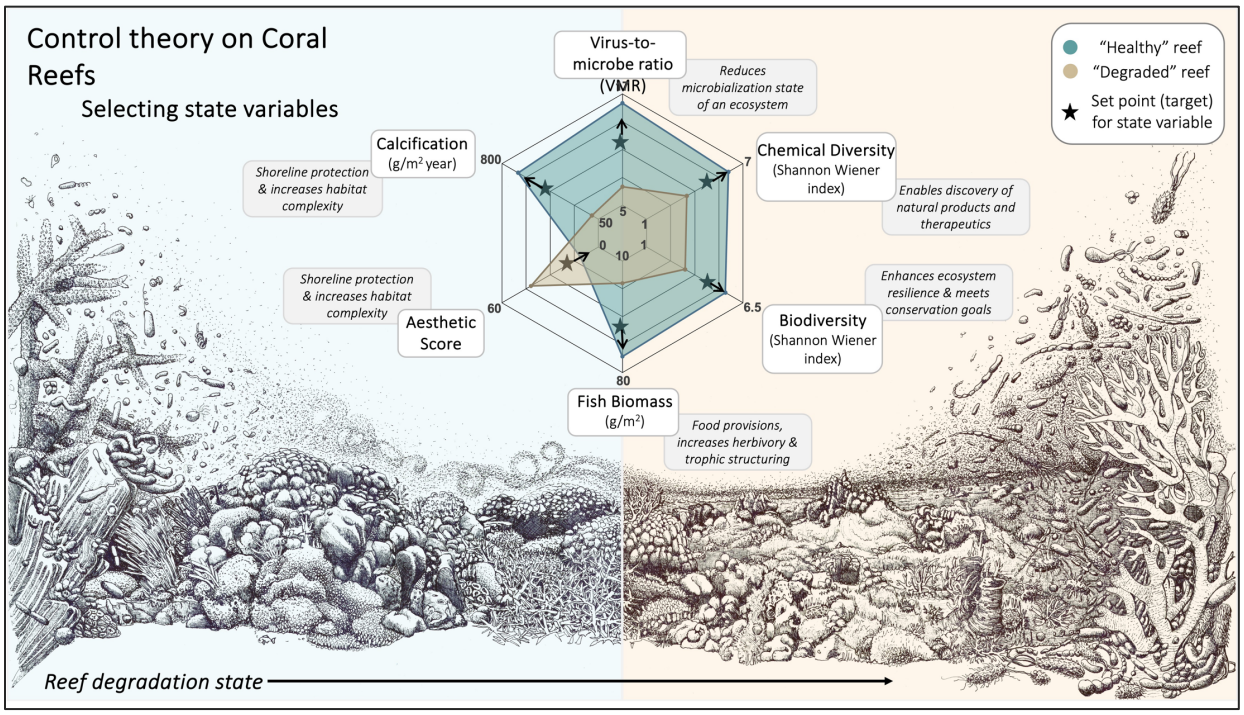


Figure 5.1 Six state variables (white boxes) representing coral reef ecosystem attributes essential to reef function and to an integrated human-reef system (gray boxes). These are the measured variables which describe a coral reef's state, with the set points (black stars on the axes of the spider plot) representing target values for the reef system. When the measured values of all state factors meet or exceed the set points, the reef is considered to be "healthy" and capable of delivering essential ecosystem services to human communities (blue data). Figure adapted from Nelson et al 2022.

Set points

Next, control theory applications require **set points** or target values that indicate the optimal system state. On coral reefs, set points are state factor values that satisfy human demand for resources and provide an explicit target for restoration efforts. The set point for reef fisheries is the amount of fish biomass required to sustain human demand for food and maintain essential reef functions (herbivory, trophic web dynamics, healthy broodstock), whereas the set point for coastal protection is the calcification rate that exceeds erosional and dissolution processes, thereby sustaining net growth of the reef framework. The set point values in Table 5.1 were selected based on literature

values collected from healthy reefs, however, local biological characteristics and history should be considered to select more realistic set points at specific sites. When all of the state factors meet or exceed their set points, a reef is considered healthy or optimized and capable of delivering ecosystem services.

Controllers

Lastly, **controllers** are targeted interventions that push the state factors towards the set points. Control in ecosystems can be implemented via three routes: adding or removing biological components (*state control, SC*), altering environmental factors that influence biological metabolic rates or responses (*parametric control, PC*), and restructuring the physical environment or geometry (*physical habitat control, PHC*) (Loehle 2006). Farmers use each of these control routes, such as through herbicides and pesticides (SC), applications of fertilizers and water (PC), and controlled burning (PHC) to regulate crop harvests. A variety of interventions have been tested on coral reefs (Table 5.2); however coral restoration has employed only a narrow range of these strategies by focusing on state controls and working almost exclusively on corals, despite the need for biodiversity and functional redundancy for healthy reef states. Existing interventions include (1) coral gardening, a branch of marine silviculture focused on asexual propagation and outplanting of coral fragments (Rinkevich 2005, 2019; Lirman et al., 2010; Horoszowski-Fridman et al., 2015), (2) sexual propagation via assisted larval fertilization and dispersal (Randall et al., 2020; Banaszak et al., 2023), and (3) herbivore stocking, although there is growing interest in leveraging other coral reef organisms, such as sponges (Biggs 2013) and microbes (Peixoto et al., 2017; Rosado et al., 2019), to support restoration. Physical habitat control methods have seen

increases in the use of artificial reefs and substrate stabilization (Higgins et al., 2022), though remain underused. Environmental factors (temperature, dissolved oxygen, alkalinity, water flow, PAR) are known to impact calcification rates, fish abundances, and microbial communities, but difficulties in controlling these variables *in situ* have stymied attempts at parametric control.

Table 5.2 Control interventions for manipulating coral reef ecosystems. Controllers are categorized as state control (biological manipulations), parametric control (environmental manipulations), or physical habitat control (substrate manipulations). Interventions are given for each controller type according to examples from the literature, including conceptual models and applied research. The controllability of each intervention, i.e., feasibility of the controller type to be manipulated, is compared between a natural reef and on Coral Arks (controllers that are currently being tested are highlighted in blue). The state factors impacted are listed as expected for each control intervention.

Control type	Intervention type	Controllability		State factors impacted	Examples
		Reef	Ark		
State control	Herbivore stocking (i.e., parrotfish, *Diadema*)	Low	High	calcification aesthetic score VMR chem diversity	Bellwood et al. 2004; Hughes et al. 2007; Maciá et al. 2007; Abelson et al. 2016; Obolski et al. 2016; Neilson et al. 2018; Shantz et al. 2020; Cortés-Useche et al. 2021; Manuel et al. 2021
	Sexual propagation (assisted larval fertilization & recruitment)	High	High	calcification aesthetic score	Nakamura et al. 2011; Chamberland et al. 2017; Cruz and Harrison 2017; Randall et al. 2020; Sellares-Blasco et al. 2021; Banaszak et al. 2023
	Assisted adaptation & evolution	Low	Med	calcification aesthetic score biodiversity	van Oppen et al. 2015; Levin et al. 2017; Chan et al. 2018; Baums et al. 2019; Humanes et al. 2021; Quigley et al. 2021; Voolstra et al. 2021
	Managed relocation & assisted gene flow	Low	High	aesthetic score biodiversity	Hoegh-Guldberg et al. 2008; Aitken and Whitlock 2013; van Oppen et al. 2017
	Asexual propagation (coral gardening, direct transplantation, & micro-fragmentation)	Med	High	Calcification fish biomass aesthetic score biodiversity	Rinkevich 2005, 2019, 2021; Lirman et al. 2010; Horoszowski-Fridman et al. 2015; Lirman & Schopmeyer 2016; Page et al. 2018; Knapp et al. 2022

Table 5.2. Control interventions for manipulating coral reef ecosystems (Continued).

Control type	Intervention type	Controllability		State factors impacted	Examples
		Reef	Ark		
State control	Trophic control (predator addition or removal)	Med	High	fish biomass biodiversity	Rivera-Posada et al. 2013; Williams et al. 2014; Ladd et al. 2016; Delgado and Sharp 2020; Fletcher et al. 2020; Plagányi et al. 2020; Kroon et al. 2021
	Microbiome engineering/ transfer	Low	High	Calcification VMR biodiversity	Peixoto et al. 2017; Epstein et al. 2019; Rosado et al. 2019; Santoro et al. 2021; Voolstra et al. 2021
	Fish biomass enhancement (fisheries management)	Low	Med	fish biomass aesthetic score biodiversity	Bellwood et al. 2004; Pikitch et al. 2004; Cox et al. 2013; Mcclanahan et al. 2015; Bozec et al. 2016; Muallil et al. 2019
	Cryptobenthic translocation (water filtering, nutrient remineralization, zooplankton)	Low	High	Calcification fish biomass biodiversity VMR chem. diversity	Shafir et al. 2006; Cabaitan et al. 2008; Enochs 2012; Biggs 2013; Champion et al. 2015; Wee et al. 2019; Ladd and Shantz 2020
	Larval recruitment using acoustic enrichment (sound) and light (light traps)	Med	High	Calcification fish biomass biodiversity	Simpson et al. 2004; Vermeij et al. 2010; Alldredge et al. 2013; Lillis et al. 2015; Gordon et al. 2019; McAfee et al. 2023
Parametric control	Reoxygenation of hypoxic zones (mechanical mixing, pumping, bubbling)	Low	Med	Calcification VMR biodiversity	Stigebrandt and Gustafsson 2007; Conley et al. 2009; Visser et al. 2016; Liu et al. 2020
	Artificial upwelling (temperature mitigation)	Low	High	Calcification biodiversity	Pan et al. 2016; Feng et al. 2020; Sawall et al. 2020; Zhang et al. 2022

Table 5.2. Control interventions for manipulating coral reef ecosystems (Continued).

Control type	Intervention type	Controllability		State factors impacted	Examples
		Reef	Ark		
Parametric control	Organic matter mitigation (reduce pollution & sedimentation)	Med - High	High	Calcification Chem diversity Biodiversity VMR	Diaz and Rosenberg 2008; Kemp et al. 2009; Jiao et al. 2011; DeMartini et al. 2013; Shelton III and Richmond 2016; Suárez-Castro et al. 2021
	Alkalinity enhancement	Low	High	Calcification aesthetic score	Albright et al. 2016; Feng et al. 2016; Renforth and Henderson 2017; Mongin et al. 2021; Zhang et al. 2022
	Flow enhancement	Low	Med	Calcification fish biomass aesthetic score	Comeau et al. 2014; Baer et al. 2023
Physical habitat control	Artificial reefs	Med	High	fish biomass aesthetic score biodiversity	Shafir et al. 2006; Amar and Rinkevich 2007; Reguero et al. 2018; Brathwaite et al. 2022; Higgins et al. 2022
	Fish aggregating devices (FADs)	Med	High	fish biomass biodiversity	Buckley et al. 1989; Bell et al. 2013, 2015; Albert et al. 2014

Table 5.2. Control interventions for manipulating coral reef ecosystems (Continued).

Control type	Intervention type	Controllability		State factors impacted	Examples
		Reef	Ark		
Physical habitat control	Engineering of new materials, geometries, & 3D printing	Low	High	Calcification fish biomass biodiversity aesthetic score chem. Diversity	Chamberland et al. 2017; Levenstein et al. 2021; Leonard et al. 2022; Levy et al. 2022; Berman et al. 2023
	Substrate stabilization & manipulation	Low	High	Calcification fish biomass biodiversity aesthetic score	Fox et al. 2005, 2019; Williams et al. 2019; Yanovski and Abelson 2019; Ceccarelli et al. 2020; Jayanthi et al. 2020
	Substrate enhancement (electrolysis)	Low	High	Calcification fish biomass biodiversity aesthetic score	Goreau and Prong 2017; Hein et al. 2020

A control framework for ecosystem restoration uses ecosystem services to define key state factors, sets measurable goals through set points, and uses controllers to iteratively perturb a system until reaching the set point (Figure 5.2). These approaches have been successful at managing crop, tree stand, and fish yields through tightly calibrated control inputs (Shea and Possingham 2000; Meza and Bhaya 2010; Ding et al., 2018) but have not yet been applied to coral reefs. Making a coral restoration control framework practicable in the field requires (1) identifying controllers which have the highest impact on the state factors, (2) characterizing the relationships between controllers and state factors, and (3) using these relationships to build a reef-specific intervention strategy. Bridging theory and practice requires *in situ*, experimental tools on which to test the controllers, characterize relationships between controllers and the

state factors, and reduce environmental noise and sampling difficulties. Coral Reef Arks, an *in situ* coral reef mesocosm, provide an experimental platform that meets these needs and a tool to develop an operable control strategy for reef restoration.

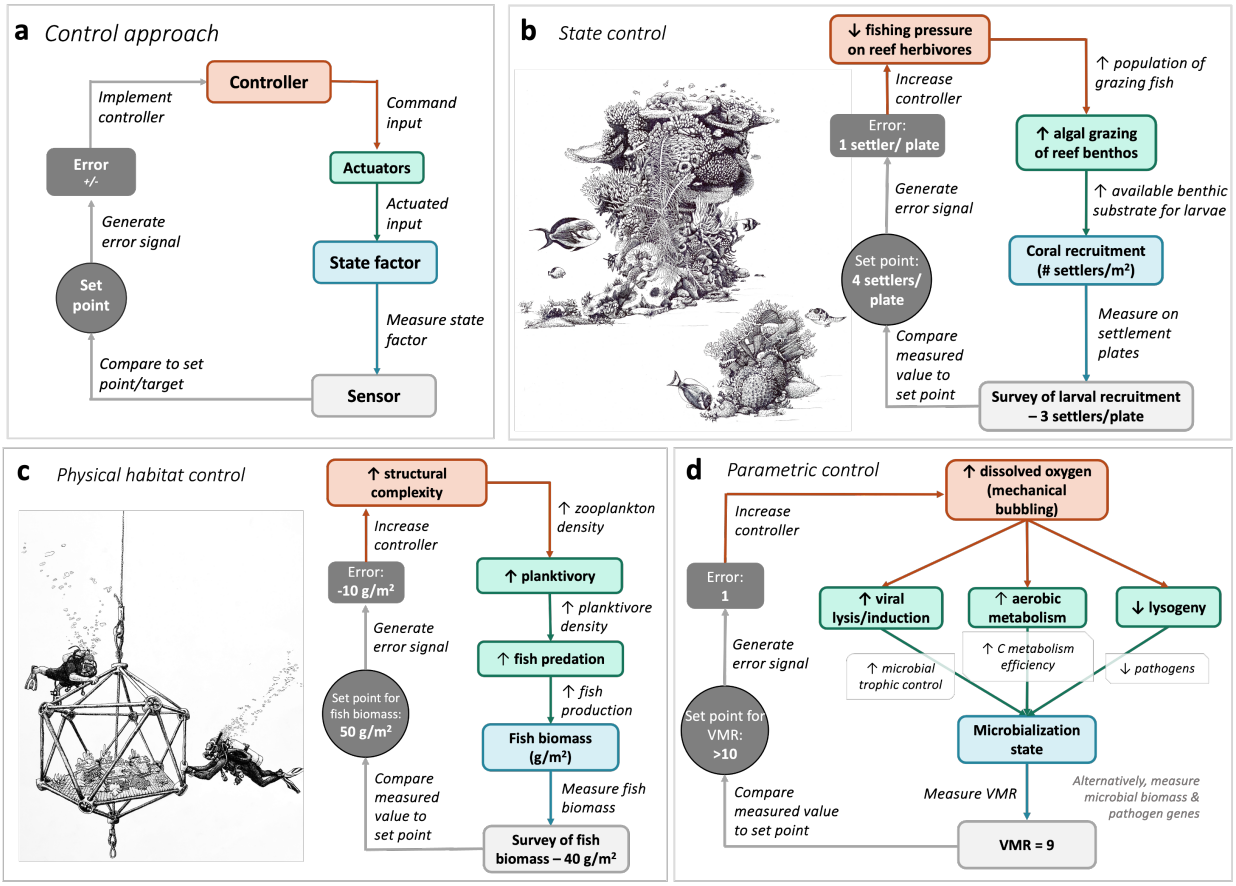


Figure 5.2 (A) Control approach to coral restoration. An intervention is applied using a controller, which acts on the state factor via an actuator. A sensor is used to measure the state factor and an error signal is generated by comparing the measured value of the state factor to its set point. The error signal is used to determine the scale at which to reapply the controller to push the state factor towards the set point. (B) An example using state control. Control is applied by decreasing fishing pressure on reef herbivores, which acts to enhance coral recruitment to the benthos (increased herbivory frees up available benthic space). Recruitment rates are assessed using settlement plates (3 settlers/plate), compared to the set point (4 settlers/plate), and the error signal (1 settler/plate) indicates the controller (decreasing fishing pressure on herbivores) should be applied again. (C) An example of physical habitat control. Control is applied by increasing structural complexity, which acts to enhance fish biomass (this schema has two actuators working in series: demersal zooplankton recruiting to the structure feed planktivores, which then enhance fish production). Fish biomass is assessed via surveys (40 g/m^2), compared to the set point (50 g/m^2), and the error signal (-10 g/m^2) indicates structural complexity should be further enhanced. (C) An example of parametric control. Control is applied by increasing nighttime dissolved oxygen via mechanical bubbling, which acts on the microbialization state of the system (this schema has three actuators working in parallel: increased viral lysis controls microbes, decreased lysogeny reduces pathogens, and efficient carbon metabolism strategies reduce microbial biomass). Microbialization state is assessed via VMR (9), compared to the set point (10), and the error signal (1) indicates that dissolved oxygen should be further enhanced.

