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Swanson, Stella Ann

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Santa Barbara

Echinoid herbivores and coral reef resilience

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution and Marine Biology

by

Stella Ann Swanson

Committee in charge:

Professor Russell Schmitt, Chair

Professor Sally Holbrook

Professor Cherie Briggs

Professor Peter Edmunds, California State University, Northridge

September 2016

The dissertation of Stella Ann Swanson is approved.

Peter Edmunds

Cherie Briggs

Sally Holbrook

Russell Schmitt, Committee Chair

September 2016

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VITA OF STELLA ANN SWANSON

September 2016

Stella.Swanson@lifesci.ucsb.edu
Department of Ecology, Evolution and Marine Biology
University of California, Santa Barbara
Santa Barbara, CA 93106-9620

EDUCATION

University of California, Santa Barbara September, 2016
PhD Ecology, Evolution and Marine Biology
Advisor: Dr. Russell Schmitt
Dissertation title: *Herbivory and coral reef resilience*

California State University, Northridge 2011
MS Biology
Advisor: Dr. Robert C. Carpenter
Thesis title: *Species-specific effects of echinoids on coral reef community structure in Moorea, French Polynesia*

California State University, Long Beach 2008
BS Marine Biology

Ocean Studies Institute, Wrigley Institute for Environmental Studies,
Santa Catalina Island, semester course of study Fall 2006

RESEARCH EXPERIENCE

University of California, Santa Barbara
Doctoral research in Moorea, French Polynesia

California State University, Northridge 2008-11
Master's research in Moorea, French Polynesia

California State University, Northridge 2006-08
Field Research Assistant in Moorea, French Polynesia
Assisted Dr. Robert C. Carpenter and his graduate students with various coral and algal community ecology sampling and field experimental manipulation

California State University, Long Beach 2008
Undergraduate directed research in Glover's Reef, Belize
Advisors: Dr. Gwen Goodmanlowe, Dr. Chris Lowe, and Dr. Bruno Pernet
Project description: Morphological adaptations in the marine sponge *Callyspongia vaginalis*

Hawaii Institute of Marine Biology 2007
Directed research
Advisor: Dr. Robert C. Carpenter
Project description: Photosynthetic performance and morphology in the Hawaiian coral *Montipora capitata* from different flow environments

Ocean Studies Institute, Marine Biology Semester, Santa Catalina Island 2006
Undergraduate directed research
Advisor: Dr. Peter J. Edmunds (California State University, Northridge)
Project description: Analysis of inducible defenses in the marine bryozoan *Membranipora membranacea* at Santa Catalina Island

WORK EXPERIENCE

Research Assistant 2007- 09
Duties: Field herbivore and benthic community survey data collection in Moorea, French Polynesia for Long-Term Ecological Research program. Community metabolism data collection for major algal and invertebrate taxa.
Supervisor: Robert C. Carpenter

Fisheries Technician Pacific States Marine Fisheries Commission 2007
Duties: Species identification, catch and size data collection for recreational fisheries. Los Angeles and Orange counties. Supervisor: Toby Carpenter

Nursing Assistant Hoag Hospital, Newport Beach California 2002-06
Nursing Assistant Flagstaff Medical Center, Flagstaff Arizona 2000-02

TEACHING EXPERIENCE

Head Teaching Associate: Methods in Aquatic Community Ecology 2011, 2012, 2013
Head Teaching Associate: Biology laboratory 2016
Teaching Associate: Biology laboratory 2012, 2013, 2015
Graduate Assistant: Invertebrate Zoology Santa Catalina Island 2010
Teaching Associate: Introductory Biology laboratory 2008-09
Third grade-science guest lecturer: Long Beach Unified School District 2008

PROFESSIONAL MEMBERSHIPS

Benthic Ecological Society
Moorea Coral Reef Long-Term Ecological Research Program
Society for Advancement of Chicanos and Native Americans in Science
Western Society of Naturalists

ANONYMOUS SCIENTIFIC REVIEW

Journal article reviewer for: *Marine Ecology Progress Series • Environmental Monitoring and Assessment*

PROFESSIONAL SERVICE

Graduate-Student Representative

Moorea Coral Reef Long-Term Ecological Research Program 2009-2015
Treasurer
Marine Biology Graduate Student Association 2008

EDUCATIONAL OUTREACH

Co-founder and writer for ecological research blog: <https://ssalterblog.wordpress.com/>
Television appearances: Voice of the Sea (Voiceofthesea.org):
<https://vimeo.com/154224087>

FELLOWSHIPS AND GRANTS

UCSB department of Ecology, Evolution and Marine Biology Block Grant (\$11,150) 2015
Worster Award for paired Undergraduate and Graduate student research (5,000) 2014
University of California Graduate Opportunity Fellowship (\$22,000) 2013-14
Summer Doctoral Research Institute Fellowship: National Science Foundation's Alliances
for Graduate Education and the Professoriate (NSF-AGEP) (\$6,000) 2011
UCSB department of Ecology, Evolution and Marine Biology Block Grant (\$12,000) 2011
Minority Biomedical Research Support – Research Initiative for Scientific
Enhancement (MBRS-RISE) Scholar 2009-11
CSUN Graduate Equity Fellowship (\$4000) 2008-10
CSUN Thesis Support Grant (\$1000) 2008
Southern California Tuna Club Marine Biology Scholarship (\$1000) 2006
CSU Louis Stokes Alliance for Minority Participation (LSAMP) Scholar (\$2500) 2006

CERTIFICATIONS

AAUS Scientific Diver, PADI Advanced SCUBA, NAUI Open Water SCUBA, French
Captain's Boating License, California Boating Safety Certification, CPR, First Aid, O₂

INVITED TALKS

Seminar speaker: California State University, Long Beach Biology Department Seminar.

Guest lecture: Richard B. Gump Field Station Moorea, French Polynesia. Colby College,
Tropical Ecology Field Course.

ORAL PRESENTATIONS

Does branching coral structure enhance the recovery of a coral reef after a disturbance?
Stella Swanson 2015 Western Society of Naturalists Meeting, Sacramento, CA.

*Rapid mortality of multiple species of sea urchins in Moorea, French Polynesia: Initial
impacts on the coral reef community.* Stella Swanson 2013 Western Society of
Naturalists Meeting, Oxnard, California.

Bioerosion by the sea urchin Echinometra mathaei modulates coral recruitment. Stella
Swanson 2013 Benthic Ecology Meeting, Savannah, Georgia.

Coral reef resilience: The role of echinoids in coral recruitment and growth. Stella
Swanson 2012 Moorea Coral Reef Long-Term Ecological Research – All Investigators
Meeting, Santa Barbara, California.

The influence of sea urchins on coral recruitment and recovery. Stella Swanson 2012 Ecology, Evolution and Marine Biology Graduate Student Symposium, University of California, Santa Barbara.

The feeding biology of the Echinoid Echinostrephus aciculatus in Moorea, French Polynesia. Stella Swanson 2011 Long-Term Ecological Research – Graduate Student Symposium, Santa Barbara, California.

Species-specific effects of echinoids on coral reefs. Stella Swanson and Robert C. Carpenter. 2011 Benthic Ecology Meeting, Mobile, Alabama.

The unique biology and ecology of the echinoid Echinostrephus aciculatus in Moorea, French Polynesia. Stella Swanson and Robert C. Carpenter 2010 Western Society of Naturalists Meeting, San Diego, California.

Species-specific effects of echinoids on coral reefs. Stella Swanson and Robert C. Carpenter 2010 Benthic Ecology Meeting, Wilmington, North Carolina.

Species-specific effects of echinoids on coral reef community structure. Stella Swanson and Robert C. Carpenter 2010 California State University, Northridge Student Symposium, Northridge, California.

POSTER PRESENTATIONS

Species-specific effects of echinoids on coral reef community structure. Stella Swanson and Robert C. Carpenter 2009 Moorea Long-Term Ecological Research All Investigators Meeting, Santa Barbara, California.

Species-specific effects of echinoids structuring coral reef communities. Stella Swanson and Robert C. Carpenter 2009 NSF Long-Term Ecological Research All Scientists Meeting, Estes Park, Colorado.

Species-specific effects of echinoids on coral reef community structure. Stella Swanson and Robert C. Carpenter 2008 California State University, Northridge Student Symposium, Northridge, California.

Species-specific effects of echinoids on coral reef community structure. Stella Swanson and Robert C. Carpenter 2008 Western Society of Naturalists, Vancouver, BC.

ABSTRACT

Echinoid herbivores and coral reef resilience

Stella Ann Swanson

Anthropogenic impacts and climate change are increasing the frequency and intensity at which ecosystems are being perturbed. On tropical reefs, disturbances can result in loss of live coral and sometimes initiate a transition to an alternative community state, frequently one dominated by macroalgae. Because algae-dominated reefs may have lower productivity, decreased species diversity and reduced ecosystem services, there has been considerable interest in elucidating the mechanisms that mediate a transition to an algae dominated state or the re-establishment of coral. In this dissertation I explore how physical attributes of a coral reef and the echinoid and fish communities control algal growth and influence the return to coral dominance.

Recent disturbances in Moorea, French Polynesia offer an opportunity to examine the effects of architectural complexity of the substrate on recruitment of new coral colonists. I explore how the success of new coral colonists is affected by variation in structural complexity, particularly with respect to the skeletons of recently-killed branching coral. I quantified growth and survival of juvenile pocilloporid corals on structurally complex *Pocillopora* skeletons and on massive *Porites*, then generated quantitative predictions about the role these different types of substrates play in the replenishment of coral populations in the lagoons of Moorea. Results revealed that recruitment to dead branching *Pocillopora* structures is high, yet very low subsequent survival of those recruits, due to fast erosion of their host, indicates that dead *Pocillopora* structures are a sink for corals at vulnerable life stages.

Microhabitats on dead coral structure can also provide important habitat for new coral colonists. Survivorship of young corals can be greater in crevices and holes than on exposed surfaces, due to incidental or targeted predation by herbivores and corallivores. Thus, other taxa that influence the availability of crevice space can indirectly mediate coral recruitment. Bioeroding echinoids have the potential to affect settlement and early survival of corals through their influence on crustose coralline algae (CCA) and/or the provision of crevice space. In Moorea, the echinoid *Echinometra mathaei* create distinctive crevices that enhance the small-scale structural complexity of the reef and are associated with high cover of CCA within and surrounding them. This study demonstrates that the microhabitats created by *E. mathaei* on slower eroding *Porites* coral provide favorable habitat for recruitment of coral, thereby bioeroding sea urchins could have an overall positive impact on the coral community.

In 2013, an unknown agent resulted in rapid mortality of echinoid populations in the lagoon of Moorea. In the final portion of this dissertation, I describe the nature of the decline in *D. savignyi* populations, and report how the benthic community responded over the first 2.5 years following the abrupt mortality event. Additionally, I experimentally tested the ability for fish and remaining sea urchin herbivores to control algal growth on this reef and determined the rate of algal colonization in the absence of these herbivores. Despite high abundances prior to their demise, the loss of *D. savignyi* did not result in an increase in macroalgae or a shift in community structure. The experimental results suggest that fish herbivores were able to compensate for the loss of the echinoids by rapidly consuming any enhanced algal growth. Furthermore, the establishment of algae in Moorea appears more slow than may occur on other tropical reefs in the absence of herbivory.

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I. Title: Structurally complex dead coral skeletons can be a sink habitat for early coral colonists

Abstract

Coral reefs worldwide are threatened by climate change and anthropogenic factors such as pollution and overfishing. Recent work has suggested that perturbations to coral reefs that do not remove complex physical structure (such as coral bleaching events) may enhance subsequent coral re-establishment by providing physically complex habitat for coral recruitment. This study addresses how complex physical structure provided by dead branching *Pocillopora* coral skeletons may influence the rate of return to coral dominance. The erosion of dead branching coral structures is rapid for dead *Pocillopora* and most of these structures are likely to erode completely within 3-5 years. However, coral recruitment to dead *Pocillopora* structures is very high, resulting in high mortality rates of these colonists as the habitat erodes. The results from this study suggest that dead *Pocillopora* skeletons are a sink for young coral colonists and a disturbance that removes this structure may actually increase the rate of coral re-establishment.

Introduction

Anthropogenic impacts and climate change are increasing the frequency and intensity at which ecosystems are being perturbed (Nyström et al. 2000, Hughes et al. 2013).

Disturbances can alter ecosystem structure and function by changing such important aspects as species composition or physical attributes of the habitat. On tropical reefs, disturbances can result in loss of live coral (Sebens 1994, Hughes 1994, Connell et al. 1997) and sometimes initiate a transition to an algae-dominated state (Hughes 1994), which can persist, in some cases, for decades (Mumby et al. 2007, Alvarez-Filip et al. 2009). Because algae-

dominated reefs may have lower productivity, decreased species diversity and reduced ecosystem services compared to coral-dominated reefs (Carpenter 1988, Hoegh-Guldberg et al. 2007, Graham et al. 2014), there has been considerable interest in elucidating the mechanisms that underlie landscape-scale re-establishment of coral (Hughes et al. 2013). The potential for coral recovery may differ depending on whether the disturbance alters the physical environment (Connell 1997, Graham et al. 2015), which in turn is related to the source of coral mortality. For example, storms can destroy complex structure by removing the hard skeletons of scleractinian corals. In the case of a severe physical disturbance, coral can be reduced to unconsolidated rubble where survival of new coral recruits can be low due to substrate instability (Birkeland 1997, Nzali et al. 1998, Fox et al. 2003). Disturbances such as coral bleaching events (Glynn 1996, Baker et al. 2008), coral disease (Harvell et al. 2007), and coral predator outbreaks (Pratchett 2005, Kayal et al. 2012), normally kill coral but leave their skeletons intact. Researchers have suggested that reefs may return to a coral dominated state faster after a disturbance that leaves coral skeletons largely intact (Connell 1997, Graham et al. 2011, 2015). The structural complexity of a tropical reef can enhance the recruitment rate of corals by providing preferred settlement microhabitat and/or enhanced post-settlement performance. Dead coral structure provides settlement sites and critical shelter for juvenile corals (DeVantier and Done 2007), and complex structures may provide microhabitats ideal for coral growth.

In addition to architectural complexity, the structural integrity of a reef following a disturbance can have profound impacts on the ability for a coral reef community to recover (Connell 1997, Birkeland 2004, Graham et al. 2006, Pratchett et al. 2008, Alvarez-Filip et al. 2009). Dead coral structure has been found on some reefs to erode within years after a major

disturbance event (Birkeland 1997, Hughes and Connell 1999, Sheppard et al. 2002). Bioeroding organisms including parrotfishes and invertebrates such as sea urchins and boring molluscs are abundant on many coral reefs and are a major cause of breakdown of the reef framework (Hutchings 1986, Birkeland 1997, Baker et al. 2008). Bioerosion can accelerate after a coral mortality event, leading to altered composition of the bioeroding community and rapid erosion of the reef framework (Birkeland 1997), yet on some reefs bioerosion may be relatively constant after coral death (Roff et al. 2015). Research has suggested that climate change, pollution and overfishing may give bioeroding organisms an advantage on coral reefs, and some reefs are experiencing accelerated bioerosion (Holmes et al. 2000, Alvarez-Filip et al. 2009). Furthermore, erosion of the coral reef framework can drive compositional and biodiversity shifts in fish (Syms and Jones 2000, Sheppard et al. 2002, Garpe et al. 2006, Graham et al. 2006, 2007, 2009) and invertebrate communities (Przeslawski et al. 2008, Norström et al. 2009).

There is marked variation among types of scleractinian coral in their vulnerability to the same disturbance depending for example on their thermal tolerance or mechanical susceptibility (Marshall and Baird 2000, Loya et al. 2001, Schuhmacher et al. 2005, Madin and Connolly 2006, Burt et al. 2008, Fabricius et al. 2011, van Woesik et al. 2011, Madin et al. 2014, Hoey et al. 2016). Mechanically robust corals such as massive forms (some *Porites* spp. and Faviids) may suffer only partial mortality during disturbance events that result in complete mortality of branching corals (Acroporidae and Pocilloporidae) (Graham et al. 2006, 2007, Burt et al. 2008, Adjeroūd et al. 2009, Trapon et al. 2011, Madin et al. 2014), and large massive growth forms are less likely to be dislodged or broken during physical disturbances (Madin and Connolly 2006). Branching growth forms are more likely to be

removed by physical disturbances (Madin and Connolly 2006, Madin et al. 2014) and can be more affected by bleaching events or coral predators (De'ath and Moran 1998, Pratchett 2005, Tokeshi and Daud 2010, Kayal et al. 2012). However, growth rates for fast-growing branching corals such as Acroporids and Pocilloporids often result in rapid re-population of these corals (Burt et al. 2008). It appears that over the past few decades, some coral reefs are shifting in coral taxonomic composition (Sebens 1994, Alvarez-Filip et al. 2013, Edmunds et al. 2014) with structurally complex branching corals becoming less common and corals with massive growth forms increasing in abundance (Loya et al. 2001, Fabricius et al. 2011, van Woesik et al. 2011). Because coral larvae often settle upon dead coral skeleton, the future resilience of coral reefs will depend in part on the suitability of the structure left behind following a coral mortality event.

