**Title**

Environmental drivers and their effect on dominant macroalgal species responses, interactions, and resilience in a fringing reef system

**Permalink**

https://escholarship.org/uc/item/9bs1d3jg

**Author**

Grier, Shalanda

**Publication Date**

2023

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Los Angeles

Environmental drivers and their effect on dominant macroalgal species responses, interactions,

and resilience in a fringing reef system.

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Shalanda Rachelle Grier

2023

ABSTRACT OF THE DISSERTATION

Environmental drivers and their effect on dominant macroalgal species responses, interactions, and resilience in a fringing reef system.

by

Shalanda Rachelle Grier

Doctor of Philosophy in Biology

University of California, Los Angeles, 2023

Professor Peggy Marie Fong, Chair

Coral reefs experience natural and anthropogenic disturbances that can shift reefs from coral to algal domination, with concurrent loss of ecosystem functions and services. Pulse (transient) disturbances, such as storms, can alter the regime of environmental drivers in reefs negatively affecting corals. However, little is known of the resilience of the shifted macroalgal community, motivating my research into the effects of storm-associated disturbance on macroalgae. Here I investigate 1) how dominant macroalgae respond to changes in environmental drivers such as light, sediment, and nutrients and 2) how light and sediment disturbances affect species interactions and resilience.

First, I explored the response of a green calcifying alga to changes in light, nutrients, and sediment. In the field, increased nutrients reduced growth, but only with added sediment, while ambient nutrients and reduced light increased growth. In microcosms, sediment acts as a buffer in high light, increasing growth. Thus, different combinations of environmental drivers produce complex interactions that can ameliorate negative effects of changes in certain environmental drivers.

Second, I examined the effects of short-term disturbances in sediment and light on growth and species interactions of two macroalgae (calcifying vs non-calcifying), demonstrating environmental drivers can have independent rather than interactive effects depending on species assemblage. Intra-specifically, light reduction negatively affected the calcifying species and had negligible effects on non-calcifying species. However, interspecifically, light reductions resulted in negative responses for both algae, with differential performance suggesting species interactions. Thus, both species and community context are needed to improve predictions for coral reefs in the Anthropocene.

Last, I studied the resilience of these macroalgae to storm-associated light and sediment disturbances. While disturbance negatively affected growth for both species, the capacity for resilience differed substantially. The calcifying species recovered quickly while the other did not; further, recovery rate was dependent on the presence of the other species, suggesting community context can affect species resilience.

Overall, this work reveals the importance of studying species-specific responses of dominant macroalgae and their interactions to short-term disturbances as these responses can be shaped by community and environmental contexts, both of which are expected to continue to change in the Anthropocene.

The dissertation of Shalanda Rachelle Grier is approved.

Richard F. Ambrose

Paul Henry Barber

Nathan Jared Boardma Kraft

Peggy Marie Fong

University of California, Los Angeles

2023

DEDICATION


To my mom, dad, the Grier Gang, family, and friends-

thank you for your love, support, and prayers. They carried me along the way.

# TABLE OF CONTENTS

# LIST OF TABLES

Chapter 3

*Main Text*

# LIST OF FIGURES

Chapter 3

*Main text*

# ACKNOWLEDGMENTS

This dissertation would not have been possible without my community, family, and friends. Thank you for always reminding me who I am and whose I am in this big ole' crazy world.

First and foremost, Peggy Fong thank you for your endless support that started well before my graduate journey. You have always believed in this dream of mine and consistently partnered with me to make my dream a reality no matter what. I will always appreciate the passion and care you have for your craft as an ecologist and mentor. I will never forget the first time we met and how excited you were to help me, and my team develop an independent research project. That experience was truly transformative. From snorkeling with you in the South Pacific for the first time, identifying various macroalgal species, learning how to conduct research, learning stick shift, experiencing challenges and so much more, you have been a consistent source of support and inspiration. Also, thank you for modeling what it looks like to have a healthy work life balance. I would also like to thank Jon Fong for the coconut bread, jokes, and support. Peggy, I am truly grateful that you were my advisor during this process, and I look forward to collaborating with you as Dr. Grier in the future.

Paul Barber, thank you for getting me out of the pool that day. Haha! Shortly after we met, during The Diversity Project, I got injured. I was so upset. I thought I would not be able to complete the program but both you and Peggy assured me that there was space for me and that I could still contribute in a meaningful way. Thank you for finding a place for me that summer in your lab until I was well again. Thank you for never placing limits around what I can do and for encouraging me to always think of my work in a broader context. Paul I will never forget how you always make things happen and include your students and mentees along the way. I aspire to

give back throughout my career as you have, and I am grateful that you were an integral part of my journey. Thank you and Jeannie for hosting dinners and creating a safe space to hangout. These will always be some of my fondest graduate school memories.

I would also like to thank my dissertation committee members Richard Ambrose, Nathan Kraft, and Paul Barber. Rich thank you for your thoughtful questions, helpful feedback, and attention to details. I truly appreciate your investment in my growth as writer and scientist. Nathan and Paul thank you for all your recommendations and suggestions throughout this journey.

To present and past members of the Fong and Barber lab thank you for your stories, laughs, and support in the field. To my TDP family thank you for your consistent support over the years. Camille and Tiara thank you both for opening your homes to me when I first arrived in Los Angeles and for serving as inspiration throughout my graduate journey. Ashlyn thank you for all the movie meetups, Korean BBQ dinners, spa days, travel adventures and venting sessions lol! Thank you for getting me OUTSIDE even when I was feeling low. You are the true epitome of a friend, and I am very thankful to have you in my life. Love you girl! Kelcie thank you for all the work and yoga sessions. They were some of my most favorite memories during this journey and I will always cherish them. Lastly, thank you and Sam for your support. I will forever be grateful. Lauren, Regina, and Katie I have truly enjoyed having you all on this journey with me from the work sessions, lab meetups, nights in Moorea and more, you all have added moments of joy throughout this journey. I would also like to thank Lauren, Emily, Ben, and Regina for your support in the field in Moorea and California. Tonya Kane thank you for all your hugs lol! Also, thank you for your support and encouragement over the years. I will always appreciate the light that you have been for me during this journey. Rachel Kennison thank you for the insightful

conversations, laughs, and inspiration. I appreciate your candor and philosophy on life. Thank you and Luna for providing a peaceful space for me during life's transitions and all the support.

I would also like to acknowledge friends, family, and staff whose support made this dissertation possible. Ben! OMG! I do not think I would have made it through this program without you lol. Thank you for your consistency, friendship, and organization. You spearheaded so many of our cohort gatherings and encouraged me to get out of my comfort zone.  Thank you for the laughs and work sessions. They truly added so much to my experience. Additionally, I would like to say thank you for being an authentic advocate for diversity and inclusion and for letting your actions speak for themselves. Nyasha, I am so glade you approached me that day! Thank you for being my beach, brunch, and church buddy. I am so grateful for your friendship and support throughout this journey. Jeannie, thank you for the laughs, hugs, hikes, and meet-ups. You are truly a light in this world, and I am grateful to call you a friend. Erick thank you for the work sessions, introductions to delicious food spots in LA, care, and support. I appreciate your friendship and creativity. Ki thank you for the QOTD's, conversations, travel dates and so much more. You have vicariously experienced so much of this journey with me and I am grateful that you were present for the ride. Thank you, friend.

Bre, Teiara, Sydney, Jasmine, and Zac thank you all for your friendship over the years. You all have added so much to my life and continue to keep a smile on my face through all life's ups and downs and especially during this journey. Thank you for your prayers, support, and friendship. Sean, thank you for being my biggest cheerleader and reminding me to never back down. Tessa, thank you for warmly welcoming into the EEB community during orientation. I greatly appreciate all your support, kind words, and care when it came to varying needs throughout this journey.

My journey to graduate school started well before my enrollment at UCLA. For this reason, I would like to thank those who have supported me throughout different stages of my academic career. Dr. Eric Engstrom thank you for taking my initial interest in research seriously and encouraging me to apply to my first research internship. That summer in Woods Hole was the start of my research journey and it would not have been possible without your encouragement and support. Dr. Abiodun Adibi and Dr. Indu Sharma thank you for pushing me to continue my journey as a researcher at Hampton University and for all the letters of recommendations. Dr. Pam Yeh, thank you for giving me space to grow as a young researcher in your lab during my summer internship at UCLA. Dr. Michelle Johnson, thank you for your mentorship and guidance throughout my adolescent. You were the first academic doctor I knew and a catalyst for my journey.

I would like to thank my family including my parents, siblings, grandparents, uncles, aunts, and cousins. Thank you all for believing in me and supporting me throughout this journey. Mommy and daddy, thank you both for instilling character, grit, respect, faith, and love. These things have truly carried me along the way. Thank you for modeling the idea that it is never too late to start over or try again. Your journeys in life have served as both inspiration and motivation and I am grateful to have you both as parents. Kevin, Austin, Sean, and Briana thank you for being 'gang'. I appreciate the love and support you all have given me throughout this journey. All of you inspire me to put my best foot forward and to go after my dreams. Love you guys!

Brotherson and the UC Berkely Gump Research Station for logistical support in Moorea, French Polynesia.

# BIOGRAPHICAL SKETCH

## SHALANDA R. GRIER

**<u>EDUCATION</u>**

2015    B.S. in Biology and Minor in Leadership Studies, Hampton University

**<u>AWARDS AND HONORS</u>** (select few)

2021    George A. Bartholomew Fellowship for Outstanding Field Biologists

2018    National Science Foundation (NSF) Graduate Research Fellowship Program (GRFP)

2018    University of California Office of the President Historically Black College and

University Fellowship

**<u>PUBLICATIONS</u>**

Hayes, HG., Kalhori, PS., Weiss, M., **Grier, SR**., Fong, P., & Fong, CR. (2021). Storms may

disrupt top-down control of algal turf on fringing reefs. *Coral Reefs*, *40*(2), 269-273.

Fong, CR., Chiquillo, KL., Gaynus, CJ., **Grier, SR.,** Hà, BA., Ryznar, ER., ... & Fong, P. (2021).

Flip it and reverse it: Reasonable changes in designated controls can flip synergisms to

antagonisms. *Science of the Total Environment*, *772*, 145243.

Ryznar, E. R., Smith, L. L., Hà, B. A., **Grier, S. R.**, & Fong, P. (2023). Functional trait

variability supports the use of mean trait values and identifies resistance trade-offs for

marine macroalgae. *Journal of Ecology*.

**<u>TEACHING APPOINTMENTS</u>**

**Fall 2022**                    Teaching Fellow, Program for Excellence in Education and
Research in the Sciences


**Spring 2021**                 Graduate Grader, Life Science Career Exploration

| | |
|---|---|
| **2020, 2021** | Special Grader, Introduction to Ecology and Animal Behavior |
| **Fall 2020** | Teaching Assistant, Introduction to Ecology and Animal Behavior |
| **Winter 2020, 2021 & Spring 2023** | Teaching Assistant, Associate & Fellow Marine Biology Field Quarter |
| **Fall 2018, 2019, 2021** | Teaching Assistant & Teaching Associate, Introduction to Marine Science |

## Conference Presentations (selected)

**Grier, S**., Ha, B., Ryznar, E., Smith, L., Fong, P. (2021, June). *Sediment, light, and interspecific interactions have strong yet independent species-specific effects on two dominant coral reef macroalgae.* American Society of Limnology and Oceanography Annual Meeting, Virtual. Oral presentation

**Grier, S**., Fong, P. (2018, Dec.). *Both species interactions and nutrients may reduce the negative effects of density on growth of a dominant macroalga on a human-impacted fringing coral reef in the South Pacific*. California Estuarine Research Society Meeting, Long Beach, CA. Poster presentation

## GUEST LECTURES

Coastal Biology, Fall 2023, University of Pennsylvania

Field Marine Biology Quarter (FMBQ), Fall 2020 and 2022, UCLA

Marine Biology Quarter (MBQ), Spring 2023, UCLA

CHAPTER 1

**Sediment, light, and interspecific interactions have strong yet independent species-specific effects on two dominant coral reef macroalgae**

**Abstract**

Storms are predicted to increase with climate change in the South Pacific, resulting in reductions in light levels and increases in sedimentation for coral reef communities. In coral reef ecosystems, light is a limiting resource to primary producers while sediment is generally considered a stressor. To test this hypothesis, we examined growth and structural responses of two macroalgae, *Padina boryana* and *Sargassum pacificum*, in response to experimental manipulations of sediment addition and light reduction on a fringing reef in Moorea, French Polynesia. This experiment was first conducted on two monospecific assemblages, *P. boryana* and *S. pacificum,* respectively, and then interspecific assemblages of these species. In monospecific assemblages, shade reduced *P. boryana* growth by 68% with no effect of sediment, while added sediment increased *S. pacificum* growth by 40.4% with no effect of light. Further, carbonate content of *P. boryana* was higher in ambient light and with added sediment, while neither factor affected thallus toughness of *S. pacificum*. In interspecific assemblages, growth of *P. boryana* was higher and calcification was lower than in monoculture. *S. pacificum* had a negative growth response to reduced light when grown with *P. boryana*, suggesting species interactions. Our study suggests *P. boryana* and *S. pacificum* have species-specific growth and structural responses to changes in light and sediment load that may occur with short-term disturbances in environmental drivers associated with storms. Further, understanding the

responses of species and the influence of community context on these responses will strengthen

coral reef predictions in the Anthropocene.


**Introduction**

As many environmental drivers of primary productivity continue to shift globally in the

Anthropocene (IPCC 2019)(IPCC 2019), it is becoming increasingly imperative to understand

their ecological effects. Presently, global climate change is predicted to alter precipitation

patterns, including increased intensity of storms in the South Pacific (Knutson 2010). Storms can

cause short-term reduction in light availability (Grémare et al. 2003; Carle and Sasser 2016) and

have been linked to increased runoff from developed watersheds into coastal marine ecosystems,

including fringing coral reefs (Edmunds et al. 2014). Additionally, storm-generated winds can

lead to resuspension and redeposition of sediments, which can profoundly affect coral reef

producer populations and communities (Tebbett and Bellwood 2020). Thus, the potential for

further alterations in environmental drivers associated with storms in coastal marine systems

(Xie et al. 2018; Luter et al. 2021) motivates further research on their effects on primary

producers.

Macroalgae are ubiquitous throughout fringing coral reef systems and provide many

ecosystem benefits. Macroalgae provide vital ecosystem functions in the form of habitat (Bittick

et al. 2019; Fulton et al. 2019), nutrient cycling (Fong and Paul 2011), bioresources (Sudhakar et

al. 2018), and potential carbon sinks (Hill et al. 2015). However, macroalgae often compete for

essential resources, such as space, with coral (Lirman 2001). This competition, along with other

environmental stressors, minimizes the space available for coral recruits to settle and survive

(Box and Mumby 2007; Bulleri et al. 2018). As such, when macroalgae dominant on coral reefs

the ecosystem is considered to be in a degraded state (McCook 1999; Mejia et al. 2012; Bruno et al. 2014; Fulton et al. 2019). Thus, understanding how reduced light and increased sediment resuspension and deposition affect macroalgae is critical as the abundance of different macroalgal species likely determines the structure and function of coral reef communities in the Anthropocene.

Light, a critical resource for all primary producers, including coral reef macroalgae, may be episodically reduced during storms (Mejia et al. 2012) due to runoff, sediment resuspension, and cloudiness. Macroalgal communities on fringing coral reefs generally receive adequate light for growth due to shallow water depths (Manuel et al. 2013). However, cloudiness associated with storms can reduce light levels in these communities for intervals from hours to days (Anthony et al. 2004; Victor et al. 2006). Macroalgal species can acclimate to and tolerate various ranges of light intensities over time Click or tap here to enter text.(Franklin and Larkum 1997; Talarico and Maranzana 2000; Dieter and Wiencke 2003) but short-term reductions in light can have negative effects. While both high and low light levels can result in decreases in photosynthetic activity (Middelboe et al. 2006) due to photoinhibition (Häder et al. 2002; Li et al. 2014b) and light limitation, respectively, generally higher light results in faster growth (O'Neal and Price 1988). Studies have captured long-term responses of macroalgae to changes in light; however, short-term responses to light linked with other storm-associated disturbances such as sediment resuspension and deposition, warrant more attention.

While wind-driven sediment resuspension and deposition is known to negatively affect corals (Storlazzi et al. 2015; Luter et al. 2021), the extent to which other benthic space holders, especially macroalgae, are affected by this process is understudied. Sediment accumulation has strong effects on tropical turf algae (Tebbett et al. 2018; Tebbett and Bellwood 2019). For

example, sediment resuspension and deposition results in light limitation and reduced growth (Tebbett et al. 2018). Additionally, Clausing et al. (2014) found sediment addition deterred turf algal growth, likely by limiting light and gas exchange leading to anoxic conditions. Sediment has also been shown to aid turf growth by limiting herbivory (Tebbett et al. 2018). For tropical macroalgae, added sediment can lead to reductions in growth (Clausing et al. 2016), but this result is not universal as *Padina boryana* and *Sargassum pacificum* both demonstrated tolerance of increased sediment loads (Johnson et al. 2018; Sura et al. 2021). These studies suggest responses of macroalgae to sediment are likely dependent on species-specific traits as seen in temperate macroalgae (Eriksson and Johansson 2005; Voerman et al. 2019). As such, investigating species-specific responses to sediment disturbances are necessary as variations in responses will likely influence species' growth and, ultimately, their composition on fringing reefs.

In addition to impacting growth, variation in environmental drivers can lead to structural changes in algae, such as variation in thallus toughness and calcium carbonate ($CaCO_3$) content. However, alteration in structural content of macroalgae in response to sediment resuspension and deposition and light reduction remain largely unexplored. In contrast, studies have demonstrated structural responses of algae to disturbances such as herbivory (Paul and Van Alstyne 1988), nutrient addition (Bergman et al. 2016; Bittick et al. 2016), and light (De Beer and Larkum 2001). To our knowledge, sediment effects on macroalgal structural responses have not been thoroughly investigated (but see Sura et al., 2021). In contrast, light has been shown to influence macroalgal structural responses, particularly calcification, in lab/aquaria experiments spanning 4-7 hrs. (Jensen et al. 1985; McNicholl and Koch 2021). Light may control calcification through both photosynthetic carbonate precipitation and the energy photosynthesis supplies for

calcification (Borowitzka and Larkum 1976, 1987; Jensen et al. 1985; Semesi et al. 2009; Prathep et al. 2018). We posit that similar relationships may exist in calcifying tropical algal species such as *Padina spp.* that deposit calcium carbonate on thalli surfaces (Benita et al. 2018). It is important to understand drivers of macroalgal structural responses to changes in sediment and light as they may have community and ecosystem level effects (Schupp and Paul 1994; Campbell et al. 2014).

Although individual algae may respond to variation in light and sediment, interspecific interactions may mediate these species-specific responses. While there is a lack of studies on coral reef algae illustrating how species-specific effects can be dependent on neighbors, there is evidence of these effects in other systems (Cheloni et al. 2019). For example, the physiological and morphological responses of two dune grasses changed based on sand burial and monoculture or mixed assemblages (Harris et al. 2017). One fared better in monoculture versus mixed assemblages due to differences in species traits such as energy allocation. This result provides evidence of species interactions influencing species responses to abiotic drivers. Given that macroalgae typically occur in mixed species assemblages rather than monocultures, it is important to investigate the intra- and interspecific responses of different macroalgal species to disturbances.

Here, we investigate: 1) the species-specific growth and structural responses (calcification, toughness) of *P. boryana* and *S. pacificum* to short-term addition of sediment, reduction in light, and their possible interactions, and 2) the effects and interactions that variations in sediment and light have on interspecific assemblages of *P. boryana* and *S. pacificum.*

**Materials and Methods**

*Experimental Approach*

To evaluate species-specific responses to short-term changes in sediment, light, and their possible interactions, we conducted three two-factor, fully-crossed experiments varying light and sediment deposition. Due to logistical constraints, experiments were conducted in three different stages. In Experiment 1 and 2, we tested the effects of these two factors on monospecific assemblages of each target algal species separately. Experiment 3, the final experiment, varied the same two factors on interspecific assemblages of the target algal species. In all experiments, algal thalli were placed in cages to deter herbivores from consuming algae and potentially removing settled sediment.

*Study Site and Species*

All three experiments took place from April - May 2019 in Moorea, French Polynesia within a fringing patch reef system at Ta'ahiamaunu Public Beach (17.491918 ºS 149.850036 ºW). This site is located along the north shore at the mouth of Opunohu Bay, in water depths ≤ 2.5 meters, and is comprised of patchy hard substrate that is structurally complex. Much of the structure within this fringing reef is dead skeletons of massive corals in the genus *Porites* remaining after prior disturbances, such as *Acanthaster planci* outbreaks and cyclones (Pratchett et al. 2011; Trapon et al. 2011; Vercelloni et al. 2019), surrounded by less complex coral rubble or sandy bottom.

We studied *Padina boryana* and *Sargassum pacificum* (hereafter *Padina* and *Sargassum*), both of which are ubiquitous species of brown algae commonly found in tropical fringing reef systems (Mayakun and Prathep 2005; Adjeroud et al. 2009). Although these species are both

brown macroalgae, they have distinct morphologies and traits. *Padina* is a lightly calcified alga (Geraldino et al. 2005) with an upright, flattened foliose thallus (Wichachucherd et al. 2014). *Sargassum* is not calcified and has upright main branches with oval shaped blades (Mattio et al. 2008).

*Environmental Context: Solar Radiation and Rainfall*

Clausing et al. (2016) found that establishing the environmental context prior to and during a field experiment was critical to interpreting results. Therefore, we downloaded post-processed meteorological data of rainfall and solar radiation with permission from the Moorea Coral Reef LTER (Washburn and Brooks 2022) for the time just prior to and including our experiments. Rainfall and solar radiation were recorded every five minutes from sensors located at the University of California Gump Station, 6m above mean sea level, about 3.3 km from the study site. We plotted the post-processed daily cumulative rainfall (mm) measurements from 01 April – 31 May 2019. We reported cumulative daily rainfall (mm) measurements for the week of each experiment (22 April – 13 May 2019). We also calculated daily averages of solar radiation ($kW/m^2$) and plotted these averages over time (01 April – 31 May 2019). Lastly, we reported solar radiation ($kW/m^2$) measurements for the week of each experiment (22 April – 13 May 2019).

*Sediment and Light Effects on Monospecific Assemblages of Brown Macroalgae*

To assess the effects of marine sediment and light on the species-specific responses of *Padina* and *Sargassum,* we conducted two independent, two-factor fully-crossed field experiments manipulating sediment (ambient/added) and light (ambient/shaded). There were ten

replicates for each treatment combination (n=40) for each algal species. The experiment was first run with *Padina* for seven days (*Padina* experiment) after which the same experiment was repeated with *Sargassum* for seven days (*Sargassum* experiment). The same location was used for both experiments to limit the possibility of site effects, though temporal effects are possible. Sediment and light were manipulated in the same manner for each experiment and target species.

As we were interested in species-specific responses to our manipulated abiotic factors unconfounded by herbivory, we enclosed all algae in cylindrical cages made from hardware cloth (13.0cm x 13.5cm, height x diameter, with 1cm$^2$ mesh openings) with tops and bottoms to protect algae from most herbivores. Experimental units of this size and material did not have significant effects on water flow or light in a previous experiment at this site (Clausing et al. 2014) (See Supplement sections SI1 and SI2 for methods of our own tests of these effects). To model short-term light reduction, such as cloudiness and turbidity during rainfall events (Anthony et al. 2004; Edmunds and Gray 2014; Fong et al. 2020)(Fig. 1A), window screen was sewed on the tops and partially down the sides of half of the experimental units using fishing line. The window screen reduced the light environment by 42% (SI1&5). To limit the effects of the window screen on water flow, we left a 2-3cm opening at the bottom of experimental units free from window screening (See Supplement SI1, 2, 5 and 6 for methods and results of tests of the effects of these experimental units on light and water flow). Treatments with ambient light conditions were free of window screening.

Algae were collected from the study site, gently rinsed to remove sediments, and spun in a salad spinner for one minute to remove excess water. To quantify initial carbonate content for *Padina*, each algal sample used in the experiment was subsampled, with proportional representation of older and younger tissues. To measure *Padina* calcium carbonate, 1.2g-1.4g

subsamples of each algal thallus were placed in individual plastic cups and covered with diluted (~8%) hydrochloric acid (HCl). HCl was replaced until samples stopped bubbling, even after reapplication of acid, signifying the calcium carbonate was dissolved (Pennings and Paul 1992; Clausing and Fong 2016). After dissolution was complete, the decalcified weight of each subsample was recorded (Martone 2010). Initial carbonate content of algal samples was calculated as loss during decalcification and standardized as a percent of initial mass.

For each experimental unit, *Padina* and *Sargassum* samples were standardized to an initial wet weight of 5g each, including intact apical meristems, randomly assigned to an experimental unit, and secured on the cage bottom in growth position using cable ties. Experimental units were randomly attached to rope and deployed in the field; ropes were secured to the benthos by covering them with loose coral rubble. For ambient sediment treatments, we allowed sediment to accumulate naturally to model current sediment regimes. To create added sediment treatments, we added 33.5mL of sediment directly from the benthos of the study site to half of the experimental units every two days. Past studies from this and nearby fringing reefs have shown that mostly silt and fine grain sediments remains on algal thalli while larger grained sands and calcium carbonate can be found in the benthos (Clausing and Fong 2016; Gaynus 2019; Sura et al. 2021). We determined this volumetric dose based on visual estimates of sediment loads after wind events, which we later confirmed (SI3&7). The experimental sediment load was greater than ambient sediment loads but less than sediment loads measured after a 4-day wind event with an average speed of 17.7 ±3.35 m/s (SI3,7&8). To determine the dry weight of sediment added by this volume, we collected one of these sediment doses, dried it in a drying oven, and weighed it. Sediment dry weight was 24.1g.

At the end of each experiment, we collected all experimental units from the field. Our response variables were growth and structural responses. Algal samples were removed from experimental units, gently rinsed in seawater, and spun in a salad spinner as described above. We measured final wet weight of each algal sample and calculated the percent change in biomass. Then, for algal structural responses in *Padina*, we measured final calcium carbonate content as described above and calculated percent change from initial values in each experimental unit.

We quantified the effects of sediment and light on the structural responses of *Sargassum* by measuring final thallus toughness with a penetrometer (Cruz-Rivera and Hay 2001). The penetrometer allowed us to measure how much weight was required for a needle to penetrate blades of each algal thallus (Bittick et al. 2016). We measured toughness on a total of five blades for eight out of the ten *Sargassum* samples due to logistical constraints. Toughness was measured in the middle of each blade by resting the penetrometer tip on the blade and adding weight until blade penetration. The weights required to penetrate each of the five blades per experimental unit were averaged and served as a replicate (n=8).

*The effect of sediment and light on* Padina *and* Sargassum *in interspecific assemblages*

To investigate the effect of sediment and light on interspecific assemblages of *Padina* and *Sargassum*, we conducted a two-factor fully-crossed field experiment using the same treatment combinations described above (n=40) (Interspecific experiment). This experiment was conducted two weeks after the first set of experiments started. *Padina* and *Sargassum* were collected and standardized to wet weights of 5g in the same manner described above. For *Padina*, initial calcium carbonate was determined as described above. Thalli from each macroalgal species were positioned ~ 5cm apart within each experimental unit, ensuring that, with water movement, algal

thalli had frequent physical contact. Experimental units were deployed in the field for six days. Final structural responses of *Padina* and *Sargassum* were measured as described above.

*Statistical Analysis*

All data met the assumptions of parametric statistics (Shapiro-Wilk test for normality and Levene's test for homoscedasticity) once monospecific and interspecific *Padina* calcification values were squared. We used two-factor ANOVA to test for effects of sediment, light and their interactions on growth and structural responses of both *Padina* and *Sargassum* for all three experiments.

*Efficacy of Experimental Treatments*

We evaluated the efficacy of our sediment manipulation as well as potential experimental artifacts to ensure our treatments were biologically significant and that our caging methods did not influence our overall results (SI2, SI3& SI4). Overall, *Padina* ambient sediment loads were naturally higher than *Sargassum* (See table in SI9 for means, SE, and statistical outcomes for all measures). Overall, immediate sediment addition did not differ between algal species. However, both algal species experienced sediment loss within the two-day intervals between experimental sediment additions. Thus, to maintain sediment loads, sediment was reapplied every two days. Immediate sediment addition for *Padina* was almost double the ambient but about half of the sediment loads naturally present after a storm-associated wind event. Immediate sediment addition for *Sargassum* was more than twenty-fold of sediment loads naturally present on *Sargassum*.