CORAL REEF ARKS: LINKING THEORY TO PRACTICE

Coral Reef Arks (hereafter “Arks”) are positively buoyant, midwater structures tethered to the seafloor which naturally recruit and assemble reef communities (Baer et al., 2023). High modularity in shape, size, and siting of the structures combined with their isolation from the benthos make controlling and measuring Arks much easier than natural coral reefs. Arks optimize control strategies for restoring coral reefs by allowing managers to (1) identify the most effective controllers, (2) determine relationships between controllers and key state variables, and (3) test a site-specific control strategy that can be replicated for statistical power, allow for the use of state controls, parametric controls, and physical habitat controls, and be practicably scaled to a natural reef.

Identify high impact controllers

Arks can be vertically adjusted in the water column, physically altered, and biologically seeded, meaning variables that cannot be easily regulated on natural reefs can be controlled relatively easily on Arks. This modularity unlocks many other potential control interventions that go untested in restoration (summarized in Table 5.2). Arks thus provide highly controllable platforms to test new methods of state, parametric, and physical habitat control on the state factors, including emerging conceptual interventions such as reoxygenation of hypoxic zones (Stigebrandt and Gustafsson 2007; Conley et al., 2009) and mitigation of temperature stress (Sawall et al., 2020). The goal of these tests is to identify interventions that push one or more state factors in the direction of their set points, with *high impact controllers* becoming candidates for intervening at the reef scale. Table 5.2 shows interventions that are currently being implemented on Arks (colored in blue) and the state factors these interventions are expected to influence.

Mathematical relationships between high impact controllers identified on Arks and the state factors are then defined to determine how to implement the controller to achieve the desired ecological response.

Define the relationship between controllers and state factors

Predictably altering a state factor is the goal of any control strategy, which requires a mathematical relationship that describes how a state factor will respond to changes in the controller (Heinimann 2010). This information gives practitioners the ability to appropriately “dial” a controller (e.g., the number of urchins translocated to a reef) in order to achieve a desired response (e.g., an amount of grazed reef substrate). This relationship is determined by testing the controller at varying intensities, measuring the response of the state factor, and producing an equation that describes their relationship (Scheffer and Carpenter 2003). Determining these relationships is challenging to accomplish on natural reefs, in which noisy boundary layers and constantly fluctuating gradients of nutrients, dissolved oxygen, organic carbon, alkalinity, and other parameters (Candy et al., 2023; Nelson et al., 2023) prevent tight regulation of the controllers and reliable measurements of the state factors. By elevating a reef community out of the reef boundary layer, Arks reduce environmental noise and increase the stability of the measurements (Baer et al., 2023), providing an observable and isolated platform on which to identify maximally effective controllers. These controllers are used to iteratively perturb an Arks community, measuring the state factors after each perturbation, until the set point is reached (Figure 5.2). The resulting relationship is used to determine the duration, intensity, and scale at which to implement the controller to achieve the desired ecological effect (Heinimann 2010). Because many

relationships between variables in ecosystems are non-linear (i.e., temperature and coral calcification rate) or interdependent (i.e., temperature and oxygen), quantifying them with Arks is particularly useful to refine and calibrate control interventions before implementing them at the reef scale.

The following perturbations were conducted on Arks communities deployed at Caribbean reef sites in Curaçao and Puerto Rico (Figure 5.3). In each case, the response of the state factors was measured and compared to a set point (Table 5.1).

Perturbation 1 (coral translocation; *state control*): A cohort of corals (n = 100) were translocated to each of two Arks deployed offshore of Isla Vieques, Puerto Rico to evaluate the effect of coral translocation on the state factor of calcification rate (Figure 5.3c). Over 6 months, total living coral surface area increased from 2000 cm^2 to 5000 cm^2. The buoyant weight of the Arks, measured using a strain gauge as tension on the mooring line (Baer et al., 2023), increased by an average of 17 kg over 6 months. Normalized to surface area on the Arks, this indicates an estimated calcification rate of 690 g/m^2/year, exceeding the set point (Figure 5.3c).

Perturbation 2 (cryptic biota translocation; *state control*): The two Arks deployed offshore of Vieques were seeded with native cryptic reef biodiversity to evaluate the effect of cryptic organisms on the state factor of fish biomass (Figure 5.3d). Autonomous Reef Monitoring Structures (ARMS), a marine biodiversity census tool (Plaisance et al., 2011a; Pearman et al., 2018), were deployed on natural reefs offshore of Vieques and passively recruited reef cryptobiota (including sponges, bryozoans, bivalves, worms, and small mobile invertebrates) for one year. The ARMS were then netted and translocated to each of two midwater Arks (n=10 per Ark) to seed Arks

communities with native reef cryptobiota. Following the addition of the ARMS to Arks, the abundance of invertivorous and planktivorous fish resident on Arks increased significantly (Figure 5.3d), with corresponding increases in fish biomass that exceeded the set point (data not shown). This suggests the establishment of a trophic network through the addition of mobile invertebrates and zooplankton (Figure 5.3d).

Perturbation 3 (water quality enhancement; *parametric control*): Two Arks deployed offshore of the southern Caribbean island of Curaçao were vertically adjusted in the water column to evaluate the effect of water quality on the state factor of virus-to-microbe ratio (VMR, Figure 5.3a). Both Arks were installed less than 2 m above a degraded reef benthos at 20 m depth. Measurements of dissolved organic carbon (DOC) concentrations, dissolved oxygen (DO), flow speeds, and VMR collected on the Arks (20 m depth) did not differ significantly from the neighboring reef. The Arks were then moved vertically to a final depth of 10 m. Following relocation, measurements of DOC, DO, flow speeds, and VMR significantly differed from the neighboring reef (10 m depth), with VMR increasing to meet the set point (Figure 5.3a) as described above (Table 5.1).

Perturbation 4 (geometry manipulation; *physical habitat control*): The internal geometry of two Arks deployed offshore of Curacao were modified to evaluate the effect of habitat geometry on the state factor of fish biomass (Figure 5.3b). On one Ark, two fiberglass platforms were added to horizontally bisect the structure, providing a habitat with overhead cover. On the other Ark, a column made from stacked limestone plates was installed vertically from the Ark bottom to the apex, providing a habitat with no overhead cover. Measurements of fish biomass collected on the Arks and compared

to the neighboring reef show a strong fish preference for the Ark with overhead cover, exceeding the set point for fish biomass (Figure 5.3b).

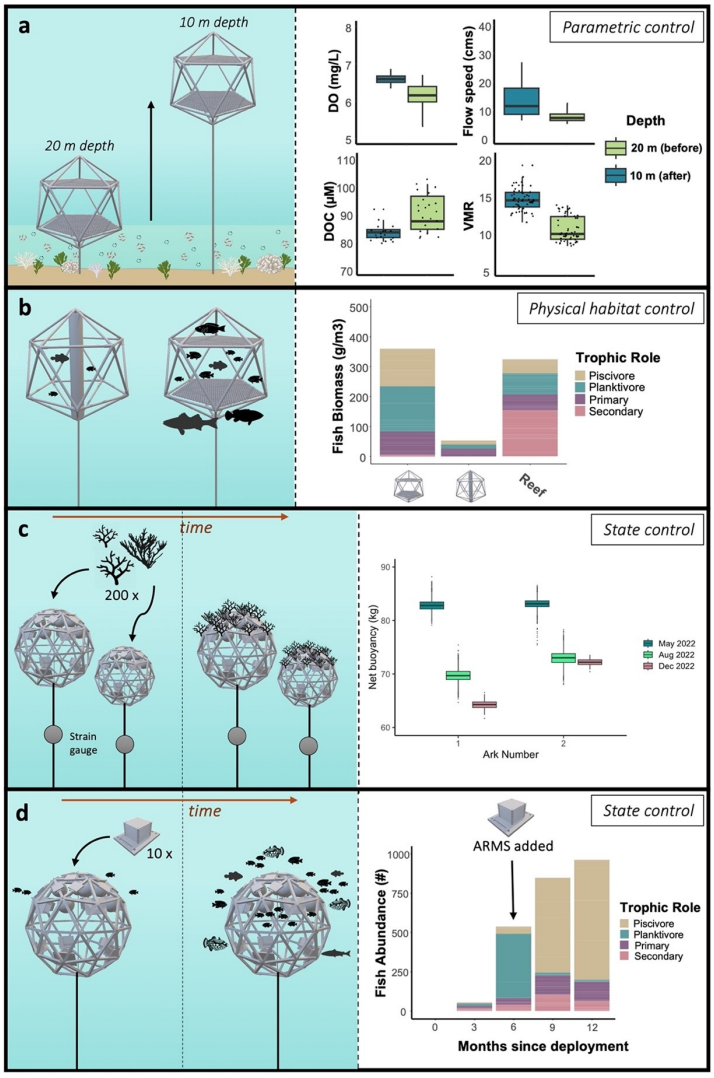


Figure 5.3 Four control interventions were applied to Coral Arks. A) (left panel) Coral Arks were vertically relocated from 20 m depth to 10 m depth. (right panel) Boxplots showing dissolved oxygen (mg/L, top left), current speed (cms, top right), DOC (μM, bottom left), and virus-to-microbe ratio (VMR, bottom right) measured on the Arks before and after vertical relocation. B) (left panel) Two different designs of Coral Arks were deployed side by side, with one Ark containing overhead cover via two platforms, and the other containing roughly the same amount of substrate, but without overhead cover. (right panel) Stacked bar charts showing fish biomass (g/m^3) on each Ark, with each fish classified into one of four broad trophic guilds - planktivores, primary consumers/herbivores, secondary consumers/omnivores, and piscivores. Data was also collected on a nearby reef plot. C) (left panel) Two Coral Arks were each seeded with 200 living coral fragments. (right panel) Measurements of the in-water weight of Coral Arks were collected via a strain gauge in May, August, and December 2022. The boxplots show the net buoyancy of the Arks structures at each time point, with a decrease in net buoyancy indicating a calcifying system that is increasing in weight. D) (left panel) 10 ARMS units seeded on a nearby natural reef were transferred to each of two Coral Arks to seed the structures with native reef biodiversity. (right panel) Stacked bar charts showing fish abundance (#) on the Coral Arks for the first year of deployment. Seeded ARMS were added to the Arks at 6 months post deployment. Note the increase in secondary consumers and piscivores at the 9-month time point.

Build site specific control strategy

A successful reef restoration strategy has predictable outcomes, which requires local knowledge of a reef's state to determine in what form and to what extent to intervene to reinstate ecosystem services. The coral restoration field has focused its efforts on propagating and outplanting coral fragments, but deteriorated reef state often results in low rates of transplant survival, growth, and fecundity (Rogers et al. 2015; Boström-Einarsson et al. 2020, Boisvert et al 2024). To address this, Coral Arks – mesocosms that reflect their surrounding environment – can be used to quickly select interventions tailored to a specific site and evaluate scalability to the neighboring reef. Importantly, Arks are not critical to the use of a control approach to restoration. Past and ongoing restoration projects are examples of experiments testing a controller at a specific scale, and the data from these projects contains useful information about site-specific responses to control inputs. These datasets can be used to extract mathematical relationships between variables using modeling and machine learning tools such as SINDy (Sparse Identification of Nonlinear Dynamics), which are designed to discover the underlying governing equations of a dynamical system from observational (time series) data (Brunton et al. 2016; Kaheman et al. 2020). SINDy and similar tools are particularly useful when dealing with systems such as coral reefs, where the underlying governing equations are unknown or difficult to formulate analytically (Champion 2019). The equations generated can then be used as a starting point to predict the magnitude of the control intervention required to create the desired effect on the state factor at the reef scale, and incorporated into restoration plans accordingly. Known relationships between variables on coral reefs, many of which have

been modeled (Figure 5.4), can also be leveraged using machine learning tools to better inform restoration interventions.

TOWARDS ECOSYSTEM LEVEL CONTROL

Coral reef scientists and restoration practitioners are becoming increasingly aware of the need for solutions to address coral reef degradation, the dire impacts of which now threaten the health and livelihoods of approximately one billion people (Burke et al., 2011). While most implemented interventions have been limited to corals, more extreme concepts, as of yet not implemented, have been proposed. These interventions include bio- and geoengineering reefs (Crabbe 2009; Feng et al., 2020; Nguyen et al., 2023; Sovacool et al., 2023), moving functional groups of corals and fish between oceans and hemispheres (Bradbury and Seymour 2009), and transforming degraded reefs into pseudo-reefs that capture only some reef functions, but nonetheless remain useful in the human-reef integrated system. The discussions these ideas stimulate should push the coral restoration field, which is both time- and resource-limited, to strongly consider whether their finite resources are being used most efficiently and to explore which interventions maximize ecosystem benefits.

Our control theory framework for coral reef restoration sets explicit goals for reinstating ecosystem services and uses an *in situ* mesocosm system to develop actionable methods for achieving these goals. The Arks technology offers a platform for manipulative experiments to narrow down the list of potential interventions to a few, maximally effective control strategies before scaling these strategies to a natural coral reef. While a control theory approach is important for identifying options supported by data from nature, a decision framework can also be used in parallel to compare

intervention choices in the broader socio-economic landscape, including human benefits (beyond ecosystem services), equity, financing, and more. Decision theory dictates how to solve complex problems and only recently has been applied to environmental conservation (Hemming et al. 2022). Decision frameworks apply a stepwise approach to define issues, determine the outcomes sought, identify key performance measures that inform those outcomes, consider interventions to address the issues, estimate the risks and tradeoffs of each intervention, choose and implement an intervention or set of interventions, and then monitor and learn (Hemming et al. 2021). Control theory can be embedded throughout a decision framework, particularly in identifying key performance measures, considering interventions, and estimating the risks and tradeoffs of each intervention. In this way, a decision framework can help ensure the success of applying control theory to coral reefs by accounting for variables beyond the natural environment.

Practically applying a control framework to ecosystems runs into three addressable challenges: (1) time lags, (2) controllability, and (3) non-linear variable relationships (Loehle 2006; Heinimann 2010; Ding et al., 2018). Similar control frameworks applied to terrestrial ecosystem restoration and resource management have been successful even when faced with these challenges (Loehle 2006; Heinimann 2010; Ding et al., 2018), and practical applications of control theory to coral reefs can surmount them in similar ways.

Time lags

The ability to rapidly measure key state factors and continually calibrate control inputs accordingly is essential to adaptive control. However, delays in time between implementing the controller and measuring a response in the state factors, known as

time lags, make it hard to adapt control inputs over short timescales. Changes to the state factors of fish biomass, biodiversity, and aesthetics will take time to measure following perturbations and are subject to hysteresis effects (i.e., historical system states and preceding perturbations), which may demand much higher control inputs than predicted by mathematical relationships to achieve the desired response (Scheffer and Carpenter 2003; Bellwood et al., 2004; Norström et al., 2009). However, time lags are common in all ecological applications of control, and models developed in fisheries management which successfully incorporate time lags and hysteresis (Meza and Bhaya 2010) can be similarly adapted for reefs. Further, new developments in sensor technologies, such as 3D photogrammetry (Burns et al., 2015), real-time DNA sequencing (Carradec et al., 2020; Chang et al., 2020), underwater multi- and hyperspectral imagery (Mills et al., 2023), stereo video (Wilson et al., 2018), and machine learning algorithms for classification (Kennedy et al., 2021) have significantly reduced the cost and labor required to generate high resolution measurements of the state factors, which can now be conducted in nearly real-time. Applying these technologies to restoration monitoring plans will enable practitioners to better understand the ecological outcomes of their interventions and adaptively adjust inputs as needed. Practitioners may also select state factors with less inherent time delays, such as microbial community composition (Glasl et al., 2019), metabolic balance (Takeshita et al., 2016), benthic cover (Kennedy et al., 2021), and acoustics (Freeman et al., 2018; Gordon et al., 2018) if these metrics align with restoration goals.