To understand the how some coral reefs may be affected by a disturbance that kills coral tissue but leaves the skeleton intact, it is important to determine how new corals will perform on dead coral structure with differing structural complexity, as well as how resistant the dead host coral structure is to erosion. Recent disturbances in Moorea (Adjeroud et al. 2009, Pratchett et al. 2010, Adam et al. 2011), offer an opportunity to examine the effects of architectural complexity of the substrate on recruitment of new coral colonists. A recent outbreak of crown-of-thorns seastars (COTS, *Acanthaster planci*) killed coral tissue over large areas, which was followed by a cyclone that removed dead coral skeletons from some (particularly the outer reefs on the north shore) but not all of the reefs affected by COTS (Adam et al. 2011, Kayal et al. 2012). In this study, I explore how recruitment of sexually-produced coral colonists is affected by variation in structural complexity, particularly with respect to the skeletons of recently-killed branching coral. I quantified growth and survival

of juvenile corals on structurally complex *Pocillopora* skeletons and on massive *Porites*, then generated quantitative predictions about the role these different types of substrates play in the replenishment of coral populations in the lagoons of Moorea. Such understanding is vital given that climate change is likely to increase the frequency of disturbances that kill coral tissue versus those that also reduce habitat complexity (Glynn 1996, Hoegh-Guldberg 1999, Pratchett et al. 2008, Baker et al. 2008).

Methods

Study site

This study location was the back reef on the north shore of Moorea, French Polynesia (17°30'S, 149°50'W), which contain a landscape of patch reefs comprised primarily of large colonies of species of massive *Porites*, eroded coral substrate (hereafter, pavement), sand and coral rubble. In addition to the massive *Porites* structures, large colonies of *Porites rus* and smaller branching corals (*Acropora* spp. and *Pocillopora* spp.) occur, the latter growing on top of massive *Porites* structure as well as stable areas of the benthos. The reefs of Moorea experienced an outbreak of crown-of-thorns seastars (*Acanthaster planci*) between 2006-2009 resulting in a reduction of live coral cover from ~40% to < 5% on the fore reef (Adam et al. 2011, Kayal et al. 2012) as well as some mortality of corals in the lagoons (pers. obs). In 2010 Cyclone Oli removed the majority of the remaining coral structure on the fore reef on the north shore, but in the sheltered back reef environment much of the dead coral structure remained intact immediately following the cyclone (Adam et al. 2014).

Availability of habitat for coral establishment and patterns of abundance of juvenile corals

The types of structure suitable for coral settlement and growth were quantified in lagoons (1.5 – 3 m depth) to evaluate how benthic community composition and structural complexity influence the return of coral. In 2011 and 2015, transect surveys were conducted on SCUBA in the mid-lagoon just east of the Cook's Bay Pass to estimate the types and availability of habitat suitable (defined as stable, dead coral structure) for coral recruitment. Using 25 x 2 m belt transects ($n = 10$) positioned parallel to the reef crest, I quantified the overall benthic community composition on habitat types suitable for coral. Excluding sand, unconsolidated coral rubble and live coral tissue, the four suitable habitat types were dead massive *Porites* spp., dead *Porites rus*, pavement and dead *Pocillopora* spp. with naturally occurring mixed communities of crustose coralline algae and turfing algae on their surfaces, but largely devoid of macroalgae.

The four habitat types were then surveyed for established juvenile corals of all genera. Densities of all live juvenile (0.5-5 cm diameter) corals (Hall and Hughes 1996) on each habitat type were assessed in 0.25 m² quadrats ($n = 20$ each for dead massive *Porites* spp., *Porites rus*, and pavement) as they were encountered along the transects described above. Due to the smaller size of dead *Pocillopora* structures compared to other habitat types, live corals growing on *Pocillopora* skeletons were surveyed in smaller (0.0625 m²) quadrats ($n = 40$). All densities were scaled to number m⁻². Following testing for homogeneity of variance I determined that data did not require transformation using a quantile-quantile plot. Juvenile coral density data were analyzed for differences among mean coral densities on the four habitat types using a one-way ANOVA followed by a

Tukey's honest significant difference post hoc analysis using JMP (v. 11) and a sequential Bonferroni correction to account for multiple comparisons.

Growth and survivorship of coral on dead massive Porites, pavement and Pocillopora

I quantified juvenile coral survivorship and growth to evaluate the effect of high and low habitat complexity on coral performance. High complexity habitat was dead *Pocillopora* skeletons, while the remaining three habitat types (dead massive and mounding *Porites*, pavement) were defined as low complexity habitats. For this analysis I focused on Pocilloporid corals because 94% of colonists belonged to this genus. To determine growth and survival of juvenile *Pocillopora*, 206 corals were marked on two low complexity habitats (remnant massive *Porites* structures and pavement) and one high complexity habitat type (dead *Pocillopora* structures). Since very few juvenile (or adult) corals were found on remnant *Porites rus* bommies, I was unable to include this habitat type in the study. In 2012, corals were marked individually by attaching numbered tags (Allflex Global Sheep Ear Tags) on dead massive *Porites* (average juvenile *Pocillopora* diameter 25.3 ± 1.5 mm, $n = 60$) and pavement (average diameter 25.5 ± 0.88 mm, $n = 60$) within 5 cm of each coral. On *Pocillopora* skeletons corals (average diameter 25.9 ± 1.7 mm, $n = 86$) were marked using color-coded acrylic beads (Pop Beads) on cable ties attached to the branch adjacent to each coral.

For each marked juvenile *Pocillopora* colony diameter (maximum diameter (L) and the axis perpendicular (l)) and height (h) were measured to the nearest 0.1 mm using Vernier calipers. Measurements were taken at the start of the study and after one year during the Austral winter of 2012 and 2013. The three measurements of juvenile coral colony size (L , l ,

and *h*) were averaged to estimate mean colony diameter, which was used to estimate colony growth (final average diameter - initial average diameter) over 1 year.

One-way ANOVA confirmed there were no initial differences in mean size of the juvenile *Pocillopora* selected to evaluate among the three habitat types (ANOVA, $F_{2, 205} = 0.3, p = 0.74$). Data were checked for normality using quantile-quantile plots and log transformed to improve normality. A one-way ANOVA was used to test whether coral growth (log final average diameter – log initial average diameter) depends on initial *Pocillopora* colony size and a one-way ANOVA with heterogeneous variances tested whether coral growth depends on habitat. For survivorship of the marked cohort, I used ANCOVA with a binomial error distribution to test whether survivorship differed among habitat types or with initial coral size after 3 years. Models were run using the statistical language R (R core development team, 2016).

Erosion of dead Pocillopora and massive Porites skeletons

Based on morphological differences between massive *Porites* and *Pocillopora*, I hypothesized that the skeletons of dead *Pocillopora* would erode more rapidly than those of massive *Porites*. To test this hypothesis I quantified (1) the erosion rates of dead massive *Porites* and *Pocillopora* over 3 years, and (2) the performance (growth or erosion) of adult *Pocillopora* colonies that were either alive or had suffered partial mortality prior to 2012. Colony growth and the erosion were quantified beginning in 2012 in four 20 x 20 m plots at the study site. Plots were selected in the survey area to represent naturally occurring *Pocillopora* varying in size and condition. Within each plot every *Pocillopora* colony > 100 cm diameter was individually marked ($n = 171$ total) using numbered tags attached with a

nail at the base of the colony. All marked *Pocillopora* were classified in 2012 as belonging to one of three categories: (1) dead with only the skeleton remaining ($n = 110$), (2) partially dead but with some living tissue ($n = 53$), or (3) entirely living ($n = 8$, few living and undamaged colonies were present). A planar photograph was taken of each colony from the closest distance required to encompass the entire colony in the frame (Canon PowerShot D20). Colony circumference and the proportion of the colony that was living and dead were quantified from photographs using ImageJ. Colony circumference was used to calculate colony surface area using an equation obtained from the aluminum foil technique (Marsh 1970, Baker et al. 2008). Using a linear regression I established the best relationship ($r^2 = 0.92$, $p < 0.0001$) between dead *Pocillopora* colony circumference and surface area (obtained by covering the entire 3-dimensional surface of a given coral with aluminum foil, and using the weight of the aluminum foil to estimate the surface area) from colonies ranging in circumference from 0.13 to 1.6 m, $n = 10$ and obtained the equation $A = 3.19 C^{2.16}$ (where A is surface area in m^2 , and C is circumference in m). This equation was then used to calculate the surface area of marked *Pocillopora* colonies in the field and their erosion over time. While this technique does not quantify erosion with high precision the aim of this study was to quantify large changes in colony size, and this technique of photograph analysis was suitable for that purpose.

In addition to determining the erosion rates of dead *Pocillopora*, I evaluated the ability of adult *Pocillopora* colonies that had suffered partial mortality to recover (either re-grow tissue over remnant skeleton or to grow laterally out from it) as well as the growth, mortality, and erosion of live *Pocillopora* colonies during the same time period. The erosion of dead massive *Porites* skeletons was estimated from photographs of the same colonies

taken in 2012 and 2015. These photographs were taken at the same site the surveys were completed. Using ImageJ software I quantified the change in planar surface area of each massive *Porites* skeleton ($n = 9$) over 3-years. I used a Student's t-test to compare the skeletal erosion rates (defined as the difference in surface area) over 3 years (2012 to 2015) of dead massive *Porites* and dead *Pocillopora* following testing for statistical assumptions and determining that data did not require transformation.

Consequences of habitat selection

The estimates of growth and survivorship of juvenile *Pocillopora* allowed me to estimate potential impacts of the presence of different types of habitat structure on replenishment of coral to the reef. I used survivorship data from *Pocillopora* growing on pavement, dead massive *Porites* and dead *Pocillopora* to calculate overall *Pocillopora* survival. This was quantified as the number of corals surviving to 3 years summed over all habitat types, per meter squared of reef habitat available for coral settlement. I excluded *Porites rus* from these calculations because no adult corals were observed growing on *P. rus*, despite a few observations of juvenile corals growing on *P. rus* initially. To determine how dead *Pocillopora* structures affected survivorship over 3 years on a larger scale, I calculated overall coral survival under two scenarios, each of which assumes no *Pocillopora* structure persists: (1) all juvenile corals found on *Pocillopora* are assumed to recruit to the other substrate types (i.e., massive *Porites*, and pavement) in proportion to the relative availability of those habitats and showed the same growth and survivorship as colonies that recruited to each of those two habitats, and (2) all juvenile corals found on *Pocillopora*

recruited to massive *Porites* only and showed the same growth and survivorship as colonies that recruited to that habitat.

The first scenario explores the case in which *Pocillopora* structures are not available as habitat for young corals to grow on and coral larvae recruit to the remaining habitat types. Because I calculated the mortality rates of juvenile *Pocillopora* on massive *Porites*, pavement and *Pocillopora* structures, it was possible to calculate the density of juvenile corals persisting to 3 years on each type using the equation

$$D_{i,final} = (P_i D_{poc} + D_{i,initial}) S_i$$

where P_i is the proportion of the habitat available for coral recruitment comprised of type i , D_{poc} is the initial density of juvenile corals on dead *Pocillopora* structure, $D_{i,initial}$ is the initial density of juvenile corals on habitat type i from my surveys, and S_i is the fraction of corals on habitat type i that survive until 3 years. This calculation makes it possible to test the hypothesis that coral survival would be greater in the absence of *Pocillopora*, if corals instead settled on other available habitats.

For Scenario (2) I assume that no *Pocillopora* skeletons remain following a disturbance, and that all juvenile corals I found on *Pocillopora* recruited to massive *Porites* only. I used the equation

$$D_{MP,final} = (D_{poc,initial} + D_{MP,initial}) S_i$$

for the massive *Porites* substratum, which has the same form as the equation for Scenario (1), except that all the juvenile corals I observed on *Pocillopora* structure were assumed to settle on massive *Porites* (MP) and not other substrate types. This calculation allows me to

test the hypothesis that overall coral survivorship would be greater if all coral recruitment on *Pocillopora* instead had occurred on *Porites*.

Results

Availability of habitat for coral establishment and patterns of abundance of juvenile corals

Of the total number of live juvenile coral counted in initial (2011) surveys, most were on dead *Pocillopora* skeletons (~ 51%, 161 corals) and dead massive *Porites* (~ 44%), while a much smaller fraction occurred on pavement and dead *Porites rus* (~ 2% each) (Fig. 1a).

This distribution did not reflect the relative availability of these habitat types (Fig. 1b). Two-thirds of the substrate suitable for coral colonization in 2011 was comprised of dead massive *Porites*, followed by dead *Pocillopora* skeletons (~ 16%) and then pavement and dead *Porites rus* (Fig 1b). The density of juvenile corals in 2011 was the highest on dead *Pocillopora* skeletons, which on a per area basis was nearly 5 times more than on massive *Porites* and 10 times greater than on pavement or dead *Porites rus* (Fig. 1c; ANOVA, $F_{3,99} = 16.84$, $P < 0.001$).

Four years later, > 98% of live corals were found on dead *Porites*, with very few colonies on pavement (9 colonies in 42 m² of reef) (Fig. 2a). Due to erosion, dead *Pocillopora* skeletons and dead *Porites rus* structures became so scarce that they did not occur in the 2015 transects. In 2015, the survey indicated that dead massive *Porites* represented ~ 86% of the habitat suitable for corals with pavement constituting (almost) all of the rest (Fig. 2b). Wider inspection (diver surveys of ~ 2000 m² of the site) revealed a few remnant *Pocillopora* skeletons remained, and also that the density of coral recruits on these skeletons in 2015 was still > 3 times greater than the density on massive *Porites* (Fig. 2c).

Growth and survivorship of coral on dead massive Porites, pavement and Pocillopora

Study of naturally occurring juvenile corals revealed that survivorship differed for colonies that recruited on dead *Pocillopora* and pavement versus massive *Porites*, with 6 % of 60, 7 % of 60 and 21 % of 85 juvenile *Pocillopora* alive after three years, respectively (Fig. 3). Survival among years differed by habitat type. Survivorship of corals alive at the start of the third year (2014-15) depended on their size and habitat, as there was a significant size by habitat interaction ($\chi^2 = 8.85$, $df = 2$, $p = 0.012$). Corals growing on pavement were more likely to survive if their initial size was larger ($\chi^2 = 8.41$, $df = 1$, $p = 0.004$), however initial coral size not influence survival on *Pocillopora* ($\chi^2 = 3.3$, $df = 1$, $p = 0.07$) and massive *Porites* ($\chi^2 = 0.36$, $df = 1$, $p = 0.54$).

Annual colony growth did not differ for juvenile *Pocillopora* spp. on massive *Porites* ($6.42 \text{ mm} \pm 1.07$ mean \pm SE growth in average colony diameter in mm) versus dead *Pocillopora* (7.94 ± 2.58 mean \pm SE) and pavement (5.53 ± 1.79 mean \pm SE) (ANOVA, $F_{2, 64} = 27.65$, $p = 0.44$). Initial juvenile colony size did not have a significant effect on coral growth (ANOVA, $F_{1, 63} = 0.06$, $p = 0.08$).

Erosion of dead Pocillopora and massive Porites structure

The rates of erosion of the different recruitment habitats at the study site differed dramatically. Dead *Pocillopora* lost 69% of their calculated surface area between 2012 and 2015 (Fig. 4). By contrast, dead massive *Porites* structures did not erode significantly during the same time period (Student's t-test, $df = 1$, $t = 0.12$, $p = 0.90$, Fig. 4).

Consequences of habitat selection

In both modeling scenarios, the effect of removing all *Pocillopora* structure resulted in an overall net positive outcome for survivorship of juvenile coral. In the first scenario where juvenile (*Pocillopora* spp.) corals that would have recruited to dead *Pocillopora* structures instead recruited to massive *Porites*, the size of the juvenile *Pocillopora* population would have been enhanced by 103 % more colonies (i.e., just over a doubling of coral abundance). In the second scenario in which juvenile corals growing on dead *Pocillopora* structure instead grew only on massive *Porites* structure, the overall *Pocillopora* population would have had 126 % more colonies.

Discussion

Reef-forming corals can be disturbed by two qualitatively different types of disturbances – those killing coral tissue, but leaving their skeletons intact, and those reducing reef architectural complexity by removing coral skeletons. A long-standing issue in ecology has been whether the likelihood of return to a coral dominated community differs between these two types of disturbances (Colgan 1987, Connell et al. 1997, Connell 1997, Tokeshi and Daud 2010, Kayal et al. 2012). There is compelling evidence that physical damage to structural components of a reef can impede the return of a high coral cover community (Connell et al. 1997, Birkeland 1997, Alvarez-Filip et al. 2009, Traçon et al. 2011). Among the proposed causes for a slow rate of return to coral dominance are the loss of settlement cues and/or habitat for new coral settlers, substratum instability that results in high mortality of coral recruits, and space preemption by macroalgae (Connell et al. 1997, Sheppard et al. 2002, Graham et al. 2006). Researchers have argued that more of these important ecological

processes remain intact when reef complexity is not reduced by a perturbation that kills coral over landscape scales (Connell et al. 1997, Alvarez-Filip et al. 2009, Graham et al. 2015), and thus a return to a coral community may be faster from disturbances that leave coral skeletons in place (Connell et al. 1997, Sheppard et al. 2002, Graham et al. 2009). Results of the work I report here reveal that some coral skeletons can serve as a sink (*sensu* Pulliam 1988) for recolonizing corals due to rapid erosion of the dead biogenic complexity.

