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UNIVERSITY OF CALIFORNIA

Los Angeles

Anthropogenic impacts on
top-down and bottom-up processes
affect coral reef resilience

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

by

Shayna Anne Sura

2021

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ABSTRACT OF THE DISSERTATION

Anthropogenic impacts on
top-down and bottom-up processes
affect coral reef resilience

by

Shayna Anne Sura

Doctor of Philosophy in Biology

University of California, Los Angeles, 2021

Professor Peggy Marie Fong, Chair

Coral reefs are among the most diverse ecosystems globally, yet many are experiencing anthropogenic disturbances leading to reef degradation. Resilience (defined as resistance to and recovery from disturbance) to disturbance influences whether reefs shift from coral-dominated to degraded algal-dominated states. Two ecological processes that support reef resilience are herbivory and nutrient limitation. Herbivory is a strong top-down control on reefs that can be reduced by overfishing. Nutrient limitation is a bottom-up process limiting growth of algae and increased anthropogenic nutrients can enhance growth and shift competitive outcomes toward algae. I address 1) the role of functional diversity of herbivorous fishes in coral reef resilience, and 2) how nutrient enrichment degrades reef resilience by changing growth and interactions among algae.

Using field experiments, I assessed the functional diversity of herbivorous fishes by examining their foraging behavior on macroalgae on a fringing reef in Moorea, French Polynesia. I found herbivorous fishes clustered into two groups based on their relative selectivity and these groups have greater functional redundancy than complementarity.

Functional diversity of herbivorous fishes has never been included in models of reef resilience and alternative stable states (ASS) despite empirical evidence of their importance in supporting reef resilience. When I incorporated herbivore functional groups into a coral reef model, I found herbivore community composition influences reef recovery and ASS. Specifically, browsers are better than grazers for promoting reef recovery. Also, ASS almost disappear for a browser-dominated community, while ASS are present even when there is no fishing pressure if the community is grazer-dominated. My findings highlight that including herbivorous fish functional groups into coral reef models is critical for recognizing complex interactions between human impacts and reef community compositions that support resilience or drive ASS of coral reefs.

Finally, I examined the effects of nutrient enrichment and macroalgal presence on algal turf growth over time. I uncovered a novel facilitative interaction where macroalgal presence increased algal turf height, which could promote shifts from short, healthy turfs to longer, less desirable turfs on coral reefs.

Overall, my dissertation quantifies resilience mechanisms and thus contributes to conserving healthy coral reefs into the future.

The dissertation of Shayna Anne Sura is approved.

Daniel T. Blumstein

James O. Lloyd-Smith

Deron Burkepile

Peggy Marie Fong, Committee Chair

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2021

DEDICATION

To my family, academic family, partner, and friends –
your love, support, and positivity made this possible.

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ACKNOWLEDGEMENTS

First, I want to acknowledge Peggy Fong for her belief in and support of my dream of becoming a marine ecologist. She helped make my dream a reality and taught me many valuable life lessons along the way. I am very grateful for her generosity, wisdom, and confidence boosts that made this possible.

I also want to thank the many Fong Lab members (past and present) I have had the pleasure to meet, know, and collaborate with during my time at UCLA. I could not have done this without your presence, support, feedback, creativity, commiseration, laughter, and joy over the past seven years!

I also want to recognize my family, my partner, my friends, and Clover for their endless encouragement through this journey, especially during the difficult times when you reminded me it was okay to struggle, but also helped nudge me forward.

Finally, I want to acknowledge my committee members, Jamie Lloyd-Smith, Dan Blumstein, and Deron Burkepille, for their advice, guidance, and support through this process and the twists and turns that arose along the way.

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 1144087. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation. My dissertation was also supported by the UC Office of the President Dissertation Year Fellowship.

Chapter 1 is a reprint of Sura SA, Molina NE, Blumstein D, & Fong P. (2021) Selective consumption of macroalgal species by herbivorous fishes suggests reduced functional complementarity on a fringing reef in Moorea, French Polynesia. *Journal of Experimental Marine Biology and Ecology*. 536: 151508. doi.org/10.1016/j.jembe.2020.151508

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Reprint Modifications:

- Journal article page numbers were removed to maintain page number consistency with the dissertation document.

Chapter 3 is reprinted by permission from Springer Nature Customer Service Centre GmbH: Springer Nature; Coral Reefs; Macroalgae and nutrients promote algal turf growth in the absence of herbivores; Sura SA, Delgadillo A, Franco N, Gu K, Turba R, & Fong P; 2019; 38: 425 – 429; doi:10.1007/s00338-019-01793-w

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- Nancy Franco contributed to the conceptualization, methodology, investigation, data curation, and writing (review and editing) of this work.
- Kelly Gu contributed to the conceptualization, methodology, investigation, data curation, and writing (review and editing) of this work.
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Reprint Modifications:

- Journal article page numbers were removed to maintain page number consistency with the dissertation document.

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Sura SA, Gehris C⁺, Liang M⁺, Lim A⁺, & Fong P. Timing of nutrient regimes and community composition influence growth and species-specific interactions of macroalgae. Ecological Society of America (ESA) 2020 Annual Meeting, virtual, August 3 – 6, 2020, poster presentation.

Sura SA, Fong P, & Lloyd-Smith JO. A functional group model demonstrates key herbivore guilds shape the resilience of coral reef ecosystems. Western Society of Naturalists 100th Annual Meeting, Ensenada, Mexico, October 31 – November 3, 2019, oral presentation.

Sura SA, Lloyd-Smith JO, & Fong P. Functional groups of herbivores and algae shape the resilience of coral reef ecosystems. Ecological Society of America (ESA) 2019 Annual Meeting, Louisville, KY, August 11 – 16, 2019, oral presentation.

Sura SA, Delgadillo A⁺, Franco N⁺, Gu K⁺, Turba R & Fong P. Macroalgae and nutrients promote algal turf growth in the absence of herbivores. 2018 Western Society of Naturalists Meeting, Tacoma, Washington, November 8 – 11, 2018, poster presentation.

Sura SA & Fong P. Herbivorous fish species differ in selectivities of macroalgae on a fringing reef in Mo'orea. 13th International Coral Reef Symposium, Honolulu, Hawaii, June 19 – 24, 2016, poster.

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CHAPTER 1:

SELECTIVE CONSUMPTION OF MACROALGAL SPECIES BY HERBIVOROUS FISHES SUGGESTS REDUCED FUNCTIONAL COMPLEMENTARITY ON A FRINGING REEF IN MOOREA, FRENCH POLYNESIA

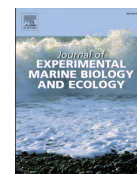
The following chapter is a reprint of

Sura SA, Molina NE, Blumstein D, & Fong P. (2021) Selective consumption of macroalgal species by herbivorous fishes suggests reduced functional complementarity on a fringing reef in Moorea, French Polynesia. *Journal of Experimental Marine Biology and Ecology*. 536: 151508. doi.org/10.1016/j.jembe.2020.151508.



Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Selective consumption of macroalgal species by herbivorous fishes suggests reduced functional complementarity on a fringing reef in Moorea, French Polynesia

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ARTICLE INFO

Keywords:

Functional redundancy
 Functional complementarity
 Herbivorous fishes
 Macroalgae
 Selectivity

ABSTRACT

Worldwide, many coral reefs are at risk of shifting to degraded algal-dominated states, due to compromised ecological conditions. Functional diversity of herbivorous fishes maintains coral reef health and promotes reef resilience to disturbances. Given previous evidence, it appears the functional roles of herbivorous fishes differ across geographical locations, indicating a need for further assessment of macroalgal consumption by herbivorous fishes. We assessed functional diversity by examining foraging behavior of herbivorous fish species on macroalgae on a fringing reef in Moorea, French Polynesia. We video-recorded choice experiments containing seven common macroalgae and used Strauss' linear resource selection index to determine macroalgal selectivities. We used cluster analysis to identify any distinct groups within herbivorous fish species, given the macroalgal species they targeted, and fitted generalized linear mixed-effects models to identify factors that best predicted the number of bites taken on macroalgae. Seven species from 3 fish families/tribes took a total of 956 bites. Fish species differed in their selectivity with some species (*Naso lituratus*, *N. unicornis*, *Calatomus carolinus*) strongly preferring one or two macroalgal species, while other fish species (*Acanthurus nigrofuscus*, *Ctenochaetus striatus*, *Chlorurus sordidus*, *Balistapus undulatus*) were less selective. This resulted in fish species forming two clusters. Only 3 of 7 macroalgae were preferred by any fish species, with two fish species both preferring the same two macroalgae. The limited differences in fish species' preferences for different macroalgae suggests limited functional complementarity. Two models (macroalgal species identity+fish functional group, macroalgal species identity+fish species) best predicted the number of bites taken on macroalgae compared to models incorporating only a single explanatory factor or fish family. In the context of this Moorean fringing reef, there is greater functional redundancy than complementarity of herbivorous fishes consuming macroalgae, and the fishes grouped together according to their relative selectivity. We observed fish species that are not classified as browsers consuming macroalgae, suggesting diets of herbivorous fishes may be broader than previously thought. Finally, we observed macroalgal selectivities and consumption that differed from previous studies for the same fish species. Our results contribute to the understanding of functional diversity of herbivorous fishes across coral reefs, and also highlight the need for additional research to further elucidate the role of context and functional diversity of herbivorous fishes consuming macroalgae on coral reefs.

1. Introduction

Coral reefs are one of the most diverse ecosystems on earth, yet many appear at risk of shifting from healthy, coral-dominated to degraded, algal-dominated states due to a combination of natural and anthropogenic disturbances (e.g., Hughes et al., 2010). Herbivorous fishes are critical for maintaining coral-dominated reefs because they consume

algae that compete with coral (e.g., Mumby et al., 2006; Hughes et al., 2007; Fong and Paul, 2011). Coral reefs contain a diversity of herbivorous fishes and algae, and herbivorous fishes can selectively forage on different algae (e.g., Mantyka and Bellwood, 2007a; Rasher et al., 2013; Humphries et al., 2015). Complementary foraging facilitates healthy coral reefs by reducing algal cover, biomass, and diversity while promoting coral survival and growth (Burkepile and Hay, 2008). On the

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<https://doi.org/10.1016/j.jembe.2020.151508>

Received 25 February 2020; Received in revised form 23 December 2020; Accepted 23 December 2020
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other hand, redundancy in herbivore foraging promotes coral reef resilience (Bellwood et al., 2004; Nash et al., 2016), which is the ability to resist and recover from phase shifts following disturbance (Holling, 1973; Hodgson et al., 2015). This is because functional redundancy safeguards functions even if some herbivore species are removed. It is important to assess the functional diversity of herbivorous fishes on coral reefs in order to understand the community's ability to promote a healthy coral reef.

To assess herbivore functional diversity on coral reefs, it is necessary to classify herbivorous fishes into groups at the appropriate resolution. Traditionally, herbivorous fishes were classified as grazers and browsers (e.g., Hiatt and Strasburg, 1960; Horn, 1989), referring to whether they consume crustose coralline algae (CCA) and turf algae (<2 cm height) versus macroalgae (>2 cm height, Littler and Littler, 2011a, 2011b), respectively. More recently Green and Bellwood (2009) defined four functional groups: 1) scrapers/small excavators, 2) large excavators/bioeroders, 3) grazers/detritivores, and 4) browsers. With either of these classifications, the functional group of browsers encompasses all herbivorous fishes that consume macroalgae. However, herbivory pressure can vary on different macroalgal species (e.g., Mantyka and Bellwood, 2007a, 2007b; Chan et al., 2012; Rasher et al., 2013; Humphries et al., 2015), on macroalgae of varying nutritional quality (e.g., Boyer et al., 2004; Fong et al., 2006; Chan et al., 2012; Bittick et al., 2016), and on macroalgal thalli of varying sizes (e.g., Hoey, 2010; Davis, 2018). In addition, individual species of herbivorous fishes can selectively forage on different macroalgal species (e.g., Mantyka and Bellwood, 2007a; Rasher et al., 2013; Humphries et al., 2015), among different parts of macroalgal thalli (Streit et al., 2015), and among macroalgal thalli of different heights (Hoey, 2010). This selective foraging on macroalgae can be attributed to the diversity of morphologies, chemical and physical defenses, and nutritional values of macroalgal species (e.g., Rasher et al., 2013). In addition, the size of macroalgal browser species can influence their selectivity of macroalgae (Feitosa and Ferreira, 2015; Duran et al., 2019). Thus classifying herbivorous fishes as browsers may be too coarse to capture the functional diversity of their foraging on macroalgae and further research may reveal the need for finer scale groupings (Mantyka and Bellwood, 2007a; Rasher et al., 2013).

Coral reefs around the world vary in the composition of their herbivorous fish and macroalgal communities, making it difficult to generalize information on the functional diversity of fishes across locations. The functional diversity of herbivorous fishes that consume macroalgae can vary with biogeographic location (e.g., Tebbett et al., 2019), seasons (e.g., Lefevre and Bellwood, 2011), reefs within a location (e.g., Bauman et al., 2017), reef habitat (e.g., Cvitanovic and Bellwood, 2009; Hoey and Bellwood, 2009), reef condition (e.g., Chong-Seng et al., 2014), macroalgal density (e.g., Bauman et al., 2019), and macroalgal height (e.g., Hoey, 2010), among others. Single-species

transplants of macroalgae can be used to assess the functional diversity of herbivorous fishes across various contexts (all above references except Tebbett et al., 2019). However, to assess the types of algae consumed by herbivorous fishes, studies often use multiple-species choice assays (e.g., Mantyka and Bellwood, 2007a, 2007b; Rasher et al., 2013; Humphries et al., 2015; Tebbett et al., 2019), focal fish follows (e.g., Fox et al., 2009; Adam et al., 2015, 2018; Kelly et al., 2016; Smith et al., 2018), or stomach content analyses (e.g., Choat et al., 2002; Hoey et al., 2013). When focusing on the types of algae consumed, the functional diversity of herbivorous fishes has been studied on coral reefs in the Great Barrier Reef (e.g., Mantyka and Bellwood, 2007a), the Caribbean (e.g., Adam et al., 2015), Kenya (Humphries et al., 2015), Fiji (Rasher et al., 2013), and the Hawaiian Islands (Kelly et al., 2016). The variation in herbivorous fish functional diversity across contexts, studies, and reefs indicates a continuing need to expand our understanding of the functional diversity of herbivorous fishes consuming macroalgae on coral reefs worldwide.

Our objective was to examine the functional diversity of herbivorous fish species in the context of their selectivity of macroalgae on a fringing reef in Moorea, French Polynesia. We had three questions:

- 1) What are the feeding selectivities of herbivorous fish species on macroalgae found on a fringing reef?
- 2) How do herbivorous fish species group together based upon their foraging on macroalgae?
- 3) What information (macroalgal species, herbivorous fish family, herbivorous fish species, functional group) best predicts the amount of foraging (number of bites) on macroalgae?