Controllability and Coral Arks

Unlike terrestrial systems, controllability of coral reefs is quite low, limiting our ability to purposefully influence the systems at scale. Here, we propose the highly controllable Coral Arks as a tool to identify control inputs with a disproportionately large impact on the state factors. Arks are modular, reasonably low cost (<$2000), and can support local restoration efforts by serving as coral nurseries, spawning systems, refuges for biodiversity, and testing platforms for emerging biological and geoengineering interventions. Using several perturbations on Arks, we demonstrate that the proposed state factors can be measurably pushed towards their set points (Figure 5.3). Less clear from these experiments is exactly which control variable is responsible for the changes to the state factors – thus, while controllability was achieved, *precision* control was not. Vertically moving the Arks to a shallower depth (Figure 5.3a) influenced the state factor of VMR and resulted in changes in dissolved oxygen, dissolved organic carbon (DOC), light intensity, flow speed, and likely several unmeasured variables. Similarly, the enhancements in fish biomass generated by seeding Arks with cryptic biodiversity using ARMS units (Figure 5.3d) may be due to the organisms living within the units themselves (i.e., zooplankton and mobile invertebrates), or to changes in Ark biogeochemistry and trophic interactions resulting from the addition of the ARMS.

Fully elucidating these variable relationships would require isolating controllers in successive, iterative perturbations/experiments to determine the impact of each control input on each reef variable. However, conducting so many isolated experiments would be unrealistic and impractical. Control approaches are designed to consider the behavior of the entire system rather than its individual components and thus do not require such specificity. The control framework treats the state factors as integrated

signals representing multiple biophysical characteristics of the system – for example, the aesthetic score encodes information about reef structural complexity, benthic cover, and color (Haas et al., 2015), while VMR describes microbial community stability and extent of trophic control of viruses on microbes (Knowles et al., 2016a; Silveira et al., 2023). By integrating multiple reef variables into a single state factor, fewer variable relationships have to be experimentally determined. Controllers identified using Arks which can maximally impact the state factors will direct the design of biological and geoengineering solutions, similar to those proposed in climate change mitigation (Kleypas et al., 2021), needed to bring restoration interventions to the reef scale. Some of these, including assisted evolution (van Oppen et al., 2015), microbiome transfer (Voolstra et al., 2021), artificial upwelling (Sawall et al., 2020), and alkalinity enhancement (Mongin et al., 2021) are already underway.

Non-linear variable relationships

Coral reefs are highly complex systems, and knowledge of the variables and relationships governing these ecosystems is incomplete. Mathematical relationships between variables are essential to a control strategy because they dictate how to apply a controller, but these relationships are not well characterized in marine systems. Experimentally determining them is challenging because many variable relationships on reefs are non-linear (changes to the input do not result in a proportional change in the output) and interdependent (changes in a single variable can alter other variables, leading to off-target effects). Arks can help determine these relationships by experimentally isolating and tightly controlling reef variables. However, much of the necessary data can be gathered from existing coral restoration projects and analyzed in

tools like SINDy to develop predictive models without any prior knowledge of the system's dynamics. Similarly, the effort to characterize variable relationships on coral reefs has been ongoing for decades through reductionist experiments and modelling (Figure 5.4, Weijerman et al., 2015). Synthesizing data extracted from these experiments and models into novel, predictive control models should be a primary focus of coral reef science in order to better support the ecosystem-based management sector and restoration practitioners (Figure 5.4).

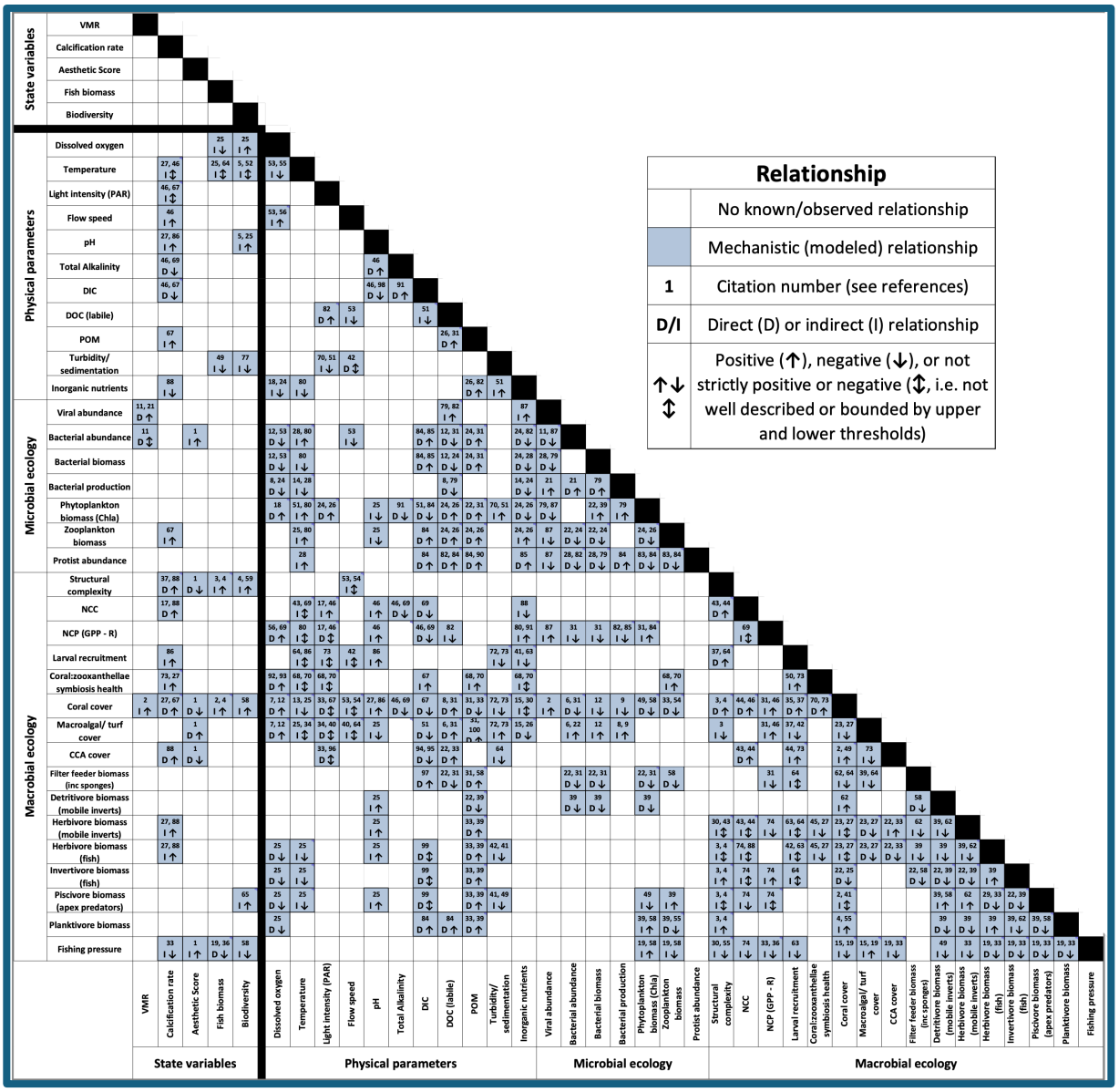


Figure 5.4 Variable relationships extracted from coral reef models (citations in Appendix 2). The variables selected on the horizontal and vertical axes were the most commonly modeled variables in coral reef models. Blue-colored boxes represent a mechanistic (i.e., modeled) relationship found between two variables. Numbers represent the citation number. “D” or “I” represent a direct or indirect relationship, with direct relationships defined as consumption/predation or production/release, and indirect relationships assumed to be made up of a number of direct relationships. When both direct and indirect relationships exist for a variable pair, their direct relationship is shown here. Arrows indicate directionality of relationship, with upward-facing arrows indicating a positive relationship (production/release/facilitation) and downward-facing arrows indicating a negative relationship (consumption/predation/antagonism). Double-sided arrows indicate relationships that have been found to be both positive or negative, or are bounded by upper and lower thresholds.

CONCLUSIONS

We have proposed a novel framework for active coral reef restoration based in control theory, which sets explicit goals for reinstating ecosystem services and uses an *in situ* mesocosm system to identify effective control strategies and appropriately scale these strategies to a coral reef. This framework does not propose specific interventions for restoring reefs, but instead provides a road map for designing goal-oriented restoration practices that can be adapted to meet local needs. Climate change and ecosystem degradation make coral restoration goals a moving target, and scientists are urging reef managers to shift their goals from what is desirable, such as protecting species and restoring ecosystems to historic baselines, to what is possible, such as engineering reefs to enable richer interaction with humans by enhancing fisheries, tourism, water quality, and reef accretion to protect shorelines (Bradbury and Seymour 2009; Coleman et al., 2020; Rinkevich 2021). Achieving these goals will require collaboration between reef restoration scientists and practitioners to synthesize fundamental and applied knowledge of reef function into predictively guided reef interventions. Control theory provides a backbone for dynamically controlling terrestrial ecosystems and, applied to coral reefs, offers a foundation for evidence-based control in reef management that will help chart a new future for coral reefs.

ACKNOWLEDGEMENTS

We thank Heather Maughan, Ryan Hanna, Ty Roach, Will Barnes, Lars ter Horst, Emily Nixon, and Basil Darby for their comments, suggestions, and stimulating discussions in the writing of this manuscript. Chapter 5 in full, is a reprint as it was submitted to the journal Nature Ecology and Evolution. Jason L Baer, Aaron Hartmann, and Forest Rohwer. The dissertation author was the primary investigator and author of this paper.

REFERENCES

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2009.0339

Baer, J. L., Carilli, J., Chadwick, B., Hatay, M., van der Geer, A., Scholten, Y., Barnes, W., Aquino, J., Ballard, A., Little, M., Brzenski, J., Liu, X., Rosen, G., Wang, P. F., Castillo, J., Haas, A. F., Hartmann, A. C., & Rohwer, F. (2023). Coral Reef Arks: An *in situ* mesocosm and toolkit for assembling reef communities. *Journal of Visualized Experiments*, *2023*(191). https://doi.org/10.3791/64778

Banaszak, A. T., Marhaver, K. L., Miller, M. W., Hartmann, A. C., Albright, R., Hagedorn, M., Harrison, P. L., Latijnhouwers, K. R. W., Mendoza Quiroz, S., Pizarro, V., & Chamberland, V. F. (2023). Applying coral breeding to reef restoration: best practices, knowledge gaps, and priority actions in a rapidly-evolving field. *Restoration Ecology*, *31*(7). https://doi.org/10.1111/rec.13913

Bates, A. E., Cooke, R. S. C., Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., Côté, I. M., Lefcheck, J. S., Costello, M. J., Barrett, N., Bird, T. J., Fenberg, P. B., & Stuart-Smith, R. D. (2019). Climate resilience in marine protected areas and the 'Protection Paradox.' *Biological Conservation*, *236*(May 2018), 305–314. https://doi.org/10.1016/j.biocon.2019.05.005

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833.

Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. S. (2006). Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1582), 101–107. https://doi.org/10.1098/rspb.2005.3276

Biggs, B. C. (2013). Harnessing natural recovery processes to improve restoration outcomes: an experimental assessment of sponge-mediated coral reef restoration. *PloS One*, *8*(6), e64945.

Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C. A., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D., Stewart-Sinclair, P. J., Vardi, T., & McLeod, I. M. (2020). Coral restoration – A systematic review of current methods, successes, failures and future directions. *PLoS ONE*, *15*(1), 1–24. https://doi.org/10.1371/journal.pone.0226631

Bradbury, R. H., & Seymour, R. M. (2009). Coral reef science and the new commons. *Coral Reefs*, *28*(4), 831–837. https://doi.org/10.1007/s00338-009-0540-6

Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment*, *17*(8), 445–454. https://doi.org/10.1002/fee.2088

Bruno, J. F., Côté, I. M., & Toth, L. T. (2019). Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Annual Review of Marine Science*, *11*, 307–334. https://doi.org/10.1146/annurev-marine-010318-095300

Brunton, S. L., Proctor, J. L., & Kutz, J. N. (2016). Sparse identification of nonlinear dynamics with control (SINDYc). *IFAC-PapersOnLine*, *49*(18), 710–715.

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2011). *Reefs at risk revisited*. Washington, DC: World Resources Institute.

Burns, J. H. R., Delparte, D., Gates, R. D., & Takabayashi, M. (2015). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ*, *3*, e1077.

Candy, A. S., Taylor Parkins, S. K., Van Duyl, F. C., Mueller, B., Arts, M. G. I., Barnes, W., Carstensen, M., Scholten, Y. J. H., El-Khaled, Y. C., Wild, C., Wegley Kelly, L., Nelson, C. E., Sandin, S. A., Vermeij, M. J. A., Rohwer, F. L., Picioreanu, C., Stocchi, P., & Haas, A. F. (2023). Small-scale oxygen distribution patterns in a coral reef. *Frontiers in Marine Science*, *10*(April), 1–13. https://doi.org/10.3389/fmars.2023.1135686

Carradec, Q., Poulain, J., Boissin, E., Hume, B. C. C., Voolstra, C. R., Ziegler, M., Engelen, S., Cruaud, C., Planes, S., & Wincker, P. (2020). A framework for *in situ* molecular characterization of coral holobionts using nanopore sequencing. *Scientific Reports*, *10*(1), 15893.

Champion, K. (2019). *From data to dynamics: discovering governing equations from data*.

Chang, J. J. M., Ip, Y. C. A., Bauman, A. G., & Huang, D. (2020). MinION-in-ARMS: nanopore sequencing to expedite barcoding of specimen-rich macrofaunal samples from autonomous reef monitoring structures. *Frontiers in Marine Science*, *7*, 448.

Coleman, M. A., Wood, G., Filbee-Dexter, K., Minne, A. J. P., Goold, H. D., Vergés, A., Marzinelli, E. M., Steinberg, P. D., & Wernberg, T. (2020). Restore or redefine: Future trajectories for restoration. *Frontiers in Marine Science*, *7*(April 2020), 1–12. https://doi.org/10.3389/fmars.2020.00237

Conley, D. J., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hansson, L. A., Rabalais, N. N., Voss, M., & Zillén, L. (2009). Tackling hypoxia in the Baltic Sea: Is engineering a solution? *Environmental Science and Technology*, *43*(10), 3407–3411. https://doi.org/10.1021/es8027633

Costanza, R., De Groot, R., Sutton, P., Van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., & Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, *26*, 152–158.

Crabbe, M. J. C. (2009). Modelling effects of geoengineering options in response to climate change and global warming: Implications for coral reefs. *Computational Biology and Chemistry*, *33*(6), 415–420.

Davis, K. L., Colefax, A. P., Tucker, J. P., Kelaher, B. P., & Santos, I. R. (2021). Global coral reef ecosystems exhibit declining calcification and increasing primary productivity. *Communications Earth & Environment*, *2*(1), 105.

Díaz-Pérez, L., Rodríguez-Zaragoza, F. A., Ortiz, M., Cupul-Magaña, A. L., Carriquiry, J. D., Ríos-Jara, E., Rodríguez-Troncoso, A. P., & Del Carmen García-Rivas, M. (2016). Coral reef health indices versus the biological, ecological and functional diversity of fish and coral assemblages in the Caribbean sea. *PLoS ONE*, *11*(8), 1–19. https://doi.org/10.1371/journal.pone.0161812

Ding, Y., Wang, L., Li, Y., & Li, D. (2018). Model predictive control and its application in agriculture: A review. *Computers and Electronics in Agriculture*, *151*(June), 104–117. https://doi.org/10.1016/j.compag.2018.06.004

Duffy, J. E. (2019). Reefs need richness. *Nature Ecology & Evolution*, *3*(2), 149–150.
Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, *4*(9), 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016

Edwards, C. B., Friedlander, A. M., Green, A. G., Hardt, M. J., Sala, E., Sweatman, H. P., Williams, I. D., Zgliczynski, B., Sandin, S. A., & Smith, J. E. (2014). Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 20131835.

Estes, J. A., & Palmisano, J. F. (1974). Sea otters: their role in structuring nearshore communities. *Science*, *185*(4156), 1058–1060.

Estrada-Saldívar, N., Jordán-Dalhgren, E., Rodríguez-Martínez, R. E., Perry, C., & Alvarez-Filip, L. (2019). Functional consequences of the long-term decline of reef-building corals in the Caribbean: evidence of across-reef functional convergence. *Royal Society Open Science*, *6*(10), 190298.

Farnum, P. (2001). Precision forestry—finding the context. *First International Precision Forestry Cooperative Symposium, Institute of Forest Resources. College of Forest Resources. University of Washington, Seattle, WA, Washington*, 3–5.

Feng, E. Y., Sawall, Y., Wall, M., Lebrato, M., & Fu, Y. (2020). Modeling coral bleaching mitigation potential of water vertical translocation–An analogue to geoengineered artificial upwelling. *Frontiers in Marine Science*, *7*, 556192.