Branching corals such as *Pocillopora* and *Acropora* can provide a substantial amount of architectural complexity to a reef, but they are more prone to complete destruction by physical forces compared to more massive forms such as *Porites* (Woodley et al. 1981, Hughes and Connell 1999, Marshall 2000, Nyström et al. 2000, Madin and Connolly 2006, Madin et al. 2014). Species of branching corals also may be more susceptible to temperature extremes (Fox et al. 2003, Baker et al. 2008) and in the Indo-Pacific are preferred by crown-of-thorns seastars (Colgan 1987, Tokeshi and Daud 2010, Kayal et al. 2012). Thus, the widespread death of branching corals may be accompanied by a substantial reduction in structural complexity of a reef. Based on the results of the present study, the presence of remnant *Pocillopora* structure can impede the rate of return to coral dominance compared to a disturbance that leaves only massive coral structures or removes coral skeletons entirely. When reefs are disturbed by a physical disturbance that removes branching coral structure and leaves more robust massive coral structure intact, as occurs periodically in Moorea via predation by crown-of-thorns seastars or coral bleaching (Trapon et al. 2011), subsequent coral colonization on the most physically robust structures can result in a more rapid return to coral dominance. Because my study and others have shown that branching skeletons tend to be colonized by coral recruits at a much greater rate - but also erode at a much faster rate -

than skeletons of massive corals, a perturbation that only kills coral tissue can produce an ecologically significant sink for colonizing corals during the time branching structure erodes. In the current study, the estimated time for the complete erosion of dead *Pocillopora* structures is on the order of 3 – 5 years. This erosion likely occurs via internal bioeroders (such as bivalves and sponges), external bioeroders (such as sea urchins) as well as through mechanical damage caused by waves and boat anchors. Scenario modeling indicated that corals at my study site 5 years after the disturbance would have been > 100% more abundant had the coral that recruited to *Pocillopora* skeletons instead colonized the low complexity habitats (assuming no change in habitat-specific juvenile coral survivorship rates). Thus at least for the back reef of Moorea, there is evidence suggesting the coral community might recover twice as fast following a disturbance that removes branching coral skeletons.

Erosion of the coral structure after disturbances has been documented on numerous reefs over short time scales of a few years (Sheppard et al. 2002, Graham et al. 2006) to longer decadal time scales (Alvarez-Filip et al. 2009). Branching corals forming complex reef structure in the Indian Ocean eroded within three years after the 1998 El Nino bleaching event (Sheppard et al. 2002), and after six years in the Maldives (Schuhmacher et al. 2005). Such erosion of the reef structure can have important and sometimes long-lived consequences for the fish and invertebrate communities following a disturbance. After a bleaching event in the Seychelles researchers attributed a time lag in the decline of some fish species to the physical breakdown of habitat over 7 years (Graham et al. 2006, 2007). Yadav (2015) observed that coral recruits preferentially settled on tabular coral skeletons (such as acroporids) in the northern Indian Ocean, despite their structural instability resulting in high mortality (Yadav et al. 2015). Such findings are similar to the structural instability and high

mortality of corals on dead *Pocillopora* in the present study. While this is not the first study to suggest that the structure of dead branching coral erodes rapidly on a coral reef (Graham et al. 2006, Adam et al. 2015, Yadav et al. 2015), it is the first to evaluate how this process might impede the return to a high coral cover community.

The fore reef of Moorea is remarkably resilient to periodic disturbances, and returns to coral dominance within a decade (Adjeroud et al. 2009, Trapon et al. 2011, Adam et al. 2011, Leray et al. 2012, Bramanti and Edmunds 2016). Back-to-back disturbances recently occurred to the north shore fore reef of Moorea; in 2006-2009, an *Acanthaster planci* outbreak resulted in massive loss of live coral (Kayal et al. 2012) and in early 2010, a category 4 cyclone removed dead branching coral structure (Adam et al. 2014). Thus the cyclone may have accelerated the rate of recovery by removing the potential ‘sink’ habitat for recolonizing juvenile coral from the exposed fore reef.

Research has suggested that some morphotypes of corals are becoming relatively more abundant in response to climate shifts and altered disturbance regimes (Fabricius et al. 2011), and there is evidence for coral community compositional shifts over geological time scales (Edmunds et al. 2014). The corals suggested to become more common on contemporary coral reefs in the Indo-Pacific are the encrusting and massive forms such as massive *Porites*, while structurally complex corals such as Acroporids and Pocilloporids may be among the genera that are likely to be less common (Loya et al. 2001, Fabricius et al. 2011, van Woesik et al. 2011). The findings in the present study suggest that a shift to dominance by corals with massive growth forms such as massive *Porites* in future decades may speed the return to coral dominance between disturbances.

The instability of branching coral structure is likely to have important consequences for the survival of young corals that settle on them, which may be compounded by the susceptibility of those same branching corals to bleaching (Marshall and Baird 2000) and predation by the crown-of-thorns seastar (Kayal et al. 2012). However, in some cases rapid regeneration (1 -5 yrs) of bleached tissue of corals has been reported (Diaz-Pulido et al. 2009, Hughes et al. 2013, Roff et al. 2014). The potential for regeneration of corals that have lost some of their living tissue through predation is not well understood (Henry and Hart 2005, De'ath et al. 2012). There is evidence for rapid regeneration for some massive forms of *Porites* (van Woesik 1998, Hughes 2003), yet little is known about the regenerative capacity for adult *Pocillopora* (Henry and Hart 2005, Mumby et al. 2007). However, results from Lenihan and Edmunds (2010) suggest that juvenile *Pocillopora* in Moorea can enhance growth in response to fish predation (Lenihan and Edmunds 2010) and this regenerative capacity exceeds that of juvenile *Porites* (Edmunds and Lenihan 2009). In the present study the majority of *Pocillopora* (95 %) were dead or had suffered partial mortality in the back reef of Moorea prior to 2012. I found limited evidence for the recovery of adult *Pocillopora* colonies after partial mortality. The majority (77 %) of adult *Pocillopora* that had undergone partial mortality prior to 2012 died and eroded by within 3 years. When combined with the erosion of dead colonies by ~ 70 %, the instability of these structures is likely to have significant consequences for young corals that settle on this habitat type.

Given the increasing intensity and frequency of perturbations to coral reef ecosystems that are likely to occur due to climate change (Hughes 2003, Hoegh-Guldberg et al. 2007), it is crucial to understand the mechanisms underlying coral recovery processes (Graham et al. 2011, Roff and Mumby 2012). Graham et al. (2015) demonstrated that for a

large network of reefs in the Indian Ocean, the two most accurate predictors of coral community recovery were habitat complexity and water depth. They found that coral larval supply was not a good predictor of recovery, however coral juvenile density, resulting from post settlement mortality processes were associated with the rate of coral recovery. The results from the present study suggest that at least for some reefs, the complexity afforded by dead *Pocillopora* structure combined with the high coral recruitment to this habitat, may be delay the coral recovery process.

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Figures

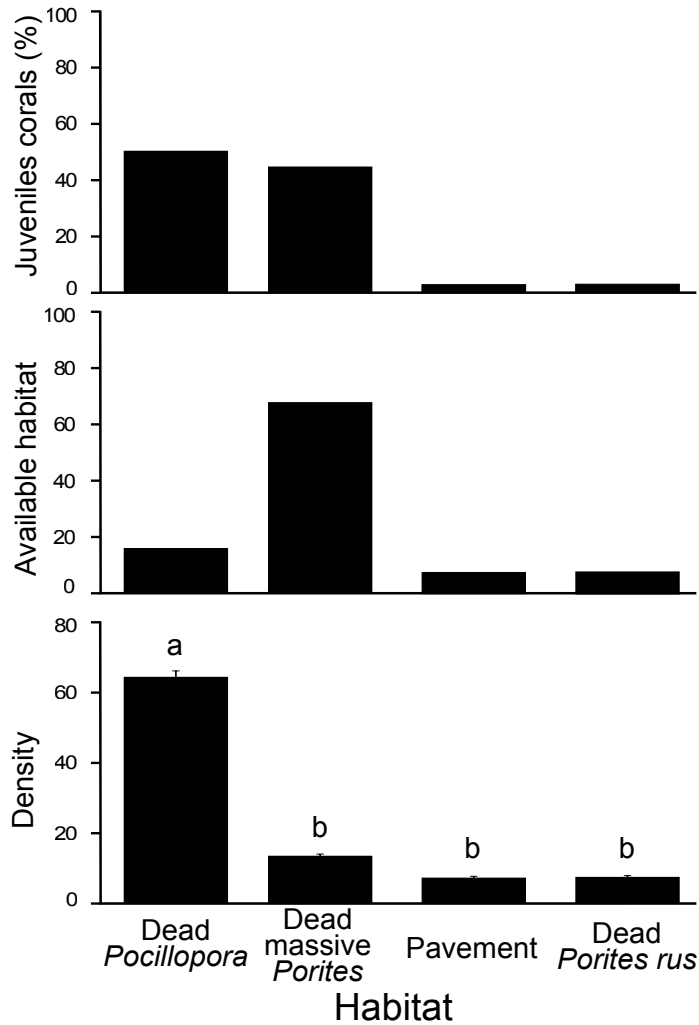


Figure 1. The percentage of the benthos that was potentially suitable for coral recruitment comprised of pavement and dead corals (massive *Porites*, *Pocillopora*, and *Porites rus*) (bottom); density (no. m⁻²) of juvenile corals on each habitat type from $n = 40$ quadrats for *Pocillopora* and $n = 20$ quadrats for all other habitats and, (middle) available settlement habitat for corals from $n = 10$ transects at the study site, (top) the percent total contribution (combined habitat availability and juvenile coral density) of each habitat to coral recruitment in 2011. Different letters indicate significant differences among means from Tukey's post hoc analysis.

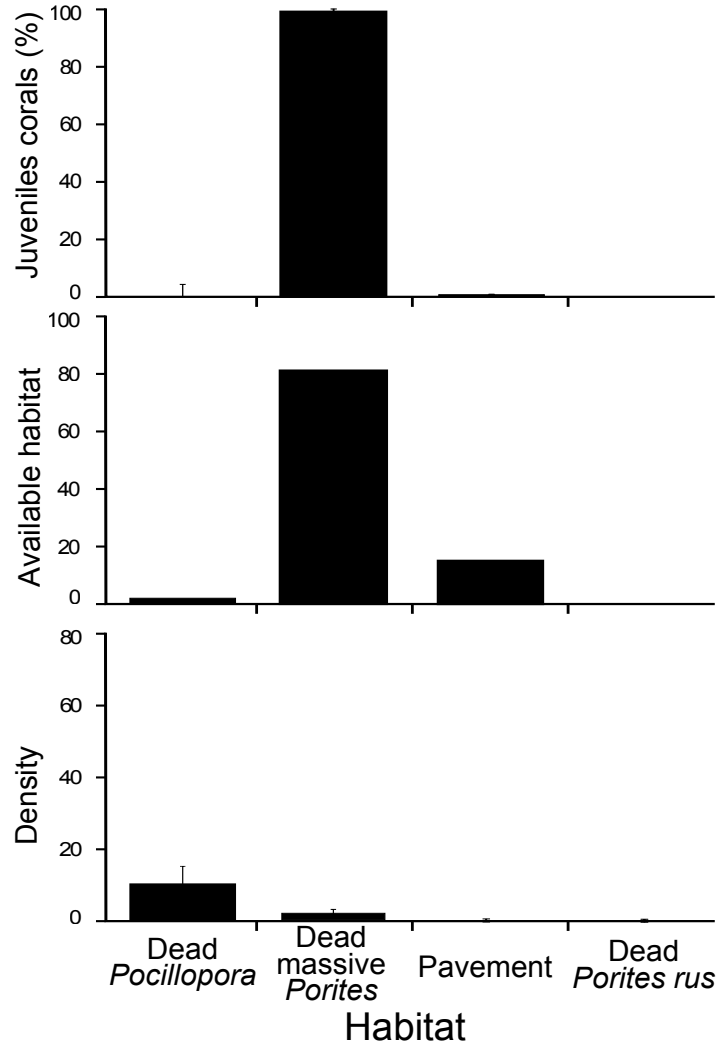


Figure. 2. The percentage of the benthos that was potentially suitable for coral recruitment in 2015 comprised of pavement and dead corals (massive *Porites*, *Pocillopora*, and *Porites rus*) (bottom); density (no. m⁻²) of juvenile corals on each habitat type from n = 40 and n = 20 quadrats for *Pocillopora* and all other habitat types, respectively, (middle) percentage of available habitat at the study site from n = 10 transects and, (top) the percent total contribution of each habitat (combined habitat availability with juvenile coral density) to coral recruitment in 2015.

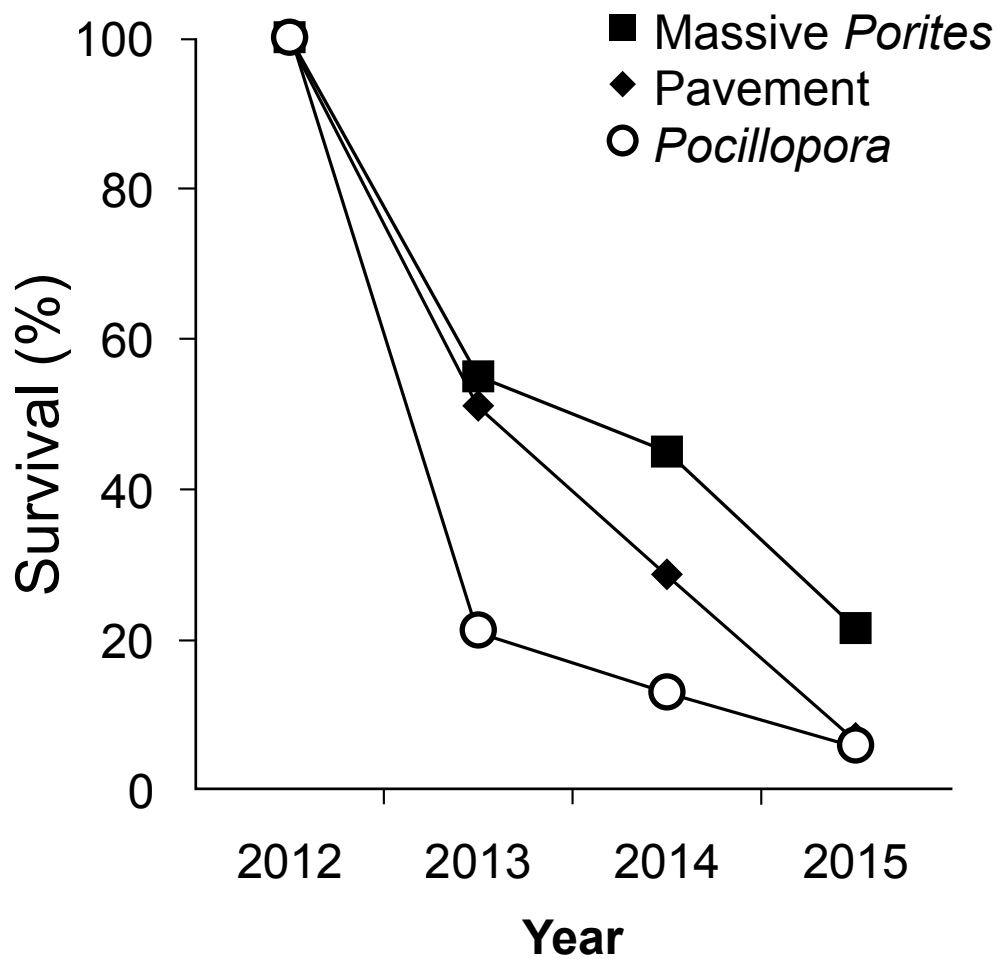


Figure 3. The percentage of surviving juvenile corals growing on dead massive *Porites*, pavement and dead *Pocillopora* from 2012 to 2015. $n = 60$ *Pocillopora* on dead massive *Porites* and pavement and $n = 85$ *Pocillopora* on dead *Pocillopora* in 2012.