To determine the effectiveness of our experimental treatments manipulating light, we placed Hobo loggers, (UA002-64 HOBO Waterproof Temperature/Light Pendant Data Logger), (lumens ft$^2$) in ambient light and shaded experimental units during each experiment (April – May 2019) for 4-6 days (n=1, readings every 2.5 minutes). Hobo loggers were placed within the experimental units but away from algae to avoid algae blocking the light. The average light level for each day was calculated using readings from 1100-1800 for each experiment. Light measurements during the monospecific *Padina* experiment began on the third day on 24 April 2019 and lasted four days. For both the monospecific *Sargassum* and the mixed assemblage experiments, light measurements began on the second day of the experiment, 30 April and 8 May 2019, respectively, and lasted five days. Light levels were also recorded in February 2020 when wind-driven sediment loads were measured (SI3). To set our sediment treatments in context of the wind environment that may have generated deposition during wind-driven resuspension and deposition, we quantified wind speeds (SI8).

**Results**

*Monospecific* Padina *experiment with initial low light and intermittent rain*

Prior to the *Padina* experiment, there was intermittent light rain, with daily accumulations of less than 6.3mm (Fig. 1A). There was a 2-day rainfall event 1 day after the start of the *Padina* experiment totaling 59.9mm. Summed weekly rainfall during this experiment spanning 22 April – 28 April 2019 totaled 105.2mm. Although variable, there was an overall reduction in mean solar radiation with increasing rainfall during this storm (Fig. 1B), contextualizing our experimental treatments.

Rainfall likely caused the initial low light levels across treatments (Fig. 2A). Cessation of rain resulted in light levels gradually increasing for the next two days and remaining so until the end of the week-long experiment as conditions remained dry. There was a small and marginally significant difference between light levels in ambient and shaded light treatments (t-test, p=0.07). Light was reduced on average by approximately 17% over the four days light was recorded during the experiment (Fig. 2A).

Reducing light level, even by this relatively small degree, negatively affected *Padina*, reducing growth by 67.6% overall compared to ambient light treatments; in contrast, there was no effect of added sediment (Fig. 2B, Table 1A). *Padina* grew in all treatments, with average daily increases ranging from 1.3 - 5.2 %. In contrast, both sediment and light had independent main effects on the structural responses of *Padina*, measured as change in carbonate content, when grown in monospecific assemblage (Fig. 2C, Table 1B). *Padina* increased carbonate content by over 2% per day in ambient light treatments while changes in carbonate content of algae in shaded treatments ranged from gains of 1% to losses of -1% per day. Further, added sediment resulted in an overall increase in carbonate content of *Padina* ranging from 1.5-2.8 % per day.

*Monospecific* Sargassum *experiment with intermediate light level and little rain*

The *Sargassum* experiment took place from 29 April – 05 May 2019, after a 1-day rainfall event that totaled 45.2mm (Fig. 1A). However, during the experiment there was little to no rainfall with daily accumulations of less than 0.3mm. As such, solar radiation remained higher and less variable during the *Sargassum* experiment than during the *Padina* experiment (Fig. 1B). *Sargassum* in monospecific assemblages consistently experienced more light with larger

differences between light treatments compared to *Padina* (Fig. 3A; note scale difference between panel A in Fig 2 and Fig. 3). There was a significant difference between ambient and shaded light treatments (t-test, p=0.005), where light was reduced by approximately 49%.

Adding sediment positively affected *Sargassum*, increasing growth by 40.4% overall (Fig. 3B, Table 2A). While there was a marginally significant trend where reduced light reduced growth of *Sargassum*, the overall reduction due to light was less than 30%, despite the large differences in availability due to light treatment. There was no significant change in *Sargassum* thallus toughness for either experimental factor.

*Interspecific experiment with intermediate light levels and little rain*

Like the previous experiment, there was a rainfall event starting the day before the interspecific experiment, which totaled 27.2mm (Fig. 1A). Rain continued throughout the first day of the experiment, which ran from 07 May – 13 May 2019. However, daily accumulations never exceeded 11.9mm. Solar radiation also remained higher and varied less during this combined experiment compared to the *Padina* experiment but was lower than the *Sargassum* experiment (Fig. 1B). As for the above-water measures, light levels in interspecific assemblages fluctuated, with fluctuations muted in shaded treatments (Fig. 4A). There was a significant difference between ambient and shaded light level measurements (t-test, p = 0.008) with an average light reduction of 44% over the experiment.

The reduction of light negatively affected *Padina,* resulting in an overall reduction in growth of 51% compared to ambient light treatment (Fig. 4B, Table 3A). As when grown alone, there was no effect of added sediment. Growth of *Padina* in full light was about 10% per day, while reducing light decreased growth to ~ 5% per day. In contrast to growth responses, both

light and sediment treatments had independent main effects on the change in carbonate content of *Padina* (Fig. 4C, Table 3B). While % calcium carbonate content of *Padina* in ambient light did not change during the experiment, shaded treatments lost an average of ~7.2% of carbonate content per day. Further, *Padina* in ambient sediment treatments lost about ~5% per day of its carbonate, while added sediment limited this reduction in carbonate to about 2% per day.

Reduction of light negatively affected *Sargassum* when grown with *Padina*, resulting in an overall reduction in growth of 68.3% compared to ambient light treatments (Fig. 4D, Table 3C). In ambient light, *Sargassum* growth averaged 2.6% per day, while light reduction resulted in a decrease in growth to ~1% per day. In contrast to the experiment when *Sargassum* was grown alone, there was no effect of added sediment when it was grown with *Padina*. Neither light nor sediment affected *Sargassum* toughness over the six days of the experiment (Fig. 4E, Table 3D). The average weight needed to penetrate *Sargassum* thalli across treatments was ~ 6.8g.

**Discussion**

Overall, our study demonstrates that *Padina* and *Sargassum* have unique and noninteractive responses to simulated storm-related disturbances that may be modified by community context. We found species-specific responses to experimental alterations of sediment and light. These algal responses varied widely; for example, small reductions in light impacted growth and calcification of *Padina*, while *Sargassum* tolerated far greater reductions in light and benefitted from added sediment. Additionally, the responses of these macroalgae to disturbances may be exacerbated or buffered by a neighbor, albeit this may also have been driven by temporal environmental variability. For example, *Sargassum*, when grown with *Padina*, lost resilience to light reduction as well as the benefit from sediment addition. In contrast, *Padina* benefited from

15

the presence of *Sargassum,* ameliorating the negative effects of reduced light on growth. Taken together, our results imply that consideration of macroalgal species identity and community context is critical to advance our ability to predict responses to changing environmental drivers.

*Responses to short term reductions in light are species-specific*

Our results show that short-term reductions in light limit algal growth and the strength of this driver varied across macroalgal species. The consistently large and negative effects of reduced light on *Padina* growth suggest this alga is relatively intolerant of short-term light limitation. Cox and Smith (2015) provided evidence that a congener, *Padina sanctae-crucis*, can acclimate to both high light and changes in light over an 8-day period in an intertidal zone in Hawaii. Possible explanations of this difference include higher overall light availability in intertidal zones compared to our subtidal study, or within-genus differences in tolerance to reduced light. Ultimately, these studies suggest that, for *Padina*, the lasting effects of short-term reduction in light level, such as that generated by storms, need further investigation.

In contrast, *Sargassum* was not as sensitive to light reductions as *Padina*; though light for this experiment started at a higher baseline, the difference between light treatments was consistent and of greater magnitude. Thus, the marginal effect of light on *Sargassum* growth indicates this species has a greater ability to sustain growth during short-term light reductions. Congeners of *Sargassum* at early life stages have also shown tolerance to a range of light levels over a two-week period, although there was a general pattern of lower growth at the lowest light level (Zou et al. 2018). Although our *Sargassum* thalli were not in early life stages, our results suggest the response to lower light is likely similar. Overall, our study suggests that *Sargassum* may be more tolerant of episodic reductions in light, such as those that occur during storms,

compared to *Padina.* This higher tolerance may provide one possible explanation for why this *Sargassum* species has increased in dominance on reefs in the Anthropocene (Stiger and Payri 1999; Li et al. 2014a; Hong et al. 2021; Zhong et al. 2021).

We found that short-term reduction in light had strong effects on macroalgal physical structure in the form of calcification, but not toughness. The structural response of *Padina* to these environmental drivers was strong while lacking in *Sargassum*. *Padina's* strong response may be explained by the considerable energy requirement for calcification, which is why it is often linked to photosynthesis (Jensen et al. 1985). For example, the intercellular uptake of $CO_2$ during photosynthesis and the subsequent increase in pH within extracellular spaces of *Halimeda spp.,* another calcifying alga, has been suggested as the main mechanism by which aragonite precipitation is initiated (Borowitzka and Larkum 1977, 1987). While calcium carbonate is deposited externally on the ventral surface of *Padina* (Okazaki et al. 1986), unlike *Halimeda* (Borowitzka and Larkum 1976), the relationship between photosynthesis and calcification may be similar (Borowitzka and Larkum 1987). Further, reduction in calcification for *Padina* due to reduced light is supported by studies showing low light often results in little or reduced calcification for many calcifying species such as coralline algae (Egilsdottir et al. 2016), coral, and macroalgae (e.g., species in genera *Millapora* and *Galaxaura,* respectively, among others) (Goreau 1963; Prathep et al. 2018). In contrast, toughness is often induced by physical damage such as herbivory and may not require energy directly from photosynthesis (Bergman et al. 2016). Our study suggests that changes in environmental conditions relating to storm disturbances, such as short-term reduction in light availability, may ultimately result in decreased physical structure, in the form of calcification, for calcifying macroalgal species such as *Padina*.

*Responses to sediment deposition range from tolerance to stimulatory*

We found that sediment can be a driver of *Sargassum* growth. Our results contrast many studies that found no or adverse effects of sediment on *Sargassum* (Umar et al. 1998; Bi et al. 2016; Sura et al. 2021). However, differences in results may be attributed to experimental sediment loads, species, and/or environmental context. For example, our experimental load on *Sargassum* was significantly higher than the ambient load, whereas Sura et al. (2021) modeled ambient sediment conditions. Additionally, our experimental load was less than the heavy sediment load we measured after a storm-related wind event (SI9). It is possible that sediment may have an indirect positive effect by providing a nutrient subsidy. This has been shown previously for *Padina* (Clausing et al. 2016) in Moorea and for macroalgae in a temperate estuary(Kamer et al. 2004). Click or tap here to enter text. Schaffelke (1999) also provides evidence of this process wherein *Sargassum linearifolious* thalli covered with particulate matter had >100% faster growth rates than thalli with particulate matter removed. Taken together, these studies imply *Sargassum* may be favored in places where global change results in increased sediment flux and/or resuspension.

In contrast, we found *Padina* is tolerant of increased sediment loads. This result contrasts studies suggesting sediment negatively affects *Padina* growth (Clausing et al. 2016). Many studies report negative sediment effects on macroalgal growth and survival at early life stages (Alestra and Schiel 2015; Bi et al. 2016; Gao et al. 2019). As such, it is possible sediment may inhibit *Padina's* growth at early life stages not captured in our study. However, another study in Moorea also showed *Padina boryana* tolerates added sediment (Johnson et al. 2018) while recent evidence has demonstrated an absence of either a positive or negative sediment effect on *Padina* growth (Sura et al. 2021). These studies all suggest that, in contrast to *Sargassum*, sediment may

not be a primary driver for *Padina* growth, and that the strength and direction of sediment effects may be highly context-dependent. Thus, as responses to sediment are species-specific, increased sediment should not be universally implicated as an environmental driver that inhibits algal growth. Instead macroalgae such as *Sargassum* may flourish on future reefs with high sediment while *Padina* simply tolerates high sediment conditions.

*Effects of light and sediment are independent, not interactive*

Results did not support our hypothesis that there would be strong and persistent interactions between light and sediment on macroalgal growth and structural responses. Our findings contradict other studies in temperate regions that have found interactions between light and sediment that can influence the assemblage of macroalgal communities (Irving and Connell 2002; Connell 2005). However, one possible explanation for these differences may be the level of investigation, as previous studies focused on algal community assembly and maintenance in temperate subtidal environments whereas our study focuses on macroalgal responses at the population level on a tropical fringing reef. Our results are consistent with another study investigating light and sediment effects on algal habitats and/or growth responses (Irving and Witman 2009), although this study focused on algal germlings as opposed to mature thalli. The lack of an interaction between sediment and light for our study may be due to low sediment retention over time for both algae and the possible removal of sediment due to whiplash motion of algal thalli in interspecific assemblages.

Both environmental drivers strongly and independently affected the ability of *Padina* to deposit calcium carbonate, with the reduction of light posing a consistent negative effect and the addition of sediment posing a consistent positive effect. Our results are similar to research that

19

demonstrated higher light availability results in higher calcification rates compared to completely dark treatments (McNicholl et al. 2020). While our study investigated ambient and reduced light availability in contrast to light and dark treatments, we found a consistent pattern of reduced calcification rates with less light availability. We also found a novel positive effect of added sediment, where sediment reduced *Padina* calcium carbonate loss in comparison to ambient sediment conditions. However, the mechanism behind these losses warrants further exploration. While light, $CO_2$, and pH have been shown to affect calcification of macroalgae (Celis-plá et al. 2015; Vogel et al. 2015), our study suggests sediment deposition may also affect calcium carbonate content. This result implies that systems that experience acute sediment disturbances may buffer against lower net algal calcification, increasing the potential for carbon sequestration (Chung et al. 2011).

*Concluding remarks and the need for future research*

We hope our results motivate future research into species-specific effects and interspecific interactions between tropical macroalgae in response to short-term sediment and light disturbances associated with storms. Additionally, we hope this work will encourage the implementation of shorter-term studies within longer-term studies to capture the dynamics of macroalgal responses overtime. While we found differences when species were grown together or alone, these results may be confounded by differences in light level and other environmental conditions across experiments. In our experiment, *Padina* grew faster with *Sargassum* than when it was grown alone. Conversely, when *Sargassum* was grown with *Padina*, growth was much slower. These results suggest *Sargassum* may provide some benefit to *Padina* while *Padina* may harm *Sargassum*. However, experiments directly manipulating presence and absence of these

species need to be conducted to further elucidate whether there is a species interaction between

*Padina* and *Sargassum* in response to storm-related environmental disturbances.

**Tables**

**Table 1.** (A) Two-way ANOVA testing the effects of sediment and light on *Padina* growth. (B)

Two-way ANOVA testing the effects of sediment and light on *Padina* calcification in

intraspecific assemblage. Bolded values represent significant p-values.

| A. *Padina* Growth | | | | |
|---|---|---|---|---|
| **Source** | **Df** | **Sum of Squares** | **F Ratio** | **P Value** |
| Light | 1 | 221.0703 | 0.3633 | **0.0117** |
| Sediment | 1 | 4304.4432 | 7.0742 | 0.5506 |
| Light*Sediment | 1 | 378.0432 | 0.6213 | 0.4359 |
| **B. *Padina* Calcification** | | | | |
| **Source** | **Df** | **Sum of Squares** | **F Ratio** | **P Value** |
| Light | 1 | 0.04252533 | 4.6432 | **0.0381** |
| Sediment | 1 | 0.10955255 | 11.9615 | **0.0014** |
| Light*Sediment | 1 | 0.00014715 | 0.0161 | 0.8999 |

**Table 2.** (A) Two-way ANOVA testing the effects of sediment and light on *Sargassum* growth.

(B) Two- way ANOVA testing the effects of sediment and light on *Sargassum* toughness in

intraspecific assemblage.

| A. *Sargassum* Growth | | | | |
|---|---|---|---|---|
| **Source** | **Df** | **Sum of Squares** | **F Ratio** | **P Value** |
| Light | 1 | 417.84839 | 3.1439 | 0.0847 |
| Sediment | 1 | 687.99628 | 5.1766 | **0.0289** |
| Light*Sediment | 1 | 202.01017 | 1.5200 | 0.2256 |
| **B. *Sargassum* Thallus Toughness** | | | | |
| **Source** | **Df** | **Sum of Squares** | **F Ratio** | **P Value** |
| Light | 1 | 2.622 | 1.920 | 0.177 |
| Sediment | 1 | 0.281 | 0.206 | 0.654 |
| Light*Sediment | 1 | 1.066 | 0.781 | 0.385 |

**Table 3.** (A) Two-way ANOVA testing the effects of sediment and light on *Padina* in interspecific assemblages. (B) Two-way ANOVA testing effects of sediment and light on transformed *Padina* calcification data over 7-day period in interspecific assemblage. (C) Two-way ANOVA testing effects of sediment and light on *Sargassum* growth in interspecific assemblages. (D) Two-way ANOVA testing effects of sediment and light on transformed *Sargassum* thallus toughness data over 7-day period in interspecific assemblage.

| A. *Padina* Growth | | | | |
|---|---|---|---|---|
| Source | Df | Sum of Squares | F Ratio | P Value |
| Light | 1 | 9457.8210 | 13.7666 | **0.0007** |
| Sediment | 1 | 245.4102 | 0.3572 | 0.5539 |
| Light*Sediment | 1 | 157.4102 | 0.2291 | 0.6352 |
| B. *Padina* Calcification | | | | |
| Source | Df | Sum of Squares | F Ratio | P Value |
| Light | 1 | 61.396276 | 9.7712 | **0.0039** |
| Sediment | 1 | 27.147886 | 4.3206 | **0.0463** |
| Light*Sediment | 1 | 9.674804 | 1.5397 | 0.8999 |
| C. *Sargassum* Growth | | | | |
| Source | Df | Sum of Squares | F Ratio | P Value |
| Light | 1 | 1050.1201 | 5.1778 | **0.0291** |
| Sediment | 1 | 111.7417 | 0.5510 | 0.4629 |
| Light*Sediment | 1 | 31.1363 | 0.1535 | 0.6976 |
| D. *Sargassum* Thallus Toughness | | | | |
| Source | Df | Sum of Squares | F Ratio | P Value |
| Light | 1 | 0.182 | 0.047 | 0.8304 |
| Sediment | 1 | 0.081 | 0.021 | 0.8862 |
| Light*Sediment | 1 | 0.170 | 0.044 | 0.8359 |

**Figure Captions**

**Fig. 1 a** Daily sum of rainfall (mm) and **b** Daily mean solar radiation (kW m$^{-2}$) taken above the sea surface from 01 April – 31 May 2019. Shaded vertical bars represent experimental periods for *Padina*, *Sargassum,* and the mixed species experiments, respectively.

**Fig. 2 a** Average daily light intensity measured under water in cages (lum/ft$^2$) for *Padina* monospecific assemblage 24 April – 27 April 2019. Mean percent daily change (±SE) in *Padina* b wet weight and c carbonate content when subjected to ambient and manipulated sediment (added) and light (shaded) treatments over 7 days. Bars are means ± SE.

**Fig. 3 a** Average daily light intensity measured under water in cages with different light treatments (lum/ft$^2$) for *Sargassum* monospecific assemblage 29 April – 05 May 2019. **b** Mean percent daily change (±SE) in *Sargassum* wet weight and **c** average weight in grams needed to penetrate *Sargassum* thalli subjected to ambient and manipulated sediment and light treatments over 7 days. Bars are means ± SE.

**Fig. 4 a** Average daily light intensity measured under water in cages with different light treatments (lum/ft$^2$) for *Padina* in interspecific assemblage 08 May – 13 May 2019. Mean percent daily change (±SE) in *Padina* **b** wet weight and **c** carbonate content in response to ambient and manipulated sediment and light treatments in interspecific assemblage. **d** Mean percent daily change (±SE) in *Sargassum* growth and **e** average weight in grams needed to penetrate *Sargassum* thalli in response to ambient and manipulated sediment and light treatments when grown in interspecific assemblage. Bars are means ± SE.

**Figures**

25
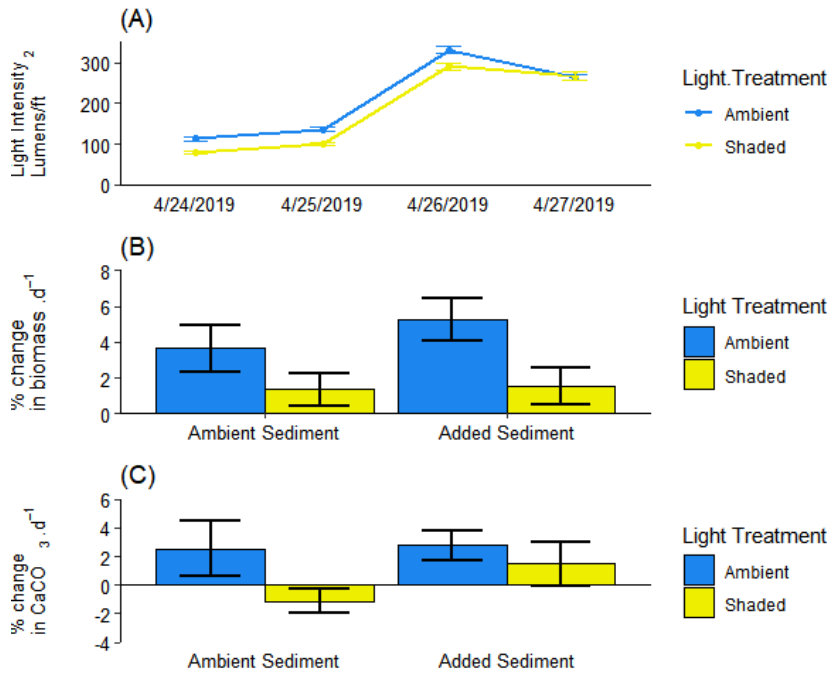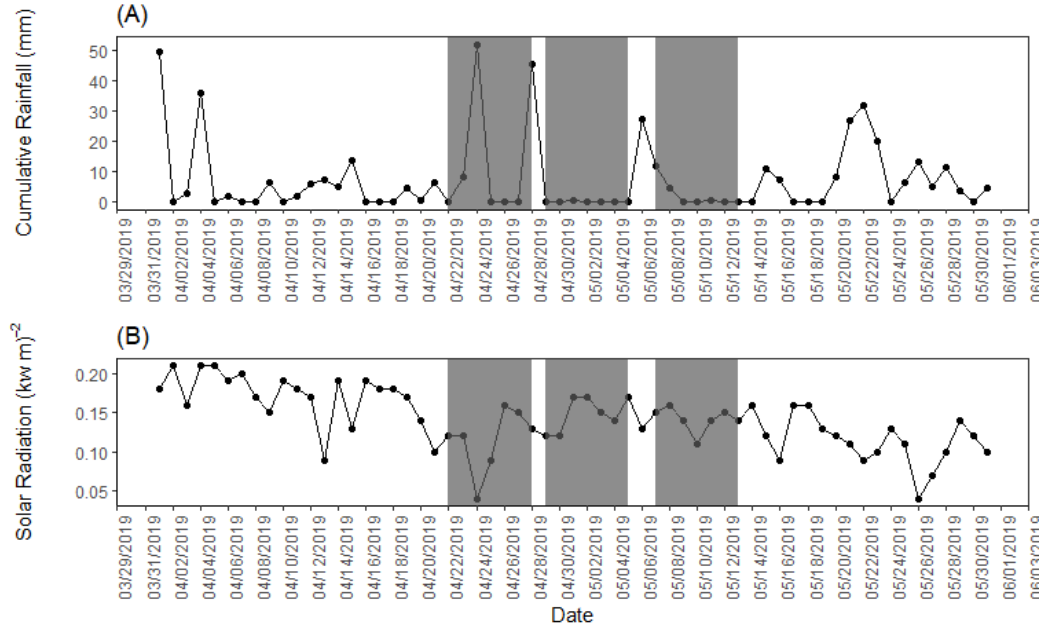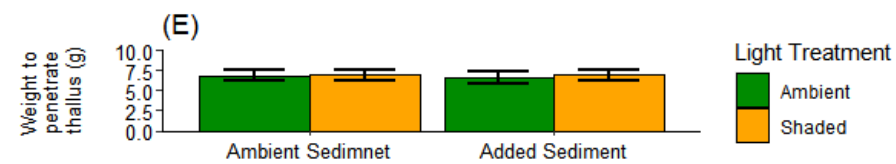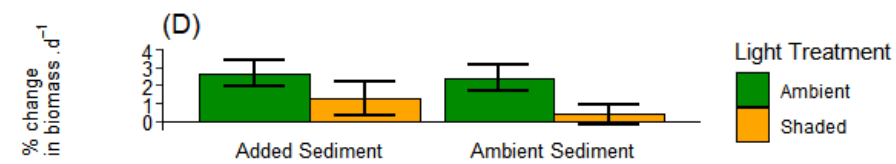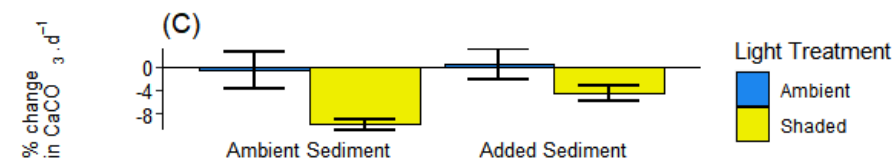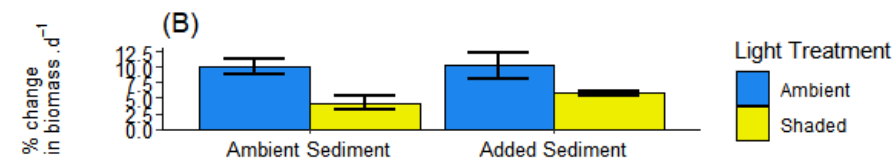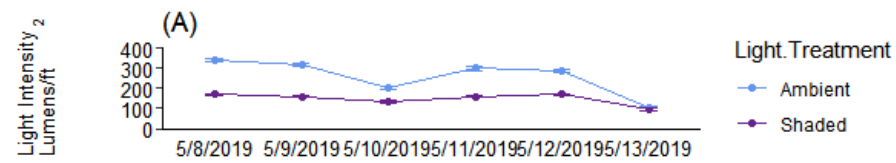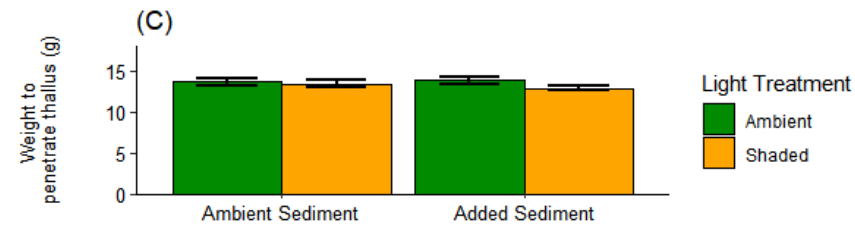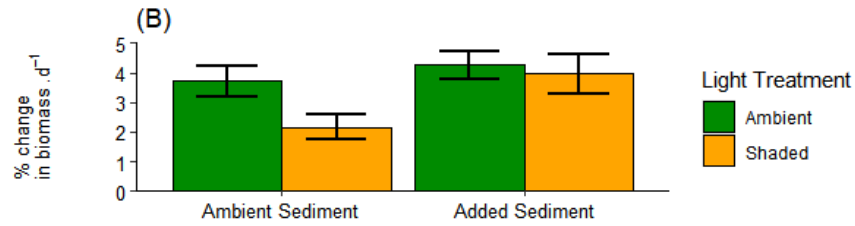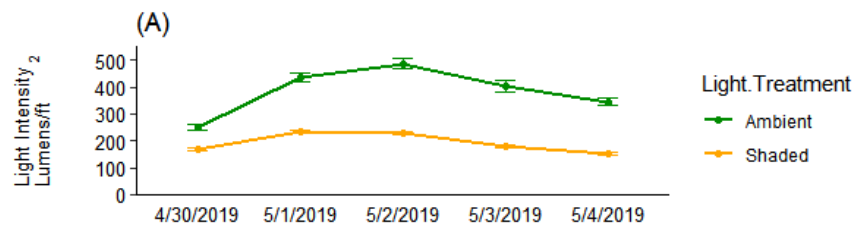
APPENDIX 1 – CHAPTER 1 SUPPLEMENT

**Supplementary Methods**

SI1. Evaluating differences in shaded and ambient treatment light measurements.

To quantify the light reduction of our shaded experimental units compared to ambient light conditions in the absence of algae, one Hobo logger was placed inside an ambient experimental unit to measure ambient light level and one Hobo logger was placed within a shaded experimental unit to measure reduced light level. Both Hobo loggers were positioned 5 cm from the benthos. The data loggers recorded light level every 10 secs for 6 minutes. The percent change from ambient light measurements and shaded light measurements was calculated and recorded on January 27, 2020.

SI2. Evaluating differences in water flow due to shading method

To evaluate the differences in flow across experiential light treatments we used clod cards and dye tests. We did a set of dye tests in Moorea in May 2019. Due to limited time in the field, we repeated and expanded the dye tests and conducted clod care measures along a tidal channel of the University of California's Carpinteria Salt Marsh Reserve on the exact same size and shape of cages used in Moorea in February 2023. This additional testing of water flow across units was repeated to gain confidence in our results. We acknowledge that the flow in this estuary likely differs from the fringing reef where we did these experiments, but reasoned that as the flow measures were relative between cage types, this was an adequate test of differences.