Freeman, S. E., Freeman, L. A., Giorli, G., & Haas, A. F. (2018). Photosynthesis by marine algae produces sound, contributing to the daytime soundscape on coral reefs. *PLoS ONE*, *13*(10), 1–14. https://doi.org/10.1371/journal.pone.0201766

Galand, P. E., Ruscheweyh, H. J., Salazar, G., Hochart, C., Henry, N., Hume, B. C. C., Oliveira, P. H., Perdereau, A., Labadie, K., Belser, C., Boissin, E., Romac, S., Poulain, J., Bourdin, G., Iwankow, G., Moulin, C., Armstrong, E. J., Paz-García, D. A., Ziegler, M., … Planes, S. (2023). Diversity of the Pacific Ocean coral reef microbiome. *Nature Communications*, *14*(1), 1–13. https://doi.org/10.1038/s41467-023-38500-x

Glasl, B., Bourne, D. G., Frade, P. R., Thomas, T., Schaffelke, B., & Webster, N. S. (2019). Microbial indicators of environmental perturbations in coral reef ecosystems. *Microbiome*, *7*(1), 1–13. https://doi.org/10.1186/s40168-019-0705-7

Gordon, T. A. C., Harding, H. R., Wong, K. E., Merchant, N. D., Meekan, M. G., McCormick, M. I., Radford, A. N., & Simpson, S. D. (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(20), 5193–5198. https://doi.org/10.1073/pnas.1719291115

Grafeld, S., Oleson, K., Barnes, M., Peng, M., Chan, C., & Weijerman, M. (2016). Divers' willingness to pay for improved coral reef conditions in Guam: An untapped source of funding for management and conservation? *Ecological Economics*, *128*, 202–213. https://doi.org/10.1016/j.ecolecon.2016.05.005

Graham, N. A. J., Ainsworth, T. D., Baird, A. H., Ban, N. C., Bay, L. K., Cinner, J. E., De Freitas, D. M., Diaz-Pulido, G., Dornelas, M., Dunn, S. R., Fidelman, P. I. J., Foret, S., Good, T. C., Kool, J., Mallela, J., Penin, L., Pratchett, M. S., & Williamson, D. H. (2011). From microbes to people: Tractable benefits of no-take areas for coral reefs. *Oceanography and Marine Biology*, *49*, 105–135.

Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y. W., Maughan, H., Pantos, O., Roach, T. N. F., Sanchez, S. E., Silveira, C. B., Sandin, S., Smith, J. E., & Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2016.42

Haas, A. F., Guibert, M., Foerschner, A., Calhoun, S., George, E., Hatay, M., Dinsdale, E., Sandin, S. A., Smith, J. E., & Vermeij, M. J. A. (2015). Can we measure beauty? Computational evaluation of coral reef aesthetics. *PeerJ*, *3*, e1390.

Hartmann, A. C., Petras, D., Quinn, R. A., Protsyuk, I., Archer, F. I., Ransome, E., Williams, G. J., Bailey, B. A., Vermeij, M. J. A., Alexandrov, T., Dorrestein, P. C., & Rohwer, F. L. (2017). Meta-mass shift chemical profiling of metabolomes from coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1710248114

Hatcher, B. G. (1997). Coral reef ecosystems: How much greater is the whole than the sum of the parts? *Coral Reefs*. https://doi.org/10.1007/s003380050244

Hein, M., Banaszack, A., Dallison, T., Deri, W., Grimsditch, G., Jacob, F., Loder, J., McLeod, I., Mead, D., & Moore, T. (2021). Mapping the global funding landscape for coral reef restoration.

Hein, M. Y., Beeden, R., Birtles, A., Gardiner, N. M., Le Berre, T., Levy, J., Marshall, N., Scott, C. M., Terry, L., & Willis, B. L. (2020). Coral restoration effectiveness: Multiregional snapshots of the long-term responses of coral assemblages to restoration. *Diversity*, *12*(4), 1–22. https://doi.org/10.3390/D12040153

Hein, M. Y., Vardi, T., Shaver, E. C., Pioch, S., Boström-Einarsson, L., Ahmed, M., Grimsditch, G., & McLeod, I. M. (2021). Perspectives on the use of coral reef restoration as a strategy to support and improve reef ecosystem services. *Frontiers in Marine Science*, *8*(April), 1–13. https://doi.org/10.3389/fmars.2021.618303

Heinimann, H. R. (2010). A concept in adaptive ecosystem management-An engineering perspective. *Forest Ecology and Management*, *259*(4), 848–856. https://doi.org/10.1016/j.foreco.2009.09.032

Hemming, V., Camaclang, A. E., Adams, M. S., Burgman, M., Carbeck, K., Carwardine, J., Chadès, I., Chalifour, L., Converse, S. J., Davidson, L. N. K., Garrard, G. E., Finn, R., Fleri, J. R., Huard, J., Mayfield, H. J., Madden, E. M. D., Naujokaitis-Lewis, I., Possingham, H. P., Rumpff, L., … Martin, T. G. (2022). An introduction to decision science for conservation. *Conservation Biology*, *36*(1), 1–16. https://doi.org/10.1111/cobi.13868

Higgins, E., Metaxas, A., & Scheibling, R. E. (2022). A systematic review of artificial reefs as platforms for coral reef research and conservation. *PLoS ONE*, *17*(1 January), 1–23. https://doi.org/10.1371/journal.pone.0261964

Hill, J. I., & Durham, S. L. (1978). Input, signals, and control in ecosystems. *ICASSP '78. IEEE International Conference on Acoustics, Speech, and Signal Processing*, *3*, 391–397. https://doi.org/10.1109/icassp.1978.1170546

Holland, J. H. (2006). Studying complex adaptive systems. *Journal of Systems Science and Complexity*, *19*(1), 1–8. https://doi.org/10.1007/s11424-006-0001-z

Horoszowski-Fridman, Y. B., Brêthes, J.-C., Rahmani, N., & Rinkevich, B. (2015). Marine silviculture: Incorporating ecosystem engineering properties into reef restoration acts. *Ecological Engineering*, *82*, 201–213.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*. https://doi.org/10.1016/j.cub.2006.12.049

Januchowski-Hartley, F. A., Graham, N. A. J., Wilson, S. K., Jennings, S., & Perry, C. T. (2017). Drivers and predictions of coral reef carbonate budget trajectories. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1847). https://doi.org/10.1098/rspb.2016.2533

Johnson, M. D., Price, N. N., & Smith, J. E. (2022). Calcification accretion units (CAUs): A standardized approach for quantifying recruitment and calcium carbonate accretion in marine habitats. *Methods in Ecology and Evolution*, *13*(7), 1436–1446. https://doi.org/10.1111/2041-210X.13867

Kaheman, K., Kutz, J. N., & Brunton, S. L. (2020). SINDy-PI: a robust algorithm for parallel implicit sparse identification of nonlinear dynamics. *Proceedings of the Royal Society A*, *476*(2242), 20200279.

Kemp, W. M., Testa, J. M., Conley, D. J., Gilbert, D., & Hagy, J. D. (2009). Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences*, *6*(12), 2985–3008.

Kennedy, E. V, Roelfsema, C. M., Lyons, M. B., Kovacs, E. M., Borrego-Acevedo, R., Roe, M., Phinn, S. R., Larsen, K., Murray, N. J., & Yuwono, D. (2021). Reef Cover, a coral reef classification for global habitat mapping from remote sensing. *Scientific Data*, *8*(1), 196.

Kleypas, J., Allemand, D., Anthony, K., Baker, A. C., Beck, M. W., Hale, L. Z., Hilmi, N., Hoegh-Guldberg, O., Hughes, T., Kaufman, L., Kayanne, H., Magnan, A. K., Mcleod, E., Mumby, P., Palumbi, S., Richmond, R. H., Rinkevich, B., Steneck, R. S., Voolstra, C. R., … Gattuso, J. P. (2021). Designing a blueprint for coral reef survival. *Biological Conservation*, *257*, 109107. https://doi.org/10.1016/j.biocon.2021.109107

Knowles, B., Silveira, C. B., Bailey, B. A., Barott, K., Cantu, V. A., Cobian-Guëmes, A. G., Coutinho, F. H., Dinsdale, E. A., Felts, B., Furby, K. A., George, E. E., Green, K. T., Gregoracci, G. B., Haas, A. F., Haggerty, J. M., Hester, E. R., Hisakawa, N., Kelly, L. W., Lim, Y. W., … Rohwer, F. (2016). Lytic to temperate switching of viral communities. *Nature*. https://doi.org/10.1038/nature17193

Ladd, M. C., Burkepile, D. E., & Shantz, A. A. (2019). Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. *Restoration Ecology*, *27*(5), 1166–1176.

Ladd, M. C., & Shantz, A. A. (2020). Trophic interactions in coral reef restoration: A review. *Food Webs*, *24*, e00149. https://doi.org/10.1016/j.fooweb.2020.e00149

Lange, I. D., Perry, C. T., & Alvarez-Filip, L. (2020). Carbonate budgets as indicators of functional reef “health”: A critical review of data underpinning census-based methods and current knowledge gaps. *Ecological Indicators*, *110*, 105857.

Lirman, D., Thyberg, T., Herlan, J., Hill, C., Young-Lahiff, C., Schopmeyer, S., Huntington, B., Santos, R., & Drury, C. (2010). Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs*, *29*(3), 729–735.

Loehle, C. (2006). Control theory and the management of ecosystems. *Journal of Applied Ecology*, *43*(5), 957–966. https://doi.org/10.1111/j.1365-2664.2006.01208.x

Marshall, N., Marshall, P., Curnock, M., Pert, P., Smith, A., & Visperas, B. (2019). Identifying indicators of aesthetics in the Great Barrier Reef for the purposes of management. *PLoS One*, *14*(2), e0210196.

Meza, M. E. M., & Bhaya, A. (2010). Control theory and the management of ecosystems: A threshold policy with hysteresis is robust. *Applied Mathematics and Computation*, *216*(11), 3133–3145. https://doi.org/10.1016/j.amc.2010.04.015

Mills, M. S., Ungermann, M., Rigot, G., den Haan, J., Leon, J. X., & Schils, T. (2023). Assessment of the utility of underwater hyperspectral imaging for surveying and monitoring coral reef ecosystems. *Scientific Reports*, *13*(1), 21103.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2), 215–233.

Mongin, M., Baird, M. E., Lenton, A., Neill, C., & Akl, J. (2021). Reversing ocean acidification along the Great Barrier Reef using alkalinity injection. *Environmental Research Letters*, *16*(6), 64068.

Mouillot, D., Parravicini, V., Bellwood, D. R., Leprieur, F., Huang, D., Cowman, P. F., Albouy, C., Hughes, T. P., Thuiller, W., & Guilhaumon, F. (2016). Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. *Nature Communications*, *7*(May 2015). https://doi.org/10.1038/ncomms10359

Nelson, C. E., Wegley Kelly, L., & Haas, A. F. (2023). Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. *Annual Review of Marine Science*, *15*, 431–460. https://doi.org/10.1146/annurev-marine-042121-080917

Newman, M. J. H., Paredes, G. A., Sala, E., & Jackson, J. B. C. (2006). Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters*, *9*(11), 1216–1227.

Nguyen, P. Q., Huang, X., Collins, D. S., Collins, J. J., & Lu, T. (2023). Harnessing synthetic biology to enhance ocean health. *Trends in Biotechnology*, *41*(7), 860–874. https://doi.org/10.1016/j.tibtech.2022.12.015

Nocentini, S., Buttoud, G., Ciancio, O., & Corona, P. (2017). Managing forests in a changing world: The need for a systemic approach. A review. *Forest Systems*, *26*(1), 1–15. https://doi.org/10.5424/fs/2017261-09443

Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series*, *376*(Hatcher 1984), 293–306. https://doi.org/10.3354/meps07815

Pearman, J. K., Leray, M., Villalobos, R., Machida, R. J., Berumen, M. L., Knowlton, N., & Carvalho, S. (2018). Cross-shelf investigation of coral reef cryptic benthic organisms reveals diversity patterns of the hidden majority. *Scientific Reports*. https://doi.org/10.1038/s41598-018-26332-5

Peixoto, R. S., Rosado, P. M., Leite, D. C. de A., Rosado, A. S., & Bourne, D. G. (2017). Beneficial microorganisms for corals (BMC): proposed mechanisms for coral health and resilience. *Frontiers in Microbiology*, *8*, 341.

Plaisance, L., Caley, M. J., Brainard, R. E., & Knowlton, N. (2011a). The diversity of coral reefs: what are we missing? *PLoS One*, *6*(10), e25026.

Price, N. N., Martz, T. R., Brainard, R. E., & Smith, J. E. (2012). Diel variability in seawater pH relates to calcification and benthic community structure on coral reefs.

Randall, C. J., Negri, A. P., Quigley, K. M., Foster, T., Ricardo, G. F., Webster, N. S., Bay, L. K., Harrison, P. L., Babcock, R. C., & Heyward, A. J. (2020). Sexual production of corals for reef restoration in the Anthropocene. *Marine Ecology Progress Series*, *635*, 203–232. https://doi.org/10.3354/MEPS13206

Randi, C. B., Becker, A. C., Willemes, M. J., Perry, C. T., Salgado, L. T., de Carvalho, R. T., Motta, F. S., de Moura, R. L., de Moraes, F. C., & Pereira-Filho, G. H. (2021). Calcium carbonate production in the southernmost subtropical Atlantic coral reef. *Marine Environmental Research*, *172*, 105490.

Ransome, E., Geller, J. B., Timmers, M., Leray, M., Mahardini, A., Sembiring, A., Collins, A. G., & Meyer, C. P. (2017). The importance of standardization for biodiversity comparisons: A case study using autonomous reef monitoring structures (ARMS) and metabarcoding to measure cryptic diversity on Mo'orea coral reefs, French Polynesia. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0175066

Reis, V. M. dos, Karez, C. S., Mariath, R., de Moraes, F. C., de Carvalho, R. T., Brasileiro, P. S., Bahia, R. da G., Lotufo, T. M. da C., Ramalho, L. V., & de Moura, R. L. (2016). Carbonate production by benthic communities on shallow coralgal reefs of Abrolhos Bank, Brazil. *PLoS One*, *11*(4), e0154417.

Rinkevich, B. (2005). Conservation of coral reefs through active restoration measures: recent approaches and last decade progress. *Environmental Science & Technology*, *39*(12), 4333–4342.

Rinkevich, B. (2019). The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. *Journal of Marine Science and Engineering*, *7*(7). https://doi.org/10.3390/jmse7070201

Rinkevich, B. (2021). Ecological engineering approaches in coral reef restoration. *ICES Journal of Marine Science*, *78*(1), 410–420. https://doi.org/10.1093/icesjms/fsaa022

Robinson, J. P. W., Wilson, S. K., Robinson, J., Gerry, C., Lucas, J., Assan, C., Govinden, R., Jennings, S., & Graham, N. A. J. (2019). Productive instability of coral reef fisheries after climate-driven regime shifts. *Nature Ecology and Evolution*, *3*(2), 183–190. https://doi.org/10.1038/s41559-018-0715-z

Rogers, A., Harborne, A. R., Brown, C. J., Bozec, Y. M., Castro, C., Chollett, I., Hock, K., Knowland, C. A., Marshell, A., Ortiz, J. C., Razak, T., Roff, G., Samper-Villarreal, J., Saunders, M. I., Wolff, N. H., & Mumby, P. J. (2015). Anticipative management for coral reef ecosystem services in the 21st century. *Global Change Biology*, *21*(2), 504–514. https://doi.org/10.1111/gcb.12725

Rosado, P. M., Leite, D. C. A., Duarte, G. A. S., Chaloub, R. M., Jospin, G., Nunes da Rocha, U., P. Saraiva, J., Dini-Andreote, F., Eisen, J. A., Bourne, D. G., & Peixoto, R. S. (2019). Marine probiotics: increasing coral resistance to bleaching through microbiome manipulation. *ISME Journal*, *13*(4), 921–936. https://doi.org/10.1038/s41396-018-0323-6

Sandin, S. A., Sampayo, E. M., & Vermeij, M. J. A. (2008). Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles. *Caribbean Journal of Science*. https://doi.org/10.18475/cjos.v44i2.a2

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., Konotchick, T., Malay, M., Maragos, J. E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R. E., Walsh, S., Jackson, J. B. C., Knowlton, N., & Sala, E. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0001548

Sawall, Y., Harris, M., Lebrato, M., Wall, M., & Feng, E. Y. (2020). Discrete pulses of cooler deep water can decelerate coral bleaching during thermal stress: Implications for artificial upwelling during heat stress events. *Frontiers in Marine Science*, *7*, 720.