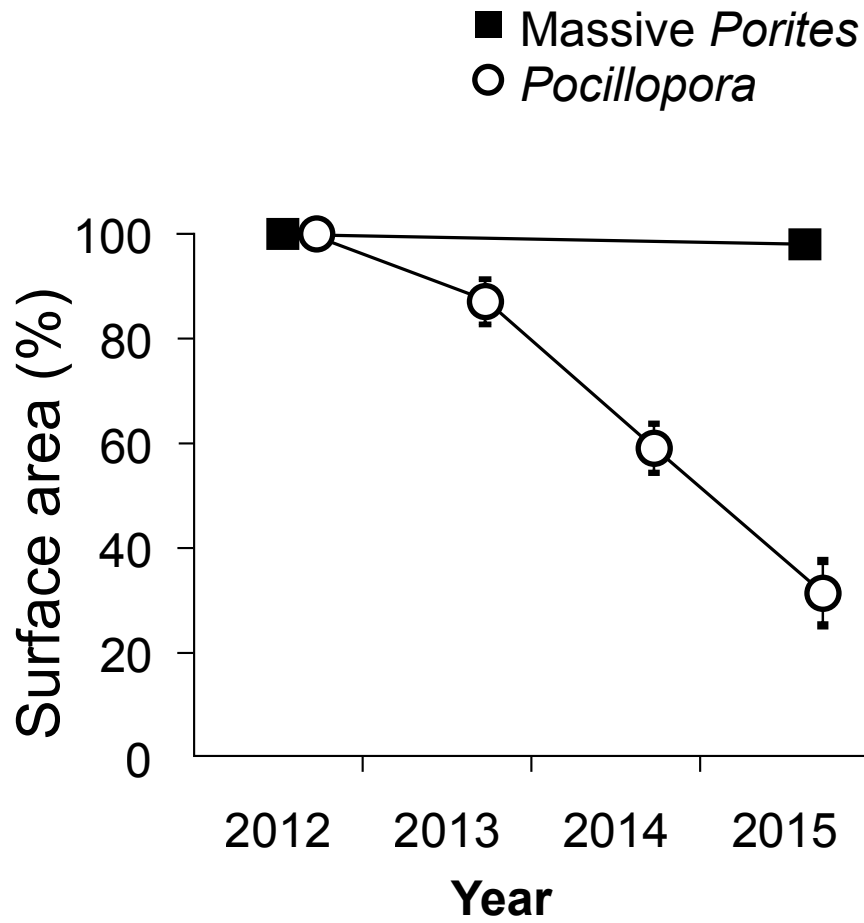


Figure. 4. Average erosion (percent change in surface area \pm SE) of dead *Pocillopora* ($n = 110$) and massive *Porites* ($n = 8$) in the back reef of Moorea from 2012 to 2015.

II. Title: Echinoids indirectly facilitate coral survival and growth through the creation of nursery habitat

Abstract

The availability of suitable recruitment habitat can be critical for the success of sessile marine organisms with a free-living larval stage. For scleractinian corals, microhabitats like cracks and crevices in the hard substrate may provide protection from predators during vulnerable life stages. The bioeroding echinoid *Echinometra mathaei* may indirectly influence the success of juvenile corals by creating habitat ideal for coral recruitment. Results from this study revealed that despite only comprising approximately 6 % of the surface area of dead massive *Porites*, *E. mathaei* crevices harbored 40 % of the juvenile corals growing on those structures, a pattern that could reflect both habitat selection at settlement and subsequent performance. Survivorship of juveniles was twice as great for colonies that settled in sea urchin crevices compared to adjacent exposed surfaces, but only when the crevice was not occupied by an urchin. This suggests that the habitat created by *E. mathaei* may have a net positive effect on coral recruitment success, yet there appears to be a tradeoff between the protection from predators within a crevice and the incidental abrasion or predation by the echinoid itself.

Introduction

The ability for species to select suitable habitat is especially important for non-motile organisms with a free-living dispersal stage such as terrestrial plants and sessile marine organisms, because individuals generally cannot move from an unfavorable location after settlement. One such group is scleractinian corals whose larvae use signals to induce settlement (Raimondi and Morse 2000). These signals include chemical cues from crustose

coralline algae (CCA) (Morse et al. 1988, Harrington et al. 2004), macroalgae (Dixson et al. 2016), and bacterial biofilms (Webster et al. 2004) as well as abiotic cues from sediments on benthic surfaces (Maida et al. 1994, Price 2010, Lenihan et al. 2011, Edmunds et al. 2014), changes in the light environment (Maida et al. 1994, Mundy and Babcock 1998), and perhaps even sound (Vermeij et al. 2010).

It has been shown for corals, that cues can signal microhabitats suitable for coral growth and survival (Arnold and Steneck 2011). For example, coral larvae have a strong positive behavioral preference at settlement for some species of CCA and not others (Harrington et al. 2004). Preferred CCA yield higher body growth and per capita survival rates compared to species of CCA that are avoided behaviorally by larvae (Harrington et al. 2004, Price 2010). Preferred species of CCA often are associated only with holes or crevices (Price 2010). Additionally, changes in light intensity and spectral characteristics have been shown to induce settlement (Maida et al. 1994, Mundy and Babcock 1998). Per capita survivorship of newly recruited corals can be greater in crevices (mm to cm in scale) than on adjacent exposed surfaces (Price 2010, Doropoulos et al. 2016), largely due to incidental or targeted predation by herbivores and corallivores respectively (Doropoulos et al. 2016). Thus, other taxa that influence the availability of crevice space can indirectly mediate coral recruitment.

Bioeroding echinoids have the potential to affect settlement and early survival of corals via enhancement (Swanson in prep.) or degradation of CCA (O'Leary et al. 2012) and/or the provision of crevice space (Birkeland and Randall 1981). When echinoid populations are large, bioeroding echinoids can reduce topographic complexity and the cover of CCA through intensive grazing, and consequentially reduce population sizes of

coral recruits (McClanahan and Muthiga 1988, O'Leary and McClanahan 2010, O'Leary et al. 2012, 2013). However, at moderate densities, these echinoids create distinctive crevices – by repeatedly scraping the benthos with their feeding structures (Birkeland and Randall 1981) – that enhance small-scale structural complexity of the reef and are associated with high cover of CCA within and surrounding them. These microhabitats could potentially provide favorable habitat for recruitment of corals, and thereby bioeroding urchins could have a positive impact on the coral community.

In the lagoon of Moorea, French Polynesia, the bioeroding echinoid *Echinometra mathaei* primarily inhabits dead massive *Porites* colonies, creating crevices on their surfaces. Dead *Porites* is one of the primary substratum types that is available in the lagoon habitat of Moorea for the establishment of branching corals (primarily *Pocillopora* spp. and to a lesser degree *Acropora* spp). Here, I test the hypothesis that the bioeroding urchin *E. mathaei* can facilitate the growth and survival of branching coral through the provision of crevice space. Results of this study shed further light on the biotic and abiotic factors that influence early success of coral on these reefs.

Methods

Study site

This research was conducted in the lagoon between Cooks Bay and Irihonu Pass on the north shore of Moorea, French Polynesia (17° 30' S, 149° 50' W), in areas where coral patch reefs ('bommies') are interspersed among stretches of sand, dead coral rubble and eroded coral structure at depths of 1 to 3 m. Many of the patch reefs are colonies of massive *Porites* spp. (including *Porites lobata* and *Porites lutea*) ranging from 0.5 – 2 m in height (for a

more detailed description see Lenihan et al. 2011). A variety of invertebrates (including bioeroding bivalves and echinoids) and numerous taxa of coral grow on the surface of dead massive *Porites* bommies. The echinoid *Echinometra mathaei* is a common bioeroding species associated with this habitat. *E. mathaei* create distinctive crevices on bommies by repeatedly scraping at the substratum with their Aristotle's lantern (Birkeland 1997), which are readily identifiable based on their dimensions and shape (McClanahan et al. 1996, Birkeland 1997). They vacate their crevices only during nocturnal feeding periods, and individuals return to their home crevices to shelter during the day (Mills et al. 2000). *Echinometra mathaei* are primarily herbivorous and in Moorea their crevices are devoid of macroalgae and often dominated by crustose coralline algae (CCA), which can act as a settlement cue for coral (Harrington et al. 2004).

Patterns of distribution and abundance of juvenile corals on Porites bommies

Preliminary observations in the lagoon of Moorea revealed juvenile corals frequently growing within the crevices created by *E. mathaei*. To quantify the frequency with which juvenile coral occupy *E. mathaei* crevices, I counted juvenile corals (≤ 4 cm diameter, *sensu* (Hall and Hughes 1996)) on 43 dead massive *Porites* (size range 0.5 – 1.6 m diameter), as well as the number of microhabitats created by *E. mathaei*. These bommies were devoid of macroalgae, but had live coral colonies of a variety of taxa living on them. I evaluated the location of all juvenile corals on massive *Porites* spp. in 2011, and classified each coral as either growing within an urchin crevice, or on an open, exposed surface (> 1 cm from any echinoid crevice). Each *Porites* bommie was measured to the nearest cm (diameter in two dimensions and height), and all *E. mathaei* on the bommie were counted. The massive

Porites bommies in the lagoon habitat in Moorea are relatively hemispherical in shape with rounded tops and flat bottoms attached to the benthos, therefore the surface area of each bommie was estimated using the equation for the surface area of a hemisphere ($2 \pi r^2$). To determine the availability of *E. mathaei* crevice space versus open space on *Porites* bommies, the dimensions of all *E. mathaei* crevices were measured to the nearest mm with Vernier calipers to calculate an average width (29 ± 1 mm, mean \pm SE) and length (113 ± 4 mm). These values were used to estimate the amount of the surface of each bommie that was comprised of *E. mathaei* crevice aperture versus open space (the remaining surface area).

Field experiment to estimate growth and survival of Pocillopora in different bommie microhabitats

Recent studies in Moorea show that the majority of newly-recruiting corals between 2011-2015 were pocilloporids (Edmunds et al. 2014, Bramanti and Edmunds 2016). I thus focused on *Pocillopora* and tested whether the habitat created by *E. mathaei* affected the post-settlement performance of corals relative to their performance on exposed surfaces. This involved evaluation of growth (over 5 months) and survivorship (over 10 months) of 120 juvenile *Pocillopora* spp. transplanted into three different microhabitats on dead *Porites* bommies: sea urchin crevices occupied by *E. mathaei*, unoccupied urchin-created crevices, and open surfaces.

Juvenile *Pocillopora* spp. (not including the brooding species *Pocillopora damicornis*), were collected from the lagoon at depths of 1 to 3 m. Juvenile corals (maximum diameter range = 12 - 28 mm, mean = 21.3 ± 0.3 SE) were carefully removed from the benthos using a chisel. Each coral was transported to the laboratory in a separate

bag with seawater, and transferred into shallow tanks supplied with flowing seawater where they were evaluated visually for signs of damage to the living tissue and corallites. Corals were randomly assigned to one of the transplant microhabitats: 1) inside an *E. mathaei* crevice occupied by a sea urchin ($n = 34$; initial maximum diameter 15.5 - 25.3 mm, mean = 20.9 ± 0.5 mm SE), 2) into an unoccupied *E. mathaei* crevice (following removal of the urchin, $n = 43$; initial maximum diameter 12.5 - 28.4 mm, mean = 20.5 ± 0.5 mm SE) or 3) onto an open surface within 10 cm of one of the marked sea urchin crevices ($n = 43$; initial maximum diameter 18.1 - 28.7 mm, mean = 22.6 ± 0.4 mm SE). ANOVA verified that there were no significant differences in the initial surface area of transplanted corals among treatments ($F_{2,117} = 2.61, p > 0.05$). Corals were placed on 10 marked massive *Porites* bommies 1-2 m apart, with each bommie receiving 5 coral transplants for each of the 3 experimental treatments that initially conformed to a randomized block design; because of unequal loss of replicates among treatments, data were analyzed using GLM with heterogeneous variances with bommie as a fixed factor (see below). Experimental corals were attached to the *Porites* bommie using Z-spar underwater epoxy. Each transplanted coral was measured to the nearest 0.1 mm (diameter in two dimensions and height) using Vernier calipers and marked using a numbered tag attached to the substratum with a nail, adjacent to the coral.

To explore the effect of orientation of coral within an urchin crevice, the position of transplanted corals within echinoid crevices was noted after they were affixed to the substrate. Positions were noted as being on the downward facing surface of the crevice ($n = 15$ survivors), a vertical surface along either edge of the crevice ($n = 16$) or an upward facing surface near the bottom of the crevice ($n = 41$).

Coral growth and survival were assessed 5 months and 10 months after transplantation, respectively. At 5 months and 10 months each coral was classified as living or dead, and their diameter and height were measured to the nearest 0.1 mm. The surface area of each transplanted juvenile coral was calculated using the equation for the surface area of a sphere ($4 \pi r^2$) as in (Kayal et al. 2011) and (Adjeroud et al. 2007) because this geometric shape has been suggested to best describe the three dimensional nature of small corals in this genus. Growth data were log transformed to achieve normality of residuals and relative change in coral surface area ($\log \text{ final} - \log \text{ initial}$) was used for analysis.

Condition of juvenile Pocillopora inside and outside microhabitats

Corals living within microhabitats can experience a tradeoff between the protection from predators and increased competition with competitors (Doropoulos et al. 2016). However, the orientation of a juvenile coral within a microhabitat may mediate the influence of some of the factors likely to result in decreased growth or survival, such as sedimentation or incidental damage due to a sea urchin occupying the same crevice. I used field surveys to determine how living within an *E. mathaei* microhabitat may influence the exposure of juvenile *Pocillopora* to factors such as predation and sedimentation. This included determining the orientation of juvenile corals within *E. mathaei* crevices (occupied and unoccupied) and on exposed surfaces of bommies as well as tissue damage to each coral. I surveyed 192 juvenile *Pocillopora* spp. growing on massive *Porites*: either within *E. mathaei* crevices ($n = 94$), or on open surfaces of the *Porites* bommie ($n = 98$), for predator damage based on the absence of living tissue exposing the skeleton or overgrowth by turf algae. For corals growing within crevices, I recorded the orientation of each coral within the

crevice as 1) on downward facing surfaces, 2) on upward facing surfaces or 3) vertical surfaces and if the crevice was occupied by a sea urchin or vacant. I classified corals as damaged if there was visible loss of coral tissue and damage to the underlying skeleton based on color and the absence of living tissue exposing the skeleton or overgrowth by turf algae following the protocol used by Lenihan (2011).

Environmental attributes of E. mathaei microhabitat and echinoid occupancy

I collected 40 CCA specimens from *E. mathaei* crevices ($n = 16$) and on open surfaces ($n = 24$) of massive *Porites* bommies. Identification in the laboratory involved identifying key characteristics including trichocyte arrangement, conceptacle shape and size (Adey et al. 1982). Samples from crevices were collected as a single continuous sample which included the same CCA thallus ≥ 2 cm outside the crevice and extending inside the crevice to a depth of 5 cm. Samples of CCA were dried and cut perpendicular to the opening of the crevice using a hand-held rotary power tool (Dremel™) to measure the thickness of the crust spanning from the outside to within the crevice. To determine if the thickness of the CCA differed inside and outside of *E. mathaei* crevices, the thickness of each CCA crust was measured at 2 mm increments (to the nearest 0.01 mm using Vernier calipers) from the opening of the crevice extending into and outside of the crevice. I calculated the change in crust thickness with distance inside and outside the crevice by subtracting the crust thickness at the edge (0 mm from the edge) from the thickness at each subsequent interval.

The light inside *E. mathaei* crevices was quantified for 8 *E. mathaei* crevices in the field at 1400 hrs during the austral summer of 2014 using the Fiber Quantum Sensor on a Pulse Amplitude Modulated (PAM) Underwater Fluorometer (Walz). Light measurements

(PAR $\mu\text{mol m}^{-2} \text{s}^{-1}$) were taken at the edge of *E. mathaei* crevices and at 1 cm increments into crevices and at 1 cm and 2 cm outside. Measurements were calibrated in the lab for accuracy against a Li-Cor LI 192 quantum sensor.

To quantify the percentage of *E. mathaei* crevices that are occupied by an echinoid versus vacated crevices, I surveyed 40 massive *Porites* structures (0.5-2.5 m maximum diameter) for crevices that were large enough to accommodate an adult *E. mathaei* using a threaded stainless steel rod (50-cm length) with a PVC disc (4 cm diameter) bolted to the end. The small disc approximated average maximum diameter of adult *E. mathaei*. The disc was inserted into every crevice (of equal or larger dimension than the disc) of each massive *Porites* to provide an estimate of the number of spaces available as refuges for adult *E. mathaei*. Then all of the *E. mathaei* inside crevices were counted on each massive *Porites* and used to quantify the number of crevices that were occupied with a sea urchin versus unoccupied.

Statistical analyses

The growth of transplanted corals at 5 months did not depend on initial coral size (regression analysis: $r^2 = 0.03$, $df = 90$, $p > 0.05$), and there was no difference in initial coral size among treatments (ANOVA $F_{119,2} = 2.6$, $p > 0.05$). The relative growth of transplanted juvenile *Pocillopora* (change in colony surface area: \log final surface area – \log initial surface area) was analyzed among treatments using a GLM with heterogeneous variances with treatment (urchin present, no urchin, and outside surfaces) as fixed factors, and a random factor of location because there was a significant effect of block or *Porites* bommie (R core development team). Another GLM with transplant orientation (for those within

urchin crevices only, downward-facing, upward-facing and side-facing) was used to test for the effect of orientation within a crevice on coral growth. GLM with a binomial error distribution determined that coral survival did not depend on initial coral size ($p = 0.55$, $t = 0.59$) prior to coral survival analysis. Coral survival was analyzed for differences among treatments using a GLM assuming a binomial error distribution to test for differences in survival at 10 months with transplant orientation (downward-facing, upward-facing and side-facing) and treatment (urchin present ($n = 39$), no urchin ($n = 36$), and outside surfaces ($n = 44$)) as fixed factors and a random effect of massive *Porites* bommie.