To create the clod cards, we mixed Plaster of Paris and water and placed the mixture into ice cube trays, which served as a mold for the mixture. Clod cards made of Plaster of Paris have been a longstanding method to measure differences in water flow (Thompson and Glenn 1994).

The mix was left to dry for two days before being removed from the plastic mold. Once removed from molding, clod cards were randomly attached to a stainless-steel fender washer 0.64 cm thick x 3,18 cm in diameter using J-B Marine Weld epoxy. The clod cards were left to dry for approximately 2 hrs. The clod card and washer were then attached to a circular base made of underwater paper using marine epoxy. Prior to attachment each base was randomly labeled with a treatment name and replicate number.

The clod cards were randomly assigned to experimental treatments either ambient (n=8) or shaded (n=8) and attached on the bottom center of each experimental unit using cable ties. Prior to deployment each clod card was weighed and recorded. Experimental units were deployed by attaching them randomly to a fabric rope secured to the benthos on February 10, 2023. They were left in the field for 22 hrs. spanning nearly 2 tidal cycles, starting with a low tide of 32.6 cm and remaining in place through a maximum high tide of 129.5 cm.

Once collected, the clod cards were detached from each experimental unit and taken back to the University of California Los Angeles. The clod cards were then placed in a food dehydrator for 30 mins to dry excess water then taken out of the food dehydrator and left to dry completely. Once completely air dried, the clod cards were reweighed.

To evaluate differences in water flow, we measured how quickly dye dissipated within the experimental units (n=10) deployed on the experimental reef in Moorea, French Polynesia. Two drops of food coloring were placed mid-height and in the center of the cylindrical experimental units. The time it took for the food coloring to move out of the cage was recorded in seconds. These times were compared between shaded and ambient experimental units with a t-test.

We repeated similar dye test using florescent water tracing dye within the Carpentaria Salt Marsh Reserve in February 2023. As before, we measured how quickly dye moved out of our experimental units. However, we expanded this test to include dispensing dye at two depths within the cages. The first set were dispensed in the center of the cylinder, but at a depth near the top of the cage. The next set were also dispensed in the center of our cylindrical experimental units but at the mid depth as these depths represented where the experimental treatments differed (no window screen vs. window screen). We used one ambient experimental unit (no window screen) and one shaded experimental unit (window screen). The units were placed parallel to one another and perpendicular to the inflowing tide to ensure one experimental unit would not disrupt the flow of the other. The same cage dimensions and materials used in the experiments were used to conduct these dye test. One drop of dye was simultaneously placed at either of the two locations mentioned above and the time it took for the dye to move out of the experimental units (ambient or shaded) was recorded at each location ten times. We conducted paired t-tests in excel to determine any statistical differences across treatments between experimental units.

SI3. Evaluating sediment treatment efficacy and context

To evaluate how our experimental sediment treatment and subsequent sediment retention on algal thalli compared to ambient and storm/wind driven sediment loads, we conducted a series of measurements of sediment on algal thalli. All measurements were conducted at the study site for each algal species. We had four approaches to verify and contextualize our added sediment treatments. We measured: 1) natural sediment accumulation on adjacent algae during our *Padina* dry season experiment, 2) immediate experimental sediment load, 3) 2-day retention of

experimentally added sediment load (just prior to re-addition), and 4) sediment accumulation during a wind/rain event in the wet season.

Average daily wind data (mph) were extracted from the FA'A'A international airport station weather data and converted to kilometer per hour (kph) during each experiment and from 30 January – 03 February 2020 during a storm (SI5). To determine if there were differences in average wind measurements across experiments, a Kruskal-Wallis analysis was conducted on the daily averages for each experiment (SI8).

*Approach 1: Natural sediment accumulation*

Our first objective was to determine the weight of sediment that naturally accumulated on our target algal species during the season of our experiments. Randomly-chosen samples of *Padina* and *Sargassum* were collected directly from the field in plastic bags with their naturally occurring sediment load (n=7 for each species). Thalli together with sediment were brought back to the lab and shaken to separate the algae from the ambient sediment. Algae were removed and wet weighed as described in the main text. Water was filtered using a three cellulose nitrate membrane filter (Sartorius AG) as we suspected there would be fine sediment on the algal thalli, as has been documented in Clausing et al (2016). However, visual observations during filtration did not support the need for this method and it was abandoned in future approaches. Due to this difference in sediment processing, the mean of the natural sediment accumulation was only compared between the two species. Sediment was dried in a drying oven until constant weight. Sediment weights were normalized to the wet weight of algal samples.

*Approach 2: Immediate experimental sediment load*

Our second objective was to determine the weight of the added volume of sediment that remained on algae immediately after addition. *Padina* and *Sargassum* samples were collected, deployed, and sediment load applied to each replicate at our field site as described above in the experiments (n=5 for each species). We immediately placed a plastic bag over each thallus with the added sediment, securely closing the bag. Thalli together with sediment were brought back to the lab, where they were shaken to separate the algae from the added sediment. Algae were removed and wet weighed as described above. Once the sediment settled in the bag, water was decanted, making sure to retain resuspended fine particles. Sediment was dried in a drying oven until constant weight. Sediment weights were normalized to the wet weight of algal samples.

*Approach 3: Two-day retention of experimental sediment load*

Our next objective was to determine the weight of the added volume of sediment that remained on algae two days after sediment addition, which was immediately before reapplication. We repeated all the methods described in approach 2 but waited two days to collect thalli with sediment that remained over the two-day period (n=5 for each species). This measurement allowed us to determine how the retention of our sediment treatment compared to natural sediment accumulation.

*Approach 4: Sediment accumulation during a wind/rain event*

To provide context for the experimental sediment treatment, in February 2020 *Padina* samples (n=8) were collected to assess the deposition of sediment during a wind/rain event in the wet season. Strong winds and persistent rainfall occurred over the course of the four days (Grier and Fong pers. obs, rainfall; Table 1, average wind speeds). Algal samples were collected,

cleared of sediment, and replaced in the field in cages to protect them from herbivory. Algal samples remained in the field for four days, after which algae with sediment that accumulated during the wind/rain event were collected and processed as described above.

SI4. Statistical analysis of sediment samples.

Data did not meet assumptions of parametric statistics. For approach 1, we performed a Mann-Whitney Test on sediment from the ambient *Padina* and *Sargassum* samples. We compared the immediate experimental sediment load for both species (approach 2), the 2-day retention of the experimental sediment load for both species (approach 3), and the mean sediment accumulation during a wind/rain event for *Padina* (approach 4) with a Kruskal-Wallis test followed by a post-hoc Dunn test to determine where the differences lie between our sediment samples. Measurements for *Sargassum* were not obtained during this wind driven sediment event as there was only a short window of time. Statistical analyses were completed in R Studio.

**Supplementary Results**

SI5. Evaluating differences in shaded and ambient treatment light measurements.

The light environment in shaded experimental units was reduced on average by 42% $\pm 3.34$ when algae were not present. A paired t-test showed that the light intensities of the ambient and shaded experimental units were statistically different ($p = 0.0005$).

SI6. Differences in water flow due to shading method

Our results from the dye test in Moorea demonstrate that there was no significant difference in the reduction in weight of the clod cards between ambient and shaded experimental units (t-test, p=0.855). Additionally, there was no significant difference in the time it took dye to dissipate from our ambient and shaded experimental units, in the Carpentaria Salt Marsh Reserve, regardless of the placement of the dye, at the top or mid-level (top, t-test, p = 0.805; mid-level, t-test, p = 0.373).

SI7. Sediment treatment efficacy and context

*Padina* naturally accumulated more ambient sediment than *Sargassum* (Mann-Whitney, p=0.005). Sediment levels on *Padina* and *Sargassum* measured two days after addition were significantly less than measured during wind driven sediment addition (SI9). These results further support the need to reapply sediment after two days to ensure the modeling of a storm event. Immediate sediment addition effectively added sediment to algal thalli, modeling increased sediment as the mean sediment levels after immediate addition were normally higher than ambient for both *Padina* and *Sargassum* (SI9), although statistical tests of his pattern were not possible due to methods change. However, immediate sediment additions remained in the bounds of reasonable sediment conditions given wind events could result in heavier sediment levels. There was no significant difference between remaining sediment accumulation approaches. However, due to the Bonferroni correction in our analysis it is possible that some power was lost thereby minimizing possible differences across experiments.

SI8. Averages of average daily wind speeds (kph) comparison across experimental treatments.

Means with shared letters do not differ significantly (Dunns' post-hoc).

| Experiment | Mean wind speed (kph) | SE |
|---|---|---|
| *Padina* Monospecific | 9.03[ab] | 0.88 |
| *Sargassum* Monospecific | 7.95[a] | 0.40 |
| Interspecific Assemblage | 13.15[b] | 0.98 |
| Wind Driven | 17.7[b] | 3.35 |

SI9. Table of Efficacy of sediment treatments. *Denotes use of filter for sediment accumulation

measurement so analyzed separately. Names with shared letters do not differ.

| Sediment Collection | Sediment Load (g dry wt. sediment/g wet wt. algae) | SE | N |
|---|---|---|---|
| *Padina* | | | |
| Immediately after addition | 0.2256[ab] | 0.0627 | 5 |
| Two days after addition | 0.0756[a] | 0.0348 | 5 |
| Wind driven sediment | 0.449[b] | 0.08 | 8 |
| *Sargassum* | | | |
| Immediately after addition | 0.2016[ab] | 0.0305 | 5 |
| Two days after addition | 0.094[a] | 0.0095 | 5 |
| *Sargassum* ambient sediment | 0.0097* | 0.0360 | 6 |
| *Padina* ambient sediment | 0.1345* | 0.0014 | 6 |

## References

Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y, de Loma TL, Penin L, Thibaut L, Vidal-Dupiol J, Salvat B, Galzin R (2009) Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. Coral Reefs 28:775–780

Alestra T, Schiel DR (2015) Impacts of local and global stressors in intertidal habitats: Influence of altered nutrient, sediment, and temperature levels on the early life history of three habitat-forming macroalgae. J Exp Mar Biol Ecol 468:29–36

Anthony KRN, Ridd P v., Orpin AR, Larcombe P, Lough J (2004) Temporal variation of light availability in coastal benthic habitats: Effects of clouds, turbidity, and tides. Limnol Oceanogr 49:2201–2211

De Beer D, Larkum AWD (2001) Photosynthesis and calcification in the calcifying algae *Halimeda discoidea* studied with microsensors. Plant Cell Environ 24:1209–1217

Benita M, Dubinsky Z, Iluz D (2018) *Padina pavonica*: Morphology and calcification functions and mechanism. Am J Plant Sci 09:1156–1168

Bergman JL, Dang BN, Tabatabaee MM, McGowan MM, Fong CR, Bittick SJ, Fong P (2016) Nutrients induce, and herbivores maintain thallus toughness, a structural anti-herbivory defense in *Turbinaria ornata*. Mar Ecol Prog Ser 559:35–43

Bi Y, Feng M, Jiang R, Wu Z, Zhang S, Wang W (2016) The effects of sediment on *Sargassum horneri* in the early life stages on rocky subtidal reefs. 132:17–23

Bittick SJ, Clausing RJ, Fong CR, Fong P (2016) Bolstered physical defenses under nutrient-enriched conditions may facilitate a secondary foundational algal species in the South Pacific. Journal of Ecology 104:646–653

Bittick SJ, Clausing RJ, Fong CR, Scoma SR, Fong P (2019) A rapidly expanding macroalga acts as a foundational species providing trophic support and habitat in the South Pacific. Ecosystems 22:165–173

Borowitzka MA, Larkum AWD (1977) Calcification in the green alga *Halimeda*. I. An ultrastructure study of thallus development. J Phycol 13:6–16

Borowitzka MA, Larkum AWD (1987) Calcification in algae: mechanisms and the role of metabolism. CRC Crit Rev Plant Sci 6:1–45

Borowitzka MiA, Larkum AWD (1976) Calcification in the green alga *Halimeda*. J Exp Bot 27:879–893

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Mar Ecol Prog Ser 342:139–149

Bruno JF, Precht WF, Vroom PS, Aronson RB (2014) Coral reef baselines: How much macroalgae is natural? Mar Pollut Bull 80:24–29

Bulleri F, Eriksson BK, Queirós A, Airoldi L, Arenas F, Arvanitidis C, Bouma TJ, Crowe TP, Davoult D, Guizien K, Iveša L, Jenkins SR, Michalet R, Olabarria C, Procaccini G, Serrão EA, Wahl M, Benedetti-Cecchi L (2018) Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLoS Biol 16:1–19

Campbell JE, Craft JD, Muehllehner N, Langdon C, Paul VJ (2014) Responses of calcifying algae (*Halimeda* spp.) to ocean acidification: Implications for herbivores. Mar Ecol Prog Ser 514:43–56

Carle MV, Sasser CE (2016) Productivity and resilience: long-term trends and storm driven fluctuations in the plant community of the accreting wax Lake Delta. Estuaries and Coasts 39:406–422

Celis-plá PSM, Hall-spencer JM, Horta PA (2015) Macroalgal responses to ocean acidification depend on nutrient and light levels. Front Mar Sci 2:1–12

Cheloni G, Gagnaux V, Slaveykova VI (2019) Species-species interactions modulate copper toxicity under different visible light conditions. Ecotoxicol Environ Saf 170:771–777

Chung IK, Beardall J, Mehta S, Sahoo D, Stojkovic S (2011) Using marine macroalgae for carbon sequestration: A critical appraisal. J Appl Phycol 23:877–886

Clausing RJ, Annunziata C, Baker G, Lee C, Bittick SJ, Fong P (2014) Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. Mar Ecol Prog Ser 517:121–129

Clausing RJ, Bittick SJ, Fong CR, Fong P (2016) Sediments influence accumulation of two macroalgal species through novel but differing interactions with nutrients and herbivory. Coral Reefs 35:1297–1309

Clausing RJ, Fong P (2016) Environmental variability drives rapid and dramatic changes in nutrient limitation of tropical macroalgae with different ecological strategies. Coral Reefs 35:669–680

Connell SD (2005) Assembly and maintenance of subtidal habitat heterogeneity: synergistic effects of light penetration and sedimentation. Marine Ecology Progress Series 289:53–61

Cox TE, Smith CM (2015) Photosynthetic rapid light curves for *Padina sanctae-crucis* vary with irradiance, aerial exposure, and tides in Hawaii's micro-intertidal zones. Mar Biol 162:1061–1076

Cruz-Rivera E, Hay ME (2001) Macroalgal traits and the feeding and fitness of an herbivorous amphipod: The roles of selectivity, mixing, and compensation. Mar Ecol Prog Ser 218:249–266

Dieter H, Wiencke C (2003) Photosynthesis in Marine Algae. Photosynthesis in Algae 14:498

Edmunds PJ, Burgess SC, Putnam HM, Baskett ML, Bramanti L, Fabina NS, Han X, Lesser MP, Madin JS, Wall CB, Yost DM, Gates RD (2014) Evaluating the causal basis of ecological success within the *Scleractinia*: an integral projection model approach. Mar Biol 161:2719–2734

Edmunds PJ, Gray SC (2014) The effects of storms, heavy rain, and sedimentation on the shallow coral reefs of St. John, US Virgin Islands. Hydrobiologia 734:143–158

Egilsdottir H, Olafsson J, Martin S (2016) Photosynthesis and calcification in the articulated coralline alga *Ellisolandia elongata* (Corallinales, Rhodophyta) from intertidal rock pools. Eur J Phycol 51:59–70

Eriksson BK, Johansson G (2005) Effects of sedimentation on macroalgae: Species-specific responses are related to reproductive traits. Oecologia 143:438–448

Fong CR, Gaynus CJ, Carpenter RC (2020) Extreme rainfall events pulse substantial nutrients and sediments from terrestrial to nearshore coastal communities: a case study from French Polynesia. Sci Rep 10:1–8

Fong P, Paul VJ (2011) Coral reef algae. Coral Reefs: An ecosystem in transition. pp 241–272

Franklin LA, Larkum AWD (1997) Multiple strategies for a high light existence in a tropical marine macroalga. Photosynth Res 53:149–159

Fulton CJ, Abesamis RA, Berkström C, Depczynski M, Graham NAJ, Holmes TH, Kulbicki M, Noble MM, Radford BT, Tano S, Tinkler P, Wernberg T, Wilson SK (2019) Form and function of tropical macroalgal reefs in the Anthropocene. Funct Ecol 33:989–999

Gao X, Lee JR, Park SK, Kim NG, Choi HG (2019) Detrimental effects of sediment on attachment, survival, and growth of the brown alga *Sargassum thunbergii* in early life stages. Phycological Res 67:77–81

Gaynus C (2019) Environmental and biotic controls affecting recruitment and proliferation of algal turf communities in coral reef systems. University of California, Los Angeles.

Geraldino PJL, Liao LM, Boo S-M (2005) Morphological study of the marine algal genus *Padina* (Dictyotales, Phaeophyceae) from Southern Philippines: 3 Species New to Philippines. Algae 20:99–112

Goreau TF (1963) Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef-builders. Annals New York Academy of Sciences 109:127–167

Grémare A, Amouroux JM, Cauwet G, Charles F, Courties C, De Bovée F, Dinet A, Devenon JL, De Madron XD, Ferre B, Fraunie P, Joux F, Lantoine F, Lebaron P, Naudin JJ, Palanques A, Pujo-Pay M, Zudaire L (2003) The effects of a strong winter storm on physical and biological variables at a shelf site in the Mediterranean. Oceanologica Acta 26:407–419

Häder DP, Lebert M, Sinha RP, Barbieri ES, Helbling EW (2002) Role of protective and repair mechanisms in the inhibition of photosynthesis in marine macroalgae. Photochemical and Photobiological Sciences 1:809–814

Harris AL, Zinnert JC, Young DR (2017) Differential response of barrier island dune grasses to species interactions and burial. Plant Ecol 218:609–619

Hill R, Bellgrove A, Macreadie PI, Petrou K, Beardall J, Steven A, Ralph PJ (2015) Can macroalgae contribute to blue carbon? An Australian perspective. Limnol Oceanogr 60:1689–1706

Hong M, Ma Z, Wang X, Shen Y, Mo Z, Wu M, Chen B, Zhang T (2021) Effects of light intensity and ammonium stress on photosynthesis in *Sargassum fusiforme* seedlings. Chemosphere 273:128605

IPCC (2019) Summary for Policymakers. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

Irving AD, Connell SD (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: Algal versus invertebrate dominated assemblages. Mar Ecol Prog Ser 245:83–91

Irving AD, Witman JD (2009) The effects of sedimentation on rocky coast assemblages. J Ecol 97:827–833

Jensen PR, Gibson RA, Littler MM, Littler DS (1985) Photosynthesis and calcification in four deep-water *Halimeda* species (Chlorophycea, Caulerpales). Deep Sea Research 32:451–464

Johnson GC, Pezner AK, Sura SA, Fong P (2018) Nutrients and herbivory, but not sediments, have opposite and independent effects on the tropical macroalga, *Padina boryana*. J Exp Mar Biol Ecol 507:17–22

Kamer K, Fong P, Kennison RL, Schiff K (2004) The relative importance of sediment and water column supplies of nutrients to the growth and tissue nutrient content of the green macroalga *Enteromorpha intestinalis* along an estuarine resource gradient. Aquat Ecol 38:45–56

Knutson TR (2010) Tropical Cyclones and Climate Change. Nat Geosci 3:157–163

Li X, Zhang Q, He J, Yu Y, Liu H (2014a) Photoacclimation characteristics of *Sargassum thunbergii* germlings under different light intensities. J Appl Phycol 26:2151–2158

Li XM, Zhang QS, Tang YZ, Yu YQ, Liu HL, Li LX (2014b) Highly efficient photoprotective responses to high light stress in *Sargassum thunbergii* germlings, a representative brown macroalga of intertidal zone. J Sea Res 85:491–498

Lirman D (2001) Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19:392–399

Luter HM, Pineda MC, Ricardo G, Francis DS, Fisher R, Jones R (2021) Assessing the risk of light reduction from natural sediment resuspension events and dredging activities in an inshore turbid reef environment. Mar Pollut Bull 170:112536

Manuel SA, Coates KA, Kenworthy WJ, Fourqurean JW (2013) Tropical species at the northern limit of their range: Composition and distribution in Bermuda's benthic habitats in relation to depth and light availability. Mar Environ Res 89:63–75

Martone PT (2010) Quantifying growth and calcium carbonate deposition of *Calliarthron cheilosporioides* (Corallinales, Rhodophyta) in the field using a persistent vital stain: Note. J Phycol 46:13–17

Mattio L, Payri CE, Stiger-Pouvreau V (2008) Taxonomic revision of *Sargassum* (Fucales, Phaeophyceae) from French Polynesia based on morphological and molecular analyses. J Phycol 44:1541–1555

Mayakun J, Prathep A (2005) Seasonal variations in diversity and abundance of macroalgae at Samui Island, Surat Thani Province, Thailand. Sci Technol 27:653–663

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367

McNicholl C, Koch MS (2021) Irradiance, photosynthesis and elevated $pCO_2$ effects on net calcification in tropical reef macroalgae. J Exp Mar Biol Ecol 535:151489

McNicholl C, Koch MS, Swarzenski PW, Oberhaensli FR, Taylor A, Batista MG, Metian M (2020) Ocean acidification effects on calcification and dissolution in tropical reef macroalgae. Coral Reefs 39:1635–1647

Mejia AY, Puncher GN, Engelen AH (2012) Macroalgae in tropical marine coastal systems. seaweed biology: Novel insights into ecophysiology, ecology and utilization. pp 329–357

Middelboe AL, Sand-Jensen K, Binzer T (2006) Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. Oecologia 150:464–476

Okazaki M, Pentecost A, Tanaka Y, Miyata M (1986) A study of calcium carbonate deposition in the genus *Padina* (Phaeophyceae, dictyotales). British Phycological Journal 21:217–224

O'Neal SW, Price JS (1988) Seasonal effects of light, temperature, nutrient concentration and salinity on the physiology and growth of *Caulerpa paspaloides* (Chlorophyceae). Mar Biol 24:17–24

Paul VJ, Van Alstyne KL (1988) Chemical defense and chemical variation in some tropical Pacific species of *Halimeda* (Halimedaceae; Chlorophyta). Coral Reefs 6:263–269

Pennings SC, Paul VJ (1992) Effect of plant toughness, calcification, and chemistry on herbivory by Dolabella Auricularia. Ecology 73:1606–1619

Pratchett MS, Trapon M, Berumen ML, Chong-Seng K (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. Coral Reefs 30:183–193

Prathep A, Kaewsrikhaw R, Mayakun J, Darakrai A (2018) The effects of light intensity and temperature on the calcification rate of *Halimeda macroloba*. J Appl Phycol 30:3405–3412

Schaffelke B (1999) Particulate organic matter as an alternative nutrient source for tropical *Sargassum* species (Fucales, Phaeophycea). J Phycol 35:1150–1157

Schupp PJ, Paul VJ (1994) Calcium carbonate and secondary metabolites in tropical seaweeds: variable effects on herbivorous fishes. Ecology 75:1172–1185

Semesi IS, Beer S, Björk M (2009) Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. Mar Ecol Prog Ser 382:41–47

Stiger V, Payri CE (1999) Spatial and seasonal variations in the biological characteristics of two invasive brown algae, *Turbinaria ornata* (Turner) J. Agardh and *Sargassum mangarevense* (grunow) setchell (Sargassaceae, Fucales) spreading on the reefs of Tahiti (French Polynesia). Botanica Marina 42:295–306

Storlazzi CD, Norris BK, Rosenberger KJ (2015) The influence of grain size, grain color, and suspended-sediment concentration on light attenuation: Why fine-grained terrestrial sediment is bad for coral reef ecosystems. Coral Reefs 34:967–975

Sudhakar K, Mamat R, Samykano M, Azmi WH, Ishak WFW, Yusaf T (2018) An overview of marine macroalgae as bioresource. Renewable and Sustainable Energy Reviews 91:165–179

Sura SA, Bell A, Kunes KL, Turba R, Songer R, Fong P (2021) Responses of two common coral reef macroalgae to nutrient addition, sediment addition, and mechanical damage. J Exp Mar Biol Ecol 536:151512

Talarico L, Maranzana G (2000) Light and adaptive responses in red macroalgae: An overview. J Photochem Photobiol B 56:1–11

Tebbett SB, Bellwood DR (2019) Algal turf sediments on coral reefs: what's known and what's next. Mar Pollut Bull 149:110542

Tebbett SB, Bellwood DR (2020) Sediments ratchet-down coral reef algal turf productivity. Science of the Total Environment 713:136709

Tebbett SB, Goatley CHR, Bellwood DR (2018) Algal turf sediments across the Great Barrier Reef: Putting coastal reefs in perspective. Mar Pollut Bull 137:518–525

Trapon ML, Pratchett MS, Penin L (2011) Comparative effects of different disturbances in coral reef habitats in Moorea, French Polynesia. J Mar Biol 2011:1–11

Umar MJ, McCook LJ, Price IR (1998) Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. Coral Reefs 17:169–177

Vercelloni J, Kayal M, Chancerelle Y, Planes S (2019) Exposure, vulnerability, and resiliency of French Polynesian coral reefs to environmental disturbances. Sci Rep 9:1–11

Victor S, Neth L, Golbuu Y, Wolanski E, Richmond RH (2006) Sedimentation in mangroves and coral reefs in a wet tropical island, Pohnpei, Micronesia. Estuar Coast Shelf Sci 66:409–416

Voerman SE, Glasby TM, Gladstone W, Gribben PE (2019) Morphological variation of a rapidly spreading native macroalga across a range of spatial scales and its tolerance to sedimentation. Mar Environ Res 149–158

Vogel N, Meyer FW, Wild C, Uthicke S (2015) Decreased light availability can amplify negative impacts of ocean acidification on calcifying coral reef organisms. Mar Ecol Prog Ser 521:49–61

Washburn, L and A. Brooks of Environmental Data Initiative. 2022. MCR LTER: Coral Reef: Gump Station Meteorological Data, ongoing since 2006. knb-lter-mcr.9.47.doi:10.6073/pasta/816b1a08e460781d6627d0c80db8ed12

Wichachucherd B, Prathep A, Zuccarello GC (2014) Phylogeography of *Padina boryana* (Dictyotales, Phaeophyceae) around the Thai-Malay Peninsula. Eur J Phycol 49:313–323

Xie X, Li M, Ni W (2018) Roles of wind-driven currents and surface waves in sediment resuspension and transport during a tropical storm. J Geophys Res Oceans 123:8638–8654

Zhong ZH, Wang Y, Qin S, Zhuang LC, Li JJ, Song WL, Liu ZY (2021) Short-term photoacclimation and photoregulation strategies of *Sargassum horneri* in response to temperature and light. Photosynthetica 59:268–276

Zou X, Xing S, Su X, Zhu J, Huang H (2018) The effects of temperature, salinity and irradiance upon the growth of *Sargassum polycystum* C. Agardh (Phaeophyceae). J Appl Phycol 30:1207–1215

CHAPTER 2

**Context-dependent growth response of *Halimeda opuntia* to sediment and nutrients in a high light environment.**

**Abstract**

Coral reefs often experience simultaneous changes in multiple environmental drivers due to human impacts that can affect species' responses and ultimately alter community structure. Presently, the bulk of coral reef research is focused on the responses of coral, fish, and opportunistic algae to multiple stressors. However, lacking are experiments investigating macroalgae typically associated with healthy reef systems. Here we explore how nutrients, sediment, and light affect a persistent macroalgal species using both field and mesocosm experiments. In the field, we quantified the response of *Halimeda opuntia*, a common calcifying alga on both less and more impacted reefs, to nutrients (ambient, enriched), sediment, and light. We found sediment and nutrient additions, conditions that are characteristic of more impacted reefs, interacted negatively to decrease *H. opuntia* growth. In a mesocosm experiment, we quantified the effects of sediment and light on *H. opuntia* growth and found in this extremely high light environment both sediment addition and light reduction positively affected *H. opuntia*. Our results demonstrate that the response of *H. opuntia* to these environmental drivers is context dependent. While the combination of nutrients and sediment may deter the growth of slower growing macroalgal species, increased sediment alone may mediate the inhibitory effects of an extremely high light environment. These results suggest that macroalgal species that are typically associated with healthy coral reefs may suffer rather than benefit from shifts in environmental drivers impacted by anthropogenic factors.