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology and Evolution*, *18*(12), 648–656. https://doi.org/10.1016/j.tree.2003.09.002

Seraphim, M. J., Sloman, K. A., Alexander, M. E., Janetski, N., Jompa, J., Ambo-Rappe, R., Snellgrove, D., Mars, F., & Harborne, A. R. (2020). Interactions between coral restoration and fish assemblages: implications for reef management. *Journal of Fish Biology*, *97*(3), 633–655. https://doi.org/10.1111/jfb.14440

Setter, R. O., Franklin, E. C., & Mora, C. (2022). Co-occurring anthropogenic stressors reduce the timeframe of environmental viability for the world's coral reefs. *PLoS Biology*, *20*(10), 1–12. https://doi.org/10.1371/journal.pbio.3001821

Shantz, A. A., Ladd, M. C., & Burkepile, D. E. (2020). Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. *Ecological Monographs*, *90*(2), 1–17. https://doi.org/10.1002/ecm.1403

Shaver, E. C., & Silliman, B. R. (2017). Time to cash in on positive interactions for coral restoration. *PeerJ*, *2017*(6). https://doi.org/10.7717/peerj.3499

Shea, K., & Possingham, H. P. (2000). Optimal release strategies for biological control agents: An application of stochastic dynamic programming to population management. *Journal of Applied Ecology*, *37*(1), 77–86. https://doi.org/10.1046/j.1365-2664.2000.00467.x

Silbiger, N. J., Guadayol, Ò., Thomas, F. I. M., & Donahue, M. J. (2014). Reefs shift from net accretion to net erosion along a natural environmental gradient. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps10999

Silveira, C. B., Coutinho, F. H., Cavalcanti, G. S., Benler, S., Doane, M. P., Dinsdale, E. A., Edwards, R. A., Francini-Filho, R. B., Thompson, C. C., Luque, A., Rohwer, F. L., & Thompson, F. (2020). Genomic and ecological attributes of marine bacteriophages encoding bacterial virulence genes. *BMC Genomics*. https://doi.org/10.1186/s12864-020-6523-2

Silveira, C. B., Luque, A., Haas, A. F., Roach, T. N. F., George, E. E., Knowles, B., Little, M., Sullivan, C. J., Varona, N. S., Wegley Kelly, L., Brainard, R., Rohwer, F., & Bailey, B. (2023). Viral predation pressure on coral reefs. *BMC Biology*, *21*(1), 77. https://doi.org/10.1186/s12915-023-01571-9

Silveira, C. B., Luque, A., Roach, T. N., Villela, H., Barno, A., Green, K., Reyes, B., Rubio-Portillo, E., Le, T., Mead, S., Hatay, M., Vermeij, M. J., Takeshita, Y., Haas, A., Bailey, B., & Rohwer, F. (2019). Biophysical and physiological processes causing oxygen loss from coral reefs. *ELife*. https://doi.org/10.7554/eLife.49114

Smith, J. G., Tomoleoni, J., Staedler, M., Lyon, S., Fujii, J., & Tinker, M. T. (2021). Behavioral responses across a mosaic of ecosystem states restructure a sea otter–urchin trophic cascade. *Proceedings of the National Academy of Sciences*, *118*(11), e2012493118.

Sovacool, B. K., Baum, C. M., Low, S., & Fritz, L. (2023). Coral reefs, cloud forests and radical climate interventions in Australia's Wet Tropics and Great Barrier Reef. *PLOS Climate*, *2*(10), e0000221.

Stigebrandt, A., & Gustafsson, B. G. (2007). Improvement of Baltic proper water quality using large-scale ecological engineering. *AMBIO: A Journal of the Human Environment*, *36*(2), 280–286.

Takeshita, Y., McGillis, W., Briggs, E. M., Carter, A. L., Donham, E. M., Martz, T. R., Price, N. N., & Smith, J. E. (2016). Assessment of net community production and calcification of a coral reef using a boundary layer approach. *Journal of Geophysical Research: Oceans*. https://doi.org/10.1002/2016JC011886

Uyarra, M. C., Watkinson, A. R., & Cote, I. M. (2009). Managing dive tourism for the sustainable use of coral reefs: validating diver perceptions of attractive site features. *Environmental Management*, *43*, 1–16.

van Oppen, M. J. H., Oliver, J. K., Putnam, H. M., & Gates, R. D. (2015). Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences*, *112*(8), 2307–2313.

Vargas-Angel, B., Richards, C. L., Vroom, P. S., Price, N. N., Schils, T., Young, C. W., Smith, J., Johnson, M. D., & Brainard, R. E. (2015). Baseline assessment of net calcium carbonate accretion rates on US Pacific reefs. *PLoS One*, *10*(12), e0142196.

Voolstra, C. R., Suggett, D. J., Peixoto, R. S., Parkinson, J. E., Quigley, K. M., Silveira, C. B., Sweet, M., Muller, E. M., Barshis, D. J., Bourne, D. G., & Aranda, M. (2021). Extending the natural adaptive capacity of coral holobionts. *Nature Reviews Earth and Environment*, *2*(11), 747–762. https://doi.org/10.1038/s43017-021-00214-3

Walters, C. J., & Hilborn, R. (1978). Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics*, *9*(1), 157–188. https://doi.org/10.1146/annurev.es.09.110178.001105

Wee, S. Y. C., Sam, S. Q., Sim, W. T., Ng, C. S. L., Taira, D., Afiq-Rosli, L., Kikuzawa, Y. P., Toh, T. C., & Chou, L. M. (2019). The role of *in situ* coral nurseries in supporting mobile invertebrate epifauna. *Journal for Nature Conservation*, *50*(May). https://doi.org/10.1016/j.jnc.2019.125710

Wegley Kelly, L., Nelson, C. E., Aluwihare, L. I., Arts, M. G. I., Dorrestein, P. C., Koester, I., Matsuda, S. B., Petras, D., Quinlan, Z. A., & Haas, A. F. (2021). Molecular commerce on coral reefs: Using metabolomics to reveal biochemical exchanges underlying holobiont biology and the ecology of coastal ecosystems. *Frontiers in Marine Science*, *8*(July). https://doi.org/10.3389/fmars.2021.630799

Wegley Kelly, L., Nelson, C. E., Petras, D., Koester, I., Quinlan, Z. A., Arts, M. G. I., Nothias, L. F., Comstock, J., White, B. M., Hopmans, E. C., van Duyl, F. C., Carlson, C. A., Aluwihare, L. I., Dorrestein, P. C., & Haas, A. F. (2022). Distinguishing the molecular diversity, nutrient content, and energetic potential of exometabolomes produced by macroalgae and reef-building corals. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(5). https://doi.org/10.1073/pnas.2110283119

Weijerman, M., Fulton, E. A., & Brainard, R. E. (2016). Management strategy evaluation applied to coral reef ecosystems in support of ecosystem-based management. *PLoS One*, *11*(3), e0152577.

Weijerman, M., Fulton, E. A., Janssen, A. B. G., Kuiper, J. J., Leemans, R., Robson, B. J., van de Leemput, I. A., & Mooij, W. M. (2015). How models can support ecosystem-based management of coral reefs. *Progress in Oceanography*, *138*, 559–570. https://doi.org/10.1016/j.pocean.2014.12.017

Williams, I. D., Richards, B. L., Sandin, S. A., Baum, J. K., Schroeder, R. E., Nadon, M. O., Zgliczynski, B., Craig, P., McIlwain, J. L., & Brainard, R. E. (2011). Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific. *Journal of Marine Sciences*, *2011*.

Wilson, S. K., Graham, N. A. J., Holmes, T. H., MacNeil, M. A., & Ryan, N. M. (2018). Visual versus video methods for estimating reef fish biomass. *Ecological Indicators*, *85*, 146–152.

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

Zhang, N., Wang, M., & Wang, N. (2002). Precision agriculture - A worldwide overview. *Computers and Electronics in Agriculture*, *36*(2–3), 113–132. https://doi.org/10.1016/S0168-1699(02)00096-0

APPENDIX 2

Supplementary material for *A control theoretic framework and in situ experimental platform for active restoration of coral reefs*

REFERENCES FOR TABLE 2 (MAIN TEXT)

Abelson, A., Obolski, U., Regoniel, P., & Hadany, L. (2016). Restocking herbivorous fish populations as a social-ecological restoration tool in coral reefs. *Frontiers in Marine Science*, *3*, 138.

Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 367–388.

Albert, J. A., Beare, D., Schwarz, A.-M., Albert, S., Warren, R., Teri, J., Siota, F., & Andrew, N. L. (2014). The contribution of nearshore fish aggregating devices (FADs) to food security and livelihoods in Solomon Islands. *PLoS One*, *9*(12), e115386.

Albright, R., Caldeira, L., Hosfelt, J., Kwiatkowski, L., Maclaren, J. K., Mason, B. M., Nebuchina, Y., Ninokawa, A., Pongratz, J., Ricke, K. L., Rivlin, T., Schneider, K., Sesboüé, M., Shamberger, K., Silverman, J., Wolfe, K., Zhu, K., & Caldeira, K. (2016). Reversal of ocean acidification enhances net coral reef calcification. *Nature*. https://doi.org/10.1038/nature17155

Alldredge, A. L., Holbrook, S. J., Schmitt, R. J., Brooks, A. J., & Stewart, H. (2013). Skeletal growth of four scleractinian corals is not enhanced by *in situ* mesozooplankton enrichment. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps10422

Amar, K. O., & Rinkevich, B. (2007). A floating mid-water coral nursery as larval dispersion hub: Testing an idea. *Marine Biology*, *151*(2), 713–718. https://doi.org/10.1007/s00227-006-0512-0

Baer, J. L., Carilli, J., Chadwick, B., Hatay, M., van der Geer, A., Scholten, Y., Barnes, W., Aquino, J., Ballard, A., Little, M., Brzenski, J., Liu, X., Rosen, G., Wang, P. F., Castillo, J., Haas, A. F., Hartmann, A. C., & Rohwer, F. (2023). Coral Reef Arks: An *in situ* mesocosm and toolkit for assembling reef communities. *Journal of Visualized Experiments*, *2023*(191). https://doi.org/10.3791/64778

Banaszak, A. T., Marhaver, K. L., Miller, M. W., Hartmann, A. C., Albright, R., Hagedorn, M., Harrison, P. L., Latijnhouwers, K. R. W., Mendoza Quiroz, S., Pizarro, V., & Chamberland, V. F. (2023). Applying coral breeding to reef restoration: best practices, knowledge gaps, and priority actions in a rapidly-evolving field. *Restoration Ecology*, 1–17. https://doi.org/10.1111/rec.13913

Baums, I. B., Baker, A. C., Davies, S. W., Grottoli, A. G., Kenkel, C. D., Kitchen, S. A., Kuffner, I. B., LaJeunesse, T. C., Matz, M. V, & Miller, M. W. (2019). Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecological Applications*, *29*(8), e01978.

Bell, J. D., Albert, J., Andréfouët, S., Andrew, N. L., Blanc, M., Bright, P., Brogan, D., Campbell, B., Govan, H., & Hampton, J. (2015). Optimising the use of nearshore fish aggregating devices for food security in the Pacific Islands. *Marine Policy*, *56*, 98–105.

Bell, J. D., Ganachaud, A., Gehrke, P. C., Griffiths, S. P., Hobday, A. J., Hoegh-Guldberg, O., Johnson, J. E., Le Borgne, R., Lehodey, P., & Lough, J. M. (2013). Mixed responses of tropical Pacific fisheries and aquaculture to climate change. *Nature Climate Change*, *3*(6), 591–599.

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833.

Berman, O., Weizman, M., Oren, A., Neri, R., Parnas, H., Shashar, N., & Tarazi, E. (2023). Design and application of a novel 3D printing method for bio-inspired artificial reefs. *Ecological Engineering*, *188*(January), 106892. https://doi.org/10.1016/j.ecoleng.2023.106892

Biggs, B. C. (2013). Harnessing natural recovery processes to improve restoration outcomes: an experimental assessment of sponge-mediated coral reef restoration. *PloS One*, *8*(6), e64945.

Bozec, Y. M., O'Farrell, S., Bruggemann, J. H., Luckhurst, B. E., & Mumby, P. J. (2016). Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(16), 4536–4541. https://doi.org/10.1073/pnas.1601529113

Brathwaite, A., Clua, E., Roach, R., & Pascal, N. (2022). Coral reef restoration for coastal protection: Crafting technical and financial solutions. *Journal of Environmental Management*, *310*, 114718.

Buckley, R. M., Itano, D. G., & Buckley, T. W. (1989). Fish aggregation device (FAD) enhancement of offshore fisheries in American Samoa. *Bulletin of Marine Science*, *44*(2), 942–949.

Cabaitan, P. C., Gomez, E. D., & Aliño, P. M. (2008). Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *Journal of Experimental Marine Biology and Ecology*, *357*(1), 85–98. https://doi.org/10.1016/j.jembe.2008.01.001

Ceccarelli, D. M., McLeod, I. M., Bostrom-Einarsson, L., Bryan, S. E., Chartrand, K. M., Emslie, M. J., Gibbs, M. T., Rivero, M. G., Hein, M. Y., Heyward, A., Kenyon, T. M., Lewis, B. M., Mattocks, N., Newlands, M., Schlappy, M. L., Suggett, D. J., & Bay, L. K. (2020). Substrate stabilization and small structures in coral restoration: State of knowledge, and considerations for management and implementation. *PLoS ONE*, *15*(10 October), 1–27. https://doi.org/10.1371/journal.pone.0240846

Chamberland, V. F., Petersen, D., Guest, J. R., Petersen, U., Brittsan, M., & Vermeij, M. J. A. (2017). New seeding approach reduces costs and time to outplant sexually propagated corals for reef restoration. *Scientific Reports*, *7*(1), 1–12. https://doi.org/10.1038/s41598-017-17555-z

Champion, C., Suthers, I. M., & Smith, J. A. (2015). Zooplanktivory is a key process for fish production on a coastal artificial reef. *Marine Ecology Progress Series*, *541*, 1–14. https://doi.org/10.3354/meps11529

Chan, W. Y., Peplow, L. M., Menéndez, P., Hoffmann, A. A., & van Oppen, M. J. H. (2018). Interspecific hybridization may provide novel opportunities for coral reef restoration. *Frontiers in Marine Science*, *5*(MAY), 1–15. https://doi.org/10.3389/fmars.2018.00160

Comeau, S., Edmunds, P. J., Lantz, C. A., & Carpenter, R. C. (2014). Water flow modulates the response of coral reef communities to ocean acidification. *Scientific Reports*, *4*, 1–6. https://doi.org/10.1038/srep06681

Conley, D. J., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hansson, L. A., Rabalais, N. N., Voss, M., & Zillén, L. (2009). Tackling hypoxia in the Baltic Sea: Is engineering a solution? *Environmental Science and Technology*, *43*(10), 3407–3411. https://doi.org/10.1021/es8027633

Cortés-Useche, C., Reyes-Gamboa, W., Cabrera-Pérez, J. L., Calle-Triviño, J., Cerón-Flores, A., Raigoza-Figueras, R., Yathiraj, R., & Arias-González, J. E. (2021). Capture, culture and release of postlarvae fishes: Proof-of-concept as a tool approach to support reef management. *Frontiers in Marine Science*, *8*(September), 1–11. https://doi.org/10.3389/fmars.2021.718526

Cox, C. E., Jones, C. D., Wares, J. P., Castillo, K. D., McField, M. D., & Bruno, J. F. (2013). Genetic testing reveals some mislabeling but general compliance with a ban on herbivorous fish harvesting in Belize. *Conservation Letters*, *6*(2), 132–140.

Cruz, D. W. D., & Harrison, P. L. (2017). Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. *Scientific Reports*, *7*(1), 1–13. https://doi.org/10.1038/s41598-017-14546-y

Delgado, G. A., & Sharp, W. C. (2020). Capitalizing on an ecological process to aid coral reef ecosystem restoration: Can gastropod trophodynamics enhance coral survival? *Coral Reefs*, *39*(2), 319–330.

DeMartini, E., Jokiel, P., Beets, J., Stender, Y., Storlazzi, C., Minton, D., & Conklin, E. (2013). Terrigenous sediment impact on coral recruitment and growth affects the use of coral habitat by recruit parrotfishes (*F. Scaridae*). *Journal of Coastal Conservation*, *17*, 417–429.

Diaz, R. J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, *321*(5891), 926–929. https://doi.org/10.1126/science.1156401

Enochs, I. C. (2012). Motile cryptofauna associated with live and dead coral substrates: Implications for coral mortality and framework erosion. *Marine Biology*, *159*(4), 709–722. https://doi.org/10.1007/s00227-011-1848-7

Epstein, H. E., Smith, H. A., Torda, G., & van Oppen, M. J. H. (2019). Microbiome engineering: enhancing climate resilience in corals. *Frontiers in Ecology and the Environment*, *17*(2), 100–108. https://doi.org/10.1002/fee.2001

Feng, E. Y., Keller, D. P., Koeve, W., & Oschlies, A. (2016). Could artificial ocean alkalinization protect tropical coral ecosystems from ocean acidification? *Environmental Research Letters*, *11*(7), 74008.

Feng, E. Y., Sawall, Y., Wall, M., Lebrato, M., & Fu, Y. (2020). Modeling coral bleaching mitigation potential of water vertical translocation–an analogue to geoengineered artificial upwelling. *Frontiers in Marine Science*, *7*, 556192.