Results

Patterns of distribution and abundance of juvenile corals on Porites bommies

A total of 311 juvenile corals were counted on 43 massive *Porites* bommies, of which ~40% occurred in *E. mathaei* crevices. The juvenile corals primarily were *Pocillopora* spp. and massive *Porites* spp. The vast majority ($94\% \pm 0.01$) of the surface of the bommies was vacant space occupied by a mixture of dead coral, algal turf and crustose coralline algae. Approximately 6 ± 0.01 % of the surface area of massive *Porites* was composed of shallow burrows made by *E. mathaei*. While there were 2 - 59 *E. mathaei* on each bommie, 62% of their crevices were unoccupied. The mean number of juvenile corals on a bommie associated with *E. mathaei* crevices was 2.9 ± 0.3 (mean \pm SE), while there were 4.5 ± 0.4 on open surfaces.

Field experiment to estimate growth and survival of Pocillopora in different bommie microhabitats

Growth of juvenile *Pocillopora* transplanted into *E. mathaei* crevices, or onto open surfaces, differed among treatments after 5 months (one-way ANOVA, $F_{2,88} = 4.80$, $p = 0.01$). Post-hoc tests revealed growth was highest for corals transplanted within crevices that lacked a resident urchin (change in surface area: 1.6 ± 0.15 , mean \pm SE), which was significantly different from growth on open surfaces (1.1 ± 0.05) (Tukey's HSD no urchin vs. outside surface $p = 0.007$). *Pocillopora* in crevices occupied by urchins (1.3 ± 0.08) grew at an intermediate rate (Fig. 1). When examining corals growing within crevices the growth of juvenile *Pocillopora* was not affected by orientation ($F_{1,2} = 0.44$, $p = 0.64$) and there was no interaction between urchin treatment and transplant orientation ($p = 0.33$, $df = 2$)

Survival of *Pocillopora* to 10 months was highest for transplants in unoccupied crevices (53 %), and much lower for the other two treatments (occupied crevices = 28 %, exposed surfaces = 27 %). The orientation of transplanted *Pocillopora* within crevices affected survival, which was consistent among urchin crevice treatments GLM effect of treatment: $df = 1$, $\chi^2 = 4.65$, $p = 0.031$; effect of orientation: $df = 2$, $\chi^2 = 8.3$, $p = 0.016$, no interaction between orientation and treatment: $df = 2$, $\chi^2 = 0.19$, $p = 0.91$ (Fig. 2). Survival in unoccupied crevices was highest (83%) for corals on downward-facing surfaces, followed by side-facing surfaces (50%), and lowest on upward-facing surfaces (43%). Survival within occupied crevices was lower than survival in unoccupied crevices: 56% for downward-facing surfaces, 29% for side-facing surfaces, and 14% for upward-facing surfaces (Fig. 2).

Field surveys of juvenile *Pocillopora* revealed that a lower percent were damaged when growing inside echinoid crevices than on open surfaces; 72% on open surfaces had

tissue damage compared to 44% in occupied crevices, and 35% in unoccupied crevices (Fig. 3). In these surveys, corals in crevices were found mostly oriented downward-facing (48%) or side-facing (44%), and comparatively few were upward-facing (8%) (Fig. 4). Damage to coral tissues was correlated with the orientation of a coral within a crevice: 60% on side-facing surfaces in occupied crevices were damaged versus 40% in unoccupied crevices. On downward-facing surfaces, 26% sustained damage in occupied crevices versus 33% in unoccupied crevices. Of the few corals found on upward-facing surfaces, 75% of those inside occupied crevices had damage and none of those in unoccupied crevices were damaged.

Attributes of the habitat within E. mathaei crevices

The light availability (PAR $\mu\text{mol m}^{-2} \text{s}^{-1}$) in *E. mathaei* crevices attenuated in a non-linear manner with distance into the crevice (Fig. 5), with the reduction in PAR reaching ~67% by 2 cm of the crevice opening (Fig. 5). The CCA community on open surfaces of massive *Porites* structures was comprised of 3 species (*Porolithon onkodes*, *Lithophyllum insipidum* and *Lithophyllum flavescens*) (Fig. 6). Within *E. mathaei* crevices, there were 5 species of CCA identified (*Neogoniolithon* sp., *Hydrolithon reinboldii*, *Pneophyllum conicum*, *Porolithon onkodes*, and *Sporolithon* sp.), 4 of which were not found on open surfaces (Fig. 6). The thickness of the CCA samples declined with distance (from 0 to 8 mm inside the crevice opening) into the sea urchin crevices from crust thickness of 2.6 mm to 1.7 mm (Fig. 7). CCA thickness increased with distance outside the crevice from 2.6 mm to 3.7 mm (from 0 to 8 mm outside the crevice opening) and average CCA thickness on exposed surfaces of bommies was 2.6 ± 0.06 (mean \pm SE).

Discussion

Microhabitat created by the echinoid *Echinometra mathaei* appears to play an important role in the recruitment of juvenile *Pocillopora* in Moorea, where massive *Porites* harbor the majority of the adult corals growing within lagoons (Lenihan et al. 2011). However, the distribution of juvenile corals on *Porites* was highly non-random between exposed surfaces and crevices on the massive structures. Despite only comprising ~ 6 % of the surface area of dead massive *Porites*, *E. mathaei* crevices harbored 40 % of the juvenile corals growing on those structures, a pattern that could reflect both habitat selection at settlement and subsequent performance. In Moorea, performance of post-settlement corals was influenced by fine-scale differences in microhabitat that was context dependent. For example, survivorship of juveniles was twice as great for colonies that settled in sea urchin crevices compared to adjacent exposed surfaces, but only when the crevice was not occupied by an urchin. At the finer, within-crevice scale, orientation of a coral had a strong effect on colony growth and survivorship with settlers facing downward from the top of a crevice having 2 to 4 times better survivorship compared to upward-facing colonies at the bottom of the crevice where sedimentation and urchin disturbance presumably are the greatest.

Recent work suggests that post-settlement corals experience tradeoffs between protection from predation within crevices and the increased competition with algae within those microhabitats (Doropoulos et al. 2016). Observed patterns of coral tissue damage in the present study support the notion that predation or incidental grazing by echinoids may affect coral performance. Other work in Moorea has suggested that predation and sedimentation can also be major determinants of coral success (Lenihan et al. 2011, 2015).

Sedimentation on upward facing surfaces limits coral recruitment (Maida et al. 1994, Nzali et al. 1998, Price 2010, Lenihan et al. 2011, Edmunds et al. 2014) and can result in decreased coral growth and survival (Price 2010, Lenihan et al. 2011, Edmunds et al. 2014). Overall, my results support the prediction that crevices created by *E. mathaei* serve as a refuge for corals during vulnerable life stages, particularly when the crevice is no longer occupied by an urchin.

Substantive differences in post-settlement performance among adjacent microhabitats, as measured in the present study, can serve as a strong evolutionary force for habitat selection during settlement (Raimondi and Morse 2000, Doropoulos et al. 2016). Indeed, coral larvae have the ability to swim and orient themselves to suitable habitat during the settlement process (Raimondi and Morse 2000) in response to the light environment (Mundy and Babcock 1998), cues from CCA (Morse et al. 1988, Harrington et al. 2004), macroalgae (Dixson et al. 2016), biofilms (Webster et al. 2004) or sediments on benthic surfaces (Maida et al. 1994, Lenihan et al. 2011). Results from my surveys evaluating the environment inside *E. mathaei* crevices, suggest that the habitat within these crevices differs from open surfaces in the light availability and composition of the community of CCA. While not directly measured in this study, the ability for larval corals to detect and settle inside *E. mathaei* crevices may be enhanced due to the rapid decrease in light with distance from the crevice opening, as has been found on other coral reefs (Morse et al. 1988, Babcock and Mundy 1996). Selection of *E. mathaei* crevices by coral larvae may also be influenced by settlement cues from CCA if some of the species of CCA found within these microhabitats induce coral recruitment.

The strongest positive facilitator of coral recruitment (*Titanoderma prototypum*) common in Moorea is a thin crust species found within cryptic, low-sedimentation habitats in the lagoon (Price 2010). This species of CCA was not found in the limited number of CCA samples collected in this study. However, the CCA samples were not collected from crevices currently occupied by juvenile corals, and it is possible that CCA collections made within crevices with living corals might have differed in CCA species composition. Nevertheless, of the species of CCA identified from collections taken within echinoid crevices in this study, one species (*Pneophyllum conicum*) facilitates the recruitment of porited corals in Moorea (Price 2010). Additionally, *Neogoniolithon* spp. that also is found inside *E. mathaei* crevices in the present study, facilitates coral recruitment in other systems. *Neogoniolithon* sp. growing on the seagrass *Thalassia testudinum* in the Caribbean can facilitate recruitment of the free living coral *Manicina areolata* and enhance its survival (Ruiz-Zárate et al. 2000). On exposed surfaces of dead massive *Porites* structures in this study, 3 species of CCA were found (*Porolithon onkodes* and *Lithophyllum insipidum*, and *Lithophyllum flavescens*). Two of these 3 negatively influence coral recruitment by *Pocillopora* spp. in Moorea (*Porolithon onkodes* and *Lithophyllum insipidum*) (Price 2010), indicating that open surfaces with these species of CCA may be avoided by coral larvae. The thickness of CCA crusts on exposed surfaces was similar to the thickness at the opening of *E. mathaei* crevices, however CCA crust thickness decreased with distance inside the crevice. Thin crust CCA have been suggested to best facilitate coral recruitment (Harrington et al. 2004, Ritson-Williams et al. 2009) and better withstand frequent grazing by echinoids than infrequent bites of fishes (Steneck 1986, O'Leary et al. 2012). Further study would be necessary to test for coral larval selection of CCA within sea urchin crevices and on open

surfaces, however the present study provides compelling evidence to suggest that the habitat created by *E. mathaei* may enhance localized coral recruitment, particularly after the echinoid has vacated the crevice. This study is the first to suggest that in moderate densities, the bioeroding echinoid *E. mathaei* may enhance coral recruitment, rather than reduce it (*sensu* O'Leary and McClanahan 2010).

Previous research has suggested that *E. mathaei* can reduce the survival and growth of coral recruits in the Caribbean, Red Sea and Kenya (Sammarco 1980, Korzen et al. 2011, O'Leary et al. 2013) and decrease coral reef topographic complexity (McClanahan 1999, O'Leary and McClanahan 2010, O'Leary et al. 2012). On an individual sea urchin basis, estimates of bioerosive behavior of *E. mathaei* in Moorea are similar to those in Kenya where *E. mathaei* are more abundant (Mills et al. 2000). However Mapstone et al. (2007) demonstrated experimentally for Moorea that only extreme reductions or increases in *E. mathaei* density within *Acropora pulchra* patches are detrimental to the coral and fish community. Additionally, other research has suggested that the fecal deposition by echinoids within *E. mathaei* crevices may fuel the growth of calcareous algae and facilitate the cementation of the reef (Mills et al. 2000). The experimental and survey data in the present study suggest that the current densities of *E. mathaei* in Moorea provide usable habitat for corals, and may enhance the framework building potential of the coral reef through the facilitation of coral recruitment. Furthermore, vacated crevices created by *E. mathaei*, are common on massive *Porites* structures in the lagoons of Moorea (~ 62 % vacancy) and may provide ideal habitat for corals during vulnerable life stages.

The most common coral occupants of *E. mathaei* crevices were pocilloporid corals, however poritids (massive forms and *P. rus*), *Montipora* spp. and acroporids were also

present. This finding is consistent with relative proportions of coral recruits on the north shore in the lagoon in Moorea belonging to these genera (Edmunds et al. 2010), and the composition of the juvenile and adult coral assemblages are relatively consistent (Penin and Adjeroud 2013). Therefore, it is likely that the results from this study provide general insight into the coral recovery process of the broader coral community on these reefs. Given that massive *Porites* structures provide the best location for coral growth and survival within the lagoon of Moorea due to protection from predators and abiotic variables such as sedimentation (Lenihan et al. 2011), it is likely that coral recruitment within *E. mathaei* crevices may enhance coral recovery in Moorea.

The outer reefs of Moorea experienced a series of disturbances to the benthic community between 2006 and 2011 (Adam et al. 2011, Bramanti and Edmunds 2016) that resulted in large loss of coral followed by an influx of coral recruits (Edmunds et al. 2015, Bramanti and Edmunds 2016). While the outer reefs suffered the greatest loss of coral and coral recruitment following the disturbances (Edmunds et al. 2015, Bramanti and Edmunds 2016), adult and juvenile corals remain abundant in the lagoon environment. It is possible that the lagoon population of adult corals may provide a portion of the coral larvae necessary for the replenishment of outer reef habitats and serve as an important mechanism by which these reefs recover from disturbances. Furthermore, the population of *Pocillopora* spp. corals in Moorea appears to be genetically different from nearby islands, suggesting that this reef may be at least partially self seeding (Edmunds et al. 2016). Therefore, the success of the juvenile corals within the lagoon is likely to play an important role in the future of these coral reefs, and the provision of microhabitats by bio-eroding sea urchins can enhance resilience of the entire coral community.

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Figures

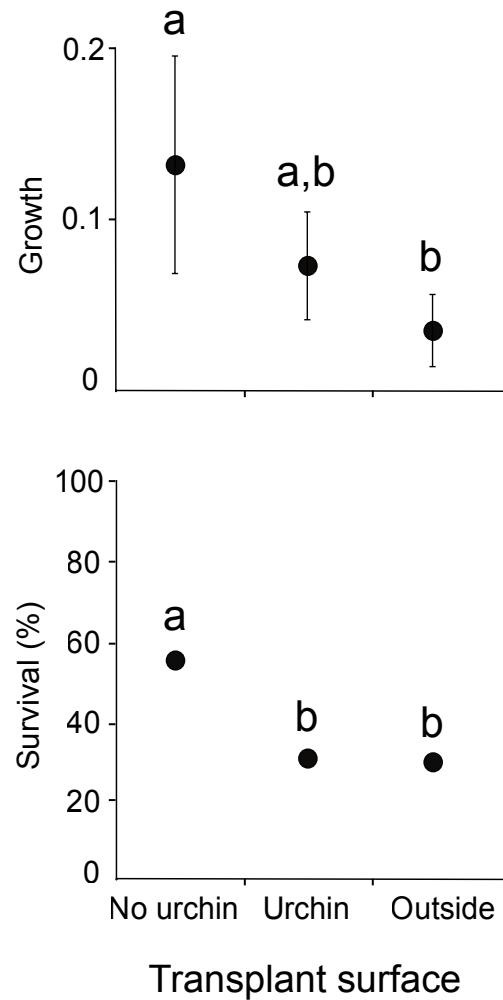


Figure 1. Coral growth (log final surface area – log initial surface area) after 5 months and survival after 10 months for juvenile *Pocillopora* spp. transplanted into crevice without a sea urchin ($n = 43$), with the sea urchin present ($n = 34$), or on an outside surface ($n = 43$). Letters that differ indicate significant differences among means from post hoc analysis.

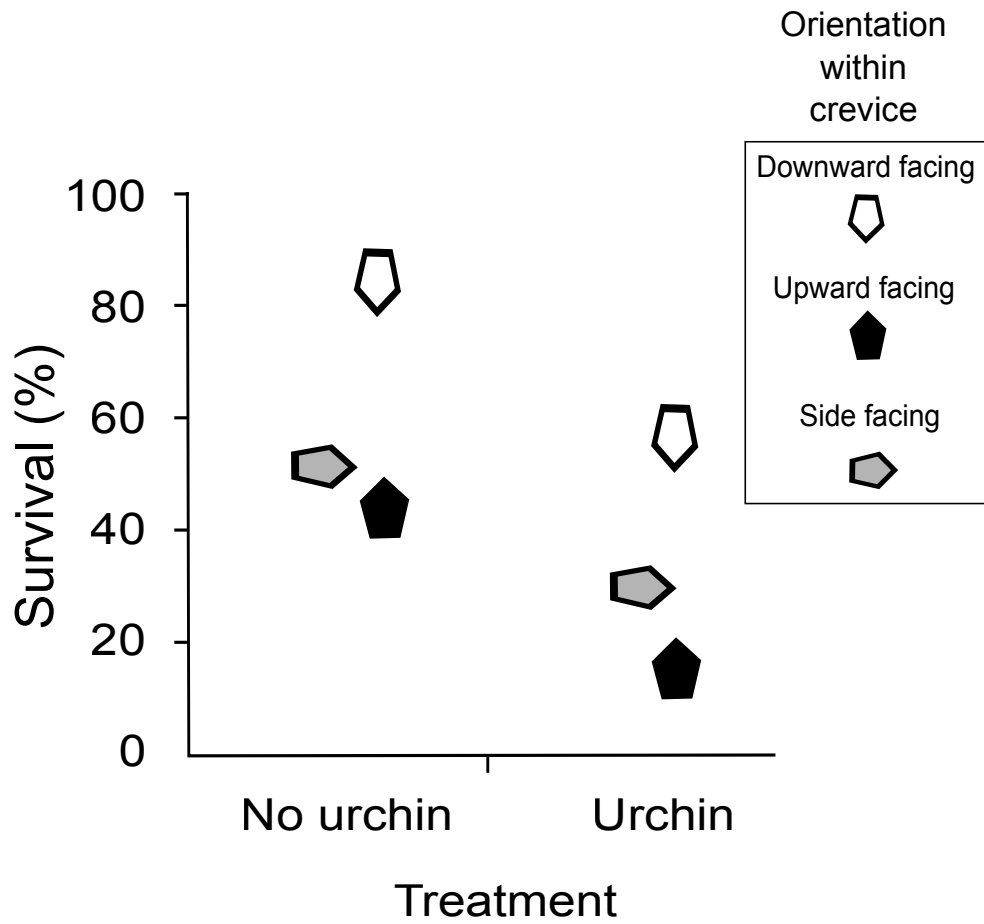


Figure 2. Percent survival of juvenile *Pocillopora* 10 months after transplant with respect to sea urchin treatment (with ($n = 37$) or without ($n = 35$) the sea urchin inside the crevice) and orientation within a crevice (downward-facing ($n = 15$), upward-facing ($n = 41$) and side-facing ($n = 16$)).