**Introduction**

      Macroalgae are important components of coral reefs, supporting a myriad of ecosystem functions, such as primary production and trophic support (Macreadie et al. 2017). Over the last 4 decades, many reefs have undergone transitions from coral-dominated states with sparse macroalgae to alternative states dominated by macroalgae (e.g., Hughes et al. 2003, 2010; Bellwood et al. 2004; Graham et al. 2013; Schmitt et al. 2018). Many studies have extensively documented the global loss of corals in response to human impacts and subsequent transitions to dominance by opportunistic macroalgae (e.g., McClanahan 1997; Knuffner et al. 2006; Bulleri et al. 2013; Johns et al. 2018). Transitions to opportunistic macroalgae have been attributed to species-specific characteristics such as fast reproduction (Stiger and Payri 1999a), especially after disturbances (Sammarco et al. 1974), increased growth in the absence of herbivory (Jessen and Wild 2013), and both positive (Done 1992; Cannon et al. 2023) and resilient responses to other anthropogenic disturbances (Schmitt et al. 2018). However, what remains unknown is how macroalgal species typical of reefs less impacted by human disturbances respond to these same stressors. Further, it is unlikely results from studies of more opportunistic, fast-growing algae that replace coral can be generalized to the slower-growing algal species typical of more natural reefs, motivating research on algae with this strategy.

      *Halimeda* is a genus of ubiquitous macroalgae that can be abundant on both healthy and degraded coral reefs (Drew and Abel 1988; Fong and Paul 2011). Historically, *Halimeda* has been common throughout more pristine reefs; however, some species in this genus can persist on degraded reefs (e.g., Halimeda opuntia, Lapointe et al. 1992; Halimeda spp., Barott et al. 2010; Halimeda spp., Cannon et al. 2023). *Halimeda* is a highly calcified green alga that is important on fringing reefs as it contributes to sediment and sand formation (Halimeda spp., Multer 1988;

Halimeda spp. including Halimeda opuntia, Price et al. 2011; Halimeda opuntia, Hofmann et al. 2014). Additionally, *Halimeda* is pan-tropical with studies being conducted on this genus across the world (Wiman and McKendree 1975; Banderia-Pedrosa et al. 2004; Pongparadon et al. 2020). While the presence of this genus of macroalgae is ubiquitous in coral reefs across the world (Cannon et al. 2023), its responses to the combination of three environmental drivers that are commonly impacted by humans, light availability, sediment loads, and nutrient supplies, are unknown. This research gains importance as these three factors will also be altered with future climate change as it will increase storms(IPCC 2019), potentially increasing run off that increases sedimentation and nutrients and reduces light.

Light is a critical environmental driver for all primary producers, but particularly for calcifying algae such as *Halimeda*, as light drives both photosynthesis and calcification (Littler and Littler 1992; Peach et al. 2017). Although one species in this genus, *Halimeda opuntia,* has a wide depth distribution (Wiman and McKendree 1975; Drew and Abel 1988; Teichberg et al. 2013) it is very common in shallow habitats where light intensities range from 300 -2000 µmoles $m^{-2}$ $s^{-1}$ (Barnes and Lazarb 1993; Yñiguez et al. 2010; Wei et al. 2022), with the highest light intensities closest to the surface. While macroalgae can adapt to various light intensities (Franklin and Larkum 1997), extremely low and extremely high light environments can hinder algal productivity (Middelboe et al. 2006) due to resource limitation or photoinhibition, which is the reduction of photosynthetic activity at very high light intensities. For example, in a 2hr. experiment, Franklin et al. (1996) demonstrated that light intensities $\geq$ 1400 µmoles $m^{-2}$ $s^{-1}$ reduced photosynthetic efficiency of several macroalgal genera, including *Halimeda*, at shallow depths < 1m. While environmental drivers, such as light availability fluctuate naturally, the duration and intensity of these fluctuations are likely to be impacted by both natural and

anthropogenic disturbances such as storms and land runoff (Anthony et al. 2004; Fabricius 2005; Victor et al. 2006; Edmunds et al. 2019; Fong et al. 2020). Thus, it is imperative to understand the effects that variable light intensities in combination with other environmental drivers that can be altered by anthropogenic impacts have on macroalgal productivity.

The effect of sediment deposition on *Halimeda* has not been thoroughly investigated. Many studies have investigated sediment effects on other macroalgal species, particularly those that are more opportunistic (Sofonia and Anthony 2008; Kawamata et al. 2012; Clausing et al. 2016; Gao et al. 2019; Sangil and Guzman 2020), demonstrating that responses to sediments can vary. As macroalgal responses to sediments are not universal, it is possible that sediment effects may be both species or group-specific and context dependent. For example, sediment can negatively affect turf algal productivity (Tebbett and Bellwood 2020) and this effect is exacerbated by sediment depth (Airoldi et al. 1997), especially in the absence of herbivory (Clausing et al. 2014). Sediments have also been shown to deter survival of macroalgal germlings and recruits via smothering and reduction of benthic cover in Mediterranean and tropical habitats (Sargassum, Umar et al. 1998; Cystoseria barbata, Irving and Witman 2009; fucoid species, Alestra and Schiel 2015). Conversely, other studies suggest that sediments have a positive effect on some macroalgae by provision of nutrients (Schaffelke 1999; Clausing et al. 2016). However, Johnson et al. (2018) and Sura et al. (2021) reported negligible sediment effects on growth and structural responses of *Sargassum pacificum* (toughness) and *Padina boryana* (calcification). While I found similar negligible results for toughness of *S. pacificum*, calcification of Padina boryana increased with added sediment (Chapter 1). As such, it will be important to explore the interactive effects on *Halimeda* of environmental drivers that are not commonly combined especially in conditions that model reefs in the Anthropocene.

Nutrients have been implicated as an influential environmental driver mediating the growth of both opportunistic (e.g., *Turbinaria*) (Sammarco et al. 1974; Adam et al. 2020) and algae characterized as slower growing (e.g., *Halimeda* spp.) (Teichberg et al. 2013). However, the response of macroalgae to nutrients is complex and can be influenced by species-specific strategies, internal nutrient storage, and temporal changes in nutrient availability (Lapointe et al. 1987; Delgado and Lapointe 1994; Fong et al. 2003; Clausing and Fong 2016). For example, Delago and Lapointe (1994) demonstrated that nutrients significantly increased the productivity of fleshy macroalgae (e.g., *Ulva* spp.) whereas the productivity of calcareous algae (e.g., *Halimeda*) was inhibited by nutrients. While *Halimeda* has been shown to respond positively to elevated nutrients (Lapointe et al. 1987; Hofmann et al. 2014), there is contrasting literature that suggest elevated nutrients may not always be stimulatory for *Halimeda* spp. (Mayakun et al. 2013). Thus, as the response of *Halimeda* to nutrient enrichment is still unclear, it is imperative to expand our understanding of how nutrients interact with other environmental drivers to affect its growth.

Understanding the response of ubiquitous calcifying macroalgal species, such as *Halimeda,* whose presence is often considered a positive on coral reefs, to variation in critical environmental divers is important as anthropogenic inputs of terrestrial runoff and natural disturbances are expected to only intensify. Thus, supplies of nutrients and sediments will increase, which also indirectly affect light availability. The objective of this study was to investigate the independent and interactive effects of combinations of light, sediments, and nutrients and their interactions on a persistent and slower-growing macroalgal species.

**Materials and Methods**

*Overall Approaches*

We utilized three approaches to understand the effects of our three environmental drivers on growth of *Halimeda opuntia,* hereafter *Halimeda.* First, to contextualize the site of our field experiment, we conducted surveys characterizing the benthic community. Second, we conducted a field experiment to investigate the effects of nutrients, sediment, and light on *Halimeda* growth in the absence of herbivory. Third, we conducted a mesocosm experiment to focus solely on the effects of sediment and light. All surveys and experiments were conducted in June 2015.

*Site Characterization*

We conducted our research on a fringing reef at Ta'ahiamaunu Public Beach (17° 30' S 149° 50' W) located along the north shore at the mouth of Opunohu Bay, in Moorea, French Polynesia. We chose to study environmental drivers on a fringing reef because these reefs may be more vulnerable to human impacts due to proximity to human population and development (Fabricius 2005). We worked on the reef flat ( $\leq 2.5$ meters deep) of a patch reef system that consisted of dead skeletons of massive corals from the genus *Porites*. These structural dead coral skeletons are what remain after prior environmental and physical disturbances, such cyclones and *Acanthaster planci* outbreaks (Adjeroud et al. 2009; Vercelloni et al. 2019). The area surrounding the structure within this fringing reef comprises less complex coral rubble and sandy bottom.

To characterize our site, we conducted benthic surveys (n=31), on snorkel, quantifying percent cover of major space occupiers, including *Halimeda opuntia*, *Padina boryana*, *Turbinaria ornata,* turf algae, crustose coralline algae (CCA), and coral. All other space occupiers were categorized as 'other' (data not shown). Surveys only included hard-bottomed

habitat suitable for algae, excluding sand patches. Within this restriction (hard-bottom), quadrats (1 m$^2$ with 81 intersections) were laid down in randomly-selected areas within the habitat, including dead massive coral structure and less complex patchy coral structures and coral rubble. We used a point contact method to quantify % cover of the target species within our quadrat. At each intersection we identified the individual directly under the point and recorded the species or category specified above. Individuals were considered under the point if algal holdfasts were present under each intersection. Thus, we did not count algal blades that may have been present under an intersection. The percent cover of each benthic space occupier was then calculated.

*Nutrient, Sediment and Light Effects on* Halimeda *Growth in the Field*

To evaluate the effects of nutrients, sediment, light and their interactions on *Halimeda* we conducted a three-factor fully-crossed field experiment manipulating nutrients (ambient /added slow-release fertilizer), sediment (ambient/added), and light (ambient/reduced) to determine their effects on the growth of *Halimeda*. We maintained a level of ambient conditions for each environmental driver to understand how the growth response of *Halimeda* under the present environmental context compares to growth under manipulated conditions that model future impacts on reefs. All 8 treatment combinations were replicated 10 times for a total of 80 experimental units.

Each experimental unit consisted of field-collected *Halimeda* thalli with initial wet weights ranging from 1.5 to 2.0 gm. To isolate the effects of our 3 environmental drivers from the biotic driver of herbivory, all algal samples were protected from herbivores by securing them to the bottom of cylindrical cages (7.5 cm diameter, 5 cm height) constructed from hardware

cloth with 1 cm openings that excluded herbivores without introducing significant cage effects in similar experiments (Clausing et al. 2014, see supplement for our own test).

To test for the impacts of elevated nutrients, we established treatments with ambient (e.g., no additional nutrients) and added nutrients (5 g of a slow-release fertilizer (Osmocote 15-9-12 N-P-K) placed in a nylon bag secured to cage bottoms. While previous studies have used higher amounts of slow-release fertilizer with more biomass we reduced the amount of fertilizer with biomass. There is a long history of using slow-release fertilizer, such as Osmocote (The Scotts Company LLC.), in various marine field experiments to investigate macroalgae and macrophyte nutrient limitation (e.g., seagrass, Koch and Snedaker 1997; mangroves, Bucolo et al. 2008; macroalgae, Gennaro et al. 2019) responses to increased nutrients (Morris et al. 2007; Fong et al. 2020) and effects on benthic community structure (Burkepile and Hay 2008; Sura et al. 2019).

To model sediment deposition we applied 3.7 ml of benthic sediment collected from the study site onto each thallus, which was enough to cover the blades to visually match areas with high sediment deposition. Past studies from this and nearby fringing reefs have shown that mostly silt and fine grain sediment remain on algal thalli compared to the larger grained sands found in the benthos (Clausing et al. 2016a; Gaynus 2019; Sura et al. 2021). Thus, we expect the sediment that remained on our *Halimeda* thalli was also finer grained, as has been demonstrated for experimental additions on *P. boryana* and *S. pacificum* (Chapter 1). Sediment was added at the beginning of the 7-day experiment and once again after three days as my previous study demonstrated that this was a reasonable interval to maintain sediment treatment (Chapter 1). While ambient sediment was removed during collection and assembly of experimental units, after deployment sediment was not removed from ambient sediment treatments, allowing for natural accumulation.

Light treatments were ambient and shaded with nylon window screening attached to the tops of cages and around the top 4 cm of the cage walls (see methods below for methods measuring treatment efficacy). We did not cover the sides entirely to minimize inhibition of water flow (see below for tests for cage artifacts). The window screen provided 45% shading of ambient light (see methods below). The cages were deployed in the field on the tops of dead coral heads at depths of ~1.5 m. Experimental duration was 7 days from 15 – 22 June 2015, after which we measured final algal wet weights.

*Effects of Sediment and Light on the Growth of* Halimeda *in Mesocosms*

We conducted a two-factor fully-crossed mesocosm experiment manipulating light (ambient, 51% reduction, 76% reduction) and sediment (absence/added) to further assess the effects of these factors on *Halimeda*. Each mesocosm had a total volume of 300ml and were made of clear plastic. The light levels were manipulated using window screens. We used 1 layer of window screen for the first level of light reduction and two layers of window screen for the second level (see below for verification methods). The window screen was secured on the top of each designated mesocosm using a rubber band. This mesocosm experiment allowed us to investigate how the main factors of sediment and light affect *Halimeda* growth, given their two-way interactions with nutrients precluded any interpretation of main effects in the field experiment. There were six experimental treatments, each with eight replicates. *Halimeda* thalli were collected from the study site and initial samples ranging from 1.5 to 2.0 grams were placed in mesocosms.

We randomly placed mesocosms in the same outdoor flow-through water table at the Gump South Pacific Research Station on the northwestern shore of Pao-Pao Bay (also known as Cook's Bay), one of two large bays on the north shore of Moorea. Mesocosm were evenly spaced

throughout the water table and positions rerandomized daily. The flow of seawater provided a water bath to maintain the ambient temperature in Pao-Pao Bay within our mesocosms (Sura et al. 2023). We placed 250 ml of ambient seawater into each mesocosm unit and we replaced the seawater every 72h. Experimental units either had ambient sediment removed or an addition of 3.7ml of sediment added as described above. Experimental sediment loads were added at the beginning of the experiment and once again after three days. The removal of sediment on *Halimeda* thalli differed from our ambient sediment treatment in the field. In the field, ambient sediment loads on *Halimeda* thalli were allowed to accumulate once algae were deployed; however, there was no natural accumulation in the mesocosms. Experimental duration was for 6 days from June 24 - June 30, 2015.

*Environmental Context: Light Measurements and Experimental Artifacts*

Light Measurements

To characterize any differences in the above water light environment between our field and mesocosm experiment we downloaded post-processed meteorological data of solar radiation with permission from the Moorea Coral Reef LTER (Washburn and Brooks 2022). Solar radiation was recorded every five minutes from sensors located at the University of California Gump station 6m above mean sea level. Daily averages of solar radiation ($kW/m^2$) were calculated and graphed for each experimental period (field, 15 June - 22 June and mesocosm, 24 June - 30 June, 2015).

Remaining light measurements were taken after the experimental period, in 2020 and 2023, due to logistical constraints. While the light measurements to provide context for the experimental treatments were taken after our experimental period, they were taken at

51

ecologically relevant time periods in the day and provide a snapshot of the relative light intensities of our light treatments. Further, we reasoned that measuring the light environment across light treatments, even if not done simultaneously with the experiment, would help contextualize relative differences in the light environment due to our shading treatments for both the field and mesocosm experiments.

To better characterize how the light environment differed across light treatments for both the field and mesocosm experiment we used Hobo data loggers, UA002-64 HOBO Waterproof Temperature/Light Pendant Data Logger, to measure light intensity (lum/ft$^2$). In 2020, the light environment of ambient (wire mesh alone) and shaded (wire mesh + window screen) experimental units were recorded in Moorea, French Polynesia. One Hobo logger was placed inside an ambient experimental unit and another Hobo logger was placed within a shaded experimental unit, in the absence of algae. Both Hobo loggers were positioned 5 cm from the benthos, which is approximately where the middle of an algal thallus would be, if present. The data loggers recorded light intensity every 10 secs for 6 minutes from 10:46 to 10:51hrs. The light intensity and the percent change between the ambient and shaded experimental units was measured and calculated on January 27, 2020.

In May 2023, hobo data loggers were placed in the ambient experimental units in the field and in our mesocosms that were filled with seawater as previously described to compare the experimental light environment in these two locations in Moorea. We converted lumens (lum/ft$^2$) to photons (μ moles/m2/s) using equations provided by Thimijan et al. (1983) and Environmental Growth Chambers (2017). We placed hobo data loggers in three mesocosms, one with each treatment of ambient, 1 screen, and 2 screens, filled with 250 ml of seawater and positioned in a flow-through water table that mimicked our initial experiment. The data loggers recorded light

level every 10 secs for 10 minutes. The percent reduction caused by each light treatment was calculated by calculating the change in each level of light reduction treatments from ambient.

<u>Evaluating Possible Artifacts of Cages in the Field</u>

To evaluate the differences in flow across experimental light treatments we used dye tests and clod cards. We did a set of dye tests in Moorea in May 2019. Due to limited time in Moorea, we repeated and expanded the dye tests and conducted clod care measures along a tidal channel of the University of California's Carpinteria Salt Marsh Reserve using cages made of the same material but of a different size (13.0cm x 13.5cm, height x diameter compared to 5cm x 7.5, height x diameter in Moorea, both cage types had 1cm2 mesh openings). This additional testing of water flow across units was repeated to gain confidence in our results. We acknowledge that the flow in this estuary likely differs from the fringing reef where we did these experiments but reasoned that as the flow measures were relative between cage types, this was an adequate test to inform differences.

In Moorea, dye was placed within experimental units (n=10) deployed on the experimental reef in Moorea, French Polynesia. Two drops of food coloring were placed mid-height and in the center of the cylindrical experimental units. To limit any additional water movement, I remained motionless after dye was placed in experimental units and only moved when each recorded session was complete. The time it took for the food coloring to visually completely move out of the cage was recorded in seconds. These times were compared between shaded and ambient experimental units with a t-test.

We repeated a similar dye test using fluorescent water tracing dye within the Carpinteria Salt Marsh Reserve in February 2023. However, we expanded this test to include dispensing dye

at two depths within the cages. The first test was dispensed in the center of the cylinder, but at a depth near the top of the cage, where the window screen covered the slides of the cage. The next test was also dispensed in the center of our cylindrical experimental units but at the mid depth nearer the place where the window screen ended. We used one ambient experimental unit (no window screen) and one shaded experimental unit (window screen) placed parallel to one another. One drop of dye was simultaneously placed at either of the two locations and the time it took for the dye to completely move out of the experimental units (ambient or shaded) was recorded at each location ten times and then averaged. Dye was considered completely moved out of the cages when all dye visually exited the cages. The two locations were tested separately, not concurrently.

Clod cards made of Plaster of Paris have been a longstanding method to measure differences in water flow (Jokiel 1993; Thompson and Glenn 1994). To create the clod cards, we mixed Plaster of Paris and water and placed the mixture into ice cube trays, which served as a mold. The mix was left to dry for two days before being removed from the plastic mold. Once removed from molding, clod cards were attached to a stainless-steel fender washer 0.64 cm thick x 3.18 cm in diameter using J-B Marine Weld epoxy and left to dry for approximately 2 hrs. The clod card and washer were then attached to a circular base made of underwater paper using marine epoxy. Prior to attachment each base was labeled with a treatment name and replicate number.

The clod cards were randomly assigned to experimental treatments either ambient (n=8) or shaded (n=8) and attached on the bottom center of each experimental unit using cable ties. Prior to deployment each clod card unit (clod card + washer and paper) was weighed.

Experimental units were deployed by attaching them randomly to a fabric rope secured to the benthos in the middle of a tidal channel in the Carpentaria estuary on February 10, 2023. They were left in the field for 22 hrs. spanning nearly 2 tidal cycles, starting with a low tide of 32.6 cm and remaining in place through a maximum high tide of 129.5 cm.

Once collected, the clod cards were detached from each experimental unit and taken back to the University of California Los Angeles. The clod cards were then placed in a food dehydrator for 30 mins to dry excess water then taken out of the food dehydrator and left to dry for two days before being reweighed.

*Statistical Analyses*

We calculated percent change in biomass as [final – initial]/initial x 100 and used it as our response variable in both experiments.

For the field experiment, we found that our data met the assumptions of homogeneity by utilizing the Levene's test (Levenes 1960) implemented in Rstudio ("R version 4.2.1 (2022-06-23)). However, a Shapiro-Wilks test (Shapiro and Wilk 1965) confirmed our data was not normally distributed. Additionally, parametric assumptions were not met with data transformations. As such, we used the "lmPerm" package in RStudio to conduct a permutational ANOVA designed for univariate responses to test the effects of light, nutrients, sediment, and their interactions on percent change in biomass of *Halimeda*. Permutational analyses have been found to be robust and account for violations against normality (Anderson and Walsh 2013; Wheeler 2016). To further explore statistical differences, we performed a pairwise post-hoc analysis when there were instances of an interaction.

For the mesocosm experiment, our data meet ANOVA assumptions (tested as above) so we used two-way ANOVA to test for the effects of light, sediment, and their interaction on percent change in biomass of *Halimeda opuntia*.

**Results**

*Site Characterization*

The study site consisted of a mixed algal community with some coral that survived the predator outbreak (Figure 1). While algal turf was the dominant space-holder, *H. opuntia* was common, with average holdfast cover of more than 10%.

*Nutrient, Sediment and Light Effects on* Halimeda *growth in the Field*

Overall, *Halimeda opuntia* grew in all 8 treatments, with growth rate ranging from an average of ~2 to over 25% in 7 days (Figure 2). Nutrients interacted significantly with sediment and marginally significantly with light (Table 1).

There was a negative effect of added sediment on *Halimeda* but only in the presence of added nutrients, generating the sediment by nutrient interaction (Figure 2, Table 1). Growth was overall lower, averaging 7% in 7 days across the two light treatments with both added nutrients and added sediment compared to 23% in the treatment with added nutrients but ambient sediment (Figure 3 a). In contrast, when nutrients are ambient, there is no difference between ambient and added sediment treatments; rather, mean growth across these 4 treatments was 21%.

There was a positive effect of reduced light when nutrients were ambient but when nutrients were added in combination with reduced light there was a reduction in growth, generating the marginal light by nutrient interaction (Figure 2, Table 1). Our post-hoc analysis

confirmed that growth differed across treatments with reduced light with either ambient or added nutrients, although marginally (Figure 3 b). Reducing light by shading more than doubled the growth of *Halimeda* in ambient nutrient conditions.

*Effects of Sediment and Light on the Growth of* Halimeda *in Mesocosms*

There were significant main effects of both sediment and light on change in biomass of *Halimeda* (Figure 4; Table 2). Overall, algae grew 3.9% in 6 days when sediment was added compared to a 1.7% loss without sediment, presumably because respiration exceeded photosynthesis. The main effect of ambient light was negative, with ambient light causing an overall loss of *Halimeda* biomass of over 4% without sediment but a gain of over 2% when sediment was added. There was an overall negative effect of light, with a 4.5% loss in biomass at ambient light, 0.5% loss in biomass at 51% reduction but a slight positive growth at 76% reduction. Here the addition of sediment shifted the pattern from loss to growth in all light treatments, with the most growth at the greatest light reduction.

*Environmental Context: Light Environment and Experimental Artifacts*

Mean solar radiation was significantly greater above the water at the LTER weather station during the mesocosm experiment compared to the field experiment (Figure 5, t-test, p = 0.004). In the field, there was a 45% difference in the light environment between the ambient, $437.47 \pm 16.38$ µmoles m$^{-2}$ s$^{-1}$, and shaded, $232.16 \pm 10.28$ µmoles m$^{-2}$ s$^{-1}$, experimental units (Table 3). In mesocosms, light was reduced by the window screen treatments, with the smallest difference in light intensity between the one (51% reduction) and two (76% reduction) screen treatments at $845.73 \pm 33.37$ µmoles m$^{-2}$ s$^{-1}$ and $400.30 \pm 17.42$ µmoles m$^{-2}$ s$^{-1}$, respectively.

Although measured at different times, it appeared that the overall light regime was 4 times higher in experimental mesocosm than experimental field units, which is likely due to differences in water depth and seasonal differences in ambient light (Table 3). However, it should be noted that these light measurements were taken at different times throughout the year, one in the dry season (experimental field units) and once at near the end of the wet season (mesocosms) in Moorea.

We assessed the potential for our light reduction method to impede water flow with three approaches. First, our results from the dye test in Moorea demonstrate there was no significant difference in the time it took for dye to flow out of the shaded and unshaded treatments (n= 10, t-test, p = 0.184). Although we could not test differences statistically (n = 1 for each experimental treatment), means from our second test (in California) when dye was repeatedly dispensed at the mid-level were 2.36 ± 1.48s (mean ± SE) in our ambient experimental unit and 2.31 ± 0.49s in our shaded experimental unit. When dye was dispensed at the top of cages the mean time for dye to dissipate was 3.78 ± 1.16s in our ambient experimental units and 3.42 ± 0.79s in our shaded experimental units. Finally, results from the clod card test in Carpentaria Salt Marsh verified there were no differences in the reduction in weight of the clod cards between ambient and shaded experimental units (t-test, p=0.855).

**Discussion**

In contrast to studies that demonstrate light is limiting for many macroalgal species (e.g., Carpenter 1990; Markager and Sand-Jensen 1992; Huntington and Boyer 2008; Van Alstyne et al. 2008), we found that our environmental context was one where light was not limiting for *Halimeda*. Instead, our results demonstrate that the very high light levels in our experiment and mesocosm were inhibitory. The range of light intensities in our experiments are biologically

relevant as similar light regimes have been reported in other shallow reefs. For example, in shallow reefs with depths < 5m, maximum light intensities in some reefs range from 800 - 1300 µmoles m$^{-2}$ s$^{-1}$ (0.5-3m, Wanders 1976)while others reach 1650 µmoles m$^{-2}$ s$^{-1}$ (1-2m Barnes and Lazerd 1993) or even as high as 2000 µmoles m$^{-2}$ s$^{-1}$ (Payri et al. 2001). As such, light intensities during our experiments fall within realistic limits of light regimes a thallus may be exposed to in a shallow reef, implying that it may be common for light to be inhibitory to *Halimeda* growth on shallow reefs.

Evidence from both our field and mesocosm experiment suggests that the inhibitory effects of light on *Halimeda* may be caused by photoinhibition (Barnes and Lazerd 1993, Wanders 1976). There was an overall pattern of increased growth with shade in both our field and mesocosm experiments, demonstrating that shade limited the negative effects that occurred in high light environments. When light levels across our experiments are ranked from low to high, the response to the lowest two light regimes (field shaded and mesocosm 76% reduction) showed the predicted increase in growth usually found in experiments that construct P/I curves (Teichberg et al. 2013; Figure 6). The higher light regimes showed decreased growth that was most pronounced in the experimental units with the highest light, reflecting the typical pattern shown in P/I curves where algae are experiencing photoinhibition (Han 2002). Further, our highest light intensity exceeds values shown to induce photoinhibition in *Halimeda spp.* (Franklin et al. 1996; Häder et al. 1996). Taken together, our results imply that the light regime in our experiments was at the higher end of the P/I curve for *Halimeda*, suggesting there was a dissipation of this energy via photoinhibition. Photoinhibition is a process that protects photosystem II, where light is absorbed for photosynthesis, from irreversible damage (Trebst 1991; Häder 2006). Thus, although *Halimeda* can be a dominant space holder on very shallow

reefs, our results show these high light environments may not be optimal; rather, in this shallow environment, *Halimeda* is likely at the top end of its tolerance to high light intensity.

Comparison with other studies confirms that the light regime on our reef, and especially in our mesocosms, was extremely high and comparable with other regimes that cause photoinhibition. For example, light intensities across different macroalgal species and habitats that lead to photoinhibition range from 500 µmoles m$^{-2}$ s$^{-1}$ in intertidal tundra habitats(Hanelt 1998) to 1400 µmoles m$^{-2}$ s$^{-1}$ in coral reef habitats (Franklin et al. 1996). When we put our experimental light regimes in context (Table 3, Figure 6), significant loss in biomass occurred when light intensities were above 800 µmoles m$^{-2}$ s$^{-1}$ and this is congruent with findings that suggest the photosynthetic activity of *H. opuntia* starts to level at light intensities > 450 µmoles m$^{-2}$ s-$^{1}$ (see, Peach et al. 2017). While macroalgae have several mechanisms (e.g., chloroplast movements and dynamic photoinhibition) to mitigate high light stress (Häder et al. 2002; Häder 2006; Figueroa et al. 2009), they are energetically costly. This trade off likely explains the reduction in biomass we reported in our study when light was extremely high and the increase in biomass in our study when the light environment was reduced.

We found that the effects of increased sedimentation on *Halimeda* are context dependent. For example, in the environmental context of extremely high light, as we measured in the mesocosm experiment, increased sedimentation had a positive effect and supported *Halimeda* growth, likely by reducing photoinhibition. These results contradict some field studies that documented negative effects of sediment on turf and other macroalgae in the absence of herbivory, which was attributed to smothering (Airoldi et al. 1997; Umar et al. 1998; Clausing et al. 2014; Tebbett et al. 2018). It is unlikely our sediment smothered our algae or inhibited photosynthetic activity for *Halimeda;* instead, sediment protected *Halimeda*. Our results also

differ from studies that reported positive sediment effects on varying macroalgal species that were attributed to a nutrient subsidy (Sargassum, Schaffelke 1999; Galaxaura, Clausing et al. 2016a). It is unlikely that sediments provided a nutrient subsidy in our study as we did not capture positive main sediment effects outside of the context of high light. Thus, factors that limit light availability by physically blocking photons, such as sedimentation, may lessen the negative effects of very high light for *Halimeda*.