Fletcher, C. S., Bonin, M. C., & Westcott, D. A. (2020). An ecologically-based operational strategy for COTS control: integrated decision making from the site to the regional scale. *Report to the NESP Tropical Water Quality Hub. RRRC, Cairns*.

Fox, H. E., Harris, J. L., Darling, E. S., Ahmadia, G. N., Estradivari, & Razak, T. B. (2019). Rebuilding coral reefs: success (and failure) 16 years after low-cost, low-tech restoration. *Restoration Ecology*, *27*(4), 862–869. https://doi.org/10.1111/rec.12935

Fox, H. E., Mous, P. J., Pet, J. S., Muljadi, A. H., & Caldwell, R. L. (2005). Experimental assessment of coral reef rehabilitation following blast fishing. *Conservation Biology*, *19*(1), 98–107. https://doi.org/10.1111/j.1523-1739.2005.00261.x

Gordon, T. A. C., Radford, A. N., Davidson, I. K., Barnes, K., McCloskey, K., Nedelec, S. L., Meekan, M. G., McCormick, M. I., & Simpson, S. D. (2019). Acoustic enrichment can enhance fish community development on degraded coral reef habitat. *Nature Communications*, *10*(1), 1–7. https://doi.org/10.1038/s41467-019-13186-2

Goreau, T. J. F. G., & Prong, P. (2017). Biorock electric reefs grow back severely eroded beaches in months. *Journal of Marine Science and Engineering*, *5*(4), 7–9. https://doi.org/10.3390/jmse5040048

Hein, M. Y., Beeden, R., Birtles, A., Gardiner, N. M., Le Berre, T., Levy, J., Marshall, N., Scott, C. M., Terry, L., & Willis, B. L. (2020). Coral restoration effectiveness: Multiregional snapshots of the long-term responses of coral assemblages to restoration. *Diversity*, *12*(4), 1–22. https://doi.org/10.3390/D12040153

Higgins, E., Metaxas, A., & Scheibling, R. E. (2022). A systematic review of artificial reefs as platforms for coral reef research and conservation. *PLoS ONE*, *17*(1 January), 1–23. https://doi.org/10.1371/journal.pone.0261964

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H. P., & Thomas, C. D. (2008). Ecology: Assisted colonization and rapid climate change. *Science*, *321*(5887), 345–346. https://doi.org/10.1126/science.1157897

Horoszowski-Fridman, Y. B., Brêthes, J.-C., Rahmani, N., & Rinkevich, B. (2015). Marine silviculture: Incorporating ecosystem engineering properties into reef restoration acts. *Ecological Engineering*, *82*, 201–213.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, *17*(4), 360–365. https://doi.org/10.1016/j.cub.2006.12.049

Humanes, A., Beauchamp, E. A., Bythell, J. C., Carl, M. K., Craggs, J. R., Edwards, A. J., Golbuu, Y., Lachs, L., Martinez, H. M., & Palmowski, P. (2021). An experimental framework for selectively breeding corals for assisted evolution. *Frontiers in Marine Science*, *8*, 626.

Jayanthi, M., Patterson Edward, J. K., Malleshappa, H., Gladwin Gnana Asir, N., Mathews, G., Diraviya Raj, K., Bilgi, D. S., Ashok Kumar, T. K., & Sannasiraj, S. A. (2020). Perforated trapezoidal artificial reefs can augment the benefits of restoration of an island and its marine ecosystem. *Restoration Ecology*, *28*(1), 233–243. https://doi.org/10.1111/rec.13041

Jiao, N., Tang, K., Cai, H., & Mao, Y. (2011). Increasing the microbial carbon sink in the sea by reducing chemical fertilization on the land. *Nature Reviews Microbiology*, *9*(1), 75. https://doi.org/10.1038/nrmicro2386-c2

Kemp, W. M., Testa, J. M., Conley, D. J., Gilbert, D., & Hagy, J. D. (2009). Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences*, *6*(12), 2985–3008.

Knapp, I. S. S., Forsman, Z. H., Greene, A., Johnston, E. C., Bardin, C. E., Chan, N., Wolke, C., Gulko, D., & Toonen, R. J. (2022). Coral micro-fragmentation assays for optimizing active reef restoration efforts. *PeerJ*, *10*, e13653.

Kroon, F. J., Barneche, D. R., & Emslie, M. J. (2021). Fish predators control outbreaks of Crown-of-Thorns Starfish. *Nature Communications*, *12*(1). https://doi.org/10.1038/s41467-021-26786-8

Ladd, M. C., & Shantz, A. A. (2020). Trophic interactions in coral reef restoration: A review. *Food Webs*, *24*, e00149. https://doi.org/10.1016/j.fooweb.2020.e00149

Ladd, M. C., Shantz, A. A., Nedimyer, K., & Burkepile, D. E. (2016). Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. *Frontiers in Marine Science*, *3*, 261.

Leonard, C., Hédouin, L., Lacorne, M. C., Dalle, J., Lapinski, M., Blanc, P., & Nugues, M. M. (2022). Performance of innovative materials as recruitment substrates for coral restoration. *Restoration Ecology*, *30*(7), 1–14. https://doi.org/10.1111/rec.13625

Levenstein, M. A., Marhaver, K. L., Quinlan, Z. A., Tholen, H. M., Tichy, L., Yus, J., Lightcap, I., Kelly, L. W., Juarez, G., Vermeij, M. J. A., & Johnson, A. J. W. (2021). Engineered substrates reveal species-specific inorganic cues for coral larval settlement. *ChemRxiv*, 1–25.

Levin, R. A., Voolstra, C. R., Agrawal, S., Steinberg, P. D., Suggett, D. J., & van Oppen, M. J. H. (2017). Engineering strategies to decode and enhance the genomes of coral symbionts. *Frontiers in Microbiology*, *8*(JUN), 1–11. https://doi.org/10.3389/fmicb.2017.01220

Levy, N., Berman, O., Yuval, M., Loya, Y., Treibitz, T., Tarazi, E., & Levy, O. (2022). Emerging 3D technologies for future reformation of coral reefs: Enhancing biodiversity using biomimetic structures based on designs by nature. *Science of the Total Environment*, *830*, 154749. https://doi.org/10.1016/j.scitotenv.2022.154749

Lillis, A., Bohnenstiehl, D. W. R., & Eggleston, D. B. (2015). Soundscape manipulation enhances larval recruitment of a reef-building mollusk. *PeerJ*, *2015*(6). https://doi.org/10.7717/peerj.999

Lirman, D., & Schopmeyer, S. (2016). Ecological solutions to reef degradation: Optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ*. https://doi.org/10.7717/peerj.2597

Lirman, D., Thyberg, T., Herlan, J., Hill, C., Young-Lahiff, C., Schopmeyer, S., Huntington, B., Santos, R., & Drury, C. (2010). Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs*, *29*(3), 729–735.

Liu, S., Zhao, L., Xiao, C., Fan, W., Cai, Y., Pan, Y., & Chen, Y. (2020). Review of artificial downwelling for mitigating. *Water*, *12*(10), 2846.

Maciá, S., Robinson, M. P., & Nalevanko, A. (2007). Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. *Marine Ecology Progress Series*, *348*, 173–182. https://doi.org/10.3354/meps06962

Manuel, O. S., Williams, S. M., Weil, E., & Cruz-Motta, J. J. (2021). Experimental evaluation of *Diadema antillarum* herbivory effects on benthic community assemblages. *Journal of Experimental Marine Biology and Ecology*, *541*(April). https://doi.org/10.1016/j.jembe.2021.151566

McAfee, D., Williams, B. R., McLeod, L., Reuter, A., Wheaton, Z., & Connell, S. D. (2023). Soundscape enrichment enhances recruitment and habitat building on new oyster reef restorations. *Journal of Applied Ecology*, *60*(1), 111–120. https://doi.org/10.1111/1365-2664.14307

Mcclanahan, T. R., Graham, N. A. J., Macneil, M. A., & Cinner, J. E. (2015). Biomass-based targets and the management of multispecies coral reef fisheries. *Conservation Biology*, *29*(2), 409–417. https://doi.org/10.1111/cobi.12430

Mongin, M., Baird, M. E., Lenton, A., Neill, C., & Akl, J. (2021). Reversing ocean acidification along the Great Barrier Reef using alkalinity injection. *Environmental Research Letters*, *16*(6), 64068.

Muallil, R. N., Deocadez, M. R., Martinez, R. J. S., Campos, W. L., Mamauag, S. S., Nañola, C. L., & Aliño, P. M. (2019). Effectiveness of small locally-managed marine protected areas for coral reef fisheries management in the Philippines. *Ocean and Coastal Management*, *179*(May). https://doi.org/10.1016/j.ocecoaman.2019.104831

Nakamura, R., Ando, W., Yamamoto, H., Kitano, M., Sato, A., Nakamura, M., Kayanne, H., & Omori, M. (2011). Corals mass-cultured from eggs and transplanted as juveniles to their native, remote coral reef. *Marine Ecology Progress Series*, *436*, 161–168.

Neilson, B. J., Wall, C. B., Mancini, F. T., & Gewecke, C. A. (2018). Herbivore biocontrol and manual removal successfully reduce invasive macroalgae on coral reefs. *PeerJ*, *6*, e5332.

Obolski, U., Hadany, L., & Abelson, A. (2016). Potential contribution of fish restocking to the recovery of deteriorated coral reefs: An alternative restoration method? *PeerJ*, *2016*(2), 1–16. https://doi.org/10.7717/peerj.1732

Page, C. A., Muller, E. M., & Vaughan, D. E. (2018). Microfragmenting for the successful restoration of slow growing massive corals. *Ecological Engineering*, *123*, 86–94.

Pan, Y. W., Fan, W., Zhang, D. H., Chen, J. W., Huang, H. C., Liu, S. X., Jiang, Z. P., Di, Y. N., Tong, M. M., & Chen, Y. (2016). Research progress in artificial upwelling and its potential environmental effects. *Science China Earth Sciences*, *59*(2), 236–248. https://doi.org/10.1007/s11430-015-5195-2

Peixoto, R. S., Rosado, P. M., Leite, D. C. de A., Rosado, A. S., & Bourne, D. G. (2017). Beneficial microorganisms for corals (BMC): proposed mechanisms for coral health and resilience. *Frontiers in Microbiology*, *8*, 341.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., & Link, J. (2004). *Olicy orum*. *July*, 346–348.Plagányi, É. E., Babcock, R. C., Rogers, J., Bonin, M., & Morello, E. B. (2020). Ecological analyses to inform management targets for the culling of crown-of-thorns starfish to prevent coral decline. *Coral Reefs*, *39*(5), 1483–1499. https://doi.org/10.1007/s00338-020-01981-z

Quigley, K. M., Alvarez Roa, C., Beltran, V. H., Leggat, B., & Willis, B. L. (2021). Experimental evolution of the coral algal endosymbiont, *Cladocopium goreaui*: lessons learnt across a decade of stress experiments to enhance coral heat tolerance. *Restoration Ecology*, *29*(3), e13342.

Randall, C. J., Negri, A. P., Quigley, K. M., Foster, T., Ricardo, G. F., Webster, N. S., Bay, L. K., Harrison, P. L., Babcock, R. C., & Heyward, A. J. (2020). Sexual production of corals for reef restoration in the Anthropocene. *Marine Ecology Progress Series*, *635*, 203–232. https://doi.org/10.3354/MEPS13206

Reguero, B. G., Beck, M. W., Agostini, V. N., Kramer, P., & Hancock, B. (2018). Coral reefs for coastal protection: A new methodological approach and engineering case study in Grenada. *Journal of Environmental Management*. https://doi.org/10.1016/j.jenvman.2018.01.024

Renforth, P., & Henderson, G. (2017). Assessing ocean alkalinity for carbon sequestration. *Reviews of Geophysics*, *55*(3), 636–674.

Rinkevich, B. (2005). Conservation of coral reefs through active restoration measures: recent approaches and last decade progress. *Environmental Science & Technology*, *39*(12), 4333–4342.

Rinkevich, B. (2019). The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. *Journal of Marine Science and Engineering*, *7*(7). https://doi.org/10.3390/jmse7070201

Rinkevich, B. (2021). Ecological engineering approaches in coral reef restoration. *ICES Journal of Marine Science*, *78*(1), 410–420. https://doi.org/10.1093/icesjms/fsaa022

Rivera-Posada, J., Caballes, C. F., & Pratchett, M. S. (2013). Lethal doses of oxbile, peptones and thiosulfate-citrate-bile-sucrose agar (TCBS) for *Acanthaster planci*; exploring alternative population control options. *Marine Pollution Bulletin*, *75*(1–2), 133–139.

Rosado, P. M., Leite, D. C. A., Duarte, G. A. S., Chaloub, R. M., Jospin, G., Nunes da Rocha, U., P. Saraiva, J., Dini-Andreote, F., Eisen, J. A., Bourne, D. G., & Peixoto, R. S. (2019). Marine probiotics: increasing coral resistance to bleaching through microbiome manipulation. *ISME Journal*, *13*(4), 921–936. https://doi.org/10.1038/s41396-018-0323-6

Santoro, E. P., Borges, R. M., Espinoza, J. L., Freire, M., Messias, C. S. M. A., Villela, H. D. M., Pereira, L. M., Vilela, C. L. S., Rosado, J. G., Cardoso, P. M., Rosado, P. M., Assis, J. M., Duarte, G. A. S., Perna, G., Rosado, A. S., Macrae, A., Dupont, C. L., Nelson, K. E., Sweet, M. J., … Peixoto, R. S. (2021). Coral microbiome manipulation elicits metabolic and genetic restructuring to mitigate heat stress and evade mortality. *Science Advances*, *7*(33), 19–21. https://doi.org/10.1126/sciadv.abg3088

Sawall, Y., Harris, M., Lebrato, M., Wall, M., & Feng, E. Y. (2020). Discrete pulses of cooler deep water can decelerate coral bleaching during thermal stress: Implications for artificial upwelling during heat stress events. *Frontiers in Marine Science*, *7*, 720.

Sellares-Blasco, R. I., Villalpando, M. F., Guendulain-García, S. D., & Croquer, A. (2021). Assisted coral reproduction in the Dominican Republic: a successful story to replicate in the Caribbean. *Frontiers in Marine Science*, *8*, 669505.

Shafir, S., Van Rijn, J., & Rinkevich, B. (2006). A mid water coral nursery. *Proceedings of the 10th International Coral Reef Symposium*.

Shantz, A. A., Ladd, M. C., & Burkepile, D. E. (2020). Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. *Ecological Monographs*, *90*(2), 1–17. https://doi.org/10.1002/ecm.1403

Shelton III, A. J., & Richmond, R. H. (2016). Watershed restoration as a tool for improving coral reef resilience against climate change and other human impacts. *Estuarine, Coastal and Shelf Science*, *183*, 430–437.

Simpson, S. D., Meekan, M. G., McCauley, R. D., & Jeffs, A. (2004). Attraction of settlement-stage coral reef fishes to reef noise. *Marine Ecology Progress Series*, *276*(1), 263–268. https://doi.org/10.3354/meps276263

Stigebrandt, A., & Gustafsson, B. G. (2007). Improvement of Baltic proper water quality using large-scale ecological engineering. *AMBIO: A Journal of the Human Environment*, *36*(2), 280–286.

Suárez-Castro, A. F., Beyer, H. L., Kuempel, C. D., Linke, S., Borrelli, P., & Hoegh-Guldberg, O. (2021). Global forest restoration opportunities to foster coral reef conservation. *Global Change Biology*, *27*(20), 5238–5252.

van Oppen, M. J. H., Gates, R. D., Blackall, L. L., Cantin, N., Chakravarti, L. J., Chan, W. Y., Cormick, C., Crean, A., Damjanovic, K., Epstein, H., Harrison, P. L., Jones, T. A., Miller, M., Pears, R. J., Peplow, L. M., Raftos, D. A., Schaffelke, B., Stewart, K., Torda, G., … Putnam, H. M. (2017). Shifting paradigms in restoration of the world's coral reefs. In *Global Change Biology*. https://doi.org/10.1111/gcb.13647

van Oppen, M. J. H., Oliver, J. K., Putnam, H. M., & Gates, R. D. (2015). Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences*, *112*(8), 2307–2313.