2. Methods

2.1. Macroalgal choice experiments

We examined the behavior of herbivorous fishes foraging on macroalgae on Taahiamanu Reef (17°29'17.68"S, 149°50'55.07"W), a fringing reef of Moorea, French Polynesia. Similar to previous studies (e.g., Mantyka and Bellwood, 2007a; Rasher et al., 2013; Humphries et al., 2015), we used videos to remove the effect of human observers (e.g., Nanninga et al., 2017) when examining fish foraging behavior. We deployed choice experiments consisting of seven common macroalgae that co-occur on fringing reefs and span a wide range of functional groups and palatabilities (Littler et al., 1983; Steneck and Dethier, 1994). Our macroalgae included *Padina boryana* Thivy, *Dictyota* sp. J.V. Lamouroux, *Acanthophora spicifera* (M. Vahl) Børgesen, *Sargassum mangarevense* (Grunow) Setchell, *Turbinaria ornata* (Turner) J. Agardh, *Galaxaura* sp. J.V. Lamouroux, and *Halimeda* sp. J.V. Lamouroux. We used "proportional-sized" choices, following the methods of Mantyka

Table 1

The fish species taking bites on macroalgae and the number of fish visits (replicates) per fish species.

| Fish Species (common name) | Fish Family (Tribe) | Functional Group | Fish Visits | Total Bites |
|---|---------------------|-------------------------|-------------|-------------|
| <i>Balistapus undulatus</i> Park (Orange-lined triggerfish) | Balistidae | N/A | 31 | 113 |
| <i>Acanthurus nigrofuscus</i> Forsskål (Brown surgeonfish) | Acanthuridae | Grazer/detritivore | 17 | 92 |
| <i>Ctenochaetus striatus</i> Quoy & Gaimard (Striped bristletooth) | Acanthuridae | Grazer/detritivore | 9 | 33 |
| <i>Naso lituratus</i> Forster (Orangespine unicornfish) | Acanthuridae | Browser | 73 | 397 |
| <i>Naso unicornis</i> Forsskål (Bluespine unicornfish) | Acanthuridae | Browser | 11 | 57 |
| <i>Calotomus carolinus</i> Valenciennes (Stareye parrotfish) | Labridae (Scarinae) | Browser | 56 | 222 |
| <i>Chlorurus sordidus</i> Forsskål (Bullethead parrotfish) | Labridae (Scarinae) | Scraper/small excavator | 4 | 42 |

We classified our fish species into functional groups based upon Green and Bellwood (2009).

and Bellwood (2007a), by visually standardizing intraspecific macroalgal volume to reflect individual species' natural sizes and growth forms. We measured initial and final wet weights (biomass) to calculate percent change in biomass (see 2.2.1 below) and for use in the selectivity index (see 2.2.2 below).

We collected macroalgae from Taahiamanu Reef two days before deployment and stored them in flow through water tables. We constructed the experimental units the afternoon prior to deployment. Choice experiments ($n = 6$ per day) and caged controls ($n = 3$ per day) were deployed >5 m apart at Taahiamanu Reef on June 24 and 26, 2015 from approximately 0900 to 1400 h. We deployed GoPro Hero3 video cameras approximately 0.7 m from each experimental unit. A scale bar was included at the beginning of each recording to estimate fish sizes. One camera malfunctioned on June 24, so $n = 11$ experimental deployments.

We defined a fish visit as the interval between when a fish entered and left the video frame. Because fish may have left and then re-entered the frame, we cannot know if a fish visit represents a unique individual. For fish that took bites on at least one macroalga, we recorded fish species, size (5 cm size classes), and number of bites on each macroalga. We excluded data from the first 10 min after deployment to limit disturbance to behavior by our presence. Following the methods of Mantyka and Bellwood (2007a), we stopped recording data once any macroalgal species was too small to be visually detected in the videos. We analyzed approximately 50 h of videos. We had limited sample sizes for some observed fish species (Table 1). While we recognize these sample sizes are low, we used all species in our analysis to expand our ability to compare our work with previous studies. However, for transparency, sample sizes are reported for each species (Table 1).

2.2. Statistical analyses

2.2.1. Loss of macroalgal biomass

We used initial and final wet weights (biomass) to calculate percent change in biomass ($\text{final} - \text{initial} / \text{initial} * 100$) of each macroalga for each choice experiment and calculated the mean \pm SE across choice experiments ($n = 11$). We used caged controls to account for handling losses and macroalgal growth. We adjusted percent change in biomasses for experimental macroalgae by subtracting the average percent change in biomass calculated from caged controls. A thalli of *T. ornata* was lost during recovery for one choice experiment, resulting in $n = 10$ for *T. ornata* change in biomass.

2.2.2. Selectivity

Previous studies assessing the foraging behavior of herbivorous fishes used several metrics and indices with no apparent standardized measure to quantify foraging behavior (e.g., Mantyka and Bellwood, 2007a; Rasher et al., 2013; Adam et al., 2015; Humphries et al., 2015; Kelly et al., 2016; Adam et al., 2018; Burkepille et al., 2019; Smith et al., 2018). Strauss' linear resource selection index (Strauss, 1979) and Manly's alpha electivity index (Manly et al., 1972; Chesson, 1978; Chesson, 1983) are commonly used indices. However, Manly's alpha electivity index assumes food resources are not being depleted during the time of observation and is often used when following herbivores and observing their foraging behavior on natural substrates. Because we used choice experiments, the macroalgae were only available in limited quantities and, thus, could be depleted. Therefore, we used Strauss' linear resource selection index (Strauss, 1979) to determine selectivity of macroalgae because it does not rely on the assumption of unlimited resources. Strauss' selection indices (L) were calculated as

$$L = r_i - p_i$$

where i is the focal macroalgal species, r_i is the proportion of the number of bites taken on that macroalgal species out of all macroalgal species during a fish visit, and p_i is the proportion of initial biomass available for

that macroalgal species out of the total biomass available across all macroalgal species. We calculated L for each macroalgal species bitten during each fish visit. Then across all fish visits per fish species, we calculated the mean L and corresponding 95% confidence intervals (CI) for each macroalga for each fish species. Selectivity preference (positive) and avoidance (negative) of a macroalgal species by a fish species were indicated by 95% CI that did not overlap zero.

2.2.3. Similarities of macroalgal selectivities

To determine the similarities of our fish species based upon their macroalgal selectivities, we performed a cluster analysis on the mean L values calculated for each fish species on each macroalgal species. Thus, fish species within a cluster exhibit similar macroalgal selectivities, while different clusters of fishes exhibit distinct macroalgal selectivities. We used R 4.0.2 and RStudio (RStudio Team, 2016; R Core Team, 2016) and the 'hclust' function from the 'dendextend' package (Galili, 2015) to determine the clustering of fish species based upon their macroalgal selectivities.

2.2.4. Bite model

We compared generalized linear mixed-effects models (GLMMs) for bites to determine what information best predicted the number of bites taken on macroalgae. Our response variable was number of bites per fish visit, and because our bite data were overdispersed (variance greater than the mean), we fit our models using a negative binomial distribution. Also, we included fish visit ($N = 201$) as a random effect to account for individual variation.

Our predictor variables included macroalgal species, fish family, fish species, and fish functional group. We excluded fish size from the analyses because fish species strongly predicted fish size (ANOVA $F_{6,1400} = 1272, p < 0.0001$). We classified herbivorous fishes into four functional groups (Green and Bellwood, 2009): 1) scrapers/small excavators, which are small (<35 cm standard length) parrotfishes that consume turf algae and scrape the substrate; 2) large excavators/bioeroders, which are large (≥ 35 cm standard length) parrotfishes that contribute to bioerosion through their excavating bites; 3) grazers/detritivores, which consume turf algae and/or associated detritus but do not scrape or excavate the substrate; and 4) browsers, which consume macroalgae.

Because fish species, fish family, and fish functional group were all nested together, none of these predictor variables were included in the same model. Our data were insufficient to fit interaction terms, so we

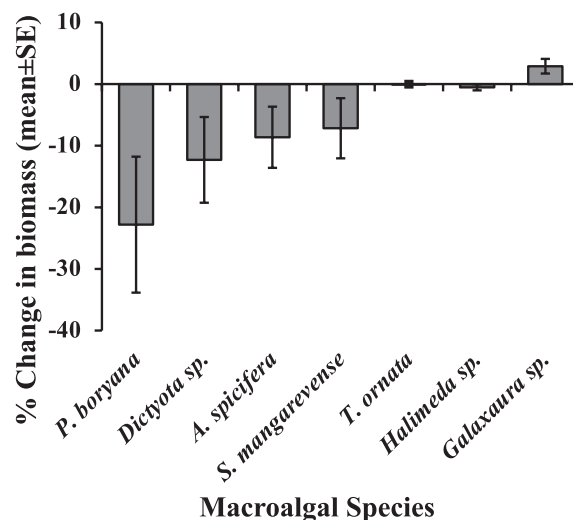


Fig. 1. Percent change in biomass (mean \pm SE) for each macroalgal species presented in choice assays ($n = 11$).

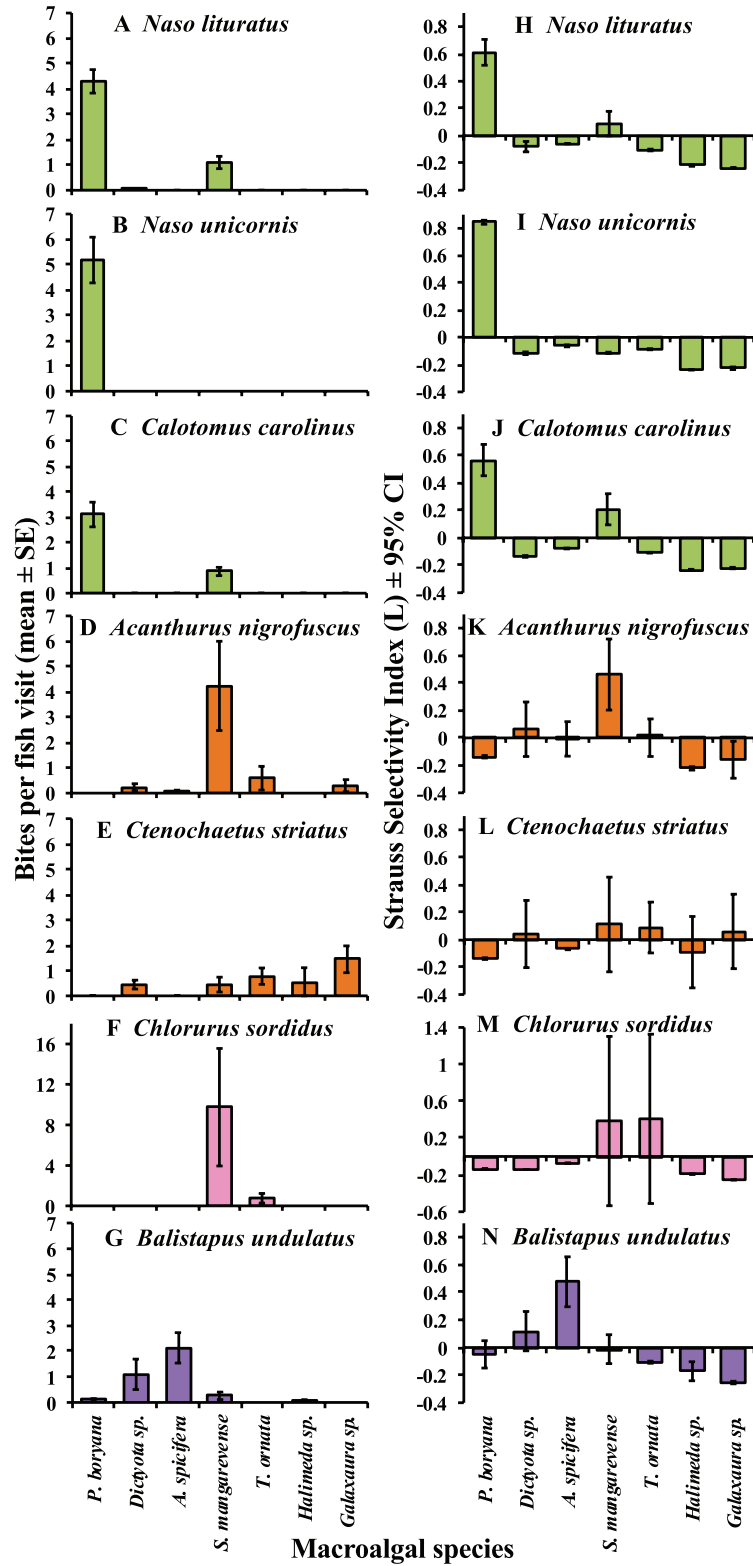


Fig. 2. Bites per fish visit (mean ± SE, column 1) and Strauss selectivity index values (±95% CI, column 2) for fish species taking bites on macroalgal choice experiments. Macroalgae are presented in order of increasing complexity and defenses against herbivory, according to [Steneck and Dethier \(1994\)](#). Fish species are color coded according to their functional group based on [Green and Bellwood \(2009\)](#): green = browser, orange = grazer/detritivore, pink = scraper/small excavator, and purple = unclassified. Note: panels F and M are on different scales than the rest. Sample sizes are the following: *Naso lituratus* n = 73, *Naso unicornis* n = 11, *Calotomus carolinus* n = 56, *Acanthurus nigrofuscus* n = 17, *Ctenochaetus striatus* n = 9, *Chlorurus sordidus* n = 4, *Balistapus undulatus* n = 31. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

compared seven main effects models to determine which variables best predicted the number of bites taken on macroalgae. Specifically, we tested models including (1) macroalgal species, (2) fish species, (3) fish family, (4) fish functional group, (5) macroalgal species + fish species, (6) macroalgal species + fish family, and (7) macroalgal species + fish functional group.

We compared Akaike Information Criterion scores corrected for small samples sizes (AICc) and AICc weights between the models to determine which information is most important (macroalgal species, fish species, fish family, or fish functional group) to predict the number of bites taken on macroalgae. To compare our models, we used differences in AICc scores (ΔAICc), where the lowest calculated value is 0. Models with ΔAICc in the range of 2–7 have support (Burnham et al., 2011), so we used a more conservative value of $\Delta\text{AICc} > 4$ (e.g. Bittick et al., 2018) and the AICc weights to indicate differences between models. We used R 4.0.2 and RStudio (RStudio Team, 2016; R Core Team, 2016) and the `glmer.nb` function with the ‘bobyqa’ optimizer from the ‘lme4’ package (Bates et al., 2015) to fit our models. We used the `aictab` function from the ‘AICcmodavg’ package (Mazerolle, 2020) to calculate AICc, ΔAICc , and AICc weights for our models. We used the `r.squaredGLMM` function from the ‘MuMIn’ package (Bartoń, 2019) to determine conditional R^2 values using the delta method (Nakagawa and Schielzeth, 2013; Nakagawa et al., 2017) for each of our models.

3. Results

We observed 7 species from 3 fish families/tribes taking a total of 956 bites on the presented macroalgae (Table 1). The number of fish visits per species varied greatly.

3.1. Loss of macroalgal biomass

Four macroalgae (*Padina boryana*, *Dictyota sp.*, *Acanthophora spicifera*, and *Sargassum mangarevense*, in rank order of greatest to least loss) lost biomass due to herbivory during our choice experiments (Fig. 1).