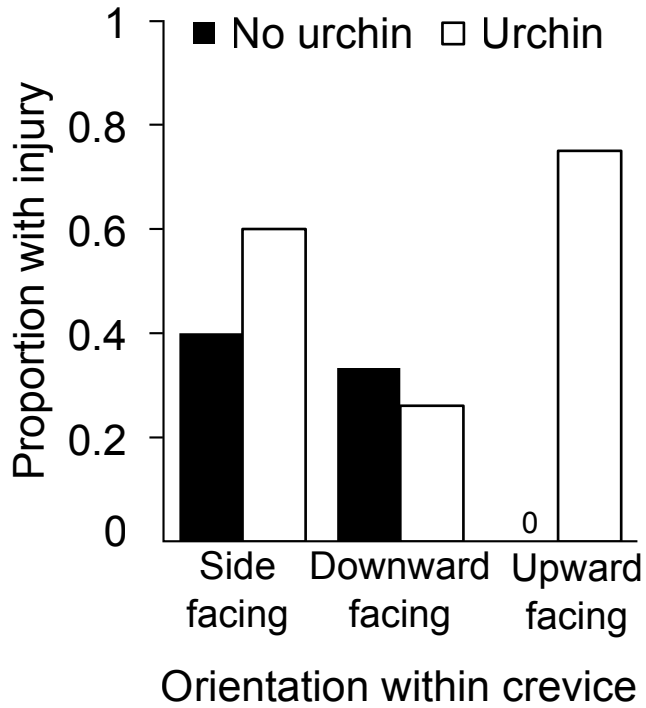


Figure 3. Proportion of naturally-occurring *Pocillopora* juveniles with damage to coral tissue and/or sclerites growing on sides (side facing), tops (downward facing) and bottoms (upward facing) of crevices occupied ($n = 42$) and unoccupied ($n = 37$) by *E. mathaei*.

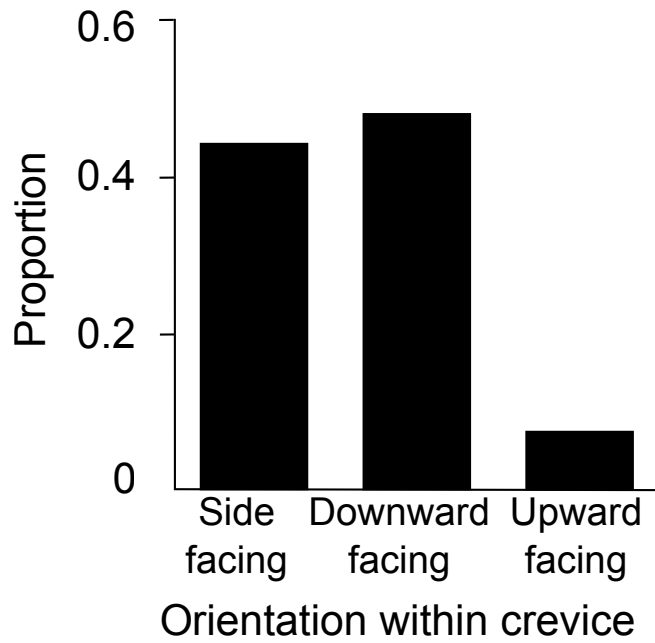


Figure 4. Proportion of naturally-occurring juvenile *Pocillopora* corals growing on sides (side facing), tops (downward facing) and bottoms (upward facing) of *E. mathaei* crevices. $n = 79$ colonies.

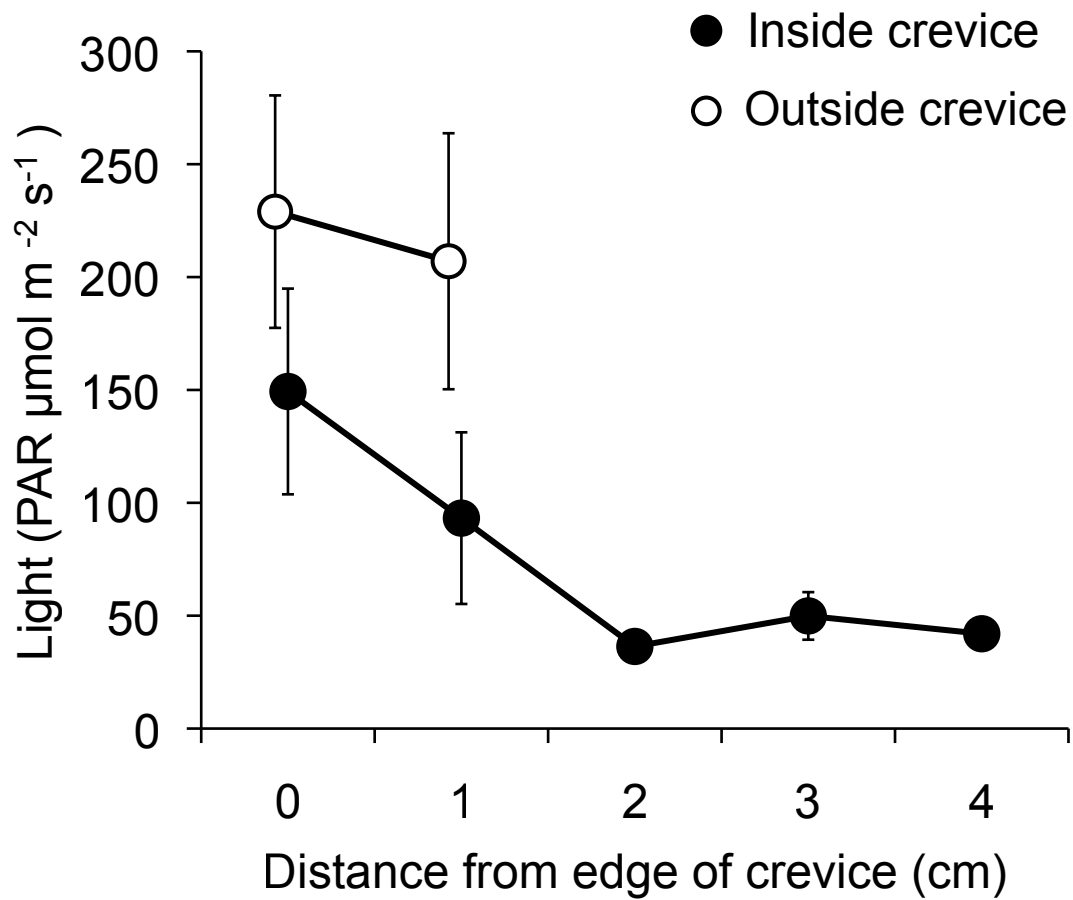


Figure 5. Mean (± 1 SE) light intensity (PAR) at the opening of an *E. mathaei* crevice and at 1 cm increments into (inside crevice) and outside onto open surfaces (outside). $n = 8$ *E. mathaei* crevices.

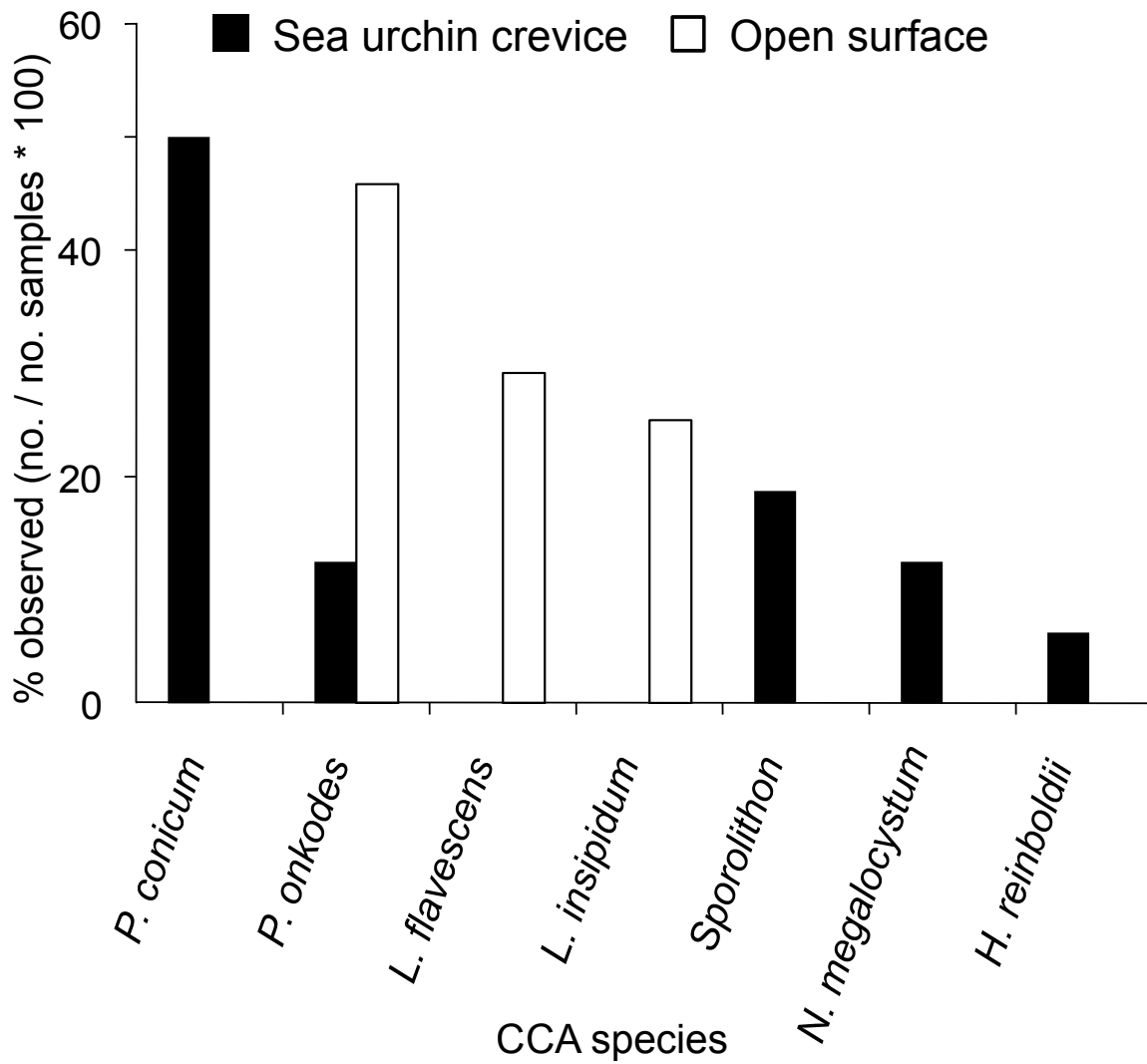


Figure 6. Percent occurrence of each species of crustose coralline algae collected from *E. mathaei* crevices ($n = 16$) and adjacent open surfaces ($n = 24$) of dead *Porites* bommies.

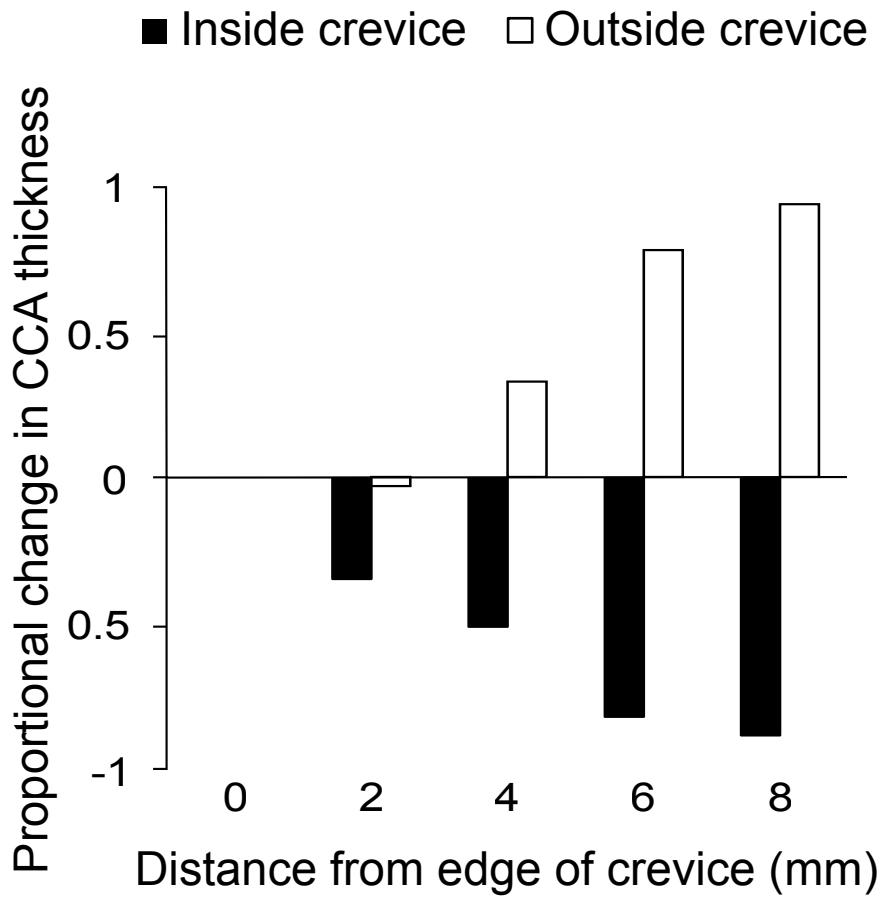


Figure 7. Proportional change in crustose coralline algae thickness with distance (mm) from the opening of the *E. mathaei* crevice ($n = 8$) and adjacent open surfaces ($n = 12$) on dead *Porites* bommies.

III. Title: Mass mortality of the abundant echinoid *Diadema savignyi* fails to trigger a coral–algal phase shift on a Pacific coral reef

Abstract

Echinoid herbivores can play an important role in controlling the growth of algae and maintaining a coral reef in a coral-dominated state. The Caribbean phase shift to macroalgal dominance following the mass mortality of *Diadema antillarum* is one of the most highlighted examples of how echinoid herbivores can play a critical role in controlling algal growth in an overfished reef. In Moorea, French Polynesia in 2013 *Diadema savignyi* populations suddenly crashed by 97% due to an unknown agent in a location where their population was previously $> 12 \text{ m}^{-2}$. The benthic cover of macroalgae did not increase dramatically following the loss of this abundant herbivore and remained $< 3\%$ 2.5 years later. Experimental fish exclusions revealed that macroalgal establishment in the same location may be slower than on other reefs that have transitioned to an algal dominated state following a disturbance. It appears that fish herbivore populations in Moorea are adequate to compensate for the sudden loss of *D. savignyi* and that a transition to an algal-dominated state is unlikely.

Introduction

Echinoids can play a critical role in maintaining tropical coral reefs in a coral-dominated state by controlling macroalgae (Hughes et al. 1987), particularly on reefs that have been subjected to disturbances (Hughes 1994). However echinoid populations can fluctuate greatly in size (Uthicke et al. 2009), which can result in loss of control of seaweeds, and thereby profoundly impact marine communities (Lessios et al. 2001, Feehan and Scheibling

2014). On Jamaican reefs prior to 1983, macroalgae covered < 5% and coral covered 40–80% of the reef despite extensive fishing, poor land use, and hurricanes (Hughes 1994, Jackson 2001). At that time, the echinoid *Diadema antillarum* occurred at high densities (reaching as high as 71 m⁻²) on most Caribbean coral reefs (Sammarco 1980, Lessios 1988). Between 1983 and 1984 an unknown pathogen devastated *D. antillarum* populations by 97%, sweeping through > 3.5 x 10⁶ km² of Caribbean coral reefs (Lessios et al. 1984a). Changes to the benthic community of Caribbean reefs were widespread following the loss of this echinoid herbivore. On some Jamaican reefs macroalgae increased from 4% to 92% cover, while coral cover declined from 52% to 3% between 1980 and 1993 (Hughes 1994). The widespread rapid changes in benthic community structure elicited by the die-off of *Diadema* has persisted for decades (Hughes et al. 2010), and has become one of the most highlighted examples of how loss of a key herbivore can have lasting impacts on ecosystem structure and function (Lessios 1995, Dudgeon et al. 2010).

Much of the research following the phase shift from coral to algal dominance in the Caribbean emphasized the need to determine factors that make a reef susceptible to phase shifts (Hughes et al. 2010). The extent of overfishing on Caribbean reefs was not well understood prior to the die off of *Diadema* (Hughes 1994) and has since been highlighted as one of the primary causes for the loss of Caribbean reef resilience (Jackson 2001). Overfishing of herbivorous fish can greatly reduce the resilience of a coral reef (Jackson 2001) and combined with anthropogenic pressures and climate change many coral reef worldwide are threatened (Bellwood et al. 2004, Cheal et al. 2010). The role of herbivore functional group and species identity has recently become a focus in coral reef ecology (Bellwood et al. 2003, 2006, Burkepile and Hay 2008, 2011, Adam et al. 2015a, 2015b).