Vermeij, M. J. A., Marhaver, K. L., Huijbers, C. M., Nagelkerken, I., & Simpson, S. D. (2010). Coral larvae move toward reef sounds. *PLoS ONE*, *5*(5), 3–6. https://doi.org/10.1371/journal.pone.0010660

Visser, P. M., Ibelings, B. W., Bormans, M., & Huisman, J. (2016). Artificial mixing to control cyanobacterial blooms: a review. *Aquatic Ecology*, *50*(3), 423–441. https://doi.org/10.1007/s10452-015-9537-0

Voolstra, C. R., Suggett, D. J., Peixoto, R. S., Parkinson, J. E., Quigley, K. M., Silveira, C. B., Sweet, M., Muller, E. M., Barshis, D. J., Bourne, D. G., & Aranda, M. (2021). Extending the natural adaptive capacity of coral holobionts. *Nature Reviews Earth and Environment*, *2*(11), 747–762. https://doi.org/10.1038/s43017-021-00214-3

Wee, S. Y. C., Sam, S. Q., Sim, W. T., Ng, C. S. L., Taira, D., Afiq-Rosli, L., Kikuzawa, Y. P., Toh, T. C., & Chou, L. M. (2019). The role of *in situ* coral nurseries in supporting mobile invertebrate epifauna. *Journal for Nature Conservation*, *50*(May). https://doi.org/10.1016/j.jnc.2019.125710

Williams, D. E., Miller, M. W., Bright, A. J., & Cameron, C. M. (2014). Removal of corallivorous snails as a proactive tool for the conservation of acroporid corals. *PeerJ*, *2*, e680.

Williams, S. L., Sur, C., Janetski, N., Hollarsmith, J. A., Rapi, S., Barron, L., Heatwole, S. J., Yusuf, A. M., Yusuf, S., Jompa, J., & Mars, F. (2019). Large-scale coral reef rehabilitation after blast fishing in Indonesia. *Restoration Ecology*, *27*(2), 447–456. https://doi.org/10.1111/rec.12866

Yanovski, R., & Abelson, A. (2019). Structural complexity enhancement as a potential coral-reef restoration tool. *Ecological Engineering*. https://doi.org/10.1016/j.ecoleng.2019.04.007

Zhang, C., Shi, T., Liu, J., He, Z., Thomas, H., Dong, H., Rinkevich, B., Wang, Y., Hyun, J. H., Weinbauer, M., López-Abbate, C., Tu, Q., Xie, S., Yamashita, Y., Tishchenko, P., Chen, Q., Zhang, R., & Jiao, N. (2022). Eco-engineering approaches for ocean negative carbon emission. *Science Bulletin*, *67*(24), 2564–2573. https://doi.org/10.1016/j.scib.2022.11.016

A synthesis of coral reef modeling and its applications to optimal control of coral reefs

Table S5.1 Variable relationships extracted from coral reef models and plotted in Figure 5.4 (main text). The following variables representing coral reef biotic and abiotic ecosystem components were identified in 100 coral reef modelling studies.

Variable	Type
Dissolved oxygen	Physical parameters/geochemistry
Temperature	Physical parameters/geochemistry
Light intensity (PAR)	Physical parameters/geochemistry
Flow speed	Physical parameters/geochemistry
pH	Physical parameters/geochemistry
Total Alkalinity	Physical parameters/geochemistry
Dissolved inorganic carbon (DIC)	Physical parameters/geochemistry
Dissolved organic carbon (labile fraction) (DOC)	Physical parameters/geochemistry
Particulate organic matter (POM)	Physical parameters/geochemistry
Turbidity/sedimentation	Physical parameters/geochemistry
Inorganic nutrients (PO_4, NO_4, NH_4)	Physical parameters/geochemistry
Viral abundance	Microbial ecology
Bacterial abundance	Microbial ecology
Bacterial biomass	Microbial ecology
Bacterial production	Microbial ecology
Phytoplankton biomass (Chla)	Microbial ecology
Zooplankton biomass	Microbial ecology
Protist abundance	Microbial ecology
Structural complexity	Macroecology
Net community calcification (NCC)	Macroecology
Net community production (NCP)	Macroecology
Larval recruitment rate	Macroecology
Coral: zooxanthellae symbiosis health (bleaching)	Macroecology
Coral % cover	Macroecology
Macroalgal/turf % cover	Macroecology
Crustose coralline algae (CCA) % cover	Macroecology

Table S5.1 Variable relationships extracted from coral reef models and plotted in Figure 5.4 (main text). The following variables representing coral reef biotic and abiotic ecosystem components were identified in 100 coral reef modelling studies (Continued).

Variable	Type
Filter feeder biomass (sponges)	Macroecology
Detritivore biomass (mobile invertebrates)	Macroecology
Herbivore biomass (mobile invertebrates)	Macroecology
Herbivore biomass (fish)	Macroecology
Invertivore/omnivore biomass (fish)	Macroecology
Piscivore biomass (fish, apex predators)	Macroecology
Planktivore biomass (fish)	Macroecology
Fishing pressure	Macroecology
Virus-to-microbe ratio (VMR)	Proposed state variables
Calcification rate	Proposed state variables
Aesthetic score	Proposed state variables
Fish biomass	Proposed state variables
Biodiversity	Proposed state variables
Chemical diversity	Proposed state variables

Relationships between the variables, include directionality, were extracted from models and plotted in Figure 5.4. In some cases, multiple different functional groups (i.e., turf and macroalgae, filter feeder biomass, inorganic nutrients) were grouped together if those groups carry out similar ecosystem functional roles. Numbers in each square correspond to the following citation list:

1. Haas, A. F., Guibert, M., Foerschner, A., Calhoun, S., George, E., Hatay, M., Dinsdale, E., Sandin, S. A., Smith, J. E., & Vermeij, M. J. A. (2015). Can we measure beauty? Computational evaluation of coral reef aesthetics. *PeerJ*, *3*, e1390.

2. Silveira, C. B., Luque, A., Haas, A. F., Roach, T. N. F., George, E. E., Knowles, B., Little, M., Sullivan, C. J., Varona, N. S., Wegley Kelly, L., Brainard, R., Rohwer, F., & Bailey, B. (2023). Viral predation pressure on coral reefs. *BMC Biology*, *21*(1), 77. https://doi.org/10.1186/s12915-023-01571-9

3. Graham, N. A. J., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*. https://doi.org/10.1007/s00338-012-0984-y

4. Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*(2), 561–575. https://doi.org/10.1007/s00338-017-1539-z

5. Timmers, M. A., Jury, C. P., Vicente, J., Bahr, K. D., Webb, M. K., & Toonen, R. J. (2021). Biodiversity of coral reef cryptobiota shuffles but does not decline under the combined stressors of ocean warming and acidification. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(39). https://doi.org/10.1073/pnas.2103275118

6. Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y. W., Maughan, H., Pantos, O., Roach, T. N. F., Sanchez, S. E., Silveira, C. B., Sandin, S., Smith, J. E., & Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*. https://doi.org/10.1038/nmicrobiol.2016.42

7. Haas, A. F., Nelson, C. E., Rohwer, F., Wegley-Kelly, L., Quistad, S. D., Carlson, C. A., Leichter, J. J., Hatay, M., & Smith, J. E. (2013). Influence of coral and algal exudates on microbially mediated reef metabolism. *PeerJ*. https://doi.org/10.7717/peerj.108

8. Haas, A. F., Nelson, C. E., Kelly, L. W., Carlson, C. A., Rohwer, F., Leichter, J. J., Wyatt, A., & Smith, J. E. (2011). Effects of coral reef benthic primary producers on dissolved organic carbon and microbial activity. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0027973

9. Nelson, C. E., Goldberg, S. J., Wegley Kelly, L., Haas, A. F., Smith, J. E., Rohwer, F., & Carlson, C. A. (2013). Coral and macroalgal exudates vary in neutral sugar composition and differentially enrich reef bacterioplankton lineages. *ISME Journal*. https://doi.org/10.1038/ismej.2012.161

10. Silveira, C. B., Coutinho, F. H., Cavalcanti, G. S., Benler, S., Doane, M. P., Dinsdale, E. A., Edwards, R. A., Francini-Filho, R. B., Thompson, C. C., Luque, A., Rohwer, F. L., & Thompson, F. (2020). Genomic and ecological attributes of marine bacteriophages encoding bacterial virulence genes. *BMC Genomics*. https://doi.org/10.1186/s12864-020-6523-2

11. Knowles, B., Silveira, C. B., Bailey, B. A., Barott, K., Cantu, V. A., Cobian-Guëmes, A. G., Coutinho, F. H., Dinsdale, E. A., Felts, B., Furby, K. A., George, E. E., Green, K. T., Gregoracci, G. B., Haas, A. F., Haggerty, J. M., Hester, E. R., Hisakawa, N., Kelly, L. W., Lim, Y. W., … Rohwer, F. (2016). Lytic to temperate switching of viral communities. *Nature*. https://doi.org/10.1038/nature17193

12. Silveira, C. B., Luque, A., Roach, T. N., Villela, H., Barno, A., Green, K., Reyes, B., Rubio-Portillo, E., Le, T., Mead, S., Hatay, M., Vermeij, M. J., Takeshita, Y., Haas, A., Bailey, B., & Rohwer, F. (2019). Biophysical and physiological processes causing oxygen loss from coral reefs. *ELife*. https://doi.org/10.7554/eLife.49114

13. Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., Heron, S. F., Hoey, A. S., Hoogenboom, M. O., Liu, G., McWilliam, M. J., Pears, R. J., Pratchett, M. S., Skirving, W. J., Stella, J. S., & Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*. https://doi.org/10.1038/s41586-018-0041-2

14. Scofield, V., Jacques, S. M. S., Guimarães, J. R. D., & Farjalla, V. F. (2015). Potential changes in bacterial metabolism associated with increased water temperature and nutrient inputs in tropical humic lagoons. *Frontiers in Microbiology*, *6*(MAR), 1–10. https://doi.org/10.3389/fmicb.2015.00310

15. Zaneveld, J. R., Burkepile, D. E., Shantz, A. A., Pritchard, C. E., McMinds, R., Payet, J. P., Welsh, R., Correa, A. M. S., Lemoine, N. P., Rosales, S., Fuchs, C., Maynard, J. A., & Thurber, R. V. (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature Communications*. https://doi.org/10.1038/ncomms11833

16. Roach, T. N. F., Abieri, M. L., George, E. E., Knowles, B., Naliboff, D. S., Smurthwaite, C. A., Kelly, L. W., Haas, A. F., & Rohwer, F. L. (2017). Microbial bioenergetics of coral-algal interactions. *PeerJ*. https://doi.org/10.7717/peerj.3423

17. Takeshita, Y., McGillis, W., Briggs, E. M., Carter, A. L., Donham, E. M., Martz, T. R., Price, N. N., & Smith, J. E. (2016). Assessment of net community production and calcification of a coral reef using a boundary layer approach. *Journal of Geophysical Research: Oceans*. https://doi.org/10.1002/2016JC011886

18. Kemp, W. M., Testa, J. M., Conley, D. J., Gilbert, D., & Hagy, J. D. (2009). Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences*, *6*(12), 2985–3008.

19. Weijerman, M., Gove, J. M., Williams, I. D., Walsh, W. J., Minton, D., & Polovina, J. J. (2018a). Evaluating management strategies to optimise coral reef ecosystem services. *Journal of Applied Ecology*, *55*(4), 1823–1833.

20. Weijerman, M., Fulton, E. A., & Brainard, R. E. (2016). Management strategy evaluation applied to coral reef ecosystems in support of ecosystem-based management. *PLoS One*, *11*(3), e0152577.

21. Brum, J. R., Hurwitz, B. L., Schofield, O., Ducklow, H. W., & Sullivan, M. B. (2016). Seasonal time bombs: dominant temperate viruses affect Southern Ocean microbial dynamics. *The ISME Journal*, *10*(2), 437–449.

22. Silveira, C. B., Silva-Lima, A. W., Francini-Filho, R. B., Marques, J. S. M., Almeida, M. G., Thompson, C. C., Rezende, C. E., Paranhos, R., Moura, R. L., Salomon, P. S., & Thompson, F. L. (2015). Microbial and sponge loops modify fish production in phase-shifting coral reefs. *Environmental Microbiology*. https://doi.org/10.1111/1462-2920.12851

23. Mumby, P. J., Hastings, A., & Edwards, H. J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, *450*(7166), 98–101. https://doi.org/10.1038/nature06252

24. Faure, V., Pinazo, C., Torréton, J. P., & Jacquet, S. (2010). Modelling the spatial and temporal variability of the SW lagoon of New Caledonia I: A new biogeochemical model based on microbial loop recycling. *Marine Pollution Bulletin*, *61*(7–12), 465–479. https://doi.org/10.1016/j.marpolbul.2010.06.041

25. Alva-Basurto, J. C., & Arias-González, J. E. (2014). Modelling the effects of climate change on a Caribbean coral reef food web. *Ecological Modelling*, *289*, 1–14. https://doi.org/10.1016/j.ecolmodel.2014.06.014

26. Wild-Allen, K., Skerratt, J., Whitehead, J., Rizwi, F., & Parslow, J. (2013). Mechanisms driving estuarine water quality: A 3D biogeochemical model for informed management. *Estuarine, Coastal and Shelf Science*, *135*, 33–45. https://doi.org/10.1016/j.ecss.2013.04.009

27. Anthony, K. R. N., Maynard, J. A., Diaz-Pulido, G., Mumby, P. J., Marshall, P. A., Cao, L., & Hoegh-Guldberg, O. (2011). Ocean acidification and warming will lower coral reef resilience. *Global Change Biology*, *17*(5), 1798–1808. https://doi.org/10.1111/j.1365-2486.2010.02364.x

28. Sarmento, H., Montoya, J. M., Vázquez-Domínguez, E., Vaqué, D., & Gasol, J. M. (2010). Warming effects on marine microbial food web processes: How far can we go when it comes to predictions? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2137–2149. https://doi.org/10.1098/rstb.2010.0045

29. Kramer, D. B. (2008). Adaptive harvesting in a multiple-species coral-reef food web. *Ecology and Society*, *13*(1). https://doi.org/10.5751/ES-02314-130117

30. Cheung, P. Y., Nozawa, Y., & Miki, T. (2021). Ecosystem engineering structures facilitate ecological resilience: A coral reef model. *Ecological Research*, *36*(4), 673–685. https://doi.org/10.1111/1440-1703.12230

31. van Hoytema, N., de Goeij, J. M., Kornder, N. A., El-Khaled, Y., van Oevelen, D., Rix, L., Cardini, U., Bednarz, V. N., Naumann, M. S., Al-Horani, F. A., & Wild, C. (2023). A carbon cycling model shows strong control of seasonality and importance of sponges on the functioning of a northern Red Sea coral reef. *Coral Reefs*, *42*(2), 367–381. https://doi.org/10.1007/s00338-022-02339-3

32. Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, *24*(9), 1000–1005.

33. Ruiz Sebastián, C., & McClanahan, T. R. (2013). Description and validation of production processes in the coral reef ecosystem model CAFFEE (Coral-Algae-Fish-Fisheries Ecosystem Energetics) with a fisheries closure and climatic disturbance. *Ecological Modelling*, *263*, 326–348. https://doi.org/10.1016/j.ecolmodel.2013.05.012

34. Yñiguez, A. T., McManus, J. W., & DeAngelis, D. L. (2008). Allowing macroalgae growth forms to emerge: Use of an agent-based model to understand the growth and spread of macroalgae in Florida coral reefs, with emphasis on *Halimeda tuna*. *Ecological Modelling*, *216*(1), 60–74. https://doi.org/10.1016/j.ecolmodel.2008.04.016

35. Langmead, O., & Sheppard, C. (2004). Coral reef community dynamics and disturbance: A simulation model. *Ecological Modelling*, *175*(3), 271–290. https://doi.org/10.1016/j.ecolmodel.2003.10.019

36. Arias-González, J. E., Nuñez-Lara, E., González-Salas, C., & Galzin, R. (2004). Trophic models for investigation of fishing effect on coral reef ecosystems. *Ecological Modelling*, *172*(2–4), 197–212. https://doi.org/10.1016/j.ecolmodel.2003.09.007

37. Blackwood, J. C., Hastings, A., & Mumby, P. J. (2011). A model-based approach to determine the long-term effects of multiple interacting stressors on coral reefs. *Ecological Applications*, *21*(7), 2722–2733. https://doi.org/10.1890/10-2195.1

38. Little, L. R., Punt, A. E., Mapstone, B. D., Pantus, F., Smith, A. D. M., Davies, C. R., & McDonald, A. D. (2007). ELFSim-A model for evaluating management options for spatially structured reef fish populations: An illustration of the “larval subsidy” effect. *Ecological Modelling*, *205*(3–4), 381–396. https://doi.org/10.1016/j.ecolmodel.2007.03.005

39. Tsehaye, I., & Nagelkerke, L. A. J. (2008). Exploring optimal fishing scenarios for the multispecies artisanal fisheries of Eritrea using a trophic model. *Ecological Modelling*, *212*(3–4), 319–333. https://doi.org/10.1016/j.ecolmodel.2007.10.044

40. Renken, H., & Mumby, P. J. (2009). Modelling the dynamics of coral reef macroalgae using a Bayesian belief network approach. *Ecological Modelling*, *220*(9–10), 1305–1314. https://doi.org/10.1016/j.ecolmodel.2009.02.022

41. Melbourne-Thomas, J., Johnson, C. R., & Fulton, E. A. (2011). Regional-scale scenario analysis for the Meso-American Reef system: Modelling coral reef futures under multiple stressors. *Ecological Modelling*, *222*(10), 1756–1770. https://doi.org/10.1016/j.ecolmodel.2011.03.008

42. Wolanski, E., Richmond, R. H., & McCook, L. (2004). A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. *Journal of Marine Systems*, *46*(1–4), 133–144. https://doi.org/10.1016/j.jmarsys.2003.11.018

43. Eakin, C. M. (2001). A tale of two ENSO events: Carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Science*, *69*(1), 171–186.