3.2. Bites and selectivity

Fish species differed in how many bites per visit they took on each macroalga (Fig. 2A–G); this resulted in differences in their selectivity of macroalgae (Fig. 2H–N). Two acanthurids, both in the genus *Naso* (*N. lituratus* and *N. unicornis*), took many bites on (Fig. 2A,B) and strongly preferred *P. boryana* (Fig. 2H,I) and avoided almost all other macroalgae. The exception was that *N. lituratus* bit *S. mangarevense* (Fig. 2A), although this did not result in a strong preference (Fig. 2H). One of the two Labridae (tribe Scarinae) species we observed, *Calatomus carolinus*, only took bites on (Fig. 2C) and preferred (Fig. 2J) *P. boryana* and *S. mangarevense* and avoided all other macroalgae. In comparison, two of the other acanthurids, *Ctenochaetus striatus* and *Acanthurus nigrofuscus*, were less selective as they bit many macroalgal species (Fig. 2D,E) and they did not exhibit preference or avoidance for at least 3 macroalgae (Fig. 2K,L). *C. striatus* was the least selective in that it did not prefer any macroalgae and avoided two macroalgae: *P. boryana* and *Acanthophora spicifera* (Fig. 2L). Slightly more selective in its foraging, *A. nigrofuscus* preferred *S. mangarevense* and avoided three macroalgae (*P. boryana*, *Halimeda sp.*, *Galaxaura sp.*) while neither preferring nor avoiding the remaining macroalgal species (Fig. 2K). For the other Labridae (tribe Scarinae) species, *Chlorurus sordidus*, we observed very few fish visits ($n = 4$), so the calculated selectivity indices were highly variable (Fig. 2M). However, *C. sordidus* was only observed to bite *S. mangarevense* and *Turbinaria ornata* (Fig. 2F). One triggerfish (Balistidae) species, *Balistapus undulatus*, took bites on five of the seven macroalgae (Fig. 2G); however, it only preferred one species: *A. spicifera* (Fig. 2N).

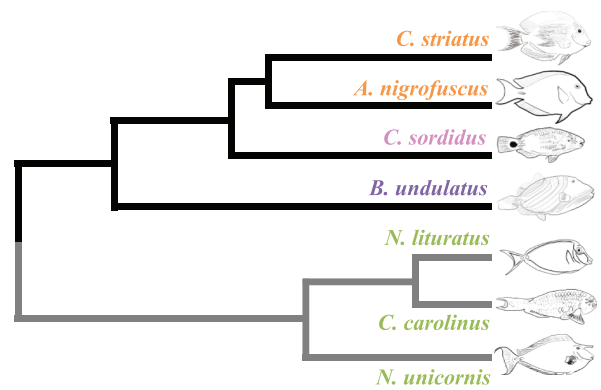


Fig. 3. Clusters of fish species based upon their Strauss' selectivity indices for macroalgae presented in choice experiments. Black versus gray lines indicate which fish species group together into each cluster. Fish species names are color coded according to their functional group based on Green and Bellwood (2009): orange = grazer/detritivore, pink = scraper/small excavator, purple = unclassified, and green = browser. Fish drawings provided by Nury Molina. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Similarities of macroalgal Selectivities

Cluster analyses indicated our herbivorous fish community was made up of two groups (Fig. 3). One group contained three species (*N. lituratus*, *N. unicornis*, and *C. carolinus*) that exhibited strong selectivity for at least one macroalga. They primarily consumed *P. boryana* and sometimes *S. mangarevense*, but avoided all other macroalgal species. In comparison, the second group contained four species (*C. striatus*, *A. nigrofuscus*, *C. sordidus*, and *B. undulatus*) that were less selective when biting macroalgae; they bit a variety of macroalgal species with minimal preferences or avoidances. The only observed preferences for these four fishes were *A. nigrofuscus* preferring *S. mangarevense*, and the triggerfish, *B. undulatus*, preferring *A. spicifera*.

3.4. Bite model

Comparison of our bite models using AICc scores and weights indicated two models best predicted the number of bites taken on macroalgae ($\Delta\text{AICc} < 4$, Table 2). Specifically, models incorporating macroalgal species identity and either fish species or fish functional group are better predictors than models incorporating fish family and

Table 2

We used ΔAICc scores and weights to evaluate which GLMM best predicted the number of bites fish took on macroalgae.

| Model Formulation | R^2 | K | AICc | ΔAICc | AICc Weight |
|--|-------|----|--------|---------------------|-------------|
| Number of Bites ~ Macroalgae + Fish Species | 0.422 | 15 | 2036.3 | 0 | 0.8 |
| Number of Bites ~ Macroalgae + Fish Functional Group | 0.403 | 12 | 2039.0 | 2.7 | 0.2 |
| Number of Bites ~ Macroalgae + Fish Family | 0.325 | 11 | 2094.6 | 58.3 | 0.0 |
| Number of Bites ~ Macroalgae | 0.306 | 9 | 2116.4 | 80.0 | 0.0 |
| Number of Bites ~ Fish Family | 0.001 | 5 | 2365.0 | 328.7 | 0.0 |
| Number of Bites ~ Fish Functional Group | 0.002 | 6 | 2366.0 | 329.7 | 0.0 |
| Number of Bites ~ Fish Species | 0.003 | 9 | 2369.9 | 333.6 | 0.0 |

Fish functional group refers to the classifications according to Green and Bellwood (2009). All models were fitted with a negative binomial distribution and included fish visit as a random effect. Presented are conditional R^2 values calculated using the delta method (Nakagawa et al., 2017).

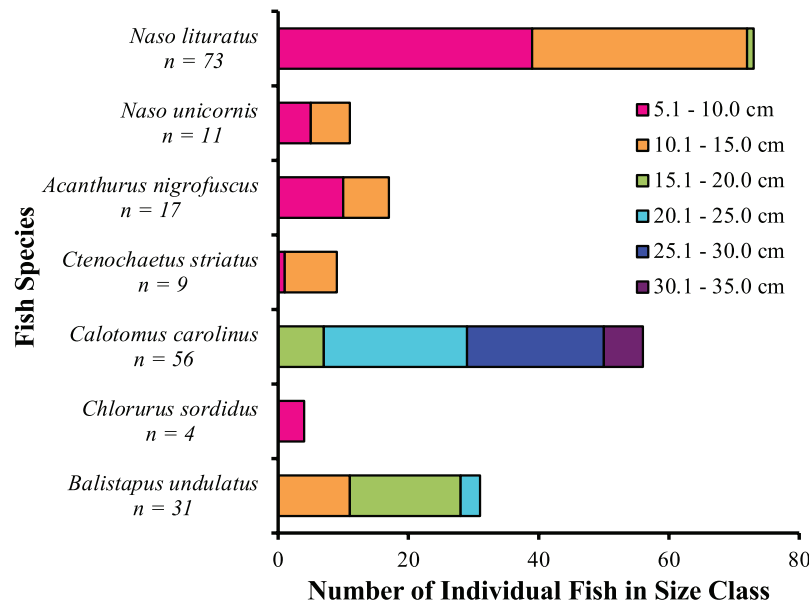


Fig. 4. Number of individual fish of each fish species within different size classes. Total number of fish visits for each species is indicated below their name.

macroalgal species identity or any of the variables by themselves (Table 2, Table S1).

3.5. Fish sizes

We primarily observed small fishes (<15 cm) taking bites on this fringing reef, although we did observe larger *C. carolinus* (Scarinae) individuals taking bites (Fig. 4). All *C. sordidus* were < 10 cm and almost all *N. unicornis* and *N. lituratus* were < 15.1 cm, with approximately half of them <10.1 cm (Fig. 4).

4. Discussion

In the context of this fringing reef in Moorea, we found the fish community has greater functional redundancy than complementarity in terms of their selectivity of macroalgae. There was high functional redundancy for two species of macroalgae (*Padina boryana* and *Sargassum mangarevense*) because they were preferred by multiple fish species. *Acanthophora spicifera* was the only other macroalga preferred by any fish species, but since it was only preferred by one fish, the triggerfish *Balistapus undulatus*, this suggests limited functional redundancy for this macroalga. Our results suggest some functional complementarity in macroalgal selectivity as three macroalgae were preferred, with some differences in the fishes preferring them. However, complementarity in terms of macroalgal selectivity on this reef appears limited since four macroalgae were never preferred. Our results are consistent with previous studies in terms of finding functional redundancy for some macroalgae (e.g., Mantyka and Bellwood, 2007a; Rasher et al., 2013; Humphries et al., 2015). However, these previous studies often found stronger functional complementarity among herbivorous fishes consuming macroalgae than we observed. The implication of functional redundancy on this Moorean reef is that herbivory on these macroalgae should be maintained after disturbances, as long as the redundant fishes exhibit response diversity to disturbances (e.g., Elmqvist et al., 2003; Bellwood et al., 2004; Nash et al., 2016). However, the limited functional complementarity suggests some functional roles are not filled by the resident fish community, which may have negative effects on this fringing coral reef (e.g., Burkepile and Hay, 2008).

The functional redundancy and complementarity we observed may be specific to the temporal, spatial, and resource availability context of our experiment. Among other factors, foraging preferences can vary depending upon which resources are available (e.g., Hanmer et al., 2017). For example, the parrotfish, *C. carolinus*, preferred *P. boryana* and *S. mangarevense*, while avoiding *T. ornata* in Moorea. However, when *P. boryana* and *S. mangarevense* were not options, this parrotfish strongly preferred *Turbinaria sp.* in Hawai'i (Kelly et al., 2016). Therefore, it is possible the fishes we observed as redundant could exhibit complementary foraging when a different number or composition of macroalgae is presented. Overall, although this is the first assessment of herbivorous fish functional diversity in terms of their macroalgal selectivity on coral reefs in Moorea, French Polynesia, additional research is necessary to further elucidate the functional diversity of Moorean herbivorous fishes in other contexts.

We did not find support for finer scale divisions for macroalgal selectivity within the broad grouping of browsers on this Moorean fringing reef. Herbivorous fishes grouped together according to their relative selectivity, with one group highly selective, albeit of the same macroalga, while the other group was less selective, eating several species of macroalgae. Our finding for this Moorean fringing reef contrasts with previous studies in Fiji (Rasher et al., 2013), Kenya (Humphries et al., 2015), and the GBR (Mantyka and Bellwood, 2007a) that observed herbivorous fishes were functionally complementary because each selected a different macroalga, or different taxonomic group of macroalgae (e.g., reds, greens, or browns). However, our two clusters reflect previous functional groups, as the fishes within our more selective cluster are usually classified as browsers (Green and Bellwood, 2009). They exhibited high redundancy in their preference of *P. boryana* and limited complementarity in consuming other macroalgae. In comparison, the fishes within our less selective cluster encompass multiple other functional groups and primarily consumed macroalgae other than *P. boryana*. *Padina boryana* is one of the most abundant macroalgae on this fringing reef (Johnson et al., 2018) and another fringing reef in Moorea (Fong and Fong, 2014). Thus, our clusters of herbivorous fishes on this fringing reef suggest high redundancy within browsers in terms of consuming one of the most abundant macroalgae, while there appears to be complementarity within herbivorous fishes more broadly as the

Table 3
Fish species observed in this study and macroalgae they took bites on from this and previous studies.

| Fish Species | Location | Sources | Methods | Macroalgae consumed |
|-------------------------------|----------------------------------|---|-------------------------|---|
| <i>Acanthurus nigrofuscus</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Dictyota</i> sp., <i>Acanthophora spicifera</i> , <i>Sargassum mangarevense</i> , <i>Turbinaria ornata</i> , <i>Galaxaura</i> sp. |
| | GBR | Hoey and Bellwood, 2009, Graba-Landry et al., 2020 | Single-species assays | <i>Sargassum swartzii</i> *, <i>Sargassum</i> sp.* |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | <i>Sargassum</i> sp. *, <i>Turbinaria</i> sp. *, <i>Acanthophora</i> sp. *, <i>Galaxaura</i> sp. *, <i>Laurencia</i> sp. |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | <i>Amansia</i> sp., <i>Asparagopsis</i> sp., <i>Tricleocarpa</i> sp., <i>Turbinaria</i> sp.* |
| <i>Balistapus undulatus</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Padina boryana</i> , <i>Dictyota</i> sp., <i>Acanthophora spicifera</i> , <i>Sargassum mangarevense</i> , <i>Halimeda</i> sp. |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | <i>Padina boryana</i> * |
| <i>Calatomus carolinus</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Padina boryana</i> , <i>Sargassum mangarevense</i> |
| | GBR | Hoey and Bellwood, 2009 | Single-species assays | <i>Sargassum swartzii</i> * |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | <i>Sargassum</i> sp. *, <i>Halimeda</i> sp. |
| | Kenya | Humphries et al., 2015 | Multiple-species assays | <i>Padina</i> sp.* |
| | Indonesia | Plass-Johnson et al., 2015 | Single-species assays | <i>Padina pavonica</i> * |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | <i>Amansia</i> sp., <i>Tolypocladia</i> sp., <i>Turbinaria</i> sp. |
| <i>Chlorurus sordidus</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Sargassum mangarevense</i> , <i>Turbinaria ornata</i> |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | <i>Padina boryana</i> |
| | GBR | Hoey and Bellwood, 2009 | Single-species assays | <i>Sargassum swartzii</i> * |
| | GBR | Bennett and Bellwood, 2011 | Single-species assays | <i>Sargassum myriocystum</i> * |
| | Ningaloo Reef, Western Australia | Vergés et al., 2012, Michael et al., 2013 | Single-species assays | <i>Sargassum myriocystum</i> * |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | <i>Sargassum polycystum</i> *, <i>Galaxaura filamentosa</i> , <i>Amphiroa crassa</i> , substrate |
| | Seychelles, West Indian Ocean | Chong-Seng et al., 2014 | Single-species assays | <i>Sargassum</i> sp.* |
| <i>Ctenochaetus striatus</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Dictyota</i> sp., <i>Sargassum mangarevense</i> , <i>Turbinaria ornata</i> , <i>Halimeda</i> sp., <i>Galaxaura</i> sp. |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | <i>Padina boryana</i> |
| | GBR | Hoey and Bellwood, 2009, Graba-Landry et al., 2020 | Single-species assays | <i>Sargassum swartzii</i> *, <i>Sargassum</i> sp.* |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | <i>Sargassum</i> sp. *, <i>Turbinaria</i> sp. *, <i>Acanthophora</i> sp., <i>Halimeda</i> sp. *, <i>Galaxaura</i> sp. *, <i>Laurencia</i> sp. |
| | Ningaloo Reef, Western Australia | Michael et al., 2013 | Single-species assays | <i>Sargassum myriocystum</i> * |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | None - fed on substrate |
| | Kenya | Humphries et al., 2015 | Multiple-species assays | <i>Cystoseira</i> sp., <i>Dictyota</i> sp. *, <i>Hypnea</i> sp., and <i>Padina</i> sp. |
| <i>Naso lituratus</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Padina boryana</i> , <i>Dictyota</i> sp., <i>Sargassum mangarevense</i> |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | <i>Padina boryana</i> * |
| | Ningaloo Reef, Western Australia | Vergés et al., 2012, Michael et al., 2013 | Single-species assays | <i>Sargassum myriocystum</i> * |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | <i>Sargassum polycystum</i> *, <i>Turbinaria conoides</i> , <i>Padina boryana</i> *, <i>Dictyota bartayresiana</i> * |
| | Indonesia | Plass-Johnson et al., 2015 | Single-species assays | <i>Sargassum</i> sp. *, <i>Padina pavonica</i> * |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | <i>Amansia</i> sp., <i>Dictyota</i> sp. *, <i>Laurencia</i> sp., <i>Tolypocladia</i> sp., <i>Turbinaria</i> sp. |
| <i>Naso unicornis</i> | Moorea, French Polynesia | This study | Multiple-species assays | <i>Padina boryana</i> |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | <i>Padina boryana</i> * |
| | GBR | Choat et al., 2002 | Stomach contents | <i>Dictyota</i> sp., <i>Turbinaria</i> sp. specified in text, otherwise macroalgal genera not specified. |
| | GBR | Hoey, 2010, Streit et al., 2015, Puk et al., 2016 - Review, Graba-Landry et al., 2020 | Single-species assays | <i>Sargassum</i> sp. |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | <i>Sargassum</i> sp., <i>Turbinaria</i> sp., <i>Acanthophora</i> sp., <i>Galaxaura</i> sp., <i>Laurencia</i> sp., <i>Halimeda</i> sp. |

(continued on next page)

Table 3 (continued)

| Fish Species | Location | Sources | Methods | Macroalgae consumed |
|--------------|-------------------------------------|----------------------------|-----------------------------|--|
| | Ningaloo Reef, Western Australia | Puk et al., 2016 - Review | Single-species assays | <i>Sargassum myriocystum</i> |
| | Fiji | Rasher et al., 2013 | Multiple- species assays | <i>Sargassum polycystum</i> , <i>Turbinaria conoides</i> , <i>Padina boryana</i> *, <i>Dictyota bartayresiana</i> |
| | Kenya | Humphries et al., 2015 | Multiple- species assays | <i>Sargassum sp.</i> |
| | Seychelles, West Indian Ocean | Chong-Seng et al., 2014 | Single-species assays | <i>Sargassum sp.</i> |
| | Indonesia | Plass-Johnson et al., 2015 | Single-species assays | <i>Sargassum sp.</i> , <i>Padina pavonica</i> * |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | <i>Amansia sp.</i> , <i>Chondrophycus sp.</i> , <i>Laurencia sp.</i> , <i>Pterocladiaella sp.</i> , <i>Tolypiocladia sp.</i> , <i>Tricleocarpa sp.</i> , <i>Turbinaria sp.</i> |

We included studies if 1) they observed at least one of the fish species from our study, 2) they included at least one of the macroalgae in our study as an option, and 3) they identified macroalgae to at least the genus level. We used an asterisk (*) to indicate macroalgae consumed in previous studies that coincide with macroalgae consumed in this study for each fish species.

second cluster of fishes provides supplemental removal of macroalgae other than *P. boryana*. Overall, the current classification scheme of grouping all browsers together appears sufficient in the context of this fringing reef in Moorea.