In contrast, in the environmental context of added nutrients and high light, as modeled in the field experiment, increased sedimentation had a negative effect on *Halimeda*. Ban et al. (2014) demonstrated that nutrients commonly interact with environmental drivers associated with storms and terrestrial runoff (e.g., sedimentation). This finding is congruent with the interaction we documented between nutrients and sediments. While nutrients can be stimulatory when interacting with biotic factors such as herbivory (Burkepile and Hay 2006), our study suggests that nutrients may not yield positive effects when interacting with sediments and this may be due to species-specific characteristics such as calcification (but see Clausing et al. 2016a). Studies have reported reductions in *Halimeda spp.* growth with increased nutrients hindering bio-remineralization (Demes et al. 2009), growth(Hofmann et al. 2014) and calcification (Delgado and Lapointe 1994). Studies have also shown that sediments can reduce the surrounding pH of other calcifiers such as corals, thereby negatively affecting $CaCO_3$ precipitation (Weber et al. 2012). Given that increases in pH initiate the process of $CaCO_3$ precipitation (Borowitzka and Larkum 1976; Semesi et al. 2009), if the presence of sediment lowered the local pH of *Halimeda* thalli, this could have prohibited calcification. Our result, taken together with other studies (Johnson et al. 2018), suggest that some opportunistic macroalgal species, such as *Sargassum spp.* that have been reported in increased abundance

across reefs (Stiger and Payri 1999b), may be more tolerant to increases in sediment and nutrients while highly calcified species such as *Halimeda* may be more susceptible to changes in these drivers.

Contrary to much of the prior research on more opportunistic species of algae (Dailer et al. 2012; Reef et al. 2012; Adam et al. 2021; Sura et al. 2023), we found overall that nutrients were inhibitory rather than stimulatory for *H. opuntia* (but see Bergman et al. 2016; Bittick et al. 2016). *Halimeda spp.* have been reported to have both a negative and positive response to nutrients in combination with environmental drivers (Teichberg et al. 2013; Hofmann et al. 2014). For example, Smith et al. (2004)reported positive effects of nutrients on *Halimeda tuna* growth with depth as nutrients may be more abundant deeper in the water column. Conversely, Hofmann et al. (2014) reported a decrease in *Halimeda opuntia* growth with elevated nutrients, in both the presence and absence of $CO_2$, and more growth over time with lower nutrient levels, suggesting that more nutrients may not have a consistent impact across different species of *Halimeda*. It is plausible that there was an excess of nutrients supplied to our *Halimeda* from our experimental nutrient enrichment and sediment supply. Other studies have characterized the genus *Halimeda* as overall slow growing with a greater contribution to resistance to disturbance than growth (Hillis-Colinvaux 1980; Littler et al. 1983). This may explain the response to nutrients we documented in our study in comparison to increased growth responses documented in fleshly macroalgal species. These opportunistic species' strategy may be to contribute more energy to growth versus resistance (Littler et al. 1983; Delgado and Lapointe 1994; Fong and Fong 2018). Overall, nutrients may not always have a stimulatory effect on all macroalgae, and the presence and directionality of this environmental driver can be influenced by environmental context (e.g., nutrient regimes) or species-specific strategies.

*Concluding Thoughts*

While a great deal of focus has been given to understanding the effects human impacts have on opportunistic coral reef macroalgae, less focus has been directed toward species that persist throughout less disturbed fringing reefs. We found that changes in environmental drivers associated with human impacts, such as increased sediment and nutrients, in high light environments will likely result in differential responses of *Halimeda*. It is likely that in this fringing reef system, *Halimeda* will continue to benefit from sedimentation in shallow environments while coral species suffer (Junjie et al. 2014; Jones et al. 2019) and other macroalgal species, such as *Padina* (Clausing et al. 2016c; Johnson et al. 2018), merely tolerate increases in this environmental driver. These different responses to increased sediments may drive changes in dominance of shallow reef communities subject to human impacts. Overall, our results suggest that at high light intensities, elevated nutrients and increased sediment are unlikely to either mitigate the negative effects of high light or bolster the stimulatory effect of added sediment; instead, these factors may result in biomass loss for *Halimeda*.

**Tables**

**Table 1.** Three-factor permutation analysis on univariate data assessing percent change in biomass of *Halimeda opuntia* over 7 days in the field experiment with nutrients (ambient/added), sediment (ambient/added), and light (ambient/reduced) as the three factors.

| | Estimate | Iteration | Pseudo p-value |
|---|---|---|---|
| **Light** | 0.99776 | 56 | 0.6429 |
| **Nutrients** | 3.00311 | 1456 | 0.0646 |
| **Sediment** | -3.33878 | 1056 | 0.0871 |
| **Light*Nutrients** | 4.25288 | 1804 | **0.0527** |
| **Light*Sediment** | -1.02328 | 68 | 0.6029 |
| **Nutrients*Sediment** | 4.92040 | 5000 | **<0.001** |
| **Light*Nutrients*Sediment** | -0.02991 | 51 | 0.9412 |

**Table 2.** Two factor ANOVA on percent change in biomass of *Halimeda opuntia* over 6 days in a mesocosm experiment with sediment (+/-), and light (0, 30%, 60% reduction) as the two factors.

| Factor | df | Sum of Squares | F Ratio | p-value |
|---|---|---|---|---|
| Sediment | 1 | 383.65485 | 22.5188 | **<0.0001** |
| Light | 2 | 174.70297 | 5.1271 | **0.0102** |
| Light*Sediment | 2 | 51.23721 | 1.5037 | 0.2340 |

**Table 3.** Average light measurements for each treatment in the field and mesocosm experiments. Field ambient and shaded light measurements were recorded in 2020 to characterize and contextualize differences in light environment due to nylon shade cloth for the shaded treatments. All mesocosm light measurements were recorded in 2023 to better characterize and contextualize the light environment and reduction caused by the nylon shade cloth(s). Light measurements provided context as to how each light environment differed based on location (field/water column vs mesocosm/water table) and light reduction (ambient/shaded).

| Light Treatment | Average Light ($\mu$moles m$^{-2}$ s$^{-1}$) |
|---|---|
| Field (January 2020) | |
| Field Ambient | $437.47 \pm 16.38$ |
| Field Shaded (45% Reduction) | $232.16 \pm 10.28$ |
| Mesocosm (May 2023) | |
| Ambient Mesocosm | $1817.06 \pm 85.36$ |
| Single Screen Mesocosm (51% Reduction) | $845. 73 \pm 33.37$ |
| Double Screen Mesocosm (76% Reduction) | $400.30 \pm 17.42$ |

**Figure Captions**

**Figure 1.** Mean (±SE) percent benthic cover at Ta'ahiamaunu Public Beach, Moorea French Polynesia, including the categories of: *Halimeda opuntia*, turf algae, coral, crustose coralline algae (CCA), *Turbinaria ornata* (n=51).

**Figure 2.** Mean percent change in wet weight (±SE) over 7 days of *H. opuntia* in a field experiment testing the effects of light, nutrients, and sediment.

**Figure 3. a)** Sediment x nutrient interaction for *H. opuntia* **b**) Post hoc analysis of light x nutrients and Bars that share the same letter or symbol are not statistically different. * Signifies marginal difference.

**Figure 4.** Mean percent change in wet weight (±SE) over 6 days of *H. opuntia* in a mesocosm experiment testing the effects of light and sediment.

**Figure 5**. Mean daily solar radiation (kw per m$^2$ ) during field and mesocosm experiments. Experiments were conducted and light readings taken from June 15th - 22nd and June 24th- 30th, 2015, respectively. Solar radiation measurements were taken by the University of California Gump Station and recorded from sensors located 6m from mean sea level. Data retrieved from Moorea LTER database.

**Figure 6.** Conceptual schematic of ranked light environment across field and mesocosm light treatments. The light environment is ranked from most reduced to highest light availability. This

schematic depicts a pattern where *H. opuntia* gained small increases in biomass with a reduced light environment followed by biomass loss when the light environment increased. Although light measurements were not measured simultaneously, calculated light measurements provide some context to differences in the light environment due to light treatments.
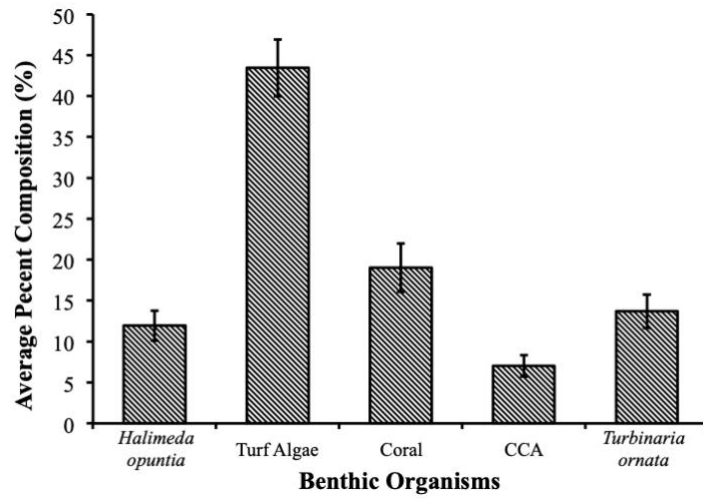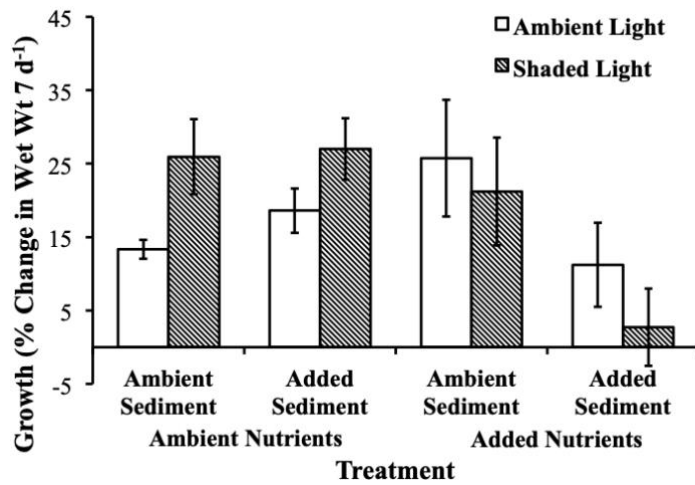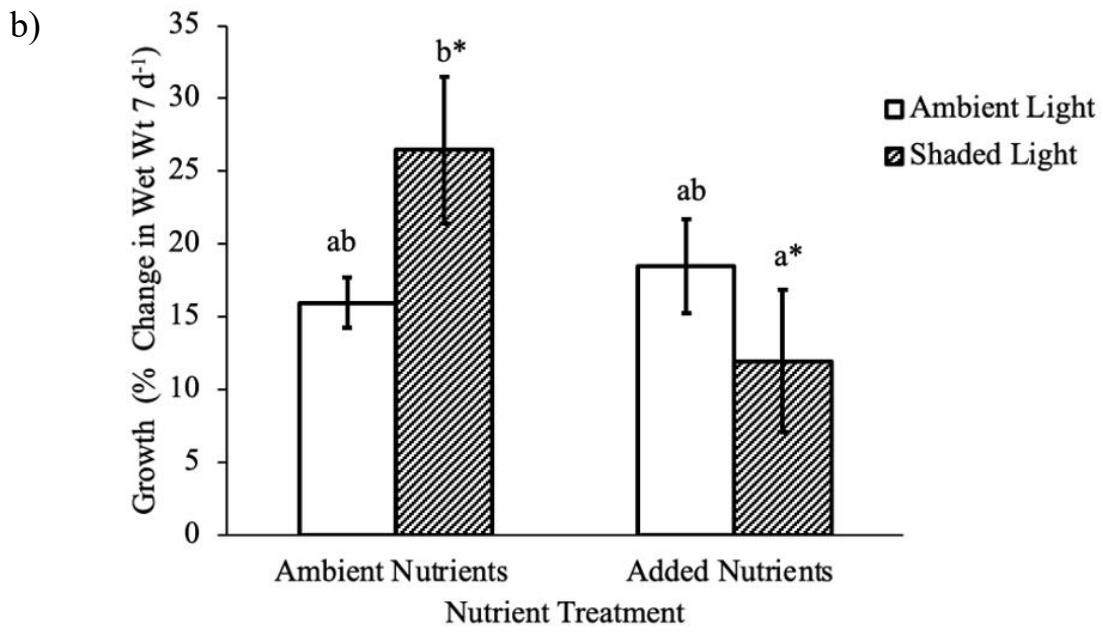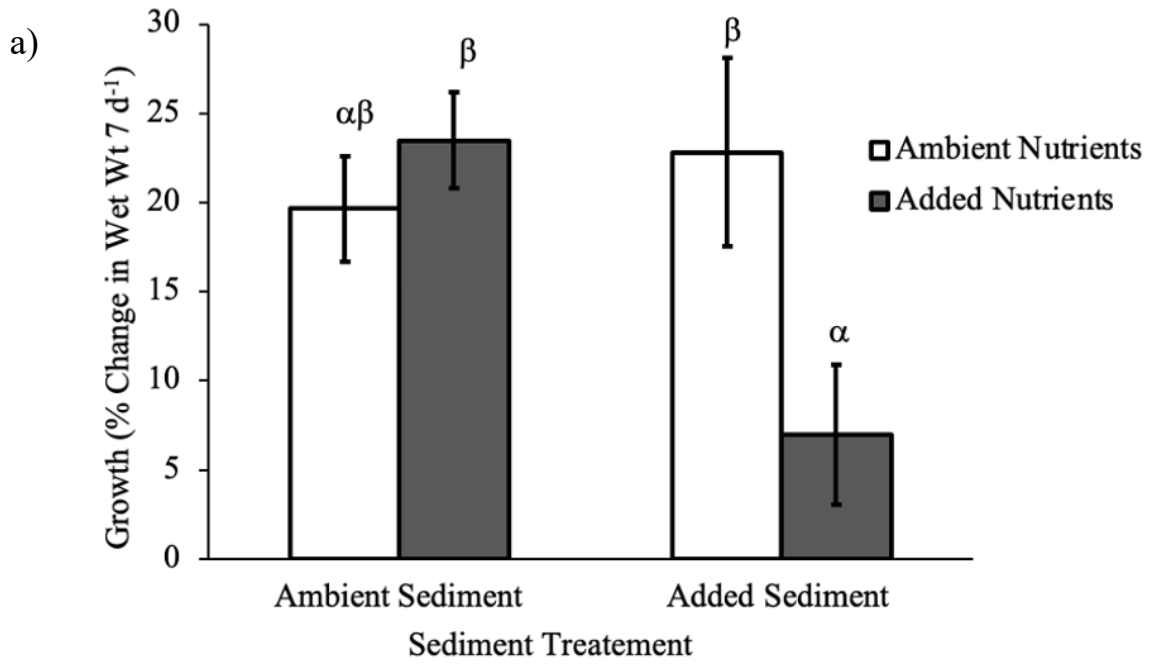
**Figures**



**Figure 1**
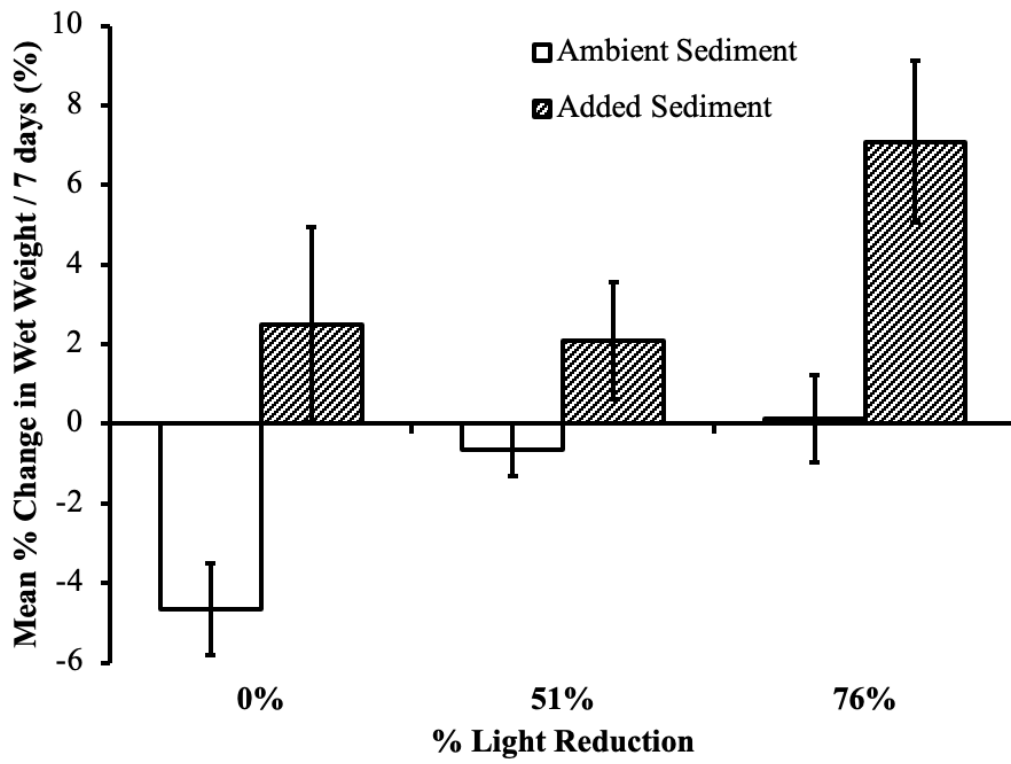


**Figure 2**

a)

b)

**Figure 3**

**Figure 4**

**Figure 5**

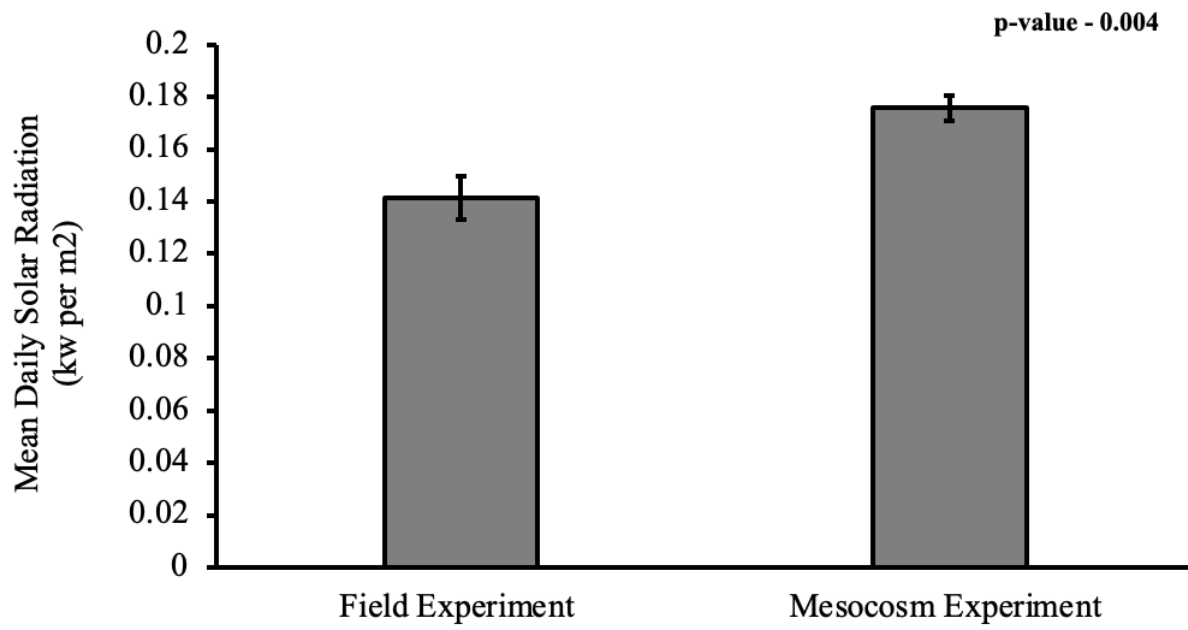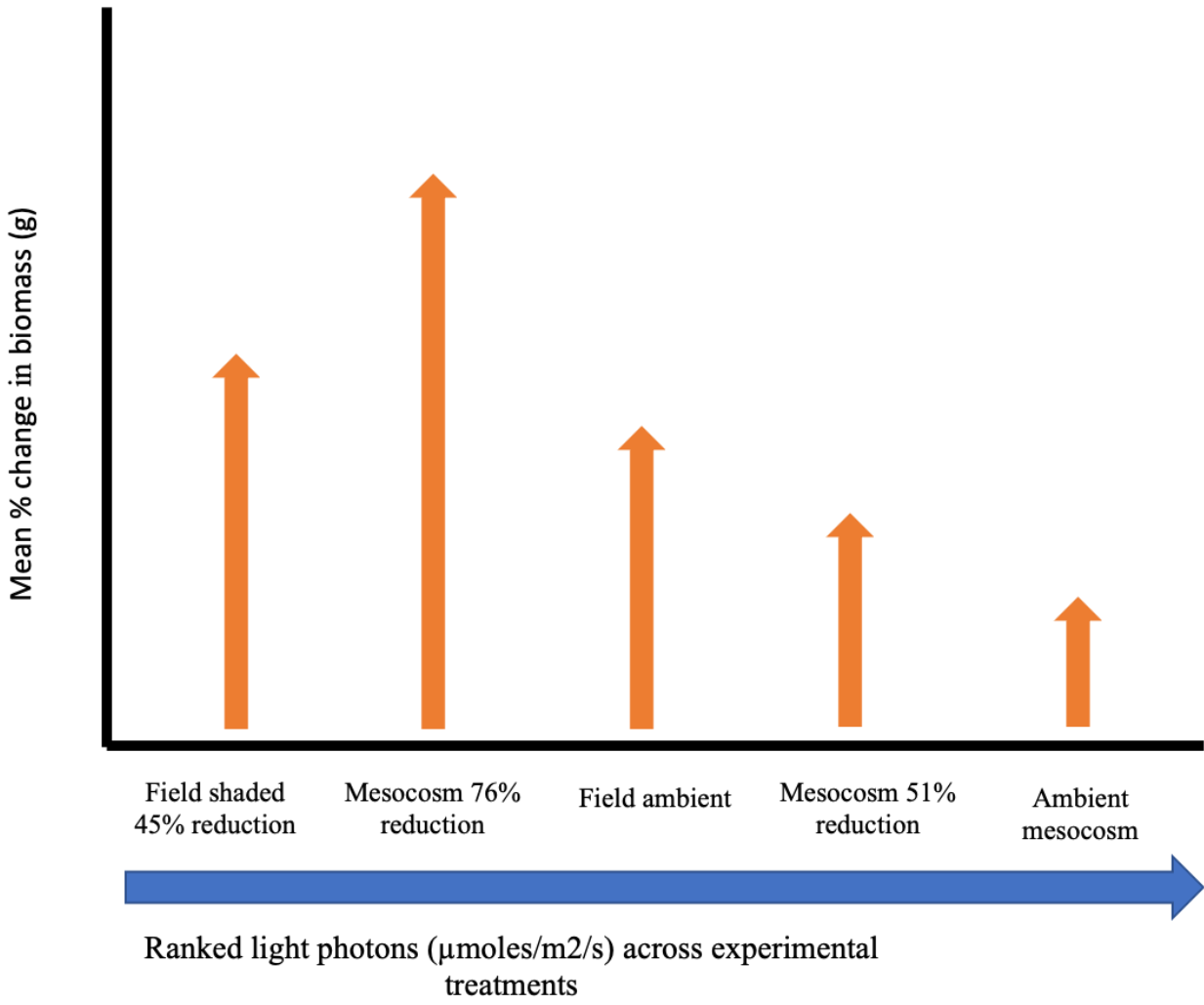**Figure 6**

**References**

Adam TC, Burkepile DE, Holbrook SJ, Carpenter RC, Claudet J, Loiseau C, Thiault L, Brooks AJ, Washburn L, Schmitt RJ, Adam TC, Burkepile DE, Holbrook SJ, Carpenter RC, Claudet J, Loiseau C, Thiault L, Brooks AJ, Washburn L, Schmitt RJ (2020) Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts. Ecological Applications 31:e02227

Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y, de Loma TL, Penin L, Thibaut L, Vidal-Dupiol J, Salvat B, Galzin R (2009) Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. Coral Reefs 28:775–780

Airoldi L, Cinelli F (1997) Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. J Exp Mar Biol Ecol 215:269–288

Alestra T, Schiel DR (2015) Impacts of local and global stressors in intertidal habitats: Influence of altered nutrient, sediment and temperature levels on the early life history of three habitat-forming macroalgae. J Exp Mar Biol Ecol 468:29–36

Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr 83:557–574

Anthony KRN, Ridd P V., Orpin AR, Larcombe P, Lough J (2004) Temporal variation of light availability in coastal benthic habitats: Effects of clouds, turbidity, and tides. Limnol Oceanogr 49:2201–2211

Ban SS, Graham NAJ, Connolly SR (2014) Evidence for multiple stressor interactions and effects on coral reefs. Glob Chang Biol 20:681–697

Banderia-Pedrosa ME, Pereira SMB, Oliveira EC (2004) Taxonomy and distribution of the green algal genus *Halimeda* (Bryopsidales, Chlorophyta) in Brazil 1. Revista Brasil Botany 27:363–377

Barnes DJ, Lazarb B (1993) Metabolic performance of a shallow reef patch near Eilat on the Red Sea. J E.up Mur Biol Ecol 174:1–13

Barott KL, Caselle JE, Dinsdale EA, Friedlander AM, Maragos JE, Obura D, Rohwer FL, Sandin SA, Smith JE, Zgliczynski B (2010) The lagoon at Caroline/Millennium Atoll, Republic of Kiribati: Natural history of a nearly pristine ecosystem. PLoS One 5:e10950

Bellwood DR, Hughes TP, Folke C, Nystrom M, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Bergman JL, Dang BN, Tabatabaee MM, McGowan MM, Fong CR, Bittick SJ, Fong P (2016) Nutrients induce, and herbivores maintain thallus toughness, a structural anti-herbivory defense in *Turbinaria ornata*. Mar Ecol Prog Ser 559:35–43

Bittick SJ, Clausing RJ, Fong CR, Fong P (2016) Bolstered physical defences under nutrient-enriched conditions may facilitate a secondary foundational algal species in the South Pacific. Journal of Ecology 104:646–653

Borowitzka MiA, Larkum AWD (1976) Calcification in the green alga *Halimeda*. J Exp Bot 27:879–893

Bucolo P, Sullivan MJ, Zimba P V. (2008) Effects of nutrient enrichment on primary production and biomass of sediment microalgae in a subtropical seagrass bed. J Phycol 44:874–881

Bulleri F, Couraudon-Reále M, Lison De Loma T, Claudet J (2013) Variability in the effects of macroalgae on the survival and growth of corals: The consumer connection. PLoS One 8:e79712

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. Ecology 87:3128–3139

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc Natl Acad Sci U S A 105:16201–16206

Cannon SE, Donner SD, Liu A, González Espinosa PC, Baird AH, Baum JK, Bauman AG, Beger M, Benkwitt CE, Birt MJ, Chancerelle Y, Cinner JE, Crane NL, Denis V, Depczynski M, Fadli N, Fenner D, Fulton CJ, Golbuu Y, Graham NAJ, Guest J, Harrison HB, Hobbs JPA, Hoey AS, Holmes TH, Houk P, Januchowski-Hartley FA, Jompa J, Kuo CY, Limmon GV, Lin Y V., McClanahan TR, Muenzel D, Paddack MJ, Planes S, Pratchett MS, Radford B, Reimer JD, Richards ZT, Ross CL, Rulmal J, Sommer B, Williams GJ, Wilson SK (2023) Macroalgae exhibit diverse responses to human disturbances on coral reefs. Glob Chang Biol 29:3318–3330

Carpenter RC (1990) Competition among marine macroalgae: A physiological perspective. J Phycol 26:6–12

Clausing RJ, Annunziata C, Baker G, Lee C, Bittick SJ, Fong P (2014) Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. Mar Ecol Prog Ser 517:121–129

Clausing RJ, Bittick SJ, Fong CR, Fong P (2016a) Sediments influence accumulation of two macroalgal species through novel but differing interactions with nutrients and herbivory. Coral Reefs 35:1297–1309

Clausing RJ, Fong P (2016) Environmental variability drives rapid and dramatic changes in nutrient limitation of tropical macroalgae with different ecological strategies. Coral Reefs 35:669–680

Dailer ML, Smith JE, Smith CM (2012) Responses of bloom forming and non-bloom forming macroalgae to nutrient enrichment in Hawai'i, USA. Harmful Algae 17:111–125

Delgado O, Lapointe BE (1994) Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. Coral Reefs 13:151–159

Demes KW, Bell SS, Dawes CJ (2009) The effects of phosphate on the biomineralization of the green alga, Halimeda incrassata (Ellis) Lam. J Exp Mar Biol Ecol 374:123–127

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132

Drew EA, Abel KM (1988) Studies on Halimeda I. The distribution and species composition of Halimeda meadows throughout the Great Barrier Reef Province. Coral Reefs 6:195-205

Edmunds PJ, Tsounis G, Boulon R, Bramanti L (2019) Acute effects of back-to-back hurricanes on the underwater light regime of a coral reef. Mar Biol 166:1–8

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. Mar Pollut Bull 50:125–146

Figueroa FL, Martínez B, Israel A, Neori A, Malta E jan, Ang P, Inken S, Marquardt R, Rachamim T, Arazi U, Frenk S, Korbee N (2009) Acclimation of Red Sea macroalgae to solar radiation: Photosynthesis and thallus absorptance. Aquat Biol 7:159–172

Fong CR, Fong P (2018) Nutrient Fluctuations in Marine Systems: Press Versus Pulse Nutrient Subsidies Affect Producer Competition and Diversity in Estuaries and Coral Reefs. Estuaries and Coasts 41:421–429

Fong CR, Gaynus CJ, Carpenter RC (2020a) Extreme rainfall events pulse substantial nutrients and sediments from terrestrial to nearshore coastal communities: a case study from French Polynesia. Sci Rep 10:1–8

Fong CR, Gaynus CJ, Carpenter RC (2020b) Complex interactions among stressors evolve over time to drive shifts from short turfs to macroalgae on tropical reefs. Ecosphere 11:e03130

Fong P, Boyer KE, Kamer K, Boyle KA (2003) Influence of initial tissue nutrient status of tropical marine algae on response to nitrogen and phosphorus additions. Marine Ecology Progress Series 262:111–123

Fong P, Paul VJ (2011) Coral reef algae. Coral Reefs: An ecosystem in transition. Z. Dubinsky and N.Stambler (eds), Springer. pp 241-272.