44. Eakin, C. M. (1996). Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs*, *15*(2), 109–119. https://doi.org/10.1007/s003380050031

45. Edwards, H. J., Elliott, I. A., Eakin, C. M., Irikawa, A., Madin, J. S., Mcfield, M., Morgan, J. A., Van Woesik, R., & Mumby, P. J. (2011). How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching? *Global Change Biology*, *17*(6), 2033–2048. https://doi.org/10.1111/j.1365-2486.2010.02366.x

46. Mongin, M., & Baird, M. (2014). The interacting effects of photosynthesis, calcification and water circulation on carbon chemistry variability on a coral reef flat: A modelling study. *Ecological Modelling*, *284*, 19–34. https://doi.org/10.1016/j.ecolmodel.2014.04.004

47. Kleypas, J. A. (1997). Modeled estimates of global reef habitat and carbonate production since the last glacial maximum. *Paleoceanography*, *12*(4), 533–545. https://doi.org/10.1029/97PA01134

48. Weijerman, M., Fulton, E. A., & Parrish, F. A. (2013). Comparison of coral reef ecosystems along a fishing pressure gradient. *PLoS ONE*, *8*(5). https://doi.org/10.1371/journal.pone.0063797

49. Weijerman, M., Fulton, E. A., Kaplan, I. C., Gorton, R., Leemans, R., Mooij, W. M., & Brainard, R. E. (2015). An integrated coral reef ecosystem model to support resource management under a changing climate. *PLoS ONE*, *10*(12), 1–23. https://doi.org/10.1371/journal.pone.0144165

50. Baskett, M. L., Nisbet, R. M., Kappel, C. V., Mumby, P. J., & Gaines, S. D. (2010). Conservation management approaches to protecting the capacity for corals to respond to climate change: A theoretical comparison. *Global Change Biology*, *16*(4), 1229–1246. https://doi.org/10.1111/j.1365-2486.2009.02062.x

51. Skerratt, J. H., Mongin, M., Baird, M. E., Wild-Allen, K. A., Robson, B. J., Schaffelke, B., Davies, C. H., Richardson, A. J., Margvelashvili, N., Soja-Wozniak, M., & Steven, A. D. L. (2019). Simulated nutrient and plankton dynamics in the Great Barrier Reef (2011–2016). *Journal of Marine Systems*, *192*(December 2018), 51–74. https://doi.org/10.1016/j.jmarsys.2018.12.006

52. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789.

53. Candy, A. S., Taylor Parkins, S. K., Van Duyl, F. C., Mueller, B., Arts, M. G. I., Barnes, W., Carstensen, M., Scholten, Y. J. H., El-Khaled, Y. C., Wild, C., Wegley Kelly, L., Nelson, C. E., Sandin, S. A., Vermeij, M. J. A., Rohwer, F. L., Picioreanu, C., Stocchi, P., & Haas, A. F. (2023). Small-scale oxygen distribution patterns in a coral reef. *Frontiers in Marine Science*, *10*(April), 1–13. https://doi.org/10.3389/fmars.2023.1135686

54. Hennige, S. J., Larsson, A. I., Orejas, C., Gori, A., De Clippele, L. H., Lee, Y. C., Jimeno, G., Georgoulas, K., Kamenos, N. A., & Roberts, J. M. (2021). Using the Goldilocks Principle to model coral ecosystem engineering. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1956). https://doi.org/10.1098/rspb.2021.1260

55. Rogers, A., Blanchard, J. L., & Mumby, P. J. (2018). Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology*, *55*(3), 1041–1049.

56. Kraines, S., Suzuki, Y., Yamada, K., & Komiyama, H. (1996). Separating biological and physical changes in dissolved oxygen concentration in a coral reef. *Limnology and Oceanography*, *41*(8), 1790–1799. https://doi.org/10.4319/lo.1996.41.8.1790

57. Lima, L. F. O., Weissman, M., Reed, M., Papudeshi, B., Alker, A. T., Morris, M. M., Edwards, R. A., De Putron, S. J., Vaidya, N. K., & Dinsdalea, E. A. (2020). Modeling of the coral microbiome: The influence of temperature and microbial network. *MBio*, *11*(2). https://doi.org/10.1128/mBio.02691-19

58. Weijerman, M., Gove, J. M., Williams, I. D., Walsh, W. J., Minton, D., & Polovina, J. J. (2018b). Evaluating management strategies to optimise coral reef ecosystem services. *Journal of Applied Ecology*, *55*(4), 1823–1833. https://doi.org/10.1111/1365-2664.13105

59. McClanahan, T. R., Donner, S. D., Maynard, J. A., MacNeil, M. A., Graham, N. A. J., Maina, J., Baker, A. C., Alemu I, J. B., Beger, M., & Campbell, S. J. (2012). Prioritizing key resilience indicators to support coral reef management in a changing climate.

60. Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, *17*(4), 360–365. https://doi.org/10.1016/j.cub.2006.12.049

61. McDonald, R. A., Neuhausler, R., Robinson, M., Larsen, L. G., Harrington, H. A., & Bruna, M. (2023). Zigzag persistence for coral reef resilience using a stochastic spatial model. *Journal of the Royal Society Interface*, *20*(205), 20230280.

62. Liu, P.-J., Shao, K.-T., Jan, R.-Q., Fan, T.-Y., Wong, S.-L., Hwang, J.-S., Chen, J.-P., Chen, C.-C., & Lin, H.-J. (2009). A trophic model of fringing coral reefs in Nanwan Bay, southern Taiwan suggests overfishing. *Marine Environmental Research*, *68*(3), 106–117.

63. Mumby, P. J., Hedley, J. D., Zychaluk, K., Harborne, A. R., & Blackwell, P. G. (2006). Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. *Ecological Modelling*, *196*(1–2), 131–148.

64. Holmes, G., & Johnstone, R. W. (2010). Modelling coral reef ecosystems with limited observational data. *Ecological Modelling*, *221*(8), 1173–1183.

65. Houk, P., Cuetos-Bueno, J., Kerr, A. M., & McCann, K. (2018). Linking fishing pressure with ecosystem thresholds and food web stability on coral reefs. *Ecological Monographs*, *88*(1), 109–119. https://doi.org/10.1002/ecm.1278

66. Meesters, E. H., Bak, R. P. M., Westmacott, S., Ridgley, M., & Dollar, S. (1998). A fuzzy logic model to predict coral reef development under nutrient and sediment stress. *Conservation Biology*, *12*(5), 957–965.

67. Gustafsson, M. S. M., Baird, M. E., & Ralph, P. J. (2013). The interchangeability of autotrophic and heterotrophic nitrogen sources in Scleractinian coral symbiotic relationships: A numerical study. *Ecological Modelling*, *250*, 183–194. https://doi.org/10.1016/j.ecolmodel.2012.11.003

68. Gustafsson, M. S. M., Baird, M. E., & Ralph, P. J. (2014). Modeling photoinhibition-driven bleaching in Scleractinian coral as a function of light, temperature, and heterotrophy. *Limnology and Oceanography*, *59*(2), 603–622. https://doi.org/10.4319/lo.2014.59.2.0603

69. Mongin, M., Baird, M. E., Tilbrook, B., Matear, R. J., Lenton, A., Herzfeld, M., Wild-Allen, K., Skerratt, J., Margvelashvili, N., Robson, B. J., Duarte, C. M., Gustafsson, M. S. M., Ralph, P. J., & Steven, A. D. L. (2016). The exposure of the Great Barrier Reef to ocean acidification. *Nature Communications*, *7*, 1–8. https://doi.org/10.1038/ncomms10732

70. Baird, M. E., Mongin, M., Rizwi, F., Bay, L. K., Cantin, N. E., Soja-Woźniak, M., & Skerratt, J. (2018). A mechanistic model of coral bleaching due to temperature-mediated light-driven reactive oxygen build-up in zooxanthellae. *Ecological Modelling*, *386*(March), 20–37. https://doi.org/10.1016/j.ecolmodel.2018.07.013

71. Baird, M. E., Cherukuru, N., Jones, E., Margvelashvili, N., Mongin, M., Oubelkheir, K., Ralph, P. J., Rizwi, F., Robson, B. J., Schroeder, T., Skerratt, J., Steven, A. D. L., & Wild-Allen, K. A. (2016). Remote-sensing reflectance and true colour produced by a coupled hydrodynamic, optical, sediment, biogeochemical model of the Great Barrier Reef, Australia: Comparison with satellite data. *Environmental Modelling and Software*, *78*, 79–96. https://doi.org/10.1016/j.envsoft.2015.11.025

72. Melbourne-Thomas, J., Johnson, C. R., Aliño, P. M., Geronimo, R. C., Villanoy, C. L., & Gurney, G. G. (2011). A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. *Environmental Modelling and Software*, *26*(1), 66–82. https://doi.org/10.1016/j.envsoft.2010.03.033

73. Carturan, B. S., Pither, J., Maréchal, J. P., Bradshaw, C. J. A., & Parrott, L. (2020). Combining agent-based, trait-based and demographic approaches to model coral-community dynamics. *ELife*, *9*, 1–223. https://doi.org/10.7554/eLife.55993

74. McClanahan, T. R. (1995). A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecological Modelling*, *80*(1), 1–19. https://doi.org/10.1016/0304-3800(94)00042-G

75. Madin, J. S., & Connolly, S. R. (2006). Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature*, *444*(7118), 477–480.

76. Brown, C. J., Jupiter, S. D., Albert, S., Klein, C. J., Mangubhai, S., Maina, J. M., Mumby, P., Olley, J., Stewart-Koster, B., Tulloch, V., & Wenger, A. (2017). Tracing the influence of land-use change on water quality and coral reefs using a Bayesian model. *Scientific Reports*, *7*(1), 1–10. https://doi.org/10.1038/s41598-017-05031-7

77. De'ath, G., & Fabricius, K. (2010). Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications*, *20*(3), 840–850.

78. Bozec, Y. M., & Mumby, P. J. (2015). Synergistic impacts of global warming on the resilience of coral reefs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 1–9. https://doi.org/10.1098/rstb.2013.0267

79. Anderson, T. R., & Ducklow, H. W. (2001). Microbial loop carbon cycling in ocean environments studied using a simple steady-state model. *Aquatic Microbial Ecology*, *26*(1), 37–49.

80. Cherabier, P., & Ferrière, R. (2022). Eco-evolutionary responses of the microbial loop to surface ocean warming and consequences for primary production. *ISME Journal*, *16*(4), 1130–1139. https://doi.org/10.1038/s41396-021-01166-8

81. Gove, J. M., Williams, G. J., Lecky, J., Brown, E., Conklin, E., Counsell, C., Davis, G., Donovan, M. K., Falinski, K., Kramer, L., Kozar, K., Li, N., Maynard, J. A., McCutcheon, A., McKenna, S. A., Neilson, B. J., Safaie, A., Teague, C., Whittier, R., & Asner, G. P. (2023). Coral reefs benefit from reduced land–sea impacts under ocean warming. *Nature*, *621*(July 2022). https://doi.org/10.1038/s41586-023-06394-w

82. Hasumi, H., & Nagata, T. (2014). Modeling the global cycle of marine dissolved organic matter and its influence on marine productivity. *Ecological Modelling*, *288*, 9–24. https://doi.org/10.1016/j.ecolmodel.2014.05.009

83. Jost, C., Lawrence, C. A., Campolongo, F., Van De Bund, W., Hill, S., & DeAngelis, D. L. (2004). The effects of mixotrophy on the stability and dynamics of a simple planktonic food web model. *Theoretical Population Biology*, *66*(1), 37–51. https://doi.org/10.1016/j.tpb.2004.02.001

84. De Laender, F., Van Oevelen, D., Soetaert, K., & Middelburg, J. J. (2009). Carbon transfer in herbivore-and microbial loop-dominated pelagic food webs in the southern Barents Sea during spring and summer. *Marine Ecology Progress Series*, *398*, 93–107. https://doi.org/10.3354/meps08335

85. Polimene, L., Allen, J. I., & Zavatarelli, M. (2006). Model of interactions between dissolved organic carbon and bacteria in marine systems. *Aquatic Microbial Ecology*, *43*(2), 127–138. https://doi.org/10.3354/ame043127

86. Madin, J. S., Hughes, T. P., & Connolly, S. R. (2012). Calcification, storm damage and population resilience of tabular corals under climate change. *PLoS ONE*, *7*(10), 1–10. https://doi.org/10.1371/journal.pone.0046637

87. Weitz, J. S., Stock, C. A., Wilhelm, S. W., Bourouiba, L., Coleman, M. L., Buchan, A., Follows, M. J., Fuhrman, J. A., Jover, L. F., Lennon, J. T., Middelboe, M., Sonderegger, D. L., Suttle, C. A., Taylor, B. P., Frede Thingstad, T., Wilson, W. H., & Eric Wommack, K. (2015). A multitrophic model to quantify the effects of marine viruses on microbial food webs and ecosystem processes. *ISME Journal*, *9*(6), 1352–1364. https://doi.org/10.1038/ismej.2014.220

88. Kennedy, E. V., Perry, C. T., Halloran, P. R., Iglesias-Prieto, R., Schönberg, C. H. L., Wisshak, M., Form, A. U., Carricart-Ganivet, J. P., Fine, M., Eakin, C. M., & Mumby, P. J. (2013). Avoiding coral reef functional collapse requires local and global action. *Current Biology*, *23*(10), 912–918. https://doi.org/10.1016/j.cub.2013.04.020

89. Kubicek, A., & Reuter, H. (2016). Mechanics of multiple feedbacks in benthic coral reef communities. *Ecological Modelling*, *329*, 29–40. https://doi.org/10.1016/j.ecolmodel.2016.02.018

90. Niquil, N., Jackson, G. A., Legendre, L., & Delesalle, B. (1998). Inverse model analysis of the planktonic food web of Takapoto Atoll (French Polynesia). *Marine Ecology Progress Series*, *165*, 17–29.

91. Palmer, J. R., & Totterdell, I. J. (2001). Production and export in a global ocean ecosystem model. *Deep Sea Research Part I: Oceanographic Research Papers*, *48*(5), 1169–1198.

92. Alderdice, R., Perna, G., Cárdenas, A., Hume, B. C. C., Wolf, M., Kühl, M., Pernice, M., Suggett, D. J., & Voolstra, C. R. (2022). Deoxygenation lowers the thermal threshold of coral bleaching. *Scientific Reports*, *12*(1), 18273.

93. Haas, A. F., Smith, J. E., Thompson, M., & Deheyn, D. D. (2014). Effects of reduced dissolved oxygen concentrations on physiology and fluorescence of hermatypic corals and benthic algae. *PeerJ*, *2014*(1), 1–19. https://doi.org/10.7717/peerj.235

94. Bergstrom, E., Ordoñez, A., Ho, M., Hurd, C., Fry, B., & Diaz-Pulido, G. (2020). Inorganic carbon uptake strategies in coralline algae: Plasticity across evolutionary lineages under ocean acidification and warming. *Marine Environmental Research*, *161*, 105107.

95. Fabricius, K. E., Kluibenschedl, A., Harrington, L., Noonan, S., & De'Ath, G. (2015). *In situ* changes of tropical crustose coralline algae along carbon dioxide gradients. *Scientific Reports*, *5*(1), 9537.

96. Dutra, E., Koch, M., Peach, K., & Manfrino, C. (2016). Tropical crustose coralline algal individual and community responses to elevated pCO2 under high and low irradiance. *ICES Journal of Marine Science*, *73*(3), 803–813.

97. De Goeij, J. M., Van Den Berg, H., Van Oostveen, M. M., Epping, E. H. G., & Van Duyl, F. C. (2008). Major bulk dissolved organic carbon (DOC) removal by encrusting coral reef cavity sponges. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps07403

98. Allison, N., Cohen, I., Finch, A. A., Erez, J., & Tudhope, A. W. (2014). Corals concentrate dissolved inorganic carbon to facilitate calcification. *Nature Communications*, *5*(1), 5741.

99. Wilson, R. W., Millero, F. J., Taylor, J. R., Walsh, P. J., Christensen, V., Jennings, S., & Grosell, M. (2009). Contribution of fish to the marine inorganic carbon cycle. *Science*, *323*(5912), 359–362.

100. Wild, C., Niggl, W., Naumann, M. S., & Haas, A. F. (2010). Organic matter release by Red Sea coral reef organisms-Potential effects on microbial activity and *in situ* O2 availability. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps08653