Fishes other than known herbivores may also play important roles in macroalgal removal on coral reefs. Triggerfishes are not considered herbivorous fishes, and they are not classified into one of the herbivorous fish functional groups since their trophic status has not been confirmed (Green and Bellwood, 2009). However, we observed the triggerfish, *B. undulatus*, taking bites on multiple species of macroalgae and preferring one macroalga. Recently, Tebbett et al. (2019) also found a triggerfish species (*Melichthys niger*) to be the dominant remover of macroalgal biomass on Caribbean reefs. More research is needed to understand the roles of additional fish species in macroalgal removal on coral reefs.

We observed macroalgal selectivities that differed from herbivorous fishes in Hawai'i. In Hawai'i, *N. unicornis* strongly preferred *Turbinaria sp.* while *N. lituratus* preferred *Dictyota sp.* (Kelly et al., 2016). In contrast, even though we offered both *Turbinaria sp.* (*T. ornata*) and *Dictyota sp.*, both *Naso sp.* avoided these two macroalgae in Moorea. The grazer *A. nigrofuscus* preferred *S. mangarevense* in Moorea, while they preferred a different macroalga, *Asparagopsis sp.*, in Hawai'i (Kelly et al., 2016). Also, as stated earlier, the parrotfish, *C. carolinus*, preferred different macroalgae between Hawai'i and Moorea. Although we had some overlap with Kelly et al. (2016) in which macroalgae were available as options, the differences in which macroalgae were available between studies may explain the observed differences in macroalgal selectivities for these fish species (e.g., Hanmer et al., 2017). Kelly et al. (2016) is the only previous study to report macroalgal selectivities for the same fishes we observed. Further research assessing variation in resource availability will help improve our understanding of foraging preferences of herbivorous fishes.

We also observed differences in which macroalgae our observed fishes took bites on in Moorea versus other locations (for a complete list see Table 3). Both *Naso sp.* are some of the only fishes found to directly consume *Turbinaria sp.* in other studies, but neither species took bites on *T. ornata* in our study. Also, both *Naso sp.* predominantly consume brown macroalgae across locations; however, they also consumed red macroalgae in Hawai'i (both species) and in the GBR (*N. unicornis* only, Table 3), but did not in our study. Similarly, *C. carolinus* often consumes the brown macroalgae, *Padina sp.* and *Sargassum sp.*, as we found in our study, although, additionally, they consumed one green and two red macroalgae in GBR and Hawai'i, respectively. The detritivore *Ctenochaetus striatus* often consumes a diversity of macroalgae, including on this fringing reef in Moorea, whereas, in Fiji, *C. striatus* only took bites on the substrate (Rasher et al., 2013, Table 3). Although these coral reefs overlap in some species of fishes and macroalgae, herbivorous fishes exhibited differences in the macroalgae they consume. Our results

support Tebbett et al. (2019) that assuming the functional roles of herbivorous fishes based upon previous work done in other reef systems may prove incorrect.

Study context, macroalgal characteristics, and fish size may help explain differences between studies. As previously stated, the functional diversity of herbivorous fishes consuming macroalgae can vary depending on the spatial, temporal, and resource availability contexts of studies (e.g., Lefèvre and Bellwood, 2011; Bauman et al., 2017; Hanmer et al., 2017). Therefore, the specific macroalgae that fishes took bites on in various locations may relate to what options were available. Also, macroalgae are diverse in their morphologies, chemical and physical defenses, and nutritional content (e.g., Paul and Hay, 1986; Steneck and Dethier, 1994; Pereira and da Gama, 2008; Fong and Paul, 2011). Inter- and intraspecific variation in these characteristics between studies and locations likely influenced selectivity and consumption of macroalgae by fishes. Finally, recent studies found diet varied with fish size for herbivorous parrotfishes (e.g., Feitosa and Ferreira, 2015; Adam et al., 2018; Smith et al., 2018) and surgeonfishes (Duran et al., 2019). However, these studies do not include any of the fish species we observed, and we could not test the role of size in fish foraging behavior within our study. Overall, our results identify the need for future studies that explore the relationships between fish size, macroalgal selectivity, macroalgal consumption, functional diversity, and algal biomass removal. This research will fill a critical knowledge gap for many herbivorous fish species that are common on coral reefs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the government of French Polynesia for providing research permission via our Protocol and the UC Berkeley Richard B. Gump South Pacific Research Station and staff for providing laboratory space and housing. We thank the UC-HBCU Diversity Project for the opportunity to conduct this research in Moorea, French Polynesia. We would like to thank Andy Brooks for his assistance with fish identifications. We are thankful to Yara Alshwairikh and Daniel Sanford for their time and effort with the many hours of videos, decalcification and grinding of macroalgal samples. We also thank three anonymous reviewers for constructive comments on a previous version.

This work was supported by the National Science Foundation Graduate Research Fellowship Program (Sura) under Grant No. 1144087 and the UC Office of the President Dissertation Year Fellowship (Sura).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2020.151508>.

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CHAPTER 2:

FUNCTIONAL GROUPS OF HERBIVORES SHAPE THE RESILIENCE OF CORAL REEFS

2.1 Abstract

Communities globally are shifting to degraded states, motivating research into attributes supporting resilience or leading to alternative stable states (ASS). Empirical studies demonstrate that functionally-diverse herbivorous fish communities support coral reef resilience; however, herbivore functional groups have not previously been included in coral reef models. We incorporated herbivore functional groups into a coral reef model and quantified their effects on reef resilience and ASS. We found herbivore community composition (relative abundance of grazers, browsers, and generalists) influences reef recovery following disturbance, with evenness becoming increasingly important as fishing pressure increases. The interaction between herbivore community composition and fishing pressure on reef recovery is further modulated by benthic algal community composition (relative amounts of turf and macroalgae), with recovery more likely when initial abundance of turf is greater than macroalgae. Finally, herbivore community composition influences the range of fishing pressures at which ASS occurs. ASS almost disappears for a browser-dominated community; but, for a grazer-dominated community ASS remains present even when there is no fishing pressure. Overall, our findings highlight that including functional groups of herbivorous fishes into coral reef models is a critical step in understanding and predicting coral reef resilience and ASS in the Anthropocene.

2.2 Introduction

As anthropogenic disturbances continue to affect virtually every ecosystem globally (e.g., Vitousek et al. 1997, Halpern et al. 2008, Ellis 2011, Sasaki et al. 2015), it is increasingly critical to understand attributes supporting community resilience. Coral reefs are among the most diverse ecosystems on earth, yet many experience coupled natural and anthropogenic disturbances leading to degradation (e.g., Lessios et al. 1983, Done 1992, Hughes et al. 2010, Graham et al. 2015, Harborne et al. 2017, Hughes et al. 2017). The prevalence of phase shifts to degraded states has spurred much research into disturbances affecting coral reefs (e.g., Harborne et al. 2017) and attributes that govern their resilience. Functional diversity of herbivorous fishes is one attribute long recognized as essential in maintaining reef resilience (e.g., Bellwood et al. 2004). In general, herbivorous fishes promote healthy coral reefs because they consume algae that compete with coral (Lewis 1986, Hughes et al. 2007, Fong and Paul 2011). However, fishing is a significant and pervasive disturbance affecting coral reefs, leading to reduced biomass and functional diversity of herbivorous fishes (e.g., Lokrantz et al. 2010, Martins et al. 2012, Edwards et al. 2014). As fishing pressure continues to impact functional diversity of herbivorous fishes in the Anthropocene, it is important to understand how these changes in functional diversity affect coral reef resilience.

Maintaining a high diversity of functional groups of herbivorous fishes supports coral reef resilience because the function each group performs can differentially promote the resistance and recovery of coral reefs. Herbivorous fishes are often classified as grazers or browsers (e.g., Hiatt and Strasburg 1960, Horn 1989, Green and Bellwood 2009) based on whether they consume turf algae (<2 cm height) versus macroalgae (>2 cm height, Littler and Littler 2011a,b), respectively. Healthy coral reefs typically have high coral cover with low cover of closely-

cropped turf (e.g., Hughes 1994). In comparison, degraded reefs have reduced coral and increased algal cover, often including macroalgae (e.g., Done 1992, Cheal et al. 2010, Graham et al. 2015). Maintaining herbivorous fish populations of both grazers and browsers is important as grazers promote resistance to phase shifts by cropping turf, while browsers can facilitate recovery following a shift by removing macroalgae (e.g., Green and Bellwood 2009, Graham et al. 2013). Therefore, coral reefs with high functional diversity of herbivorous fishes are more resilient to disturbances (e.g., Burkepile and Hay 2008, Burkepile and Hay 2010, Cheal et al. 2010, Graham et al. 2015, Nash et al. 2016). Despite the well-known importance of maintaining a diversity of herbivore functional groups for supporting coral reef resilience, these groups have not been incorporated into modeling studies of reef resilience.

Models have emerged as critical tools to study coral reef resilience because they can incorporate specific mechanisms affecting resilience and can generalize from focused field studies to broader spatial and temporal scales, often providing informative predictions of future trajectories (e.g., Muthukrishnan et al. 2016, van de Leemput et al. 2016). One important aspect of coral reef resilience is knowing whether rapid shifts to degraded states are smooth, threshold responses versus sharp bifurcations indicating alternative stable states (ASS). Bistability and hysteresis are two hallmarks of ASS. Bistability is when a community can exist in two different states for a single condition of an external driver (e.g., Blackwood et al. 2011, Muthukrishnan et al. 2016). Hysteresis is when a community has different thresholds (or tipping points) for transitions between states depending on the direction of change in an external driver (e.g., Scheffer et al. 2001, Muthukrishnan et al. 2016). One recent study (Schmitt et al. 2019) experimentally tested for and found evidence of hysteresis for Moorean coral reefs to shift between macroalgal and turf dominated states in response to varying levels of herbivory

pressure. However, empirical studies for ASS are rare, and models are often used to assess coral reef resilience and ASS. Coral reef resilience models have illuminated how reductions in grazing intensity (Mumby 2006, Mumby et al. 2007), herbivorous fish population dynamics (Blackwood et al. 2012), variations in the spatial scale of herbivory (Eynaud et al. 2016), stage-structured macroalgal refuges from herbivory (Briggs et al. 2018), and different functional responses between grazing rate and coral cover (McManus et al. 2019) affect reef resilience and/or the presence of ASS. Recent modeling work has highlighted how the strength (Muthukrishnan et al. 2016) and number of positive feedbacks (van de Leemput et al. 2016) affect reef resilience and the occurrence of ASS. One coral reef model (Eynaud et al. 2016) explored how differential loss of different types of algae (not explicitly linked to herbivore groups) influences reef recovery, and another simulation model (Miñarro et al. 2018) incorporates fish functional groups more broadly (i.e., scrapers, carnivores, and browsers and grazers as one group). However, to our knowledge, there are no models that explicitly incorporate herbivorous fish functional groups (i.e., browsers versus grazers) to evaluate coral reef resilience and ASS. Incorporating herbivore functional groups and their targeted algal resources into coral reef models allows the assessment of reef conditions that are otherwise difficult or unethical to observe or manipulate with field studies, providing essential insights into conditions influencing resilience and ASS.

Our aim was to evaluate how functional groups of herbivorous fishes shape coral reef resilience and ASS, building on growing themes in the empirical literature to develop new theoretical insights into reef ecology in the Anthropocene. Here, we expand an existing coral reef model to include herbivorous fish functional groups and their targeted algal groups, and explore how this addition affects predictions of resilience and ASS under different scenarios of human impacts. Our findings highlight the crucial importance of including herbivore functional groups

into coral reef models since we found reef recovery is more likely when initial herbivore abundances are skewed towards browsers over grazers and when herbivore community composition is more even, especially as fishing pressure increases. We also found the nature of ASS is strongly impacted by herbivore community composition, with ASS almost disappearing for a browser-dominated community. Overall, we demonstrate the usefulness of our model in predicting responses to human impacts that will only accelerate in the Anthropocene.

2.3 Methods

We expanded a previous coral reef model to incorporate three herbivore functional groups (grazers, browsers, generalists) and the two algal groups (turf, macroalgae) upon which they specialize. We examined coral reef resilience (as recovery after a disturbance) and characteristics of alternative stable states (bistability and hysteresis) under varying levels of fishing pressure, herbivorous fish communities (dominated by grazers, browsers, or generalists), and benthic communities (dominated by coral, turf, or macroalgae).

Basic Model Structure (from van de Leemput et al. 2016) – We recreated a portion of the basic model (Fig. 1A, Table S1) from van de Leemput et al. (2016), which has coral, herbivores, and algae as 3 state variables. The model is continuous time and deterministic. Coral, algae, and herbivores all have density-dependent negative feedbacks to prevent unlimited population growth. The basic model also incorporated 3 de-stabilizing positive feedbacks: 1) decreased herbivory rate with increased algal cover via a Holling type II functional response for the herbivore, 2) negative effects of algal cover on coral recruitment and growth, and 3) increased herbivore carrying capacity with increased coral cover.

In the basic model, benthic cover of each state variable is modeled as the proportion of space occupied, with coral (C) and algae (A) competing for benthic space, and unoccupied space (S) not covered by coral or algae.

$$(1) \quad S = 1 - C - A$$

Both coral (C) and algal (A) cover expand into unoccupied space through importation of propagules (i_C, i_A) and expansion of existing cover (b_C, b_A). Expansion of coral cover is negatively affected by the competitive effect of algae (α_A) on coral recruitment and growth, which is proportional to the cover of algae. Coral cover decreases via a constant decay rate (d_C) representing coral mortality. Herbivores negatively affect algae via consumption, but there is a positive feedback between algal cover and herbivory rate, which is incorporated as the Holling type II functional response. Thus, grazing rate (g_A) saturates with increasing algal cover and is affected by the handling time of algae for herbivores (η_A).

$$(2) \quad \frac{dC}{dt} = (i_C + b_C C)S(1 - \alpha_A A) - d_C C$$

$$(3) \quad \frac{dA}{dt} = (i_A + b_A A)S - \frac{g_A A H}{g_A \eta_A A + 1}$$

Herbivores (H) are modeled as a proportion of herbivore carrying capacity. Herbivores increase based upon a growth rate (r) and decrease based upon fishing pressure (f). Coral has a positive effect on herbivores by providing habitat and shelter; therefore, herbivore carrying capacity is affected by coral cover based upon the parameter σ . As σ increases, coral cover increasingly influences herbivore carrying capacity.

$$(4) \quad \frac{dH}{dt} = rH\left(1 - \frac{H}{(1 - \sigma) + \sigma C}\right) - fH$$

Basic Model Analyses – We reconstructed the van de Leemput et al. (2016) model (Fig. 1A) in R (hereafter referred to as the basic model). We tested our basic model by replicating their Figure 3e, which evaluates hysteresis, and we also evaluated bistability of the basic model (see supplement for details of methods).