Franklin LA, Larkum AWD (1997) Multiple strategies for a high light existence in a tropical marine macroalga. Photosynth Res 53:149–159

Franklin LA, Seaton GGR, Lovelock CE, Larkum AWD (1996) Photoinhibition of photosynthesis on a coral reef. Plant Cell Environ 19:825–836

Gao X, Lee JR, Park SK, Kim NG, Choi HG (2019) Detrimental effects of sediment on attachment , survival and growth of the brown alga Sargassum thunbergii in early life stages. Phycological Res 67:77–81

Gaynus C (2019) Environmental and biotic controls affecting recruitment and proliferation of algal turf communities in coral reef systems. University of California Los Angeles

Gennaro P, Piazzi L, Persia E, Porrello S (2019) Responses of macroalgal assemblages dominated by three Mediterranean brown macroalgae with different life strategies to nutrient enrichment. Eur J Phycol 54:432–446

Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norström A V., Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. Front Ecol Environ 11:541–548

Häder D-P (2006) Photoinhibition and UV Response in the Aquatic Environment. Photoprotection, Photoinhibition, Gene Regulation, and Environment . pp 87–105

Häder DP, Lebert M, Sinha RP, Barbieri ES, Helbling EW (2002) Role of protective and repair mechanisms in the inhibition of photosynthesis in marine macroalgae. Photochemical and Photobiological Sciences 1:809–814

Häder D-P, Porst M, Herman H, Schäfer J, Santas R (1996) Photoinhibition in Halimeda tuna. Photochemistry and Photobiology 64:428–434

Han BP (2002) A mechanistic model of algal photoinhibition induced by photodamage to photosystem-II. J Theor Biol 214:519–527

Hanelt D (1998) Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth distribution. Mar Biol 131:361–369

Hillis-Colinvaux L (1980) Ecology and taxonomy of Halimeda: Primary producer of coral reefs. Adv Mar Biol 17:1–327

Hofmann LC, Heiden J, Bischof K, Teichberg M (2014) Nutrient availability affects the response of the calcifying chlorophyte Halimeda opuntia (L.) J.V. Lamouroux to low pH. Planta 239:231–242

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, J. M. Pandolfi, B. Rosen, J. Roughgarden (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. Science (1979) 301:929–933

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633–642

Huntington BE, Boyer KE (2008) Effects of red macroalgal (Gracilariopsis sp.) abundance on eelgrass Zostera marina in Tomales Bay, California, USA. Mar Ecol Prog Ser 367:133–142

IPCC (2019) Summary for Policymakers. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

Irving AD, Witman JD (2009) The effects of sedimentation on rocky coast assemblages. J Ecol 97:827–833

Jessen C, Wild C (2013) Herbivory effects on benthic algal composition and growth on a coral reef flat in the Egyptian Red Sea. Mar Ecol Prog Ser 476:9–21

Johns KA, Emslie MJ, Hoey AS, Osborne K, Jonker MJ, Cheal AJ (2018) Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9:e02349

Johnson GC, Pezner AK, Sura SA, Fong P (2018) Nutrients and herbivory, but not sediments, have opposite and independent effects on the tropical macroalga, Padina boryana. J Exp Mar Biol Ecol 507:17–22

Jokiel PL and MJI (1993) Water motion on coral reefs: evaluation of the "clod card" technique. 9 Mar Ecol Prog Ser 3:175–181

Jones R, Fisher R, Bessell-Browne P (2019) Sediment deposition and coral smothering. PLoS One 14:e0216248

Junjie RK, Browne NK, Erftemeijer PLA, Todd PA (2014) Impacts of sediments on coral energetics: Partitioning the effects of turbidity and settling particles. PLoS One 9:e107195

Kawamata S, Yoshimitsu S, Tokunaga S, Kubo S, Tanaka T (2012) Sediment tolerance of Sargassum algae inhabiting sediment-covered rocky reefs. Mar Biol 159:723–733

Knuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323:107–117

Koch MS, Snedaker SC (1997) Aquatic botany Factors influencing Rhizophora mangle L. seedling development in Everglades carbonate soils. Aquat Bot 59:87–98

Lapointe BE, Littler MM, Littler DS (1987) A comparison of nutrient-limited productivity in macroalgae from a caribbean barrier reef and from a mangrove ecosystem. Aquat Bot 28:243–255

Lapointe BE, Littler MM, Littler DS (1992) Modification of Benthic Community Structure by Natural Eutrophication: the Belize Barrier Reef. Proceedings of Seventh International Coral Reef Symposium.

Levene, H., 1960. Robust tests for equality of variances. In: I. Olkin, S.G. Ghurye, W. Hoeffding, W.G. Madow & H.B. Mann (Eds.) Contributions to probability and statistics. Essays in honor of Harold Hotelling. Stanford University Press, Stanford, Carolina, p. 278–292.

Littler MM, Littler DS (1992) Photosynthesis vs. irradiance curves for six species of macroalgae from the Seychelles Islands under four levels of nutrient enrichment. Atoll Research Bulletin

Littler MM, Littler DS, Taylor PR (1983) Evolutionary Strategies in a Tropical Barrier Reef System: Functional-Form Groups of Marine Macroalgae. J Phycol 19:229–237

Macreadie PI, Jarvis J, Trevathan-Tackett SM, Bellgrove A (2017) Seagrasses and macroalgae: importance, vulnerability and impacts. Climate Change Impacts on Fisheries and Aquaculture: A Global Analysis. pp 729–770

Markager S, Sand-Jensen K (1992) Light requirements and depth zonation of marine macroalgae. Mar Ecol Prog Ser 88:83–92

Mayakun J, Kim JH, Lapointe BrianE, Prathep A (2013) Algal response to nutrient enrichment; insights into growth and chemical concentrations in two algae, Halimeda macroloba Decaisne and Turbinaria conoides (J. Agardh) Kützing. Songklanakarin Journal of Science and Technology 35:389–395

Mcclanahan TR (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. J Exp Mar Biol Ecol 218:77–102

Middelboe AL, Sand-Jensen K, Binzer T (2006) Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. Oecologia 150:464–476

Morris L, Jenkins G, Hatton D, Smith T (2007) Effects of nutrient additions on intertidal seagrass (Zostera muelleri) habitat in Western Port, Victoria, Australia. Mar Freshw Res 58:666–674

Multer HG (1988) Coral Reefs Growth rate, ultrastructure and sediment contribution of Halimeda incrassata and Halimeda monile, Nonsuch and Falmouth Bays, Antigua, W.I. Coral Reefs 6:179–186

Payri CE, Maritorena S, Bizeau C, Rodière M (2001) Photoacclimation in the tropical Coralline alga Hydrolithon Onkodes (Rhodophyta, Corallinaceae) from a French Polynesian Reef. J Phycol 37:223–234

Peach KE, Koch MS, Blackwelder PL, Manfrino C (2017) Calcification and photophysiology responses to elevated pCO2 in six Halimeda species from contrasting irradiance environments on Little Cayman Island reefs. J Exp Mar Biol Ecol 486:114–126

Pongparadon S, Nooek S, Prathep A (2020) Phenotypic plasticity and morphological adaptation of Halimeda opuntia (Bryopsidales, Chlorophyta) to light intensity. Phycological Res 68:115–125

Price NN, Hamilton SL, Tootell JS, Smith JE (2011) Species-specific consequences of ocean acidification for the calcareous tropical green algae Halimeda. Mar Ecol Prog Ser 440:67–78

Reef R, Pandolfi JM, Lovelock CE (2012) The effect of nutrient enrichment on the growth, nucleic acid concentrations, and elemental stoichiometry of coral reef macroalgae. Ecol Evol 2:1985–1995

Sammarco P, Levinton JS, Ogden JC (1974) Grazing and Control of Coral Reef Community Structure by Grazing and Control of Coral Reef Community Structure by Diadema antillarum Philippi (Echinodermata: Echinoidea): A (Echinodermata: Echinoidea): A Preliminary Study Preliminary Study. Journal of Marine Research 32:47–53

Sangil C, Guzman HM (2020) Macroalgal community response to herbivores and sediment deposition: an indicator of coral reef degradation. J Appl Phycol 32:1405–1419

Schaffelke B (1999) Particulate organic matter as an alternative nutrient source for tropical Sargassum species (Fucales, Phaeophycea). J Phycol 35:1150–1157

Schmitt RJ, Holbrook SJ, Davis SL, Brooks AJ, Adam TC, Estes JA (2018) Experimental support for alternative attractors on coral reefs. PNAS 116:4372–4381

Semesi IS, Beer S, Björk M (2009) Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. Mar Ecol Prog Ser 382:41–47

Shapiro SS, Wilk MB (1965) An Analysis of Variance Test for Normality. Biometrika Trust 52:591–611

Smith JE, Smith CM, Vroom PS, Beach KL, Miller S (2004) Nutrient and growth dynamics of Halimeda tuna on Conch Reef, Florida Keys: Possible influence of internal tides on nutrient status and physiology. Limnol Oceanogr 49:1923–1936

Sofonia JJ, Anthony KRN (2008) High-sediment tolerance in the reef coral Turbinaria
        mesenterina from the inner Great Barrier Reef lagoon (Australia). Estuar Coast Shelf Sci
        78:748–752

Stiger V, Payri CE (1999a) Spatial and seasonal variations in the biological characteristics of two
        invasive brown algae, turbinaria ornata (turner) j. agardh and sargassum mangarevense
        (grunow) setchell (sargassaceae, fucales) spreading on the reefs of Tahiti (French
        Polynesia). Botanica Marina 42:295–306

Stiger V, Payri CE (1999b) Spatial and temporal patterns of settlement of the brown macroalgae
        Turbinaria ornata and Sargassum mangarevense in a coral reef on Tahiti. Mar Ecol Prog
        Ser 191:91-100

Sura SA, Bell A, Kunes KL, Turba R, Songer R, Fong P (2021) Responses of two common coral
        reef macroalgae to nutrient addition, sediment addition, and mechanical damage. J Exp
        Mar Biol Ecol 536:151512

Sura SA, Delgadillo A, Franco N, Gu K, Turba R, Fong P (2019) Macroalgae and nutrients
        promote algal turf growth in the absence of herbivores. Coral Reefs 38:425–429

Sura SA, Gehris CG, Liang MY, Lim AN, Fong P (2023) Press versus pulse nutrient supply and
        species interactions mediate growth of coral reef macroalgae. Oikos e09716

Tebbett SB, Bellwood DR (2020) Sediments ratchet-down coral reef algal turf productivity.
        Science of the Total Environment 713:136709

Tebbett SB, Goatley CHR, Bellwood DR (2018) Algal turf sediments across the Great Barrier
        Reef: Putting coastal reefs in perspective. Mar Pollut Bull 137:518–525

Teichberg M, Fricke A, Bischof K (2013) Increased physiological performance of the calcifying
        green macroalga Halimeda opuntia in response to experimental nutrient enrichment on a
        Caribbean coral reef. Aquat Bot 104:25–33

Thimijan RW, Heins RD, Thimijan RW, Heins RD (1983) Photometric, radiometric, and
        quantum light units of measure a review of procedures for interconversion. HortScience
        18:818–822

Thompson TL, Glenn EP (1994) Plaster standards to measure water motion. Limnol Oceanogr
        39:1768–1779

Trebst A (1991) A Contact Site between the Two Reaction Center Polypeptides of Photosystem II
        Is Involved in Photoinhibition. Z Naturforsch 46c:557–562

Umar MJ, McCook LJ, Price IR (1998) Effects of sediment deposition on the seaweed
        Sargassum on a fringing coral reef. Coral Reefs 17:169–177

Van Alstyne KL, Nelson TA, Haberlin K, Nelson A V., Ribarich H, Hotchikiss R, Buckingham L, Simunds DJ (2008) Ecological and Physiological Controls of Species Composition in Green Macroalgal Blooms. Shannon Point Marine Center Publications (2).

Vercelloni J, Kayal M, Chancerelle Y, Planes S (2019) Exposure, vulnerability, and resiliency of French Polynesian coral reefs to environmental disturbances. Sci Rep 9:1–11

Victor S, Neth L, Golbuu Y, Wolanski E, Richmond RH (2006) Sedimentation in mangroves and coral reefs in a wet tropical island, Pohnpei, Micronesia. Estuar Coast Shelf Sci 66:409–416

Wanders JBW (1976) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I : Primary productivity in the coral reef. Aquat Bot 2:235

Weber M, De Beer D, Lott C, Polerecky L, Kohls K, Abed RMM, Ferdelman TG, Fabricius KE (2012) Mechanisms of damage to corals exposed to sedimentation. Proc Natl Acad Sci U S A 109:e1558–e1567

Wei Z, Zhang Y, Yang F, Long L (2022) Increased light availability enhances tolerance against ocean acidification-related stress in the calcifying macroalga Halimeda opuntia. Acta Oceanologica Sinica 41:123–132

Wheeler RE (2016) Permutation tests for linear models in R. R package version, 2(0).

Wiman SK, McKendree WG (1975) Distribution of Halimeda Plants and Sediments on and around a patch reef near old Rhodes Key, Florida. Journal of Sedimentary Petrology 45:415–421

Yñiguez AT, McManus JW, Collado-Vides L (2010) Capturing the dynamics in benthic structures: Environmental effects on morphology in the macroalgal genera Halimeda and Dictyota. Mar Ecol Prog Ser 411:17–32

# CHAPTER 3

**Both response to disturbance and recovery of two opportunistic coral reef macroalgae are context-dependent and governed by species interactions**

## Abstract

Previous works have investigated how disturbances shift coral reefs from dominance by coral to macroalgae. However, studies investigating resilience of the resultant dominant macroalgal species in response to disturbance are lacking. The first objective of this study was to assess how species interactions influence growth of two dominant macroalgal species within dense macroalgal stands dominated by intra- vs interspecific natural communities. Then, in low-density assembled communities, we assessed how species interactions influence both their response to (phase 1) and recovery from (phase 2) an episodic light disturbance. In the first experiment, we transplanted individuals of *Padina boryana* and *Sargassum pacificum* to dense intra- or interspecific dominated patches. We found species interactions significantly affected *P. boryana* growth with greater growth in dense conspecific patches than those dominated by *S. pacificum*. In contrast, *S. pacificum* did not respond to patch type. Phase 1 was investigated with a two-factor fully-crossed field experiment manipulating light and community context while in Phase 2, we quantified recovery once disturbance ceased. Light and phase interacted significantly for *P. boryana,* resulting in less growth with light reduction during phase 1, but rapid recovery once ambient light was restored. Thus, *P. boryana* shows little resistance but substantial resilience in the form of rapid recovery. In contrast, although *S. pacificum* performed better in intraspecific communities than interspecific regardless of phase, demonstrating some resistance when with conspecifics, there was net biomass loss rather than recovery in phase 2.

Taken together, these two experiments demonstrated that, under at least some contexts, both *P. boryana* and *S. pacificum* can grow better with conspecifics, suggesting that these macroalgal species are affected by interspecific interactions. Our study highlights the importance of understanding macroalgal species resilience to environmental disturbances as resilience is likely to be influenced by neighbors and traits and will ultimately shape the ecosystem functions coral reefs provide.

**INTRODUCTION**

The resilience of individual species to changes in environmental drivers will ultimately determine the nature of communities and the functions they provide in the Anthropocene. Ecological resilience is measured as resistance to and recovery from disturbance (Scheffer et al. 2001; Hodgson et al. 2015) and has historically been defined as the ability to absorb disturbance while still maintaining the same ecological relationships (Holling 1973). Since, resistance has been defined as a system's ability to maintain its state in the presence of a disturbance and recovery is the ability to return to its initial state after cessation of disturbance (Hughes et al. 2010; Hodgson et al. 2015). As species are subjected to both episodic and chronic disturbances (e.g., Oliveira et al. 2019; Williams et al. 2019; Simmons et al. 2021), to be resilient they must either tolerate these disturbances or recover rapidly once the disturbance has ceased. While some species demonstrate responses that suggests resilience, others do not (Dandan et al. 2015; Vitasse et al. 2019; Lisovski et al. 2021), providing evidence that disturbances may differentially affect species, ultimately affecting their persistence and role in a community. Evaluating species' resilience to disturbances produced by shifting environmental drivers will provide valuable information as to how they will respond to global change.

A species' responses to environmental disturbances are determined, at least in part, by the traits of that particular species (Kennedy et al. 2010; Williams et al. 2010; Zawada et al. 2019) that bolster tolerance or facilitate rapid recovery. For example, in terrestrial systems that are drought prone, primary producers that have lower water potential or greater leaf mass per area fare better in arid conditions in comparison to species that have the opposite traits (Craine et al. 2013). Other traits such as resource uptake (Kennison et al. 2011; Martínez et al. 2012), fast vs slow growth (Riegl et al. 2013) and height (Hauxwell et al. 2001; Chen and Pannell 2022), among many others, contribute to the ability of a species to recover from disturbance. Thus, exploring the responses of species with different traits to changes in environmental drivers is critical.

In addition to species-specific traits, an individual's response to variation in environmental drivers can also be influenced by their neighbors via interspecific and intraspecific interactions (Grant et al. 2014; Blanco-Cano et al. 2022). Species-species interactions that can shift responses to disturbances include facilitation and competition (Huxham et al. 2010; Napier et al. 2016). Facilitative interactions can lessen the negative effects of disturbance by providing release from disturbances (Pretzsch et al. 2013). For example, Sarneel et al. (2022) demonstrated that neighbors facilitated stem elongation of wetland species during a flood treatment, and this allowed individuals to perform better during this disturbance when with neighbors. In similar context, another study demonstrated that this trait, elongation of stems, lessened the negative effects of flooding as long stems allow plants to be at least partially emergent during a flood disturbance (Kende et al. 1998). Further, tolerant and opportunistic species can become stronger competitors under changing environmental drivers, effectively out competing neighbors via exploitative competitive (Perkol-Finkel and Airoldi 2010). For

example, recovery from disturbance can be by neighbors preemptively colonizing space or hindering resource utilization (O'Brien and Scheibling 2018). Given their differential impacts, understanding how the presence of neighbors shifts the responses of different species to changes in environmental drivers is imperative as environmental disturbances and alterations in species composition are expected to increase in the Anthropocene.

One ecosystem subject to drastic shifts due to multiple environmental disturbances is coral reefs (Trapon et al. 2011; Razak et al. 2020). Many reefs have undergone transitions from a coral to an algal dominated state over the last four decades (Hughes 1994; McManus and Polsenberg 2004; Graham et al. 2013; Kubicek et al. 2019), often favoring species with greater resilience to disturbances (de Bakker et al. 2016). While many studies have focused on the drivers of this transition (e.g., De'Ath et al. 2012; Houk et al. 2014; Adam et al. 2020; Ceccarelli et al. 2020; McManus et al. 2020), few focus on the alternate dominant species that can be more opportunistic and provide different ecosystem functions than corals (Roth et al. 2021). Understanding how different species of macroalgae respond to both shifts in environmental drivers and neighbors can help inform predictions as to how resultant communities may continue to change in the Anthropocene.

Episodic disturbances such as storms and rainfall events alter light availability in reefs (Edmunds et al. 2019; Fong et al. 2020) and significantly affect the primary productivity of corals (Edmunds and Gray 2014). However, we lack a thorough understanding of macroalgal resilience to similar disturbances in the light environment or how species interactions may mediate macroalgal resilience. As macroalgae continue to grow in dominance across coral reef ecosystems, it is imperative to understand their resilient to better predict if their dominance will continue under global change or if a lack of resilience provides opportunity for coral to recover.

Macroalgal species utilize light to fuel photosynthesis (Raven and Hurd 2012) and calcification (McNicholl and Koch 2021) and can readily adapt to changes in light availability. However, macroalgae are negatively affected by extremely high and low light levels (Middelboe et al. 2006), which ultimately deter these processes. Therefore, light availability can also influence macroalgal assemblages in reefs (Tait et al. 2014). For example, Connell (2005) demonstrated in an approximately yearlong experiment that light reduction favored the assembly of encrusting coralline algae while full light favored the colonization of turf-algae. However, that study assessed long term light reduction and did not experimentally test species interactions or resilience to short term changes in light availability nor how species recover once conditions return to ambient, motivating our investigation.

The first objective of this study was to assess how species interactions influence the growth of two dominant macroalgal species within dense macroalgal stands dominated by intra- and interspecific natural communities. Then, in low density assembled communities, we assessed how species interactions influence both their response to and recovery from an episodic light disturbance that models those that occur with storm events.

**MATERIALS AND METHODS**

*Overall Approach*

To explore the nature of species interactions and evaluate resilience of two dominant macroalgal species, we conducted two field experiments within the fringing reef system of Moorea, French Polynesia. In the first experiment, we evaluated the nature of species interactions by conducting a transplant experiment. This experiment provided a baseline depiction of how these species interacted in dense intra- and interspecific communities under

ambient abiotic and biotic conditions. To complement this experiment, we conducted a second experiment investigating species interactions and resilience to a short-term light disturbance in lower density, assembled intra- and interspecific communities. In this experiment, we excluded herbivores to focus on these two factors. This experiment was conducted in two phases, disturbance and recovery, to capture species resistance to treatments and rates of recovery after treatments were removed.

*Study Site and Species*

This study was conducted at two sites within the fringing reef system of Moorea, French Polynesia. The first is located on the Piha'ena fringing reef located northwest of the Gump Station (17°29'9.48" S 149°49'39.13" W) and the second at the Public Beach Ta'ahiamanu (17.491918 °S 149.850036 °W). Both sites are along the island's north shore and are shallow with depths < 2.5 m. The sites are dominated by dead coral heads and rubble with minimal live coral coverage due to prior disturbances by *Acanthaster planci* and cyclones (Pratchett et al. 2011; Vercelloni et al. 2019).

*Padina boryana* and *Sargassum pacificum* are ubiquitous brown algae commonly found co-occurring in tropical fringing reef systems. Although both are considered opportunistic, they have some distinct traits. *Padina spp.* are lightly calcified (Geraldino et al. 2005) with an upright, flattened foliose thallus (Wichachucherd et al. 2014). *Sargassum spp.* are not calcified and have upright main branches with oval shaped blades (Mattio et al. 2008). *Padina spp.* are usually closer to the benthos spreading horizontally while *Sargassum spp.* are taller in the water column due to is upright thallus and buoyant pneumatocysts. The fan shaped blades of *Padina spp.* range from 12-150 mm in width (Kyawt Wai and Soe-Htun 2008; Benita et al. 2018) and 15-60 mm in

height (Benita et al. 2018). The thalli of *Padina spp.* generally have more surface area than tropical *Sargassum spp.* (Smith 2023) as the oval blades of *Sargassum spp.*, while numerous, are characteristically smaller. For instance, the length of *Sargassum spp.* blades can range from 22 to 80 mm in length and 6-10 mm in width (Titlyanov et al. 2016). However, *Sargassum* spp. generally exist higher up in the water column, growing up to 1-2 m in height (Titlyanov et al. 2017) and supported by gas filled pneumatocysts.

*Evaluating the species interaction between* P. boryana *and* S. pacificum *using transplants*

To evaluate the nature of the species interaction between *P. boryana* and *S. pacificum*, we conducted a field experiment where we transplanted individuals of each species collected from an algal patch dominated by intraspecifics into dense algal patches dominated by either *P. boryana* or *S. pacificum*. The transplants were as follows: *P. boryana* into *P. boryana* dominated patches, *P. boryana* into *S. pacificum* dominated patches, *S. pacificum* into *P. boryana* dominated patches and *S. pacificum* into *S. pacificum* dominated patches. Patches were characterized as dominated by a species if more than a 95% visual estimate of the $\sim 0.25 - 0.50$m m$^2$ area was covered with one of the focal species. For each transplant combination there was a total of ten replicates totaling 40 experimental units representing interactions that are either intraspecific or interspecific.

To examine changes resulting from species interactions, *P. boryana* and *S. pacificum* thalli were haphazardly collected from the fringing reef (17°29'9.48" S 149°49'39.13" W) and brought back to Gump Station. *P. boryana* and *S. pacificum* were collected from intraspecific dominated sites to limit prior interspecific interactions. All algal samples were rinsed in seawater to remove sediments and spun in a salad spinner to remove excess water so that we could

89

standardize all samples to an initial wet weight of 5g. For the experimental deployments, the basal end of each algal sample was attached to a metal nail using a gardening twist tie, with each constituting an experimental unit.

Experimental units were then returned to the collection site and deployed. To subject experimental units to either intra- or interspecific interactions, deployment sites were haphazardly selected on dead coral heads with visually dense patches of macroalgae dominated by either *P. boryana* or *S. pacificum*. Each nail with an algal sample was hammered into the hard substrate located within the center of each patch to ensure they were surrounded by either an intraspecific or an interspecific transplant patch depending on the transplant type. Experimental units were left in the field for 5 days as previous studies have demonstrated that these species can respond to environmental drivers within similar time periods (Clausing et al. 2016; Johnson et al. 2018).

After 5 days, experimental units were collected, and the algal samples processed and weighed as described above. The percent change in biomass for each algal sample was calculated and used as the response variable. Data were analyzed using a 2-way ANOVA after testing assumptions of normality using Shapiro-Wilks test (Shapiro and Wilk 1965) and heterogeneity of variances using Levene's test (Levene 1960) in Rstudio ("R version 4.2.1 (2022-06-23). To determine where statistical differences arose across our experimental treatments we ran a Tukey-post hoc analysis on our model.

*Evaluating how disturbance and recovery from short-term light reduction affects species interactions.*

**The effect of short-term light disturbance and species interactions on the resistance of *P. boryana* and *S. pacificum*.**

In the first, disturbance phase of this experiment, we assessed the effects of short-term light reduction on resilience and species interactions between *P. boryana* and *S. pacificum* in low density assembled communities. To do so, we conducted a two-factor fully-crossed field experiment manipulating light (ambient/shaded) and total community (intraspecific *P. boryana*, intraspecific *S. pacificum* or both species) at low density (1-2 thallus, depending on community context treatment). To set up this experiment, we collected and weighed 40 individual thalli per algal species (n=40 individual/species). These replicates were randomly placed into the 6 treatment combinations as follows: 1) the ambient light and intraspecific community context treatment for *P. boryana* alone comprised 1 individual of *P. boryana,* 2) the ambient light and intraspecific community context treatment for *S. pacificum* alone comprised 1 individual of *S. pacificum* 3) the shaded light and intraspecific community context treatment for *P. boryana* alone comprised 1 individual of *P. boryana,* 4) the shaded light and intraspecific community context treatment for *S. pacificum* alone comprised 1 individual of *S. pacific,* 5) the ambient light and interspecific community context treatment comprised 1 individual of *Padina* + 1 individual of *Sargassum* thalli, and 6) the shaded light and interspecific community context treatment also comprised 1 individual of *Padina* + 1 individual of *Sargassum* thalli. Each treatment was replicated 10 times for 60 experimental units all of which were placed in individual cages to limit herbivory (see cage description below). When together (treatments 6 and 7 above) individual

*Padina* and *Sargassum* thalli were placed 5cm apart in the same cage, ensuring that, with water movement, algal thalli had frequent physical contact within their community.