Specifically coral reefs with low herbivorous fish diversity and coral reefs lacking browsing and grazing functional groups have been suggested to be particularly susceptible to phase shifts (Cheal et al. 2010, Adam et al. 2015b).

In 2013, an unknown agent resulted in rapid mortality of echinoid populations in the lagoons of Moorea. In January 2013, *D. savignyi* were observed venturing outside refuges during the day, with sloughing tissue around the Aristotle's lantern, and specimens brought into the laboratory quickly progressed from tissue and spine loss to mortality within 24 hrs. These observations were similar to descriptions of rapid mortality of *D. antillarum* in the Caribbean during the 1983 die-off (Lessios et al. 1984b). Here I describe the decline in population size of *D. savignyi* on Moorea, and then report how the benthic community responded over 2-30 months following the mortality event. Additionally, I experimentally tested the hypothesis that fish would be more likely to control algal growth on this reef than remaining sea urchin herbivores and determined the rate of algal colonization in the absence of these herbivores.

Methods

During January 2013, rapid mortality of a formerly abundant population of *Diadema savignyi* was observed at Temae (NE Moorea) in the back reef between 0.5 – 3 m depth (Carpenter, R.C. pers. comm.). To test the hypothesis that loss of this herbivore would result in an increase in macroalgal cover, surveys were initiated to evaluate echinoid density, biomass of algal turf, and benthic community composition in the ~ 3 km area where high-density aggregations ($> 10 \text{ m}^{-2}$) of *D. savignyi* historically occurred before the die off. Surveys were conducted on replicate coral patch reefs (~ 2 m diameter) to measure echinoid

densities and benthic community composition during the echinoid mortality event in January of 2013 and during the Austral summer and Austral winter between 2013 and 2015.

Additionally, data from patch reefs in the same locations in 2009 and 2010 were used to contrast *D. savignyi* densities and benthic community composition prior to the mortality event with data collected following the 2013 echinoid mortality.

Community composition was assessed using quadrats (0.25 m²) placed end-to-end centered along a band spanning the patch reef and parallel to the shore. The percent cover of coral, algal turf, crustose coralline algae (CCA), and macroalgae were estimated within each of 25 squares of a subdivided quadrat and averaged for each patch reef. In January 2010 ($n = 20$ patch reefs), during the echinoid mortality (January 2013, $n = 20$) and every six months thereafter ($n = 16$), echinoids were counted on each patch reef and densities standardized to area calculated from the diameter of the patch reef assuming it approximated a hemisphere. Data from haphazardly tossed 1 m² quadrat from July 2009 ($n = 85$) and July 2010 ($n = 88$) provided estimates of *Diadema savignyi* density in the same location prior to the mass mortality event (Han 2013).

Because turf algae biomass can increase within days following the loss or removal of echinoid herbivores (Carpenter 1986, 1988), I tested the hypothesis that turf algae biomass would increase rapidly following the mortality of *D. savignyi* in Moorea. Algal turf biomass (ash free dry mass [AFDM]) was estimated from three samples of turf collected with the underlying coral skeleton from each patch reef during the brief period echinoids were observed dying (January 2013), 20 d later to for comparison with algal turf growth estimates 20 d following the *D. antillarum* die off in the Caribbean (Carpenter 1988), and approximately every six months thereafter. A subsample of turf algae (1 cm², $n = 3$ /patch

reef) was scraped to 1 mm depth from the calcium carbonate surface from each algal turf sample and dried at 60 °C for 24 h, then ashed at 550 °C for 4 h to provide the ash free dry mass of turf algae.

Fish exclusion experiment

To test the hypotheses that fish herbivores can 1) control the growth of algal turf and 2) reduce areas of high turf biomass and remove newly established macroalgae, I established an herbivore exclusion experiment. At the same location described above, plots (25 x 25 cm) of turf algae were marked on massive *Porites* bommies during the Austral winter of 2014. Turf plots were assigned to 1) caged herbivore exclusion treatment, 2) full herbivore access or 3) a cage control treatment ($n = 15$ for each treatment), in a fully factorial blocked design. Full cages were 25 cm high with 1.5 cm plastic mesh (Vexar®) whereas cage controls had half of the top and side. At the start of the experiment and after 38 days, biomass of turf was quantified in each plot using the method described above and turf height was measured to the nearest 0.1 mm using Vernier calipers.

To determine if fish or remaining echinoid herbivores could remove algal growth within herbivore exclusion plots at the end of the experiment cages were removed for diurnal (fish) and nocturnal (echinoid) feeding periods. After 38 days, experiment cages were removed from ~ half of the fully caged plots ($n = 8$) in the morning to allow free access by diurnal fish herbivores for a 10 hr period. Fish feeding behavior was recorded using GoPro video cameras and videos were analyzed for herbivore bite rate for the first 20 minutes of exposure to herbivores within high turf plots (after cage removal) and adjacent plots with ambient turf biomass. The remaining fully caged plots ($n = 7$) were uncaged at

dusk and allowing access by nocturnal echinoid herbivores for 12 hr. Photographs taken at the time of cage removal (prior to herbivore access) and 10 (after fish herbivore access) or 12 hrs later (after echinoid herbivore access) were analyzed using ImageJ for the percent cover of turf algae, macroalgae and bare space.

Statistical analyses

Diadema savignyi density prior to 2013 was compared to the average density from all post-mortality time periods using a generalized least squares model allowing for differences in variance among groups (variance was higher before the mortality event). To determine whether changes in the benthic community occurred, I used a Student's t-test to compare the percentage of the benthic community comprised of algal turf in 2010 to the proportion of the benthic community comprised of algal turf in January 2013; data were arcsin transformed to meet assumptions and normality of residuals was confirmed using quantile-quantile plots prior to analyses for turf algae and coral. The percentage of the benthos comprised of macroalgae and crustose coralline algae was zero in nearly all samples, so these data were not formally analyzed. To determine whether response variables (percent algal turf and coral) changed over time after the mortality event (2013-2015), I used a linear regression for each benthic variable as a function of time with a random effect of bommie (random intercept model) using the statistical software package *nlme* R (R Core Team, 2014). Data from the removal of experimental turf plots comparing the benthic community in plots before and after herbivore access, and fish bite rate between high algal biomass plots and ambient plots were analyzed using *t-tests*.

Results

Prior to the mortality event, most *D. savignyi* individuals were found during the day clustered together in high aggregations and were extremely abundant (Han et al. 2016). These high-density aggregations persisted between 2010 and 2012 (pers. obs.) but were nearly extirpated by January 2013 (Fig. 1) as the mean density declined abruptly by 97%. In the 4 years prior to January 2013, the density of *D. savignyi* averaged $\sim 12 \pm 0.9 \text{ m}^{-2}$ (mean \pm SE), but fell two orders of magnitude during the Austral summer of 2012-13 to $\sim 0.2 \pm 0.02 \text{ m}^{-2}$ by January 2013 immediately following the observed mass die off of sea urchins (ANOVA $F_{3, 206} = 164.41, p < 0.0001$). Subsequent surveys between January 2013 ($0.2 \pm 0.02 \text{ m}^{-2}$) and July 2013 ($0.05 \pm 0.04 \text{ m}^{-2}$) revealed that *D. savignyi* populations continued to decline for at least six months following the mortality event and remained $< 0.05 \text{ m}^{-2}$ until sampling ended 2 years later (Fig. 2a, ANOVA $F_{2, 15} = 3.58, p = 0.005$).

Macroalgal cover at the study site in Moorea was $< 1\%$ in 2010, and remained at that low level during the echinoid die-off and remained $< 3\%$ for the following 2.5 years (Fig. 2b). Similarly, the cover of crustose coralline algae remained low in 2010 through 2015. The percent coral cover at the Moorea study site declined gradually from 56% to 45% of the benthos 2.5 years following the *D. savignyi* population reduction ($F_{2, 81} = 7.38, p = 0.008$). However, the percent cover of algal turfs increased from 43% to 52% between January 2013 during the *D. savignyi* mortality and July 2015 ($F_{2, 81} = 2.58, p = 0.01$). Algal turf biomass in Moorea did not increase immediately following the *Diadema* mortality, 20-days later, or six-months later and fluctuated somewhat over time thereafter (Fig. 2b).

In the field experiment testing the effect of fish herbivores on the growth of turf algae, after 5 days of herbivore exclusion the height of turf algae increased by 12%

(ANOVA, $F_{2,14} = 4.27$, $p = 0.02$) but there was no detectable difference in turf biomass (ANOVA $F_{2,14} = 0.22$, $p = 0.80$). After 38 days turf biomass increased by ~ 15 % (ANOVA $p = 0.001$, $F_{2,14} = 8.61$) and grew in height by ~ 150 % (ANOVA $p < 0.0001$, $F_{2,14} = 75.3$, Fig. 3). During this period, turf height and biomass decreased in both open and cage control plots, and there was no difference in these values between the herbivore exposed (open) and cage control treatments (Tukey's post hoc, $p < 0.05$).

Sequential exposure of the algae in the cage treatment to herbivores after 38 days revealed that fish and not sea urchins rapidly consumed the lush growth of turf and emerging macroalgae on patches that had not been recently grazed. Within 10 hrs fish herbivores reduced the percent cover of turf from 85% to 20% ($t_{1,13} = 0.02$, $p = 0.98$) and macroalgae from 11% to 0.5% ($t_{1,13} = 0.17$, $p = 0.87$), which resulted in an increase in bare space from 3% to 79% ($t_{1,13} = 1.06$, $p = 0.3$, Fig. 4 a). By contrast, after a 12-hour nocturnal grazing period, echinoid herbivores did not reduce the lush cover of turf or macroalgae and there was no increase in cover of bare space ($t_{1,12} = 0.2$, $p = 0.84$, $t_{1,12} = 0.32$, $p = 0.75$, $t_{1,12} = 0.5$, $p = 0.62$, respectively, Fig. 4 b). Fish concentrated their feeding in the lush algal patches immediately following removal of the cages; the bite rate for herbivorous fishes was 0.6 ± 0.1 bites s^{-1} in plots where cages had just been removed, whereas they feed at an exceedingly low rate (0.002 ± 0.01 bites s^{-1}) on adjacent plots of the same area (Figs. 5 and 6).

Discussion

Densities of *Diadema savignyi* prior to 2013 were qualitatively similar to those of *Diadema antillarum* in St. Croix, US Virgin Islands, which were reduced 96% by a mortality event

between 1983 and 1985 (Carpenter 1990, Levitan et al. 2014). In St. Croix, the impacts of the *D. antillarum* die-off on the productivity of algal turfs was detectable within 5 d, the benthic community was dominated by a filamentous brown alga within four months, and unit-area net primary productivity declined 37% (Carpenter 1988, Uthicke et al. 2009). Despite the nearly identical two-order of magnitude decline of echinoid populations in Moorea and Jamaica, the benthic communities responded completely differently, at least in the initial 2.5 years following the mortality event. The percent of the benthic community in Moorea comprised of macroalgae had not changed 2.5 years following the collapse of *D. savignyi* populations, whereas on some reefs in St. Croix, US Virgin Islands, the cover of macroalgae had increased from 0 to > 20% within two months of the loss of *D. antillarum* (Carpenter 1990). Additionally, in the back reef and shallow fore reef zones in St. Croix, algal turf biomass growing on settlement tiles increased by 20% within five days of *D. antillarum* dying, it doubled within two months, and continued to increase steadily for one year following the loss of *D. antillarum* (Carpenter 1988). In Moorea, considering the 97% reduction in the *D. savignyi* population that had occurred by January 2013, observed, relatively small fluctuations in turf biomass are unlikely related to the sea urchin decline. Furthermore the rapid loss of *D. savignyi* seems unlikely to have influenced the gradual change between 2010 and 2015 (increase in cover of turf 27%-52%) and gradual decline in coral (57-45%). Thus, the sudden loss of high densities of a major putative herbivore – a Diadematid sea urchin – had contrasting effects on community dynamics between the Caribbean and Moorea.

There are at least five explanations for the lack of a rapid increase in macroalgae in the back reef of Moorea following the mass mortality of *D. savignyi*. The first is that this sea

urchin does not have the same functional role in controlling macroalgae on reefs of Moorea as does *D. antillarum* in the Caribbean, although *D. savignyi* certainly consumes macroalgal species that are potential dominant space holders in Moorea (Swanson 2011). Second, it is possible that macroalgal populations respond much slower to release of herbivore pressure in Moorea than in the Caribbean, and there is some evidence to suggest shorter lags in response of macroalgae to released herbivore pressure in the Caribbean than in the Indo-Pacific (Roff and Mumby 2012). Results of the herbivore exclusion experiment reported here also suggest that the production of algal turf and establishment of macroalgae may be slower in Moorea than in St. Croix following the die off of *D. antillarum* (Carpenter 1988) or in experimental enclosures (Carpenter 1986).

A third potential explanation for the lack of increased macroalgae following the *D. savignyi* die off is that the spatial scale of the *D. savignyi* mortality event may have been too small to trigger a phase shift, although this is unlikely given the large area of lagoon reefs (~ 3 km²) subjected to the rapid, two-order of magnitude decline in sea urchin abundance. Indeed, patch reefs in other lagoons of Moorea have in past decades transitioned to dominance by macroalgae that have persisted for some time (Done et al. 1991). Fourth, the sparse, residual population density of *D. savignyi* following the die off may have been sufficient to keep macroalgae under control, although at 1 sea urchin per 20 m² it is difficult to conceive they could exert sufficient grazing pressure over the landscape to keep macroalgal populations in check.

A fifth, highly plausible explanation is that there was either functional redundancy in the herbivore guild or compensation for the loss of *D. savignyi* by fish herbivores. Behavioral observations reported here indicate that fish herbivores in Moorea can rapidly

respond to increased food availability, at least on local scales. Adam et al. (2011, 2014) and Han et al. (2016) report a similar response of herbivorous fishes in Moorea to a rapid increase in cover of turf algae at much larger, landscape scales, which has been invoked as a prime reason why macroalgae did not become a major space holder of the fore reef of Moorea following a sudden, rapid decline in cover of coral due to pulse perturbations that ended in 2010 (Adam et al. 2011, 2014). Following a much larger- and longer-scale herbivore exclusion experiment, Bellwood et al. (2006) found the mature stands of macroalgae that developed in the absence of herbivores were rapidly consumed by herbivorous batfish. Taken together, these results indicate that different functional groups of herbivorous fishes are capable of either suppressing the development of macroalgae or removing mature plants that escape consumption by grazers.

In the present study, the observed time lag between the loss of *D. savignyi* and a reduction in algal turf biomass (2012-2015) may be a result of the response of the herbivorous fish (and possibly other members of the echinoid community i.e., *Echinometra mathaei* and *Echinothrix* spp.) to increased food availability following the reduction in the *D. savignyi* population. However, turf biomass increased for at least 6 months in 2015 seemingly unrelated to herbivore populations, a time when fish herbivore biomass was continuing to increase. A rapid functional response in the composition of the fish community and a longer-term numerical response may have resulted if herbivorous fishes were in competition with *D. savignyi* for food. Herbivorous fishes on the fore reef of Moorea, where echinoid biomass historically is low, responded to a sudden, widespread increase in turfing algae caused by an outbreak of the corallivorous sea star *Acanthaster planci* both with faster body growth and subsequently numerically (Adam et al. 2011). For

the lagoon, based on the lack of an increase in macroalgal cover 2.5 years after the echinoid mortality event (i.e. 2015), it appears unlikely that the cover of macroalgae will increase further given the current community of herbivorous fishes.

There are considerable differences between the herbivore fish communities in the 1980's Caribbean and current Moorean reefs. The herbivorous fish on Caribbean reefs during the *Diadema* die off had been greatly altered from centuries of overfishing (Jackson 2001). Moorea is much less affected by fishing and parrotfish populations rapidly respond numerically and behaviorally following increases in food availability (Adam et al. 2011, Han et al. 2016). In the Caribbean, during the large-scale phase shift to macroalgal dominance, those reefs with the most degraded populations of herbivorous fishes were the most negatively affected and parrotfish populations appear inversely related to *Diadema* populations (Lessios 1988, Jackson et al. 2014). In general herbivorous fish biomass is greater in the Pacific than Caribbean reefs (Roff and Mumby 2012) and recent estimates suggest that herbivore biomass is increasing in the lagoons of Moorea. It is important to consider how human activities including overfishing can weaken coral reef resilience to sudden perturbations including disease outbreaks which may remove a critical herbivore functional group (Hughes 2003). The present study provides further support for the importance of herbivore functional redundancy in coral reef communities and suggests that a moderately fished herbivore community can compensate for the sudden loss of an abundant herbivore.