Expanded Model Structure – We expanded the basic model, maintaining the same structure as above, by incorporating three herbivore functional groups (grazers (G), browsers (B), generalists (R)) and their targeted algal resources (turf (T), macroalgae (M)) (Fig. 1B, Table 1). All herbivore functional groups contribute to the overall herbivore carrying capacity. Thus, their relative abundances are in proportion to the overall herbivore carrying capacity, and they each grow (r) and experience fishing pressure (f) in relation to their abundance. All additions to the basic model are in **bold**.

$$(5) \quad \frac{dG}{dt} = r\mathbf{G} \left(1 - \frac{(\mathbf{G} + \mathbf{R} + \mathbf{B})}{(1 - \sigma) + \sigma C} \right) - f\mathbf{G}$$

$$(6) \quad \frac{dB}{dt} = r\mathbf{B} \left(1 - \frac{(\mathbf{G} + \mathbf{R} + \mathbf{B})}{(1 - \sigma) + \sigma C} \right) - f\mathbf{B}$$

$$(7) \quad \frac{dR}{dt} = r\mathbf{R} \left(1 - \frac{(\mathbf{G} + \mathbf{R} + \mathbf{B})}{(1 - \sigma) + \sigma C} \right) - f\mathbf{R}$$

Following the definitions used in Sandin and McNamara (2012), turf algae (T) are sparse to dense assemblages of fast-growing filamentous algae and juvenile macroalgae that are cropped short by herbivores (Littler and Littler 2011a). Macroalgae (M) are an assemblage of erect, fleshy algae >2 cm tall (Littler and Littler 2011b). Turf can experience uncontrolled

growth and transition into macroalgae at a rate of γ , when it is not cropped by grazer and/or generalist herbivores.

Removal of turf and macroalgae by herbivores is affected by the abundance of the herbivore functional groups that consume each of them. For our model, grazers only consume turf algae, browsers only consume macroalgae, and generalists consume both turf and macroalgae in proportion to their availability. While herbivorous fishes classified as grazers or browsers may not be entirely specialized (e.g., Adam et al. 2015, Adam et al. 2018, Kelly et al. 2016, Smith et al. 2018, Duran et al. 2019), we assumed complete specialization for our model. Both turf and macroalgae have handling times (η_T, η_M) and competitive effects on coral (α_T, α_M).

$$(8) \quad \frac{dT}{dt} = (i_T + b_T T)S - \gamma T - \left(\frac{g_T T G}{g_T \eta_T T + 1} + \frac{g_T T R}{g_T \eta_T T + g_M \eta_M M + 1} \right)$$

$$(9) \quad \frac{dM}{dt} = (i_M + b_M M)S + \gamma T - \left(\frac{g_M M B}{g_M \eta_M M + 1} + \frac{g_M M R}{g_T \eta_T T + g_M \eta_M M + 1} \right)$$

$$(10) \quad \frac{dC}{dt} = (i_C + b_C C)S(1 - (\alpha_T T + \alpha_M M)) - d_C C$$

$$(11) \quad S = 1 - C - T - M$$

Expanded Model Analyses – To confirm the relationship of our model to the basic model, we first tested whether our output matched that of the basic model for appropriate initial conditions and parameter values (Table 1 – collapsed model values). We ran the basic model and our collapsed model for 1000 years (in order to reach equilibrium) under fishing pressures of 0.1, 0.5, and 0.9, and compared changes in herbivores and coral and algal cover over time.

For further analyses of our expanded model, we changed the parameter values based upon the following assumptions for a coral reef system with multiple herbivore functional groups and their targeted algal resources (Table 1 “Expanded Model Values”, see supplement for justification of assumptions):

- No handling time for turf algae ($\eta_T = 0$).
- Expansion rate of existing macroalgae is slower than expansion of turf ($b_M < b_T$).
- No importation of macroalgal propagules because it grows from turf ($i_M = 0$).
- Mortality due to herbivory is greater for turf than macroalgae ($g_T > g_M$).
- Competitive effect on coral is greater for macroalgae than turf ($\alpha_M > \alpha_T$).

We addressed four questions with our expanded model. For our first three questions, we explored a crucial aspect of coral reef resilience: the recovery of coral cover following a disturbance that reduced coral cover. We asked if coral reef resilience is affected by varying levels of fishing pressure in combination with 1) varying abundance of herbivore functional groups in the herbivore community, 2) varying amounts of benthic cover of coral, turf, and macroalgae following the disturbance, and 3) both varying herbivore communities and benthic cover. For our final question, 4) we explored how the functional group composition of the herbivore community influenced the range of fishing pressures where the characteristics of alternative stable states (bistability and hysteresis) are observed.

Unless stated otherwise, for all analyses, we used the expanded model parameter values and initial conditions from Table 1; ran the model for 1000 years because this is long enough for the system to reach equilibrium; and presented the final coral cover for each analysis.

Question 1: How do varying abundances of herbivore functional groups influence the recovery of coral reefs after a disturbance, for different levels of fishing pressure?

We set initial cover to 0.15, 0.1, and 0, for coral, turf, and macroalgae, respectively. We varied initial abundance of grazers and browsers (0 – 0.9 in 0.025 increments) for initial generalist abundance set to 0, 0.2, or 0.4. The total initial herbivore abundance (grazers + browsers + generalists) was not held constant in these simulations; rather it ranged from 0 to 0.9, so we could assess how variation in the total initial herbivore abundance (due to previous fishing pressure) affected final coral cover. Also, we set total initial herbivore abundance less than or equal to 0.9, to ensure herbivore populations began below their carrying capacity. We set fishing pressure to 0 – 0.7 in increments of 0.1. We present scenarios with fishing pressure = 0, 0.3, and 0.5 in the main text figures, and present all scenarios in the supplement.

Question 2: How does varying initial benthic cover of coral, turf, and macroalgae influence the recovery of coral reefs after a disturbance, for different levels of fishing pressure?

Disturbances may reduce coral cover by differing amounts. To explore how this might influence reef recovery, we set initial coral cover to 0.15, 0.35, 0.55, and 0.75, but only present 0.15 – 0.55 in the main text figures (we present all scenarios in the supplement). For each initial coral cover, we varied initial cover of turf and macroalgae from 0 – 0.7, or up to the appropriate level given that we held initial unoccupied space (S) to a minimum of 0.15 for all simulations. Therefore, we constrained the total initial benthic cover (turf + macroalgae + coral) so it did not exceed 0.85. We set fishing pressure to 0 – 0.7 in increments of 0.1. We present scenarios with fishing pressure = 0.4, 0.5, and 0.6 in the main text figures, and present all scenarios in the supplement.

Question 3: How does variation in the dominant herbivore functional group and benthic cover of their targeted resources influence the recovery of coral reefs after a disturbance, for different levels of fishing pressure?

We varied initial cover of turf and macroalgae, for initial herbivore abundance set to one of three scenarios: 1) **generalist-dominated**: generalists = 0.6, grazers = 0.15, browsers = 0.15; 2) **browser-dominated**: browsers = 0.6, generalists = 0.15, grazers = 0.15; or 3) **grazer-dominated**: grazers = 0.6, generalists = 0.15, browsers = 0.15. We set initial coral cover at 0.15 for all simulations, and we varied initial turf and macroalgal cover from 0 – 0.7. As above, we constrained the total initial benthic cover (turf + macroalgae + coral) so it did not exceed 0.85. We set fishing pressure to 0 – 0.7 in increments of 0.1. We present scenarios with fishing pressure = 0, 0.3, and 0.6 in the main text figures, and present all scenarios in the supplement.

Question 4: How does variation in the dominant herbivore functional group in a community influence the characteristics of alternative stable states (bistability and hysteresis) in response to fishing pressure?

Bistability is evidenced in our model when final coral cover is split between high (>0.6) coral cover and low (<0.2) coral cover equilibrium states for the same level of fishing pressure, depending upon initial coral cover conditions. For different scenarios of herbivore community and coral cover, we compared levels of fishing pressure resulting in bistability. As a baseline, we examined bistability for our model using the parameter values and initial conditions that allow it to collapse to the van de Leemput et al (2016) model. Next, we examined bistability using our expanded model parameter values from Table 1 and even initial abundances of the herbivore

functional groups (i.e., generalists = grazers = browsers = 0.3). Finally, we examined bistability for the 3 scenarios of initial herbivore abundances as above: 1) **generalist-dominated**, 2) **browser-dominated**, and 3) **grazer-dominated**. To do this, we examined combinations of initial coral cover and fishing pressures ranging from 0 – 1 in increments of 0.01. After subtracting initial coral cover and empty space (0.05) from total benthic space available, the remaining space was evenly split between turf and macroalgae for their initial condition values. For each combination of initial coral cover and fishing pressure, we ran the model for 1000 years (to reach equilibrium) and examined final coral cover.

To examine the model for hysteresis, we did “forward” and “reverse” simulations, reflecting increasing or decreasing fishing pressure, respectively. Then we determined whether the transitions from coral-dominated to algal-dominated states differed. Specifically, for the “forward” simulations, we increased fishing pressure from 0 – 1 in 0.005 increments, and for the “reverse” simulations, we decreased fishing pressure from 1 – 0 in 0.005 increments. We ran each simulation for 1000 years to ensure the system reached equilibrium. For each fishing pressure, we used the end conditions for the state variables from the previous fishing pressure as the initial conditions for the next fishing pressure. We examined hysteresis for the same five scenarios in which we examined bistability.

2.4 Results

Basic Model – Our basic model exhibits hysteresis for the same fishing pressures as those from van de Leemput et al. (2016), indicating we adequately reconstructed their model in R (Fig. S1). The van de Leemput et al. (2016) basic model exhibits bistability, with final coral cover dependent on initial coral cover, for fishing pressures between 0.33 – 0.51 (Fig. S2).

Expanded Model – Our expanded model collapses into the basic model for initial conditions and parameter values in Table 1, and the results are identical for a range of fishing pressures (Fig. 1C). When using our expanded model parameters based on our assumptions (Fig. 1D), the model behaves similarly to the basic and collapsed model (Fig. 1C); however, we can assess changes in the herbivore functional groups and their algal resources. As expected, all three herbivore functional groups respond the same to fishing pressure (Fig. 1D) since they were subject to the same fishing pressure. However, increased fishing pressure results in dramatic differences in the relative proportion of turf versus macroalgae, where turf is slightly more prevalent when fishing pressure is low, while macroalgae strongly dominates at high fishing pressure (Fig. 1D).

Question 1: How do varying abundances of herbivore functional groups influence the recovery of coral reefs after a disturbance, for different levels of fishing pressure?

Coral reef recovery is impacted dramatically by herbivore community composition (i.e., final coral cover, Fig. 2, see Fig. S3 for all scenarios). As expected, increased fishing pressure leads to more scenarios where the reef does not recover to high coral cover (Fig. 2 compare from top to bottom row). However, regardless of fishing pressure, recovery to high coral cover is more likely with increasing initial abundance of generalist herbivores (Fig. 2 compare from left to right columns).

Further, the reef recovers to higher coral cover when the initial abundances of grazers versus browsers are more similar (band of lighter color in middle of triangles in Fig. 2 panels), while a skew in the herbivorous fish community towards dominance by either grazers or browsers results in lower coral cover (dark edges of triangles in Fig. 2 panels). More subtly, the

reef is more likely to recover to higher coral cover if the skew favors browsers over grazers (compare dark edges of triangles within Fig. 2).

Question 2: How does varying benthic cover of coral, turf, and macroalgae influence the recovery of coral reefs after a disturbance, for different levels of fishing pressure?

Coral reef recovery is less likely on highly disturbed reefs. The negative effect of fishing pressure on coral reef recovery is reduced as initial coral cover increases (Fig. 3 compare columns from left to right, see Fig. S4 for all scenarios). In contrast, initial cover of turf and macroalgae have relatively little effect on reef recovery. The relative initial cover of turf versus macroalgae only affects reef recovery when fishing pressure is intermediate (0.5) and initial coral cover is low (≤ 0.35 , Fig. 3B,E). Overall, for scenarios with lower initial coral cover and higher fishing pressure, coral reefs can recover better when there is higher initial cover of turf compared to macroalgae (Fig. 3B, light band along x-axis).

Question 3: How does variation in the dominant herbivore functional group and benthic cover of their targeted resources (turf and macroalgae) influence the recovery of coral reefs after a disturbance, for different levels of fishing pressure?

Herbivore community composition interacts with benthic community composition to influence coral reef recovery. Overall, recovery decreased as herbivorous fish communities changed in dominance from generalists to browsers to grazers (Fig. 4 compare columns from left to right), and recovery was negatively impacted by increased fishing pressure (Fig. 4 compare rows from top to bottom, see Fig. S5 for all scenarios). While all scenarios experienced a disturbance reducing coral cover to 15%, the dependence of coral recovery on initial benthic

cover varied strongly depending on herbivore community composition. In a generalist-dominated community, the reef recovers to high final coral cover for low and intermediate fishing pressures, regardless of initial amounts of turf or macroalgae (Fig. 4A,B). However, for high fishing pressure (0.6), this community can only recover when initial turf and macroalgae are both low, so there is ample open space for coral recovery (Fig. 4C). Also, in this scenario, the relative initial cover of turf versus macroalgae has a minor effect on coral recovery, with better recovery when initial turf cover is similar to or exceeds macroalgal cover. In contrast, and surprisingly, reef recovery in a browser-dominated community shows no dependence on initial cover of turf versus macroalgae, and fishing pressure is the only important factor (Fig. 4D-F). Finally, when grazers dominate the herbivore community, reef recovery depends sharply on the initial cover of macroalgae when fishing pressures are low (≤ 0.2 , Fig. 4G, Fig. S5). The threshold of macroalgal cover that prevents coral recovery decreases as fishing pressure increases, while initial turf cover has relatively little effect on reef recovery (Fig. 4G, Fig. S5).

Question 4: How does variation in the dominant herbivore functional group in a community influence the characteristics of alternative stable states (bistability and hysteresis)?

When initial herbivore abundances are even, our model exhibits bistability for a very similar, although slightly contracted, range of fishing pressures as the van de Leemput et al. (2016) model (Fig. 5A,B).

Herbivore community composition has dramatic impacts on the existence and nature of ASS in this system (Fig. 5C-E). The generalist-dominated scenario has the broadest range of fishing pressures in which the coral reef can end up in a high coral cover state (Fig. 5C), and it is most similar to the scenario with even initial herbivore abundances (Fig. 5B). For the browser-

dominated scenario the final coral cover is slightly lower across all fishing pressures compared to the generalist-dominated scenario (Fig. 5C,D – compare brightness of yellow). Also, the browser-dominated scenario has only a sliver of bistability, and closely resembles a threshold transition (Fig. 5D). The grazer-dominated scenario has the broadest range of fishing pressures in which the coral reef exhibits bistability; even with no fishing pressure, there is bistability where the coral reef can only end up in a high coral cover state if it begins with initial coral cover greater than ~ 0.27 (Fig. 5E).