To eliminate potentially confounding impacts of herbivory, we placed all algae thalli in fully-enclosed cylindrical cages made from hardware cloth (13.0cm x 13.5cm, height x diameter, with 1cm$^2$ mesh openings) with tops and bottoms to protect algae from most herbivores. Cages of this size and material did not have significant effects on water flow or light in a previous experiment at this site (Clausing et al. 2014) or in our own tests (SI.1). All algal thalli were collected and prepared as described in the prior experiment. As such, all thalli were initially standardized to a wet weight of 5 g. To model short-term light reduction, window screen was sewed on the tops and partially down the sides of half of the experimental cages using fishing line. The window screen reduced the ambient light by 42% (SI.2). To limit the effects of the window screen on water flow (see SI.1 for tests), we left a 2-3cm opening at the bottom of experimental cages free from window screening. Treatments with ambient light conditions were free of window screening. Algal thalli were deployed in the field for seven days. Algal thalli were then collected, rinsed of sediments, spun in a salad spinner, and wet weighed.

We calculated percent change in biomass of the total community (community was intraspecific *P. boryana*, intraspecific specific *S. pacificum*, or 2 species combined) for each community context. The final biomass of each thallus at the end of this first phase was used as the starting biomass for the second phase of this experiment. Additionally, the same thalli from this first phase were used in the second phase of this study and the change in biomass was used the response variable for phase 2 further described below.

**The effect of removal of disturbance and species interactions on the recovery of *P. boryana* and *S. pacificum*.**

In the second phase of this experiment, we evaluated the rate of recovery after the short-term light disturbance by measuring the growth of these same algae in their community after experimental manipulations ceased. After measuring wet weight post the disturbance phase, algal thalli were re-secured back in their respective experimental units in the same manner described above and re-deployed in our study site without shading material. Thalli were left to recover in the field for seven days. Final wet weights were collected as above. The percent change in the total community biomass (community was either intraspecific or with 2 species) for each experimental unit was calculated and used as a response variable. The biomass measured at the experiment's end for each species was also used as a second response variable.

**Statistical analysis of the percent change in total community biomass in response to and recovery from short-term light disturbance and species interactions**.

To evaluate the effects of community context and light treatment across the two experimental phases (disturbance and recovery) on the growth and resilience of these algal species, we conducted a two-way repeated measures ANOVA. In this model, percent change in total community biomass was the response variable. After log transformation, data passed parametric assumptions for normality (Shapiro-Wilks) and homogeneity (Levene's Test). We used the 'aov_ez' function in R from the 'afex' package to perform a two-way repeated measures ANOVA. Phase was set as the within subject factor and community context and light were set as the between subject factors while replicate number was set as a random factor. To obtain the p-values for our model we used the 'summary' function in R. When there were interactions, we

conducted pairwise t-tests using Bonferroni correction on the interacting factors to assess differences within the significant pairwise combinations.

**Statistical analyses of the final biomass of each algal species in response to and recovery from short-term light disturbances and species interactions**.

We performed two separate two-way repeated measures ANOVAs, one for each species, in the same manner previously described above, as our data met assumptions for parametric statistics. However, in these two models, final biomass for each species after each phase was set as the response variable. When an interaction occurred a post-hoc analysis was performed on the significant pairwise combinations as described above.

 RESULTS

*Evaluating the species interaction between* P. boryana *and* S. pacificum *using transplants*

P. boryana grew faster when transplanted into *P. boryana*-dominated patches than when transplanted to *S. pacificum* patches; in contrast, *S. pacificum* did not respond to host patch type (Fig. 1). This difference in the pattern of the species growth responses across patch types resulted in a significant interaction (Table 1). *P. boryana* increased biomass by more than 35% over 6 days when transplanted into a patch of conspecifics. However, *P. boryana* biomass did not change measurably when transplanted into a *S. pacificum* patch. In contrast, there was no significant difference in the biomass of *S. pacificum* regardless of the host patch type; rather, change in biomass was low in both treatments.

*Evaluating how disturbance and recovery from short-term light reduction affects species interactions.*

**Community resistance and recovery response to short-term light disturbance and species interactions.**

Overall, the community comprised of *P. boryana* alone grew the fastest, *S. pacificum* alone the slowest, and the mixed community composed of both species grew intermediate during the disturbance phase, while during the recovery phase *S. pacificum* alone loss mass (Fig. 2a). There was a significant within subjects' interaction between phase and community context (Table 2). We explored this 2-way interaction with post-hoc analysis on the average of the light (ambient and shaded) treatment across phase and community as light did not have significant main or interactive effects at the community level. The phase by community context interaction was generated by a positive effect of recovery on *P. boryana* compared to a lack of an effect of phase for either *S. pacificum* or the mixed community (Fig. 2b).

***P. boryana* resistance and recovery in response to species interactions after short-term light disturbance**.

There was a significant interaction between light and phase on *P. boryana* final biomass (Fig. 3a, Table 3). This interaction was driven by the significantly lower biomass when light was reduced during the disturbance period versus no effect of the previous light treatment during the recovery period (Fig. 3b). On average, the biomass of *P. boryana* previously experiencing light disturbance increased by 1.5g from the disturbance to the recovery phase. However, this positive effect of restoring the light environment during phase 2 was marginal (Table 3, p= 0.073,

Community context * Phase interaction). Our post-hoc analysis confirmed that there was a statistical difference between our ambient and reduced light treatments during the disturbance period (Fig 3b).

**_S. pacificum_ resistance and recovery in response to species interactions after short-term light disturbance**.

Overall, *S. pacificum* biomass was significantly lower after the recovery phase than the disturbance phase (Fig. 4, Table 4). *S. pacificum* did not gain biomass during the recovery period regardless of prior light treatment. Instead, algae had an average of 0.9g less biomass after the recovery period compared to the average biomass after the disturbance period. There was a significant effect of community context on *S. pacificum* biomass. *S. pacificum* had higher biomass in intraspecific communities than in interspecific communities regardless of the phase (Fig. 4).

**DISCUSSION**

Overall, our study demonstrates that macroalgal biomass is affected by both community context and short-term light disturbances. We demonstrated that under some, but not all, contexts both *P. boryana* and *S. pacificum* can grow better with conspecifics than with heterospecifics, suggesting that these macroalgal species are affected by interspecific interactions. Further, while *P. boryana* was less resistant to lower light levels, it also had the greatest ability to recover after the disturbance ceased. Conversely, *S. pacificum* demonstrated more resistance to lower light levels limiting our ability to assess recovery. While competition for light has been investigated among macroalgal species (Quartino et al. 2001; Nabivailo and Titlyanov 2006; Edwards and

Connell 2012; García-Gómez et al. 2021), how species interactions affect response to short-term light disturbance and species resilience to this disturbance has not been thoroughly investigated. As such, the results of our study suggest that the composition of communities should be considered when investigating the resilience of individual species to short-term light disturbance. This topic gains importance in the Anthropocene as short-term light reduction is likely to increase with the predicted increase in storms and rainfall events that result in land runoff predicted for the South Pacific due to climate change.

*Species interactions are context-dependent, influenced by density and traits.*

Our results demonstrate that, under the context of a high-density community, interspecific interactions were negative for *P. borayna*. This is evidenced in the transplant experiment, where *P. boryana* performed better in patches dominated by its own species compared to when it was with *S. pacificum*. One possible explanation is that the *P. boryana* thalli may have leaked nutrients providing a nutrient subsidy to neighbors facilitating internal nutrient cycling within *P. boryana* patches. Studies have documented the "leaky" nature of some macroalgae species (Aisha et al. 1995), and this leakiness likely supports growth. Another possible explanation is that a dense community comprised of many *S. pacificum* individuals may have reduced the light environment for *P. boryana* as *S. pacificum* thalli are generally taller than *P. boryana* (Kyawt Wai and Soe-Htun 2008; Titlyanov et al. 2017). As such, surrounding *S. pacificum* may act as a canopy that out competes a single *P. boryana* thallus in the understory by preemptively capturing light resources. Similarly, in temperate intertidal environments and kelp forest canopies, negative effects have been attributed to reduction in light availability (Reed and Foster 1984; Desmond et al. 2017).

In the context of a low-density community, as in the resilience experiment, interspecific interactions were not important in controlling growth of *P. boryana*, as the presence of *S. pacificum* did not affect *P. boryana*. This result suggests that at lower densities, community context may not affect *P. boryana* resilience to shorter-term light disturbance. We reason that *P. boryana* was readily able to take up resources, such as light, when *S. pacificum* was at low densities. Our results are consistent with a plethora of previous work that demonstrates higher densities intensify species interactions (e.g., Krajicek et al.; Boyden et al. 2009; Huxham et al. 2010; Cameron et al. 2019). For example, Peckol and Rivers (1995) reported no difference in growth rate of two macroalgal species at low densities in mono and mixed assemblages. However, at higher density, one species had higher growth in mono vs mixed species assemblages, suggesting strong interspecific competition. A similar density effect in mono vs mixed assemblages has also been reported between different species of *Caulerpa*, illustrating that at lower densities interspecific assemblages may have little to no effect on macroalgal responses but once densities increase species grow best in intraspecific assemblages (Piazzi and Ceccherelli 2002). Future resilience studies should assess species resilience to disturbance in relation to density to determine if changes in density also affect species resilience to disturbance. Our results suggest species interactions of macroalgae are influenced by density and these factors should be considered when investigating macroalgal growth throughout fringing reefs.

We also demonstrate that the responses of *S. pacificum* to *P. boryana* depend on community context, but in the opposite direction as for *P. boryana*. For *S. pacificum,* there was more biomass gained in intraspecific versus interspecific communities in the resilience experiment but a lack of statistical differences in growth at higher densities in the transplant experiment. One possible explanation is that any negative effects high densities of *P. boryana*

may have had on *S. pacificum* in the transplant experiment may have been obscured by high variability in comparison to the relatively slow growth of *S. pacificum* individuals in this experiment. However, it is unlikely *S. pacificum* experienced a reduced light environment due to *P. boryana* as *S. pacificum* is taller than *P. boryana*. These results imply that *S. pacificum* may be a better competitor for light than *P. boryana* in high density communities, and this likely can be attributed to differences in resource acquisition traits. Alternatively, it is also possible that, like many fast-growing algae (e.g., Fong et al. 1996), *P. boryana* may have 'leaked' nutrients, providing a subsidy to *S. pacificum* as mentioned earlier. Earlier studies have shown that some macroalgae leak nutrients (Fong et al. 1996; Sura et al. 2023), possibly providing a nutrient subsidy to neighbors. In this way, the presence of the leaky high-density macroalgal stand may have negated any negative effects due to competition for resources.

Conversely, in the resilience experiment when density was lower, *P. boryana* had a negative effect on *S. pacificum* growth and this may be attributed to exploitative competition. In this scenario, *P. boryana* is the stronger competitor for nutrients, preemptively taking up nutrient resources more efficiently than *S. pacificum*. However, at this low density, leaking of nutrients may not supply adequate subsidies to significantly impact *S. pacificum* growth. Sura et al. (2023) demonstrated that under ambient conditions *S. pacificum* grew best when in a community of the same species. However, *S. pacificum* growth was negatively impacted when the nutrients were supplied in a pressed or pulsed regime, especially when paired with *P. boryana*. Taken together, these results suggest that changes in environmental drivers many not be as influential in *S. pacificum* growth as its neighbors.

*Resilience in the form of rapid recovery is limited to* P. boryana.

The ecological strategy for resilience of *P. boryana* is to 'bounce back' rapidly once the disturbance ceases rather than to be able to resist it during the disturbance event. While *P. boryana* is sensitive to short-term light reduction, this species can readily recover after the disturbance is over. The ability of *P. boryana* to recover rapidly after light disturbance is likely attributed to this species' ability to grow rapidly. This has been documented in many plant species (Grime 1977), where there is a tradeoff between growth rate and resistance to disturbance (Baraloto et al. 2010). Our study supports previous studies that suggest *P. boryana* has opportunistic traits, including fast growth (e.g., Sammarco et al. 1974; Littler et al. 1983), and this was reflected in the higher gain in biomass and responsiveness to environmental changes in comparison to *S. pacificum. P. boryana* is likely very efficient at capturing resources such as light when not shaded by a taller canopy due to its broad thallus with high surface area. Additionally, research investigating *P. boryana* and *S. pacificum* have consistently reported more rapid growth of *P. boryana* compared to *S. pacificum* under varying environmental conditions (Sura et al. 2021, 2023). As such, it is likely that high light availability is required to support rapid growth, for some species. However, while P. *boryana* is sensitive to short-term light disturbances it can readily recover biomass once light conditions return to ambient.

*Resilience in the form of resistance and limited to* S. pacificum.

In our study, *S. pacificum* demonstrated resistance to reduction in light availability, precluding our ability to measure post-disturbance recovery. Experimental studies have shown that germling and adult individuals in the genus *S. pacificum* can have a range of tolerances to both high and low light (Li et al. 2014a; Zhong et al. 2021; Hong et al. 2021) and one of the

contributing factors may be an individual's ability to efficiently acclimate to changes in light (Zhong et al. 2021). While the resistance of *S. pacificum* to light disturbance has some support in the literature (Li et al. 2014b; Hong et al. 2021; Zhong et al. 2021), because of its resistance in our study, information on its ability to recover is still lacking. However, because of its slower growth compared to *P. boryana,* we hypothesize it may not have the same ability to recover rapidly, once disturbed. Further the overall reduction of biomass in individuals of *S. pacificism* we measured in the recovery phase suggests that factors outside of our treatments likely affected the growth of *S. pacificum,* such as resource availability or experimental artifacts. Thus, further research is needed on *S. pacificism's* resilience to disturbance, particularly in the form of recovery.

Our results support the idea that the resilience of different species falls along a spectrum from resistance to recovery, and that the position of each species along this spectrum is governed by its traits (e.g., Moretti et al. 2006; Bernhardt-Römermann et al. 2011; Buma and Wessman 2012; Sánchez-Salguero et al. 2018). For example, in our experimental communities, *P. boryana* and *S. pacificum* demonstrated resilience in opposing ways, recovery vs resistance, respectively, which we attributed to differences in traits such as surface area, height, and the ability to photo-acclimate. The differences that we found in the mechanisms underlying resilience are similar to many resilience studies across ecosystems and communities, such as tropical rainforests, ant communities, and deserts (Bellingham et al. 1995; Curran et al. 2008; Thion and Prosser 2014; Andersen 2019). These studies suggest that diversity in species responses bolster overall community resilience as different individuals either maintain functioning or recover quickly after disturbance (Allison 2004; Steiner et al. 2006; Mori et al. 2013). In a broader context, our results suggest that the nature of a community's resilience will likely depend on the traits of species

within communities and this idea is supported by findings of earlier resilience work (e.g., De Lange et al. 2013; Lipoma et al. 2016). However, it is important to keep in mind that our "communities" were at a low density and consisted of two species. As such, future resilience studies should seek to investigate a range of species, densities, and community compositions that have diverse traits to gather more insights regarding resilience to disturbances.

*Concluding remarks*

Overall, our findings demonstrate that the composition of communities in combination with species traits can influence species interactions and resilience to disturbance. We propose that short term changes in environmental drivers may shift algal community composition toward more opportunistic species able to bounce back after disturbance ceases. In our study it was clear that having an ecological strategy such as fast growth allowed for the recouping of losses in biomass with the cessation of disturbance. Fast growth is often grouped with other ecological strategies such as dispersal that support recovery across scales after disturbance (e.g., Grime 1977; Gårdmark et al. 2003; Sánchez-Salguero et al. 2018; Harvey et al. 2022), suggesting that this is a consistent characteristic of recovery after disturbance. In contrast, the slower growing *S. pacificum* demonstrated resistance, yet lost biomass after disturbance ceased, suggesting a possible longer-term cost to resisting this disturbance. It is likely that resilient communities will comprise species with responses that fall along a spectrum of resilience with species traits conferring either resistance or recovery as both are needed for community resilience. We hope this study encourages more experimental studies investigating the positioning of species with varying traits along the resilience spectrum to better understand community resilience to disturbance.

**Tables**

**Table 1**. Results of a two-way ANOVA for the transplant experiment evaluating the effects of location, species, and their interactions on growth of *P. boryana,* and *S. pacificum.* Bold values signify significant effects.

| Factor | Df | Sum sq | F value | p- value |
|---|---|---|---|---|
| Location | 1 | 1620 | 5.05 | **0.032** |
| Species | 1 | 3311 | 10.32 | **0.003** |
| Location*Species | 1 | 3369 | 10.50 | **0.003** |
| Residuals | 31 | 9946 | 321 | |

**Table 2.** Results of a two-way repeated measures ANOVA testing the effects of community context and light over the 2 experimental phases on *P. boryana*, *S. pacificum,* and community growth. Bolded values signify significance.

| | SS | df | *F* | *p* |
|---|---|---|---|---|
| **Between Subjects** | | | | |
| Community context | 2.240 | 2 | 46.781 | **< 0.000** |
| Light | 0.076 | 1 | 3.154 | 0.084 |
| Community context* Light | 0.044 | 2 | 0.929 | 0.404 |
| **Within Subjects** | | | | |
| Phase | 0.070 | 1 | 3.266 | 0.079* |
| Community context* Phase | 0.403 | 2 | 9.344 | **0.001** |
| Light*Phase | 0.009 | 1 | 0.423 | 0.520 |
| Community context*Light*Phase | 0.028 | 2 | 0.656 | 0.525 |

**Table 3.** Two-way repeated measures ANOVA testing the effects of community context and light over the two experimental phases on *P. boryana* growth. Bold values signify significant effects. Asterisk (*) signify marginal effects.

| | SS | df | *F* | *p* |
|---|---|---|---|---|
| **Between Subjects** | | | | |
| Community context | 248 | 1 | 0.591 | 0.449 |
| Light | 1641 | 1 | 3.905 | 0.059* |
| Community context* Light | 10 | 1 | 0.024 | 0.879 |
| **Within Subjects** | | | | |
| Phase | 19895 | 1 | 25.563 | **0.022** |
| Community context* Phase | 2722 | 1 | 3.498 | 0.073* |
| Light*Phase | 7231 | 1 | 9.292 | **0.005** |
| Community context*Light*Phase | 707 | 1 | 0.908 | 0.350 |

**Table 4.** Two-way repeated measures ANOVA testing the effects of community context and light over the two experimental phases on *S. pacificum* growth. Bold values signify significant effects.

| | SS | df | *F* | *p* |
|---|---|---|---|---|
| Between Subjects | | | | |
| Community context | 988.7 | 1 | 6.790 | **0.014** |
| Light | 232 | 1 | 1.593 | 0.216 |
| Community context* Light | 48 | 1 | 0.330 | 0.570 |
| Within Subjects | | | | |
| Phase | 4702.01 | 1 | 9.806 | **0.004** |
| Community context* Phase | 62 | 1 | 0.129 | 0.722 |
| Light*Phase | 20 | 1 | 0.044 | 0.836 |
| Community context*Light*Phase | 416.7 | 1 | 0.869 | 0.358 |

**Figures**

**Fig. 1** Mean percent change (±SE) in *P. boryana* and *S. pacificum* wet weight in reciprocal transplant experiment. Bars that share letters are not significantly different.

**Fig. 2**. **a)** Mean percent change (±SE) in *P. boryana*, *S. pacificum* and community wet weight in response to reduced light disturbance during the recovery period and return of ambient light conditions during recovery period. **b)** Exploring the community context x phase interaction by collapsing the 3-factor design into these two interacting factors and conducting a Tukey's post-hoc analysis.

**Fig. 3**. **a)** Mean biomass (±SE) in *P. boryana* wet weight in response to reduced light, phase, and community context at the end of the Phase 1 disturbance and end of the Phase 2 recovery. **b)** Post-hoc analysis of phase x light treatment interaction for *P. boryana*. Bars that share letters are not significantly different.

**Fig. 4** a) Mean biomass (±SE) in *S. pacificum* wet weight in response to reduced light, phase, and community context at the end of the Phase 1 disturbance and end of the Phase 2 recovery.
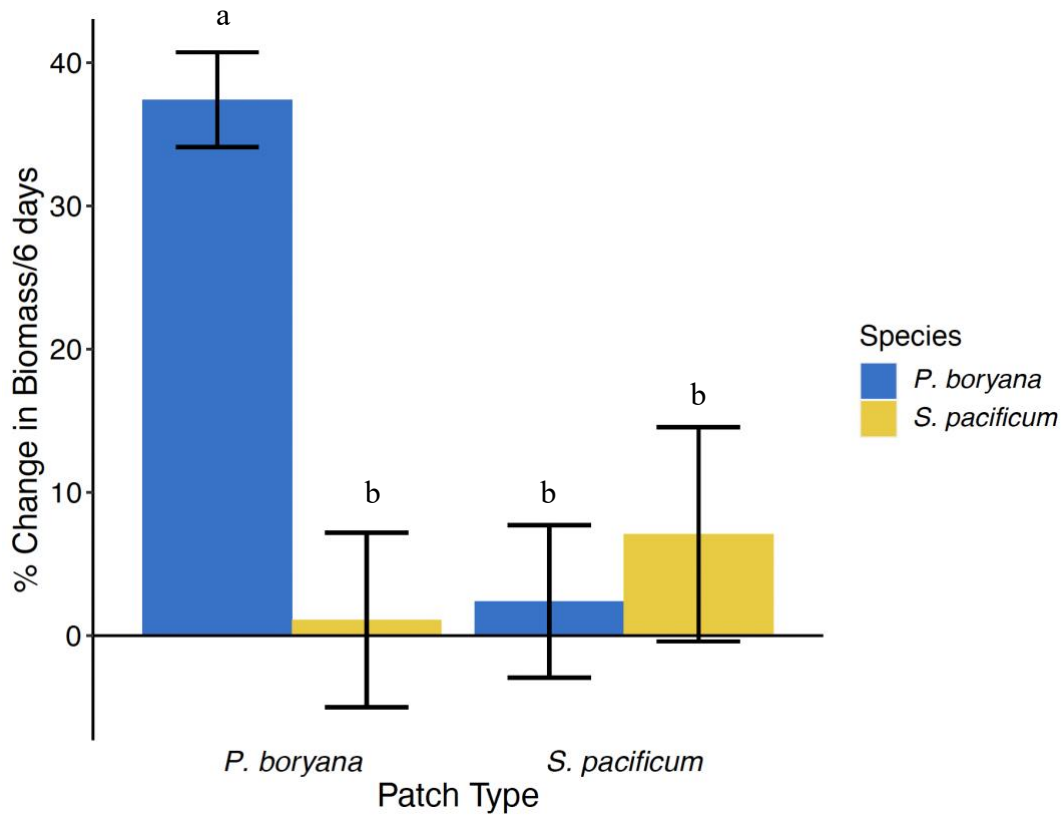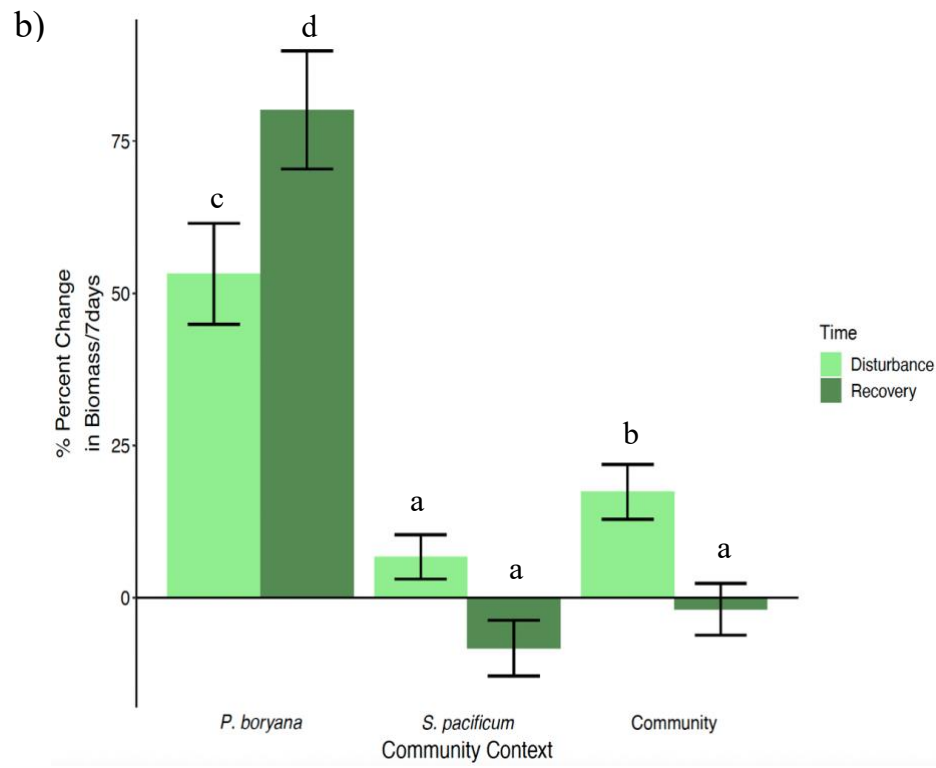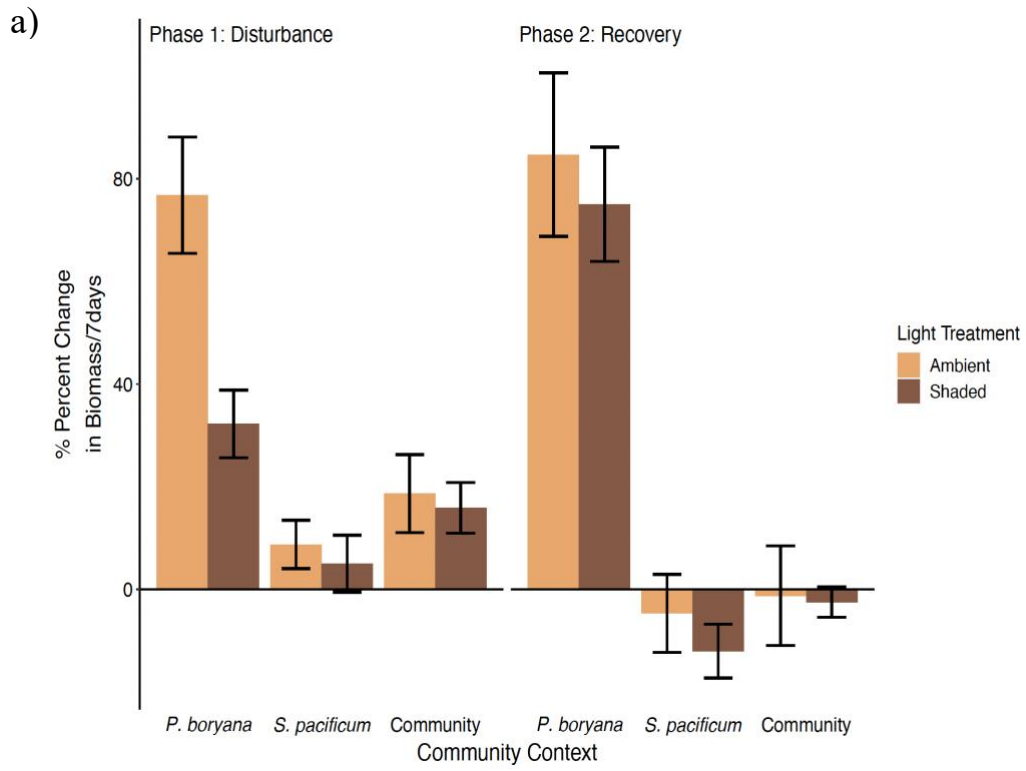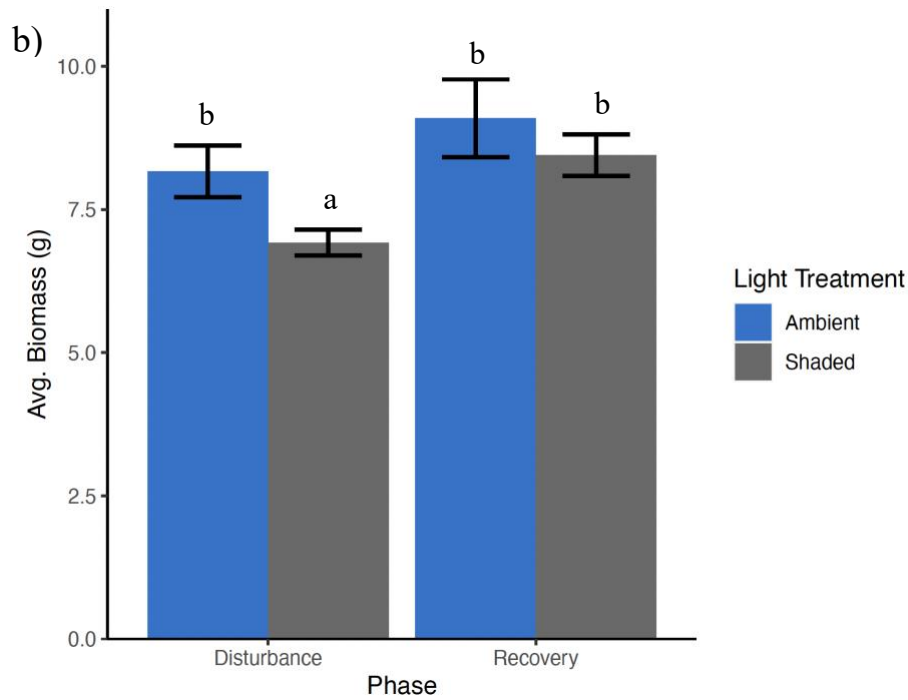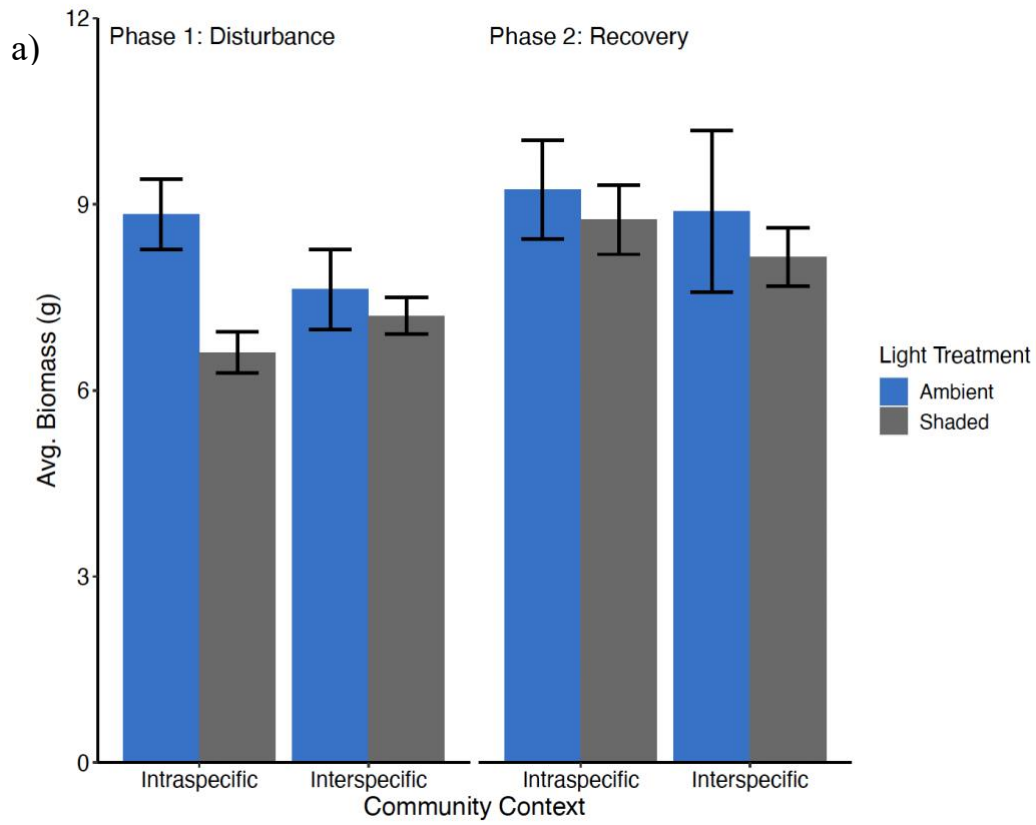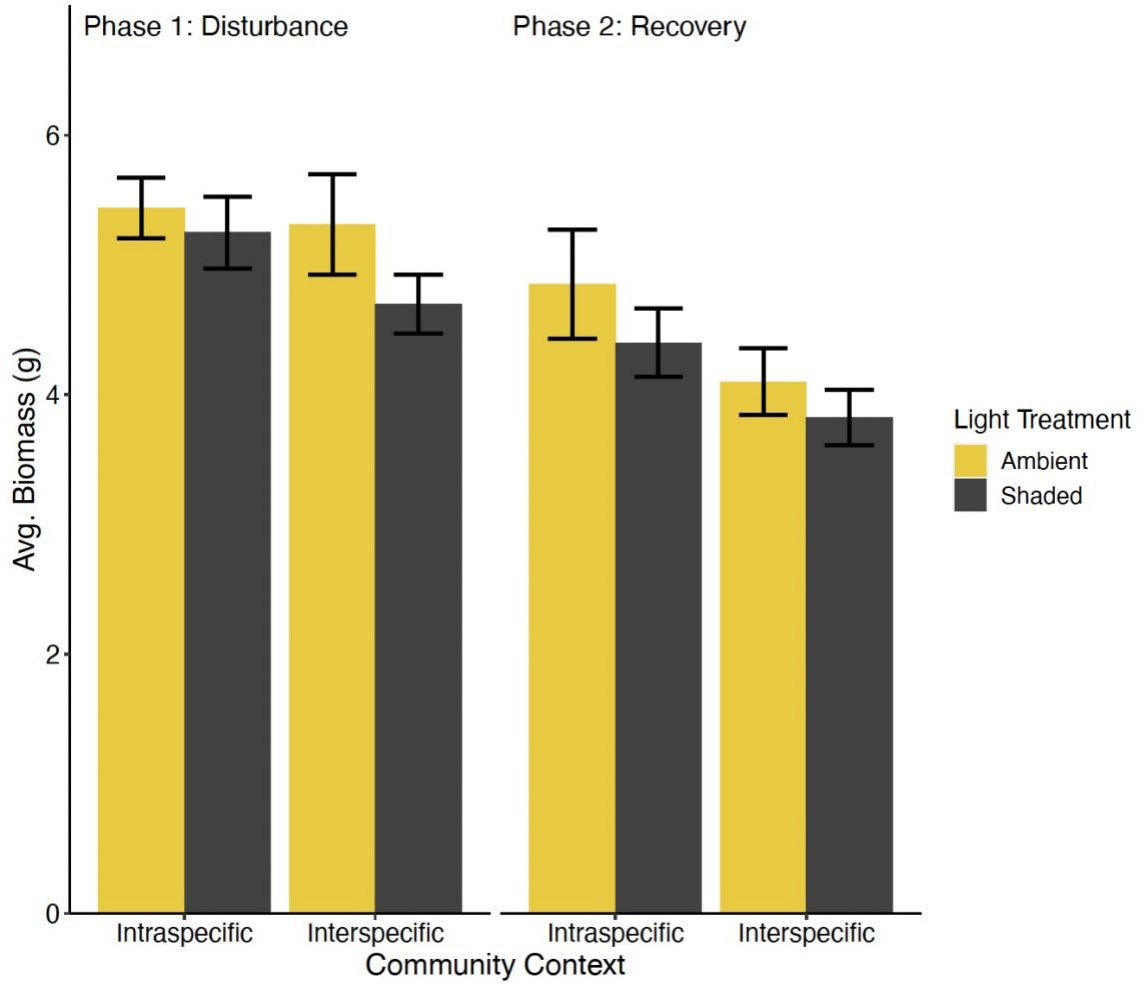
**Figure 1**