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Figures

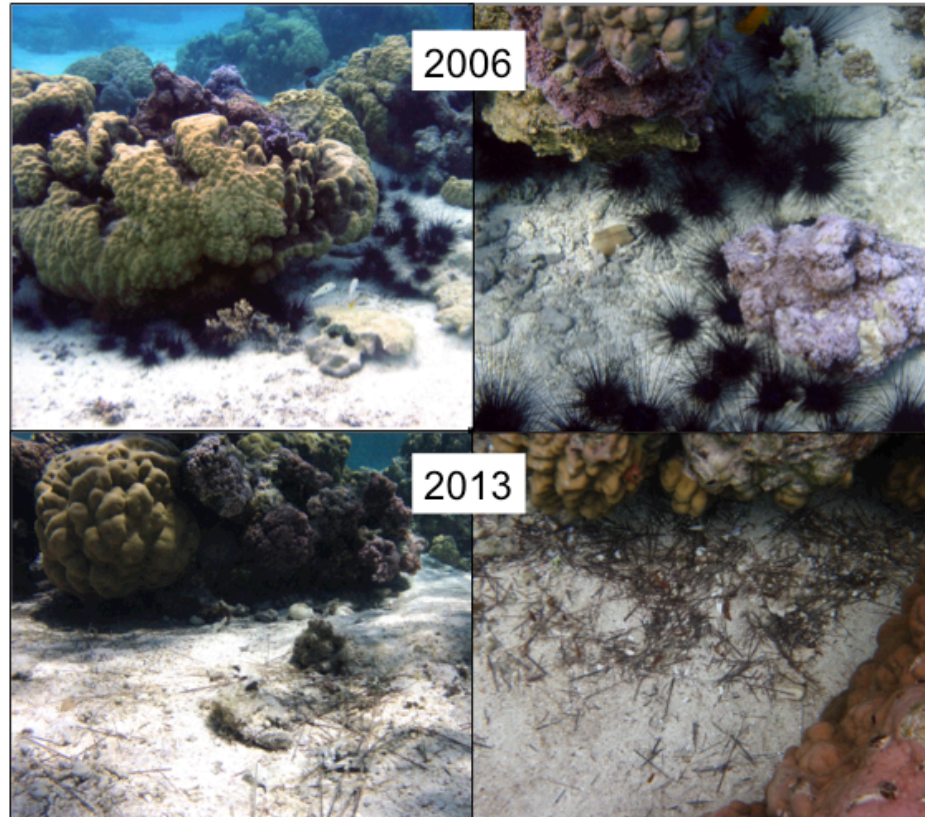


Figure 1. Photographs from the back reef on the eastern shore of Moorea, French Polynesia in 2006 and 2013 showing high density *Diadema savignyi* aggregations and sea urchin spines and tests that remained following mortality of *D. savignyi*. Mass mortality reduced high-density ($> 10 \text{ m}^2$) aggregations of *D. savignyi* over the $\sim 3 \text{ km}^2$ area of this lagoon (see Fig. 2a) (Photo credit: top photographs, M.D. Johnson, bottom photographs, S.A. Swanson).

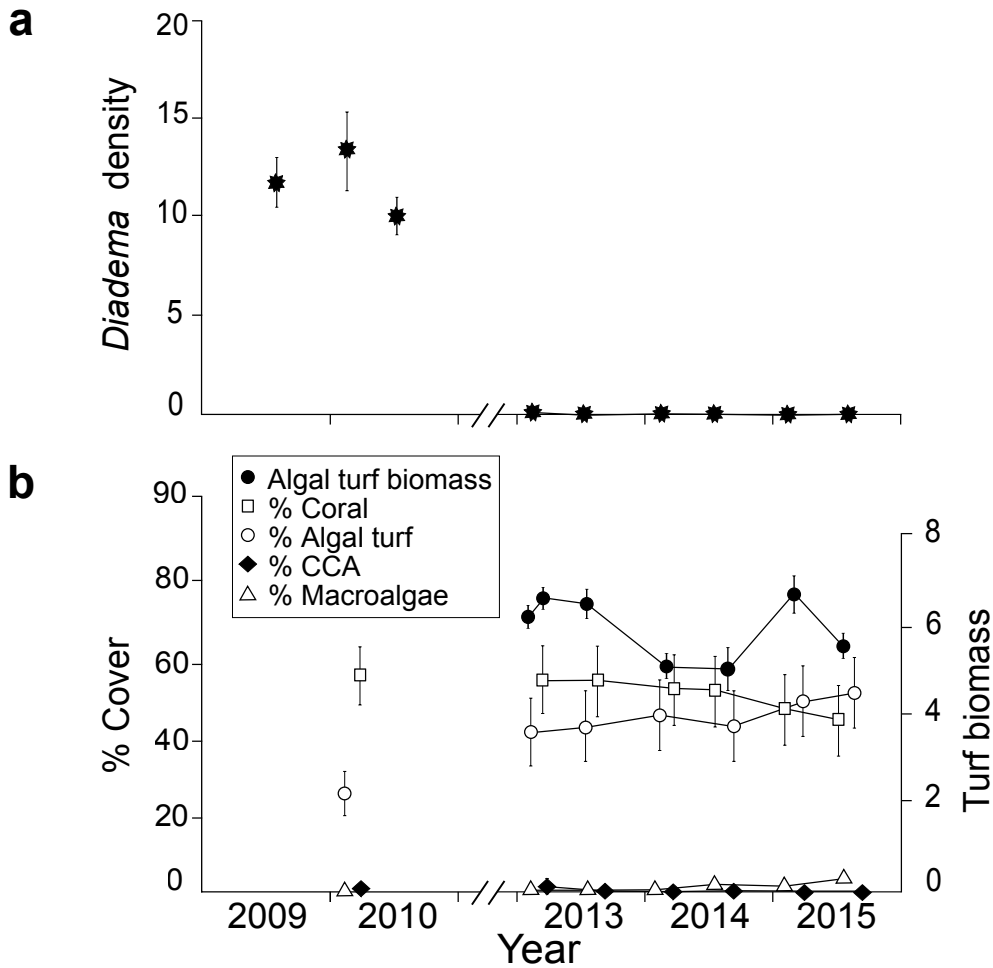


Figure 2. a) *Diadema savignyi* density (no. m⁻², mean ± SE) on patch reefs in Temae lagoon, Moorea in 2009 and 2010 prior to the mortality event and during the Austral summer and winter from 2013-2015 ($n = 85, 20, 88, 20,$ and 16 thereafter patch reefs). b) Primary Y-axis shows the percent of cover (mean ± SE) comprised of macroalgae, algal turfs, coral and crustose coralline algae (CCA) on patch reefs in 2010 ($n = 20$), and during the Austral summer and winter from 2013-2015 ($n = 20, 20, 17$ and 16 thereafter, respectively); the secondary Y-axis shows mean algal turf biomass (mg AFDM cm⁻² ± SE) during the mortality event, 2 weeks after and at each Austral summer and winter.

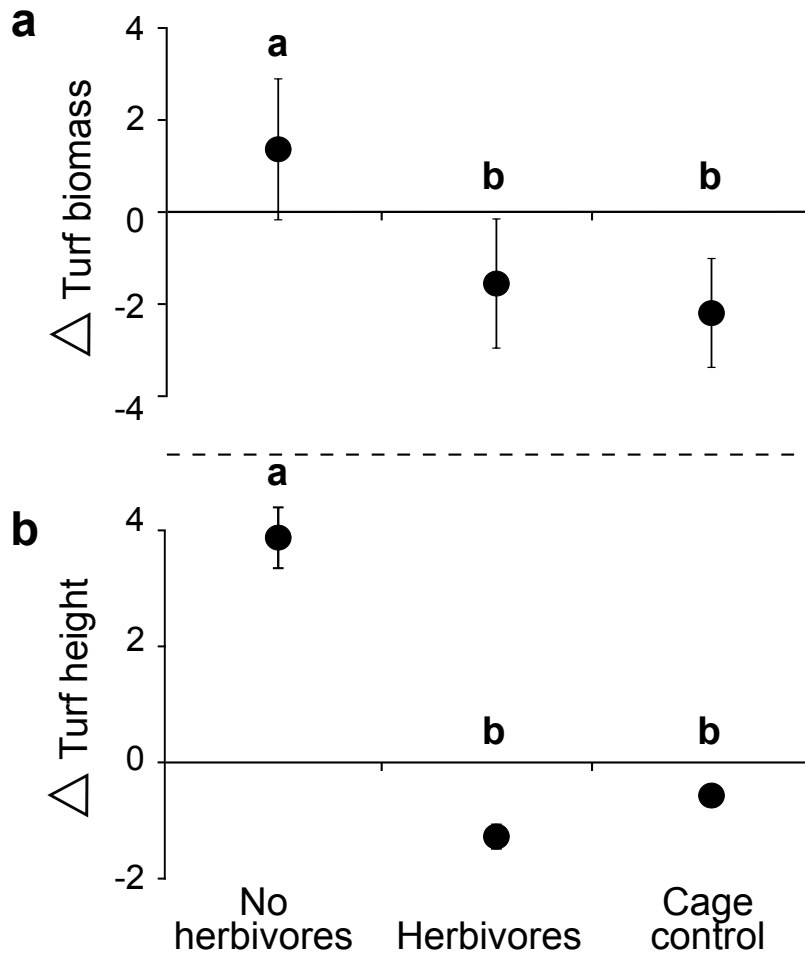


Figure 3. a) Change (Δ) in average turf biomass ($\text{mg AFDM cm}^{-2} \pm \text{SE}$) and b) turf height ($\text{mm} \pm \text{SE}$) after a 38 day experiment ($n = 15$ for each treatment). Differing letters indicate significant differences among means from Tukey's post hoc analysis ($p < 0.05$).

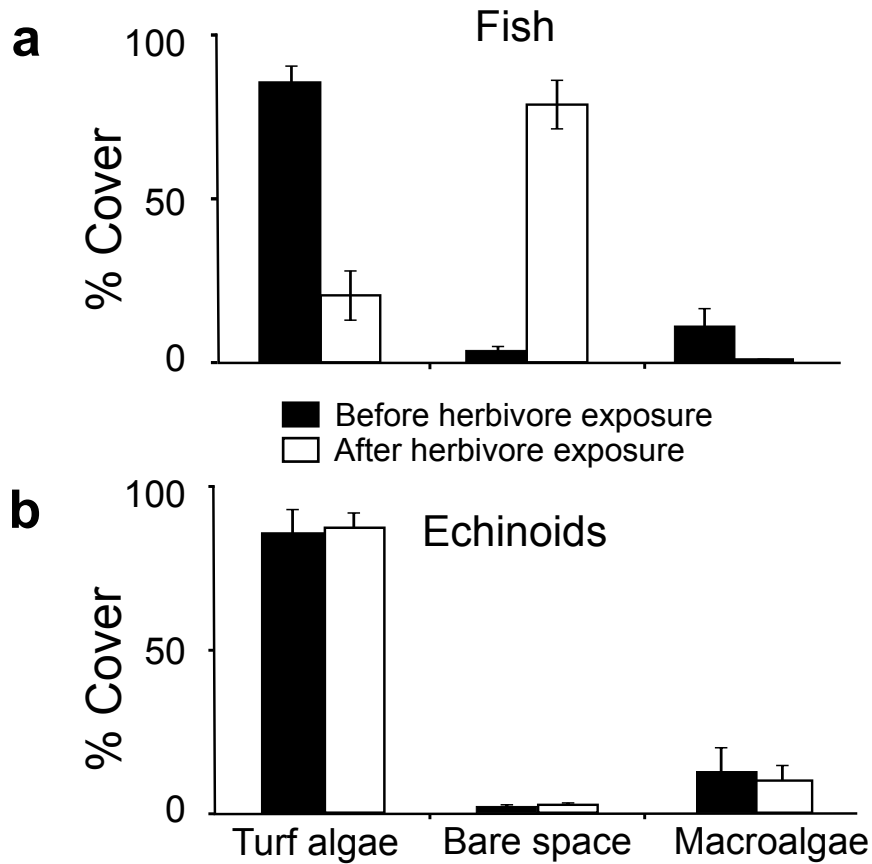


Figure 4. Change in relative cover of benthic substrates (turf algae, bare space and macroalgae) immediately before and 10 hours following exposure to a) fish herbivores ($n = 8$) and b) echinoid herbivores ($n = 7$).

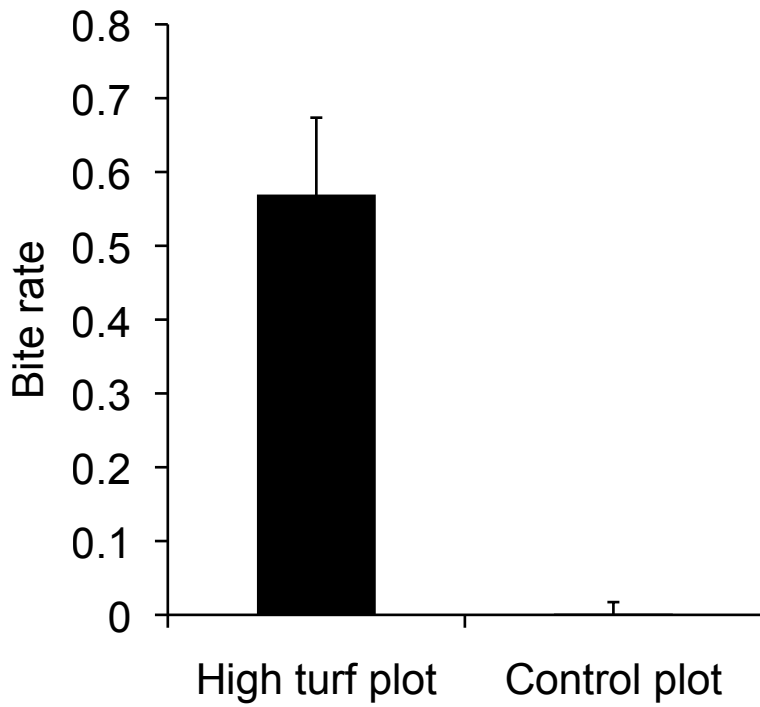


Figure 5. Herbivorous fish bite rate (no. sec⁻¹) for high turf plots immediately following exposure to fish herbivores and for similar sized control plots containing ambient turf biomass ($n = 8$ plots for each).

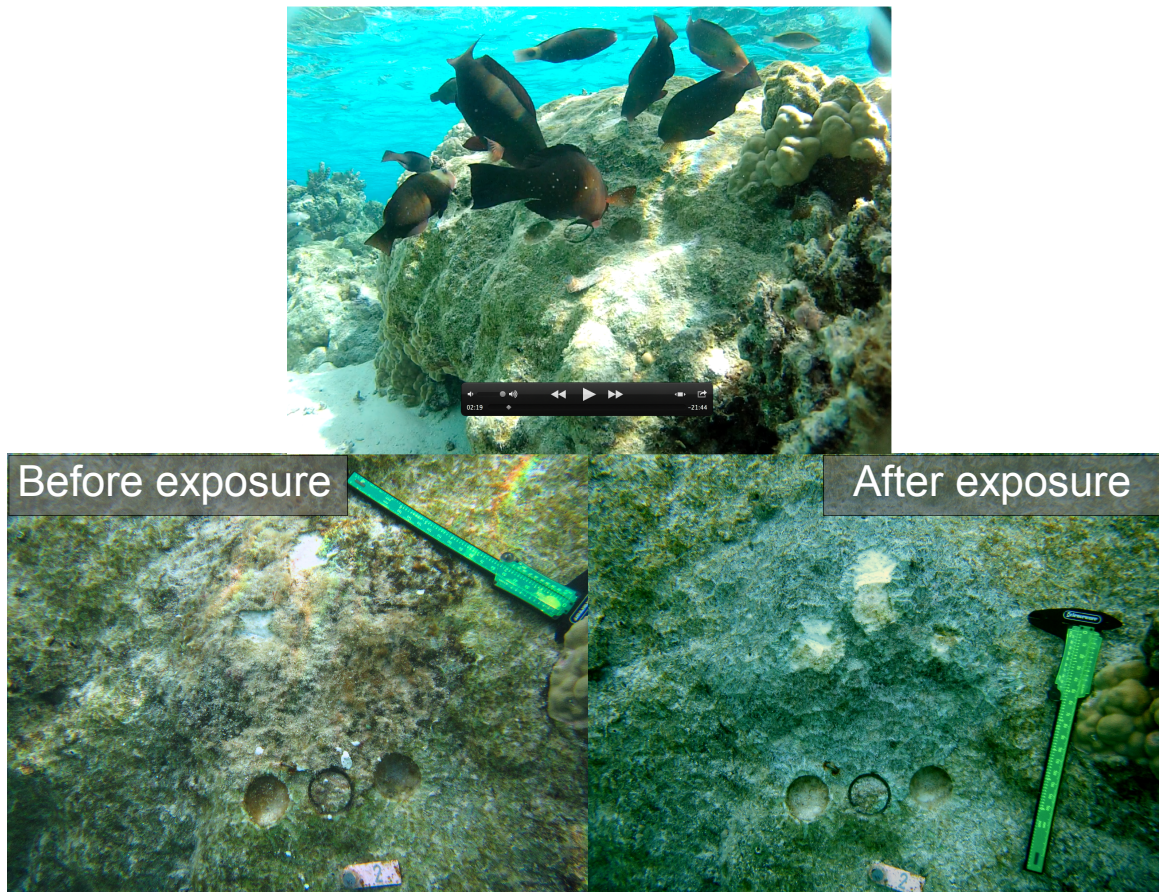


Figure 6. Experimental turf plots after cage removal before (bottom left), during (top), and after (bottom right) 10 hour exposure to fish herbivores.