The hysteresis results follow the same patterns as for bistability. The collapsed model and even herbivore community scenario show similar hysteresis curves, although the even herbivore community scenario has a slightly contracted range of hysteresis (Fig. 5F,G). Whether the model produces hysteresis depends on the herbivore community composition scenarios (Fig. 5H-J). The generalist-dominated scenario exhibits hysteresis for intermediate to high fishing pressures (Fig. 5H), and is most similar to the even herbivore community scenario (Fig. 5G). For the browser-dominated scenario, there is a very limited range of fishing pressures for which the system exhibits hysteresis (Fig. 5I); rather the relationship resembles a simple threshold. Lastly, similar to the bistability results, the grazer-dominated scenario exhibits hysteresis for the widest range of fishing pressures, and once the system is degraded, it cannot recover (during the time frame we examined) to high coral cover even if fishing pressure is reduced to 0 (Fig. 5J).

2.5 Discussion

Summary of Results

We examined how incorporating realistic herbivore functional diversity in coral reef communities can modulate – and sometimes qualitatively alter – the resilience and ASS of coral

reefs in response to human disturbance. We found herbivorous fish community composition influenced the recovery of reefs from low coral cover, even for coral reefs experiencing no fishing pressure. Also, the herbivorous fish community compositions that best promote recovery varied depending upon fishing pressure intensity, with evenness becoming increasingly important as fishing pressure increased. Similarly, our model demonstrated that benthic community structure interacted with herbivore community composition to influence reef recovery and these relationships were further influenced by fishing pressure. Finally, our model demonstrated the range of fishing pressures where coral reefs exhibited ASS changed depending on the herbivorous fish community composition, with an almost complete loss of ASS for a community dominated by browsers. Taken together, our results demonstrate the importance of incorporating herbivorous fish functional groups into coral reef models in order to recognize complex interactions between human impacts and reef community state that support resilience or drive ASS of coral reefs.

Including functional groups of herbivorous fishes was critical to understanding reef resilience

Decomposing herbivorous fishes into functional groups improved our understanding of their role in reef resilience by unmasking conditions that limit resilience that are obscured in existing models. For example, our analysis showed that reefs dominated by grazers are less resilient than reefs dominated by browsers and can exhibit ASS even when the coral reef experienced no fishing pressure. Although previous coral reef models that assess resilience or ASS have not incorporated functional groups of herbivorous fishes, some existing studies support the importance of this finer-scale knowledge. For example, species identity and relative abundance of herbivorous parrotfishes, rather than higher taxonomic levels or biomass, strongly

impacted three ecosystem processes (area of reef grazed, amount of macroalgae removed, and rate of bioerosion) in the Caribbean (Ruttenberg et al. 2019). Also, analysis of a large data set showed that incorporation of functional groups of herbivorous fishes and benthic groups helped distinguish five reef regimes in the Hawaiian Islands compared to the two (coral vs. algae) traditionally considered (Donovan et al. 2018). In addition, some coral reef models have begun incorporating finer-scale information about corals, such as including resistant versus resilient coral species when examining resilience (Baskett et al. 2015) or incorporating species richness and functional diversity of corals to examine their influence on benthic community dynamics (Carturan et al. 2020). These studies further highlight the impetus to and importance of incorporating essential dimensions of ecological function (i.e., herbivorous fish functional groups) into coral reef models. To our knowledge, our coral reef model is the first to incorporate herbivorous fish functional groups, and the first to demonstrate their crucial role in determining conditions preventing reef recovery and resulting in ASS on coral reefs.

Our research aligns with findings across other ecosystems that incorporating key structure within trophic levels into models can yield important insights about community dynamics and improved predictive capabilities. For example, the incorporation of phytoplankton and zooplankton functional groups into a complex aquatic biogeochemical model helped reveal phytoplankton competition patterns under nutrient enrichment conditions (Zhao et al. 2008). Similarly, water quality models were improved when phytoplankton were classified based on functional groups compared to taxonomic groups (Di Maggio et al. 2016), and size-spectrum models were improved with the inclusion of zooplankton functional groups (Heneghan et al. 2016). Contrary to our results, however, one ASS model for freshwater lakes found that including finer scale information about floating plants (e.g., species composition or traits) had

little impact on the final state of the system (McCann 2016). However, their ASS model assessed the trophic level that defines regime shifts (e.g., coral vs. algae, floating plants vs. submerged plants), whereas we focused on a higher trophic level. Overall, incorporating functional groups and/or key structures of trophic levels into models is often an important next step in understanding and predicting ecosystem dynamics.

Incorporating herbivorous fish functional groups into our model also revealed the importance of considering both community context and human impacts when assessing resilience to disturbances. This principle is well established in empirical studies of reef systems, including studies that showed recovery from disturbance is promoted by high diversity (Burkepile and Hay 2010, Cheal et al. 2010, Graham et al. 2015) and evenness (Nash et al. 2016) of herbivorous fish communities on coral reefs and predator diversity in kelp forests (Burt et al. 2018). Our analysis further explored how herbivore community composition influences reef recovery by examining how it changes with the human impact of fishing pressure. We found that as fishing pressure increases, the evenness of herbivore functions also needs to increase for reefs to recover from disturbance. Similarly, we found fishing pressure interacted with benthic community composition to influence reef recovery, such that recovery is only influenced by the benthic community composition when fishing pressure is high. A recent empirical study (Ford et al. 2020) found the capacity of different herbivorous fish functional groups to predict coral reef benthic communities varied with the level of local human impact. Although Ford et al. (2020) did not assess reef resilience or ASS, it supports our finding of the importance of decomposing herbivorous fish into functional groups when assessing coral reefs. Further, a recent model of shallow lakes found the abundance of herbivorous birds interacted with the human impact of nutrient loading to influence the resilience of the clear-water state (van Altena et al. 2016),

although this study did not examine community composition. Incorporating functional groups into coral reef models allows for increased understanding of how community context and continuing human impacts, such as fishing pressure, impact reef resilience.

Modeling integrates and advances our understanding of coral reef ecosystems

Our model enables us to test conceptual frameworks and examine scenarios that would be logistically or ethically prohibitive in nature, thus advancing our understanding of coral reef ecosystems. For example, browsers are widely considered more important than grazers for reef recovery from shifts to macroalgal-dominance (Green and Bellwood 2009, Graham et al. 2013). This conceptual framework is rarely tested experimentally due to valid concerns about manipulating coral cover and herbivorous fish communities on coral reefs already threatened by local and global impacts (Hughes et al. 2017), but our analysis confirms the expected importance of browsers. Similarly, long-term data have provided insights into the relationship between the abundances of herbivore functional groups and phase shifts on coral reefs. For example, low abundances of both grazers and browsers were strongly associated with phase shifts to macroalgal-dominance (Cheal et al. 2010). However, the relative contribution of these two functional groups could not be distinguished from field data; whereas, our model provided a novel way to test the concept that browsers are more important for reef recovery. Our model demonstrates that coral reefs skewed towards browsers are more resilient to disturbances and exhibit ASS for a much narrower range of fishing pressures compared to reefs with fish communities skewed towards grazers, thus supporting this concept.

As a second example, to our knowledge, previous studies have not explicitly addressed how the amount of turf and macroalgae interacts with herbivore community composition to

influence reef recovery. This is important because there is increased recognition that coral reef phase shifts are more complex than shifting between coral-dominance to macroalgal-dominance and that increased cover of turf algae can also represent coral reef degradation (e.g., Jouffray et al. 2015, Smith et al. 2016). Recent empirical studies have focused on assessing the amount of turf and macroalgae on degraded coral reefs (e.g., Smith et al. 2016) and quantifying the resident herbivorous fish community (e.g., Jouffray et al. 2015, Donovan et al. 2018), to characterize coral reef regimes. With our model, we found that algal community composition can have tremendous impacts on reef recovery, but only if the reef is degraded due to overfishing or there is massive coral loss after a disturbance. Thus, using a modeling framework allowed us to identify scenarios where knowing increased detail about benthic and herbivorous fish functional groups is important for assessing reef resilience.

Conclusions

Our findings highlight that including functional groups of herbivorous fishes into coral reef models is a critical step in understanding and predicting coral reef resilience and ASS in the Anthropocene. Models for other ecosystems that incorporate essential structures within trophic levels are already discovering important insights and improving their predictive capabilities. Our study makes this advancement for coral reef models and improves our understanding of how community context and human impacts affect reef resilience. In addition, our modeling approach allowed us to verify conceptual frameworks and identify community contexts that influence reef resilience, which would be logistically or ethically prohibitive to assess empirically in nature. Understanding the attributes supporting community resilience is especially crucial in the

Anthropocene as we try to conserve communities experiencing numerous anthropogenic disturbances, and our study advances this understanding for coral reefs.

2.6 Acknowledgements

I want to acknowledge Ana Carolina Ribeiro Gomez for her effort and guidance as a TA for EEB C219B, which was invaluable to this project.

2.7 Tables

Table 2.1 Equations for the expanded model, with state variables and parameters listed below. The collapsed model parameter values allow the expanded model to collapse down to the basic model. The expanded model parameter values are based upon assumptions given in the text.

| | | | | | |
|---|--|--|---|-------------------------------|----------------------------------|
| $S = 1 - C - T - M$ | | | $\frac{dC}{dt} = (i_C + b_C C)S(1 - (\alpha_T T + \alpha_M M)) - d_C C$ | | |
| $\frac{dT}{dt} = (i_T + b_T T)S - \gamma T$ $-\left(\frac{g_T T G}{g_T \eta_T T + 1} + \frac{g_T T R}{g_T \eta_T T + g_M \eta_M M + 1}\right)$ | | | $\frac{dG}{dt} = rG \left(1 - \frac{(G + R + B)}{(1 - \sigma) + \sigma C}\right) - fG$ | | |
| $\frac{dM}{dt} = (i_M + b_M M)S + \gamma T$ $-\left(\frac{g_M M B}{g_M \eta_M M + 1} + \frac{g_M M R}{g_T \eta_T T + g_M \eta_M M + 1}\right)$ | | | $\frac{dR}{dt} = rR \left(1 - \frac{(G + R + B)}{(1 - \sigma) + \sigma C}\right) - fR$ | | |
| $\frac{dB}{dt} = rB \left(1 - \frac{(G + R + B)}{(1 - \sigma) + \sigma C}\right) - fB$ | | | | | |
| State Variables: | S = unoccupied space C = coral cover | T = turf algal cover M = macroalgal cover | G = grazer herbivore abundance R = generalist herbivore abundance B = browser herbivore abundance | | |
| Initial Condition Values (unless otherwise indicated in analyses or text) | | | | | |
| Collapsed Model | | | Expanded Model | | |
| S0 = 0.15 C0 = 0.75 | T0 = 0.05 M0 = 0.05 | G0 = 0.45 R0 = 0 B0 = 0.45 | S0 = 0.15 C0 = 0.75 | T0 = 0.10 M0 = 0 | G0 = 0.3 R0 = 0.3 B0 = 0.3 |
| Parameters: | | | | Collapsed Model Values | Expanded Model Values |
| i_C | import of coral propagules | | | 0.05 yr ⁻¹ | 0.05 yr ⁻¹ |
| i_T | import of turf propagules | | | 0.025 yr ⁻¹ | 0.05 yr ⁻¹ |
| i_M | import of macroalgal propagules | | | 0.025 yr ⁻¹ | 0 yr ⁻¹ |
| b_C | expansion of existing coral (proportional to existing cover) | | | 0.3 yr ⁻¹ | 0.3 yr ⁻¹ |
| b_T | expansion of existing turf (proportional to existing cover) | | | 0.8 yr ⁻¹ | 0.8 yr ⁻¹ |
| b_M | expansion of existing macroalgae (proportional to existing cover) | | | 0.8 yr ⁻¹ | 0.5 yr ⁻¹ |
| d_C | mortality of coral (constant decay rate) | | | 0.1 yr ⁻¹ | 0.1 yr ⁻¹ |
| g_T | mortality of turf algae (constant grazing rate per herbivore) | | | 2 yr ⁻¹ | 2 yr ⁻¹ |
| g_M | mortality of macroalgae (constant grazing rate per herbivore) | | | 2 yr ⁻¹ | 1 yr ⁻¹ |
| r | growth rate of herbivores | | | 1 yr ⁻¹ | 1 yr ⁻¹ |
| f | herbivore mortality (constant fishing pressure) | | | 0.1 yr ⁻¹ | 0.1 yr ⁻¹ |
| η_T | turf algae handling time of herbivores | | | 1 | 0 |
| η_M | macroalgae handling time of herbivores | | | 1 | 1 |
| α_T | competition effect of turf algae on coral recruitment and growth | | | 0.5 | 0.25 |
| α_M | competition effect of macroalgae on coral recruitment and growth | | | 0.5 | 0.5 |
| σ | strength of relationship between coral cover and herbivore carrying capacity | | | 0.6 | 0.6 |
| γ | transition probability from turf algae to macroalgae | | | 0 yr ⁻¹ | 0.1 yr ⁻¹ |

2.8 Figures

Figure 2.1 A) Diagram of the basic model (adapted from van de Leemput et al. 2016) showing the interactions and feedbacks (labeled 1-3 corresponding to their descriptions in the text) incorporated in the model. B) Diagram of the expanded model structure that incorporates three herbivore functional groups (grazer, generalist, browser) and two algal resources (turf, macroalgae). Green arrow (γ) between “Turf Algae” and “Macroalgae” is a transition from turf to macroalgae. C) Comparing outputs of basic and collapsed model under 3 levels of fishing pressure for initial conditions and parameter values given in Tables S1 and 1. D) Output of expanded model under 3 levels of fishing pressure for initial conditions and parameter values given in Table 1. For both the collapsed and expanded models (C, D), the Herbivores and Algae state variables are sums of their corresponding state variables (i.e., $H = G+B+R$, and $A = T+M$).