**Figure 2**

**Figure 3**

**Figure 4**

**Supplementary Methods and Results**

*SI. 1 Evaluating Possible Artifacts of Cages on Water Flow in the Field*

SI. 1.1 Methods

To evaluate the differences in water flow across experiential light treatments we used dye tests and clod cards. We did a set of dye tests in Moorea in May 2019. Due to limited time in the field, we repeated and expanded the dye tests and conducted clod care measures along a tidal channel of the University of California's Carpinteria Salt Marsh Reserve using cages made of the same material but of a different size (13.0cm x 13.5cm, height x diameter compared to 5cm x 7.5, height x diameter in Moorea, both cage types had 1cm$^2$ mesh openings). This additional testing of water flow across units was repeated to gain confidence in our results. We acknowledge that the flow in this estuary likely differs from the fringing reef where we did these experiments but reasoned that as the flow measures were relative between cage types, this was an adequate test to inform differences.

To evaluate differences in water flow between cage types, we measured how quickly dye dissipated from cages both in Moorea, French Polynesia and repeated these measurements in California. In Moorea, dye was placed within experimental units (n=10) deployed on the experimental reef. Two drops of food coloring were placed mid-height and in the center of the cylindrical experimental units. The time it took for the food coloring to move out of the cage was recorded in seconds. These times were compared between shaded and ambient experimental units with a t-test.

We repeated a similar dye test using fluorescent water tracing dye within the Carpinteria Salt Marsh Reserve in February 2023. However, we expanded this test to include dispensing dye at two depths within the cages. The first test was dispensed in the center of the cylinder, but at a depth near the top of the cage, where the window screen covered the slides of the cage. The next test was also dispensed in the center of our cylindrical experimental units but at the mid depth nearer the place where the window screen ended. We used one ambient experimental unit (no window screen) and one shaded experimental unit (window screen) placed parallel to one another. One drop of dye was simultaneously placed at both of the two locations and the time it took for the dye to move out of the experimental units (ambient or shaded) was recorded at each location ten times and then averaged. The two locations were tested separately, not concurrently.

We used dissolution of clod cards as another test of the effect of cages on water flow. To create the clod cards, we mixed Plaster of Paris and water and placed the mixture into ice cube trays, which served as a mold. Clod cards made of Plaster of Paris have been a longstanding method to measure differences in water flow (Jokiel and Morrissey 1993; Thompson and Glenn 1994). The mix was left to dry for two days before being removed from the plastic mold. Once removed from molding, clod cards were randomly attached to a stainless-steel fender washer 0.64 cm thick x 3.18 cm in diameter using J-B Marine Weld epoxy and left to dry for approximately 2 hrs. The clod card and washer were then attached to a circular base made of underwater paper using marine epoxy. Prior to attachment each base was randomly labeled with a treatment name and replicate number.

The clod cards were randomly assigned to experimental treatments either ambient (n=8) or shaded (n=8) and attached on the bottom center of each experimental unit using cable ties. Prior to deployment each clod card unit (clod card + washer and paper) was weighed.

Experimental units were deployed by attaching them randomly to a fabric rope secured to the benthos on February 10, 2023. They were left in the field for 22 hrs. spanning nearly 2 tidal cycles, starting with a low tide of 32.6 cm and remaining in place through a maximum high tide of 129.5 cm.

Once collected, the clod cards were detached from each experimental unit and taken back to the University of California Los Angeles. The clod cards were then placed in a food dehydrator for 30 mins to dry excess water then taken out of the food dehydrator and left to dry for two days and reweighed.

SI. 1.2 Results

The results from the dye test in Moorea demonstrate there was no significant difference in the time it took for dye to flow out of the shaded and unshaded treatments (n= 10, t-test, p = 0.184). Although we could not test differences statistically (n = 1 for each experimental treatment), means from our second test (in California) when dye was repeated dispensed at the mid-level were 2.36 ± 1.48s (this and all subsequent data are mean ± SE) in our ambient experimental unit and 2.31 ± 0.49s in our shaded experimental unit. Additionally, when dye was dispensed at the top of cages the mean time for dye to dissipate was 3.78 ± 1.16s in our ambient experimental units and 3.42 ± 0.79s in our shaded experimental units. The results from our clod card test in Carpentaria Salt Marsh verified there were no differences in the reduction in weight of the clod cards between ambient and shaded experimental units (t-test, p=0.855). Thus, all 3 tests of water flow show there were no treatment artifacts.

*SI.2 Characterization of light reduction due to experimental shading*

SI.2.1 Methods

To characterize how the light environment differed across light treatments for both the field and mesocosm experiment we used Hobo data loggers, UA002-64 HOBO Waterproof Temperature/Light Pendant Data Logger, to measure light intensity (lum/ft$^2$). In 2020, the light environment of ambient (wire mesh alone) and shaded experimental units (wire mesh + window screen was recorded in Moorea, French Polynesia. One Hobo logger was placed inside an ambient experimental unit and another Hobo logger was placed within a shaded experimental unit; neither unit contained algae in this test. Both Hobo loggers were positioned 5 cm above the benthos, which is approximately where the middle of an algal thallus would be, if present. The data loggers recorded light level every 10 secs for 6 minutes. The light intensity and the percent change between the ambient and shaded experimental units was measured and calculated on January 27, 2020, to characterize light reduction.

SI.2.2 Results

Results from our Hobo logger measurements showed that there was a 45% difference in the light environment between the ambient and shaded experimental units. This demonstrated that we were reducing light with our experimental manipulation.

# References

Adam TC, Burkepile DE, Holbrook SJ, Carpenter RC, Claudet J, Loiseau C, Thiault L, Brooks AJ, Washburn L, Schmitt RJ, Adam TC, Burkepile DE, Holbrook SJ, Carpenter RC, Claudet J, Loiseau C, Thiault L, Brooks AJ, Washburn L, Schmitt RJ (2020) Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts. Ecological Applications 31:e02227

Aisha KA, Shabana EF, El-abyad MS, Kobbia IA, Schanz F (1995) Pulse feeding with nitrate and phosphate in relation to tissue composition and nutrient uptake by some macroalgae from the Red Sea at Ghardaqa (Egypt). J Basic Microbiol 35:135–145

Allison G (2004) The influence of species diversity and stress intensity on community resistance and resilience. Ecol Monogr 74:117–134

Andersen AN (2019) Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. Journal of Animal Ecology 88:350–362

de Bakker DM, Meesters EH, Bak RPM, Nieuwland G, van Duyl FC (2016) Long-term shifts in coral communities on shallow to deep reef slopes of Curaçao and Bonaire: Are there any winners? Front Mar Sci 3:247

Baraloto C, Paine CET, Poorter L, Beauchene J, Bonal D, Domenach AM, Hérault B, Patiño S, Roggy JC, Chave J (2010) Decoupled leaf and stem economics in rain forest trees. Ecol Lett 13:1338–1347

Bellingham PJ, Tanner V, Healey J (1995) Damage and responsiveness of Jamaican Montane tree species after disturbance by Hurricane. Ecology 76:2562–2580

Benita M, Dubinsky Z, Iluz D (2018) *Padina pavonica*: Morphology and calcification functions and mechanism. Am J Plant Sci 09:1156–1168

Bernhardt-Römermann M, Gray A, Vanbergen AJ, Bergès L, Bohner A, Brooker RW, De Bruyn L, De Cinti B, Dirnböck T, Grandin U, Hester AJ, Kanka R, Klotz S, Loucougaray G, Lundin L, Matteucci G, Mészáros I, Oláh V, Preda E, Prévosto B, Pykälä J, Schmidt W, Taylor ME, Vadineanu A, Waldmann T, Stadler J (2011) Functional traits and local environment predict vegetation responses to disturbance: A pan-European multi-site experiment. Journal of Ecology 99:777–787

Blanco-Cano L, Navarro-Cerrillo RM, González-Moreno P (2022) Biotic and abiotic effects determining the resilience of conifer mountain forests: The case study of the endangered Spanish fir. For Ecol Manage 520:1–11

Boyden SB, Reich PB, Puettmann KJ, Baker TR (2009) Effects of density and ontogeny on size and growth ranks of three competing tree species. Journal of Ecology 97:277–288

Buma B, Wessman CA (2012) Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. For Ecol Manage 266:25–33

Cameron H, Coulson T, Marshall DJ (2019) Size and density mediate transitions between competition and facilitation. Ecol Lett 22:1879–1888

Ceccarelli DM, Evans RD, Logan M, Mantel P, Puotinen M, Petus C, Russ GR, Williamson DH (2020) Long-term dynamics and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. Ecological Applications 30:e02008

Chen KH, Pannell JR (2022) Disruptive selection via pollinators and seed predators on the height of flowers on a wind-dispersed alpine herb. Am J Bot 109:1717–1729

Clausing RJ, Annunziata C, Baker G, Lee C, Bittick SJ, Fong P (2014) Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. Mar Ecol Prog Ser 517:121–129

Craine JM, Ocheltree TW, Nippert JB, Towne EG, Skibbe AM, Kembel SW, Fargione JE (2013) Global diversity of drought tolerance and grassland climate-change resilience. Nat Clim Chang 3:63–67

Curran TJ, Gersbach LN, Edwards W, Krockenberger AK (2008) Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of North Queensland, Australia. Austral Ecol 33:442–450

Dandan SS, Falter JL, Lowe RJ, McCulloch MT (2015) Resilience of coral calcification to extreme temperature variations in the Kimberley region, northwest Australia. Coral Reefs 34:1151–1163

De'Ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci U S A 109:17995–17999

Desmond MJ, Pritchard DW, Hepburn CD (2017) Light dose versus rate of delivery: implications for macroalgal productivity. Photosynth Res 132:257–264

Edmunds PJ, Gray SC (2014) The effects of storms, heavy rain, and sedimentation on the shallow coral reefs of St. John, US Virgin Islands. Hydrobiologia 734:143–158

Edmunds PJ, Tsounis G, Boulon R, Bramanti L (2019) Acute effects of back-to-back hurricanes on the underwater light regime of a coral reef. Mar Biol 166:1–8

Edwards MS, Connell SD (2012) Competition, a major factor structuring seaweed communities. Seaweed Biology. pp 135–156

Fong CR, Gaynus CJ, Carpenter RC (2020) Extreme rainfall events pulse substantial nutrients and sediments from terrestrial to nearshore coastal communities: a case study from French Polynesia. Sci Rep 10:1–8

Fong P, Boyer KE, Desmond JS, Zedler JB (1996) Salinity stress, nitrogen competition, and facilitation: what controls seasonal succession of two opportunistic green macroalgae? J Exp Mar Biol Ecol 206:3–221

García-Gómez JC, Florido M, Olaya-Ponzone L, Sempere-Valverde J, Megina C (2021) The invasive macroalga *Rugulopteryx okamurae*: Substrata plasticity and spatial colonization pressure on resident macroalgae. Front Ecol Evol 9:631754

Gårdmark A, Enberg A, Ripa K, Laakso J, Kaitala J (2003) The ecology of recovery. Ann Zool Fennici 40:131–144

Geraldino PJL, Liao LM, Boo S-M (2005) Morphological study of the marine algal genus *Padina* (Dictyotales, Phaeophyceae) from Southern Philippines: 3 Species New to Philippines. Algae 20:99–112

Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norström A V., Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. Front Ecol Environ 11:541–548

Grant K, Kreyling J, Heilmeier H, Beierkuhnlein C, Jentsch A (2014) Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. Ecol Res 29:991–1001

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169–1194

Harvey BP, Marshall KE, Harley CDG, Russell BD (2022) Predicting responses to marine heatwaves using functional traits. Trends Ecol Evol 37:20–29

Hauxwell J, Cebria´n J, Cebria´n C, Furlong C, Valiela I (2001) Macroalgal canopies contribute to eelgrass (*Zostera Marina*) decline in temperate estuarine ecosystems. Ecology 82:1007–1022

Hodgson D, McDonald JL, Hosken DJ (2015) What do you mean, "resilient"? Trends Ecol Evol 30:503–506

Holling CS (1973) Resilience and Stability of Ecological Systems. Annu Rev Ecol Syst 4:1–23

Hong M, Ma Z, Wang X, Shen Y, Mo Z, Wu M, Chen B, Zhang T (2021) Effects of light intensity and ammonium stress on photosynthesis in *Sargassum fusiforme* seedlings. Chemosphere 273:128605

Houk P, Benavente D, Iguel J, Johnson S, Okano R (2014) Coral reef disturbance and recovery dynamics differ across gradients of localized stressors in the Mariana Islands. PLoS One 9:e105731

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633–642

Huxham M, Kumara MP, Jayatissa LP, Krauss KW, Kairo J, Langat J, Mencuccini M, Skov MW, Kirui B (2010) Intra- and interspecific facilitation in mangroves may increase resilience to climate change threats. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2127–2135

Kende H, Van Der Knaap E, Cho H-T (1998) Deepwater rice: A model plant to study stem elongation. Plant Physiology 118:1105–1110

Kennedy CM, Marra PP, Fagan WF, Neel MC (2010) Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. Ecol Monogr 80:651–669

Kennison RL, Kamer K, Fong P (2011) Rapid nitrate uptake rates and large short-term storage capacities may explain why opportunistic green macroalgae dominate shallow eutrophic estuaries. J Phycol 47:483–494

Krajicek JE, Brinkman KA, Gingrich SF (1961) Crown competition - A measure of density. Forest science 7:35–42

Kubicek A, Breckling B, Hoegh-Guldberg O, Reuter H (2019) Climate change drives trait-shifts in coral reef communities. Sci Rep 9:1–10

Kyawt Wai M, Soe-Htun U (2008) Studies on the morphology and distribution of *Padina boryana* Thivy (Dictyotales, Phaeophyta) from Myanmar. Universities Research Journal 1:335–348

De Lange HJ, Kramer K, Faber JH (2013) Two approaches using traits to assess ecological resilience: A case study on earthworm communities. Basic Appl Ecol 14:64–73

Levene, H., 1960. Robust tests for equality of variances. In: I. Olkin, S.G. Ghurye, W. Hoeffding, W.G. Madow & H.B. Mann (Eds.) Contributions to probability and statistics. Essays in honor of Harold Hotelling. Stanford University Press, Stanford, Carolina, p. 278–292

Li X, Zhang Q, He J, Yu Y, Liu H (2014a) Photoacclimation characteristics of *Sargassum thunbergii* germlings under different light intensities. J Appl Phycol 26:2151–2158

Li XM, Zhang QS, Tang YZ, Yu YQ, Liu HL, Li LX (2014b) Highly efficient photoprotective responses to high light stress in *Sargassum thunbergii* germlings, a representative brown macroalga of intertidal zone. J Sea Res 85:491–498

Lipoma ML, Gurvich DE, Urcelay C, Díaz S (2016) Plant community resilience in the face of fire: experimental evidence from a semi-arid shrubland. Austral Ecol 41:501–511

Lisovski S, Gosbell K, Minton C, Klaassen M (2021) Migration strategy as an indicator of resilience to change in two shorebird species with contrasting population trajectories. Journal of Animal Ecology 90:2005–2014

Littler MM, Littler DS, Taylor PR (1983) Evolutionary strategies in a tropical barrier reef system: Functional-form groups of marine macroalgae. J Phycol 19:229–237

Martínez B, Pato LS, Rico JM (2012) Nutrient uptake and growth responses of three intertidal macroalgae with perennial, opportunistic and summer-annual strategies. Aquat Bot 96:14–22

Mattio L, Payri CE, Stiger-Pouvreau V (2008) Taxonomic revision of *Sargassum* (Fucales, Phaeophyceae) from French Polynesia based on morphological and molecular analyses. J Phycol 44:1541–1555

McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: Ecological and environmental aspects. Prog Oceanogr 60:263–279

McManus LC, Vasconcelos V V., Levin SA, Thompson DM, Kleypas JA, Castruccio FS, Curchitser EN, Watson JR (2020) Extreme temperature events will drive coral decline in the Coral Triangle. Glob Chang Biol 26:2120–2133

McNicholl C, Koch MS (2021) Irradiance, photosynthesis and elevated $pCO_2$ effects on net calcification in tropical reef macroalgae. J Exp Mar Biol Ecol 535:151489

Middelboe AL, Sand-Jensen K, Binzer T (2006) Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. Oecologia 150:464–476

Moretti M, Duelli P, Obrist MK (2006) Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149:312–327

Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews 88:349–364

Nabivailo Y V., Titlyanov EA (2006) Competitive relationships in natural and artificial algal communities. Russ J Mar Biol 32:S21–S31

Napier JD, Mordecai EA, Heckman RW (2016) The role of drought- and disturbance-mediated competition in shaping community responses to varied environments. Oecologia 181:621–632

Oliveira FMP, Andersen AN, Arnan X, Ribeiro-Neto JD, Arcoverde GB, Leal IR (2019) Effects of increasing aridity and chronic anthropogenic disturbance on seed dispersal by ants in Brazilian Caatinga. Journal of Animal Ecology 88:870–880

Peckol P, Rivers JS (1995) Competitive interactions between the opportunistic macroalgae *Cladophora Vagabunda* (Chlorophyta) and *Gracilaria Tikvahiae* (Rhodophyta) under eutrophic conditions. J Phycol 31:229–232

Perkol-Finkel S, Airoldi L (2010) Loss and recovery potential of marine habitats: An experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. PLoS One 5:e10791

Piazzi L, Ceccherelli G (2002) Effects of competition between two introduced *Caulerpa*. Marine Ecology Progress Series 225:189–195

Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. Plant Biol 15:483–495

Quartino ML, Klöser H, Schloss IR, Wiencke C (2001) Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate. Polar Biol 24:349–355

Raven JA, Hurd CL (2012) Ecophysiology of photosynthesis in macroalgae. 113:105–125

Razak TB, Roff G, Lough JM, Mumby PJ (2020) Growth responses of branching versus massive corals to ocean warming on the Great Barrier Reef, Australia. Science of the Total Environment 705:135908

Reed DC, Foster MS (1984) The effects of canopy shadings on algal recruitment and Growth in a Giant Kelp Forest. Ecology 65:937–948

Riegl B, Berumen M, Bruckner A (2013) Coral population trajectories, increased disturbance and management intervention: A sensitivity analysis. Ecol Evol 3:1050–1064

Roth F, RAdecker N, Carvalho S, Duarte CM, Saderne V, Anton A, Silva L, Calleja ML, MorÁn XAG, Voolstra CR, Kürten B, Jones BH, Wild C (2021) High summer temperatures amplify functional differences between coral- and algae-dominated reef communities. Ecology 102:e03226

Sammarco P, Levinton JS, Ogden JC (1974) Grazing and control of coral reef community structure by *Diadema Antillarum* Philippi (Echinodermata: Echinoidea): A preliminary study. Journal of Marine Research 32:47–53

Sánchez-Salguero R, Camarero JJ, Rozas V, Génova M, Olano JM, Arzac A, Gazol A, Caminero L, Tejedor E, de Luis M, Linares JC (2018) Resist, recover or both? Growth plasticity in

response to drought is geographically structured and linked to intraspecific variability in *Pinus pinaster*. J Biogeogr 45:1126–1139

Sarneel JM, Hefting MM, Visser EJW, Díaz-Sierra R, Voesenek LACJ, Kowalchuk GA (2022) Species traits interact with stress level to determine intraspecific facilitation and competition. Journal of Vegetation Science 33:e13145

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality. Biometrika Trust 52:591–611

Simmons KR, Eggleston DB, Bohnenstiehl DWR (2021) Hurricane impacts on a coral reef soundscape. PLoS One 16:e0244599

Steiner CF, Long ZT, Krumins JA, Morin PJ (2006) Population and community resilience in multitrophich communities. Ecology 87:996–1007

Sura SA, Bell A, Kunes KL, Turba R, Songer R, Fong P (2021) Responses of two common coral reef macroalgae to nutrient addition, sediment addition, and mechanical damage. J Exp Mar Biol Ecol 536:151512

Sura SA, Gehris CG, Liang MY, Lim AN, Fong P (2023) Press versus pulse nutrient supply and species interactions mediate growth of coral reef macroalgae. Oikos e09716

Tait LW, Hawes I, Schiel DR (2014) Shining light on benthic macroalgae: Mechanisms of complementarity in layered macroalgal assemblages. PLoS One 9:1–19

Thion C, Prosser JI (2014) Differential response of nonadapted ammonia-oxidising archaea and bacteria to drying-rewetting stress. FEMS Microbiol Ecol 90:380–389

Titlyanov EA, Titlyanova T V., Xia B, Bartsch I (2016) Retrospective analysis of diversity and species composition of marine macroalgae of Hainan Island (China). Ocean Science Journal 51:485–506

Titlyanov EA, Titlyanova TV, Li X, Huang H (2017) Common marine algae of Hainan Island (Guidebook). Coral Reef Marine Plants of Hainan Island. Elsevier, pp 75–228

Trapon ML, Pratchett MS, Penin L (2011) Comparative effects of different disturbances in coral reef habitats in Moorea, French Polynesia. J Mar Biol 2011:1–11

Vitasse Y, Bottero A, Cailleret M, Bigler C, Fonti P, Gessler A, Lévesque M, Rohner B, Weber P, Rigling A, Wohlgemuth T (2019) Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob Chang Biol 25:3781–3792

Wichachucherd B, Prathep A, Zuccarello GC (2014) Phylogeography of *Padina boryana* (Dictyotales, Phaeophyceae) around the Thai-Malay Peninsula. Eur J Phycol 49:313–323

Williams GJ, Graham NAJ, Jouffray JB, Norström A V., Nyström M, Gove JM, Heenan A, Wedding LM (2019) Coral reef ecology in the Anthropocene. Funct Ecol 33:1014–1022

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. Biol Conserv 143:2280–2291

Zawada KJA, Madin JS, Baird AH, Bridge TCL, Dornelas M (2019) Morphological traits can track coral reef responses to the Anthropocene. Funct Ecol 33:962–975

Zhong ZH, Wang Y, Qin S, Zhuang LC, Li JJ, Song WL, Liu ZY (2021) Short-term photoacclimation and photoregulation strategies of *Sargassum horneri* in response to temperature and light. Photosynthetica 59:268–276