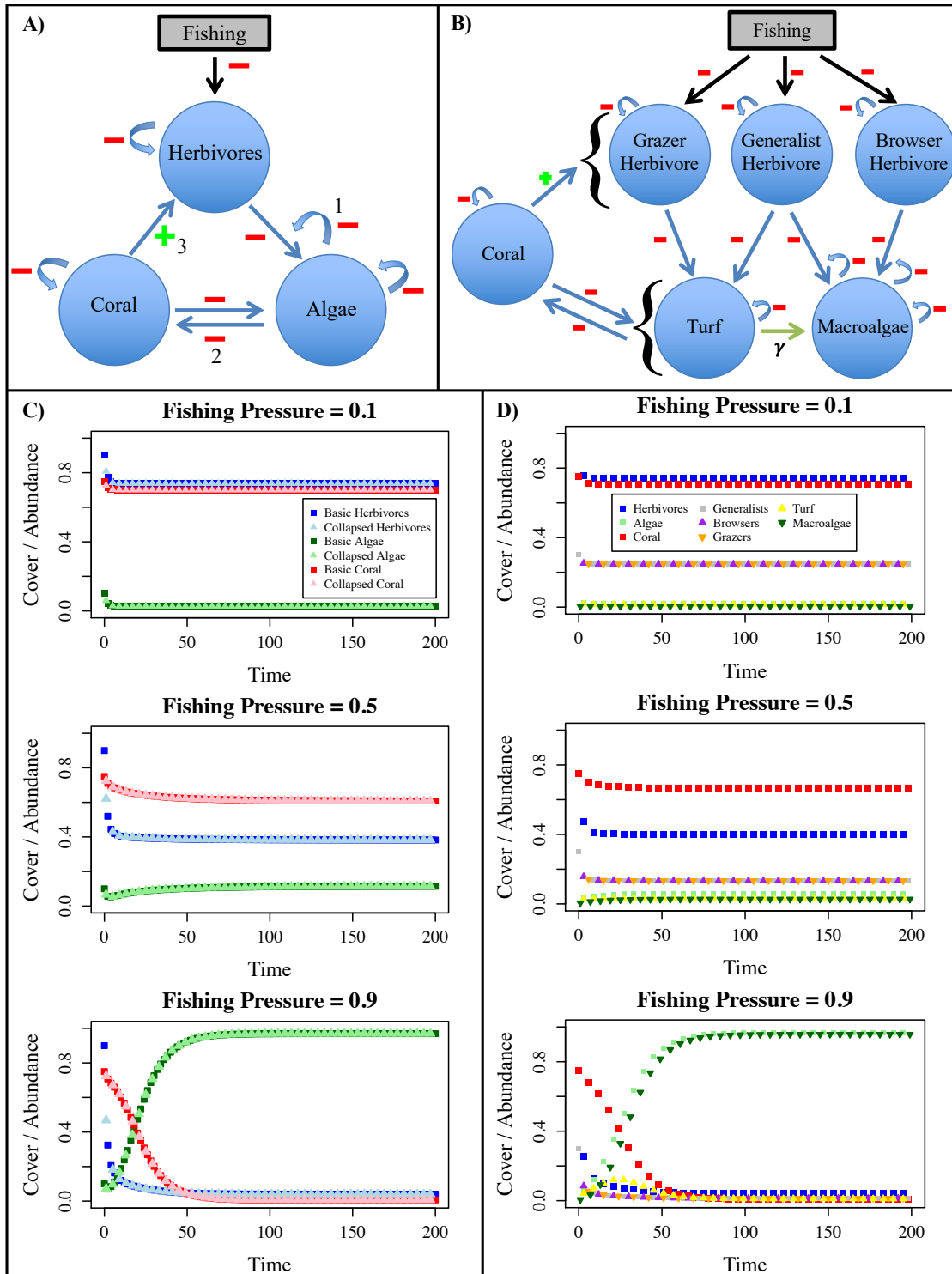


Figure 2.2 Heatmaps showing how the initial abundance of herbivorous fishes that are grazers versus browsers affect final coral cover for fishing pressures ranging from 0 to 0.5 (rows) and for initial generalist abundance set to 0 (A-C), 0.2 (D-F), or 0.4 (G-I). Total herbivore abundance is restricted to ≤ 0.9 ; therefore, as initial generalist abundance increases, the abundance of browsers+grazers has to decrease accordingly, resulting in smaller response spaces in the panels. Other initial conditions include $C_0 = 0.15$, $T_0 = 0.1$, and $M_0 = 0$.

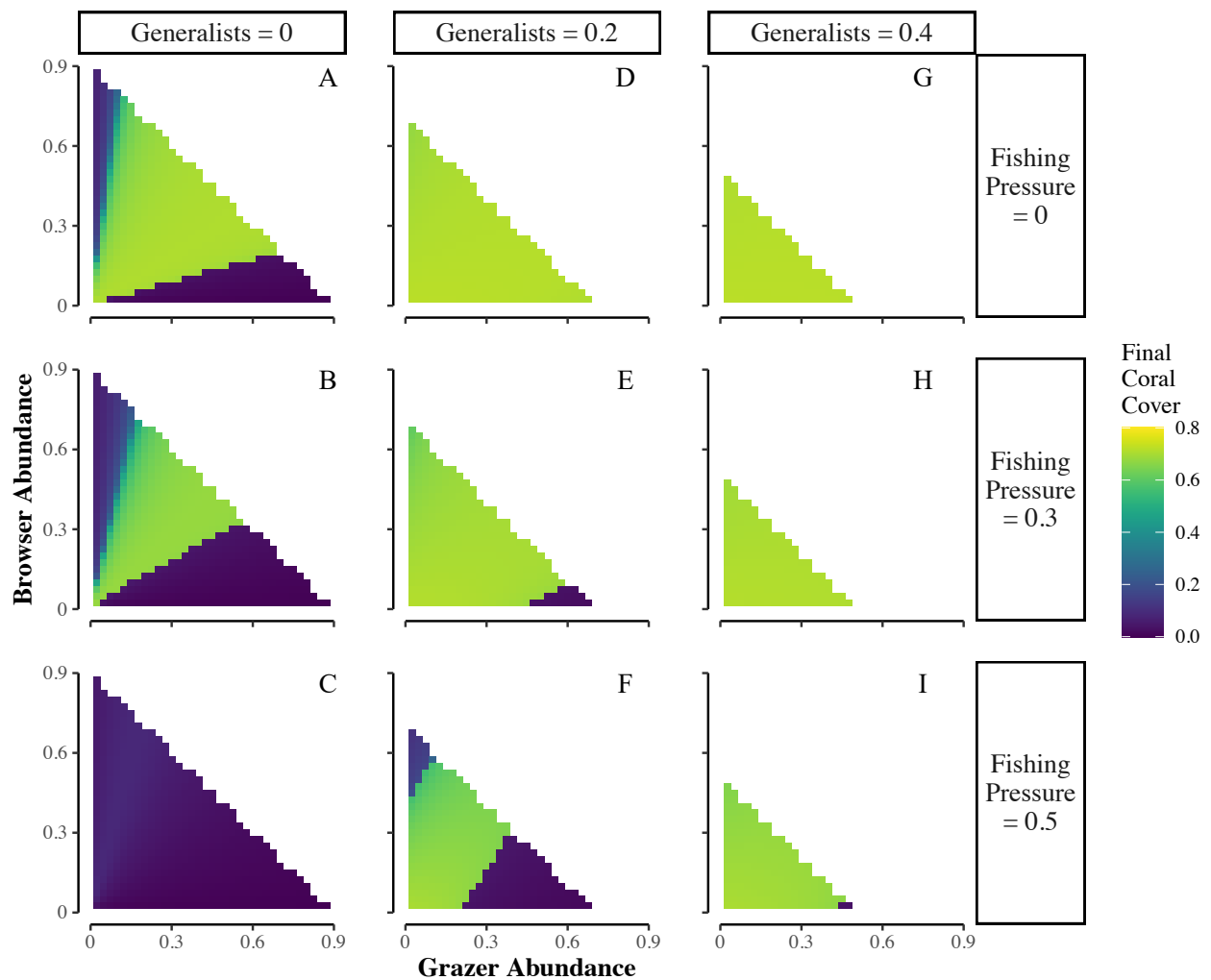


Figure 2.3 Heatmaps showing how initial cover of turf and macroalgae affect final coral cover for fishing pressures set to 0.4, 0.5 and 0.6 (rows) and for initial coral cover set to 0.15 (A-C), 0.35 (D-F), and 0.55 (G-I). Total initial benthic cover is restricted to ≤ 0.85 ; therefore, as initial coral cover increases, the initial cover of turf+macroalgae has to decrease accordingly, resulting in smaller response spaces in the panels. Initial herbivore abundances: $G_0 = 0.3$, $B_0 = 0.3$, $R_0 = 0.3$.

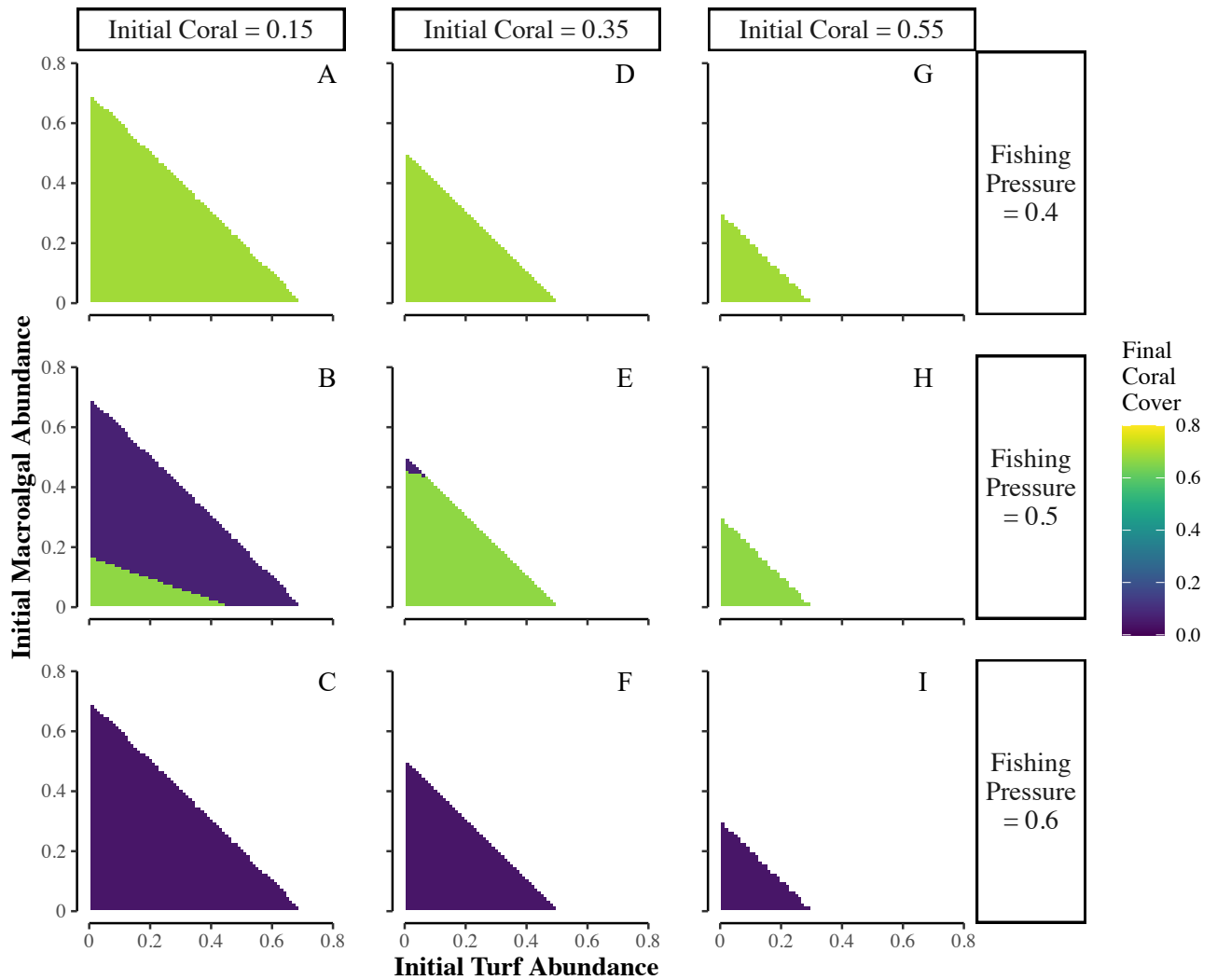


Figure 2.4 Heatmaps showing how initial cover of turf and macroalgae affect final coral cover for fishing pressures ranging from 0 to 0.6 (rows) and for initial herbivore proportions set to 1 of 3 scenarios: 1) generalists-dominated (A-C): generalists = 0.6, grazers = 0.15, browsers = 0.15; 2) browsers-dominated (D-F): browsers = 0.6, generalists = 0.15, grazers = 0.15; or 3) grazers-dominated (G-I): grazers = 0.6, generalists = 0.15, browsers = 0.15. Total initial benthic cover is restricted to ≤ 0.85 , and initial coral cover (C_0) = 0.15; therefore, the amount of unoccupied space changes for each combination of initial turf and macroalgae abundance.

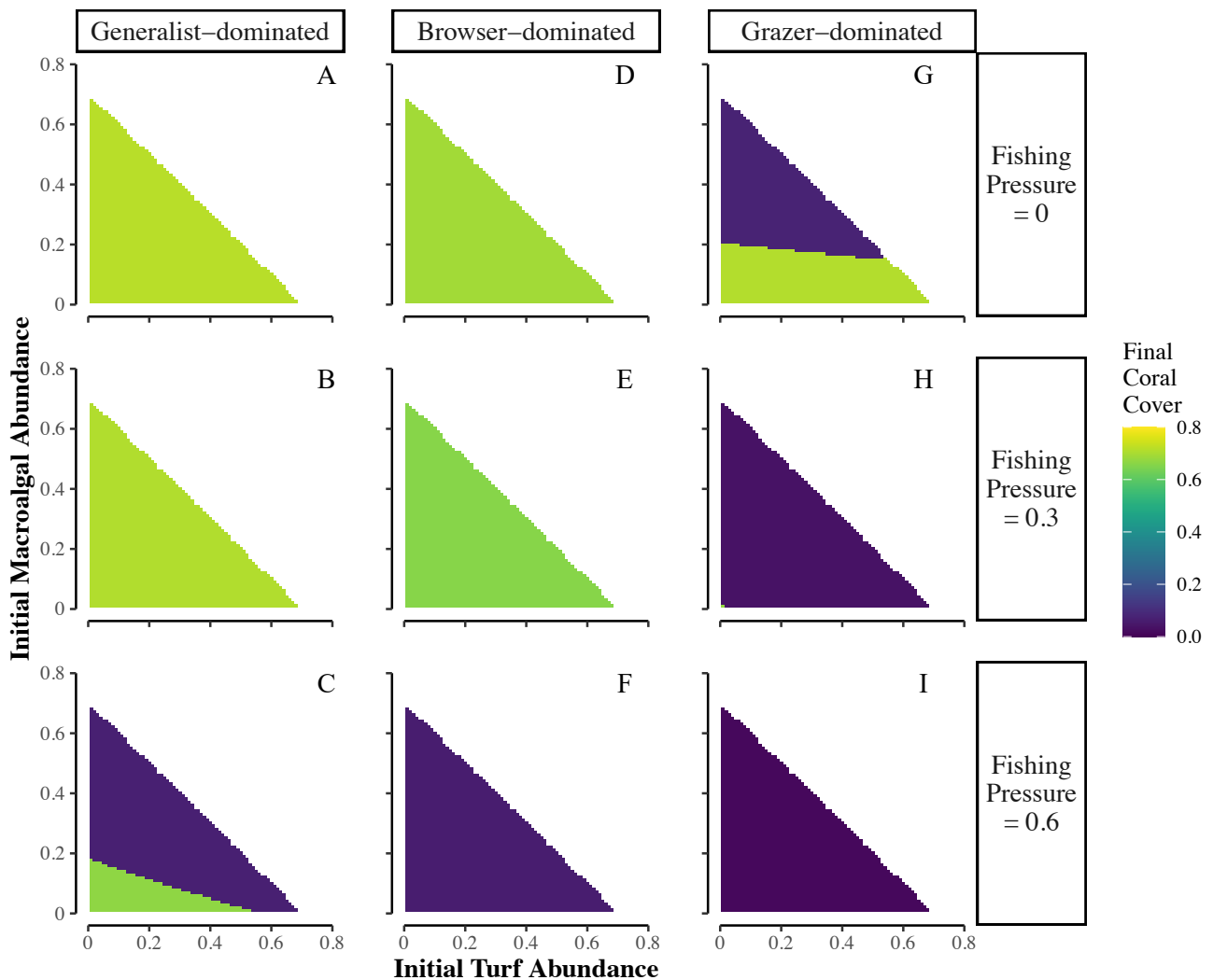
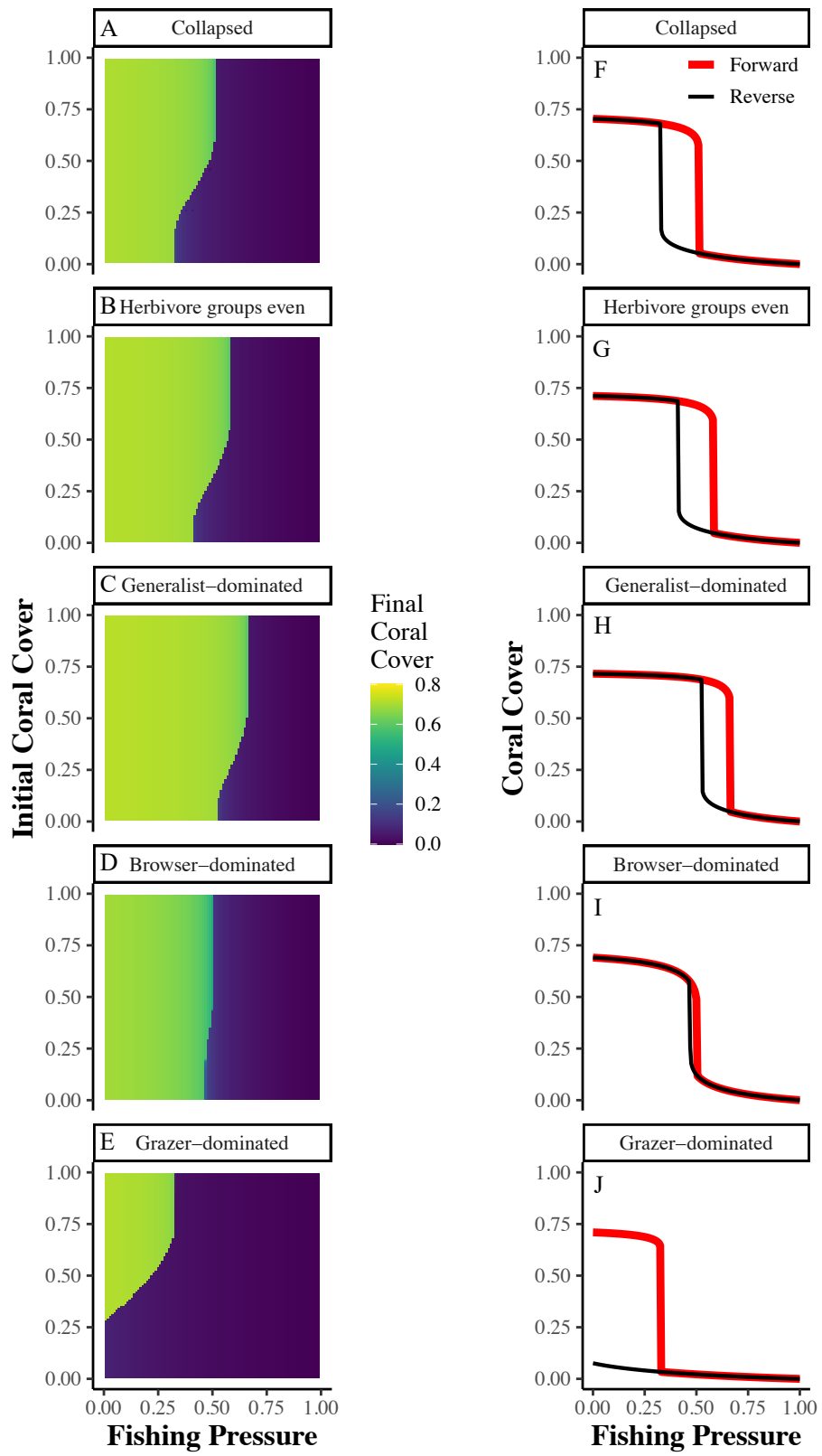


Figure 2.5 Bistability plots (A-E) showing final coral cover for each combination of fishing pressure and initial coral cover conditions. Bistability is evident when for a given fishing pressure, both low (<0.2) and high (>0.6) final coral covers occur, depending only upon the initial coral cover. Hysteresis plots (F-J) showing the final coral cover as fishing pressure is increased (forward) or decreased (reverse). Hysteresis is evident when there is a range of fishing pressures where the forward (red) and reverse (black) lines do not overlap. First, we examined bistability and hysteresis for our model using the parameter values and initial conditions that allow it to collapse to the van de Leemput et al (2016) model: collapsed (A,F). Next, we examined four scenarios using our expanded model parameter values from Table 1 with different initial herbivore community compositions: herbivore groups even (B,G): generalists = grazers = browsers = 0.3; generalists-dominated (C,H): generalists = 0.6, grazers = 0.15, browsers = 0.15; browsers-dominated (D,I): browsers = 0.6, generalists = 0.15, grazers = 0.15; or grazers-dominated (E,J): grazers = 0.6, generalists = 0.15, browsers = 0.15.



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CHAPTER 3:

MACROALGAE AND NUTRIENTS PROMOTE ALGAL TURF GROWTH IN THE ABSENCE OF HERBIVORES

The following chapter is reprinted by permission from Springer Nature Customer Service Centre GmbH: Springer Nature; Coral Reefs; Macroalgae and nutrients promote algal turf growth in the absence of herbivores; Sura SA, Delgadillo A, Franco N, Gu K, Turba R, & Fong P; 2019; 38: 425 – 429; doi:10.1007/s00338-019-01793-w



NOTE

Macroalgae and nutrients promote algal turf growth in the absence of herbivores

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Received: 19 November 2018 / Accepted: 19 March 2019 / Published online: 29 March 2019
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Abstract Closely cropped algal turfs are characteristic of healthy coral reefs, but unchecked growth can cause transitions into long sediment-laden turfs, which may be an alternative degraded state. While control by herbivores is well established, potential interactions between nutrients and macroalgae have not been evaluated. We varied macroalgal presence and nutrient addition and measured turf height and sediment accumulation over 18 d on an algal-dominated fringing reef. We found a novel facilitative effect of macroalgal presence on turf height as macroalgal presence increased growth by 34% over its absence. Nutrient addition also significantly, but independently, increased turf height by 127% compared to no nutrient addition. Macroalgal presence reduced sediment accumulation, possibly by trapping the sediment and/or by a whiplash effect. Thus, overfished coral reefs experiencing macroalgal blooms and/or nutrient additions may be at risk of developing long algal turfs, which could maintain a persistent shift to a degraded state.

Keywords Macroalgal–turf interaction · Nutrients · Algal turf · *Padina boryana*

Topic Editor Morgan S. Pratchett

Aaron Delgadillo, Nancy Franco and Kelly Gu are co-second authors.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00338-019-01793-w>) contains supplementary material, which is available to authorized users.

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Introduction

Closely cropped turf algae are part of healthy coral reef ecosystems (Fong and Paul 2011) but if their growth is unchecked, they can transition into long algal turfs (e.g., Goatley and Bellwood 2013; Clausing et al. 2014; Fong et al. 2018), overgrow neighboring corals (e.g., Vermeij et al. 2010), and represent a degraded reef state (e.g., Jouffray et al. 2015; Smith et al. 2016). Turf algae, which are multispecies assemblages of algae less than 2 cm in height (Littler and Littler 2013), are an important part of coral reefs as they are primary producers, provide trophic support, and contribute to nutrient retention and recycling (Fong and Paul 2011). Turf is typically maintained in a cropped state through herbivory (Fong and Paul 2011). However, this top-down control of algal turfs can be reduced either by overfishing of herbivores (e.g., Jackson et al. 2001) or by processes such as increased sedimentation that inhibit the feeding of herbivores on existing turfs (Bellwood and Fulton 2008; Goatley and Bellwood 2013). Furthermore, reduced herbivory pressure can cause turfs to transition into long sediment-laden algal turfs (Bellwood and Fulton 2008; Goatley and Bellwood 2013; Goatley et al. 2016) leading to a reinforcing feedback. As long sediment-laden algal turfs are suggested as an alternative stable state for coral reefs (Bellwood and Fulton 2008; Goatley and Bellwood 2013; Goatley et al. 2016), it is important to know what factors contribute to their development.

Increased nutrient supplies may facilitate algal turf growth both directly and through interactions with other stressors. While nutrient effects on macroalgae (see Burkpile and Hay 2006 for a meta-analysis), on turf cover (e.g., McClanahan et al. 2007; Sotka and Hay 2009; Muthukrishnan and Fong 2014), and on the relative cover

of short versus long algal turfs (e.g., Burkepile and Hay 2009; Rasher et al. 2012) have been investigated, Fong et al. (2018) is currently the only study that addresses and observes the role of nutrients in causing transitions from short to long turf by specifically measuring turf height over time. Herbivory can interact with and mask nutrient effects (e.g., Fong et al. 2018); therefore, examining the effects of nutrients on algal turf height is best done in the absence of herbivores. As only one previous study has measured turf height in order to test whether increased nutrients can increase algal turf height, this topic warrants further investigation.

Macroalgae are becoming more abundant on coral reefs (Fong and Paul 2011), which means interactions between algal functional forms are likely to have also increased; however, there is a lack of studies examining how the presence of macroalgae may affect turf. Algae of different forms may interact by competing for resources (e.g., space, light, nutrients; Fong and Paul 2011), through exploitative (e.g., shading) or interference competition (e.g., scouring, allelopathy) or by facilitating another alga by providing a refuge (e.g., Fong et al. 2006; Bittick et al. 2010; Roff et al. 2015). Experimental studies on algal–algal interactions are rare on coral reefs; however, two studies examined interactions between different macroalgae and both found facilitative effects by providing refuge from herbivory (Bittick et al. 2010; Roff et al. 2015). Two studies in temperate intertidal zones explored the effects of macroalgae on turf algae and found a negative effect of canopy-forming macroalgae on turf (Kim 2002; Kim et al. 2004). After testing various mechanisms (shading, scouring, allelopathy), they found shading was the mechanism causing this negative effect (Kim 2002). The effects of macroalgae on turf have rarely been studied, and to our knowledge, have not been studied at all in tropical coral reef systems despite many reefs experiencing increased presence of macroalgae.

Algal turfs are an integral part of coral reefs but can contribute to reef degradation if growth is unchecked. Macroalgal presence is becoming more common on coral reefs, yet there is a lack of studies examining how macroalgal presence may affect turfs. Nutrients can affect both macroalgae and turf algae and thus may modify how macroalgae affect turf. Therefore, our objective was to examine the effects of macroalgal presence and nutrient addition on algal turfs. We predicted nutrient addition would have a positive effect on algal turf height as shown by previous studies (e.g., Fong et al. 2018), while macroalgal presence would have a negative effect on algal turf height, likely because of competition (e.g., Fong and Paul 2011). We predicted macroalgal presence would reduce sediment accumulation on the algal turfs because macroalgae also accumulate sediments (e.g., Clausing et al.

2016); alternatively, the algal thallus could slow water movement and increase sedimentation. Further, we predicted nutrient addition would increase sediment accumulation as previously shown (e.g., Fong et al. 2018). Finally, we predicted nutrient addition and macroalgal presence would interact and effectively cancel each other out such that algal turf height and sediment depth would be similar to turfs without nutrients, in the absence of macroalgae.

Methods

We conducted a two-factor fully crossed experiment to examine the effects of nutrients (\pm slow-release fertilizer) and macroalgae (\pm presence of the brown macroalga *Padina boryana*) on algal turf growth over time (days from initial). This study took place April 23 to May 24, 2017 on a shallow (1–2 m) fringing reef (17.48°S, 149.48°W) near the mouth of Cook's Bay in Mo'orea, French Polynesia. This is a patch reef system that experienced a crown-of-thorns sea star (*Acanthaster planci*) outbreak (Adam et al. 2011) and now consists of dead *Porites lobata* colonies covered in turf and macroalgae interspersed among sand planes. We chose to model an overfished reef system because this is where algal–algal interactions are likely to be most important; therefore, we excluded herbivorous fishes from all treatments using cages. We haphazardly selected 40 25 × 25 cm plots of natural turf on the tops of dead coral colonies that lacked crevices and had a relatively flat surface. Plots were > 1 m apart to prevent spillover effects of nutrient additions (e.g., Fong et al. 2018). Each plot was haphazardly assigned to one of our four treatments (–nutrients/–macroalgae, –nutrients/+ macroalgae, +nutrients/–macroalgae, +nutrients/+ macroalgae, $n = 10$). Cages were 25 × 25 × 20 cm (length × width × height) and made of wire mesh with 1 cm² openings. We had a small strip (25 × 6 cm length × width) of wire mesh at the bottom of each cage, which left the remaining area of each plot uncovered by cage material. We used this strip to attach our nutrient and macroalgae treatments within our cages. In previous studies in this location, this caging material was shown to exclude herbivores with minimal caging artifacts, including no differences in water flow (Clausing et al. 2014). Though we do not have information on how these cages may have affected sedimentation, cages were used in all treatments, so any potential effect was equal across treatments.

For +nutrient treatments, we attached 30 g of slow-release fertilizer (Osmocote) in nylon bags to the center of the bottom strip of each experimental unit. For macroalgal treatments, we used *Padina boryana* due to its abundance on this fringing reef (Fong and Fong 2014). Macroalgal treatments were two 10 g (wet weight) subsamples of *P.*

boryana attached to the bottom strip of each experimental unit, which covered $\sim 25\%$ of the plot when quantified by photographs; however, the area affected by whiplash due to wave action was visually observed to affect approximately 75% of the plot area. We experienced a storm during our experiment that detached some of the *P. boryana*, which we replaced with new thalli.

Turf heights and sediment depths (measured to nearest 0.5 mm) were first measured on May 2, 2017 (day 1) and then every 6 d for 18 d using a wire mesh “comb” with teeth heights in 1 mm gradations (e.g., Fong et al. 2018). We measured these response variables in the sections of the plot that were not covered by the wire mesh strip to avoid potential abrasion. Due to increased within-plot variability over time, we increased the number of turf height and sediment depth measurements done per plot from 6 to 12 on day 12 and used average height or depth per plot as our response variable.

To account for initial differences in turf height, we calculated the difference in average turf height for each plot from each time point (day 6, 12, and 18) to day 1 (initial) turf heights. For sediment depths, we also calculated the difference in average sediment depth for each plot from each time point (day 6, 12, and 18) to day 1 (initial) sediment depths. We ran linear mixed-effects models on difference in turf height and difference in sediment depth. We included nutrients (\pm), macroalgae (\pm), and day (6, 12, 18) as fixed effects and plot as a random effect in the full model. After running the initial full model, we simplified the model to the lowest possible value of Akaike Information Criterion. We used ANOVAs to ensure model simplification did not lose significant terms. We performed all statistical analyses using R (R Core Team 2016), and we used the “nlme” (Pinheiro et al. 2016) library for fitting linear mixed models (LMMs).

One plot (+nutrients/+macroalgae) was excluded from all statistical analyses since it became a damselfish territory. Two plots (both +nutrients/+ macroalgae) were not located for turf height day 18 measurements but were still included in statistical analyses for days 6 and 12. Our final sample sizes were $n = 9$ for days 1, 6, 12 and $n = 7$ for day 18 for the +nutrients/+ macroalgae treatment and $n = 10$ for the remaining three treatments ($N = 39$).

Results and discussion

Initial turf height and sediment depth were 1.4 ± 0.1 mm and 0.3 ± 0.1 mm (mean \pm SE), respectively. Nutrients and macroalgae did not interact to affect turf height and were not included in the final model (Table S1). The independent effects of nutrient addition and macroalgal presence on turf height developed over time (Table S1,

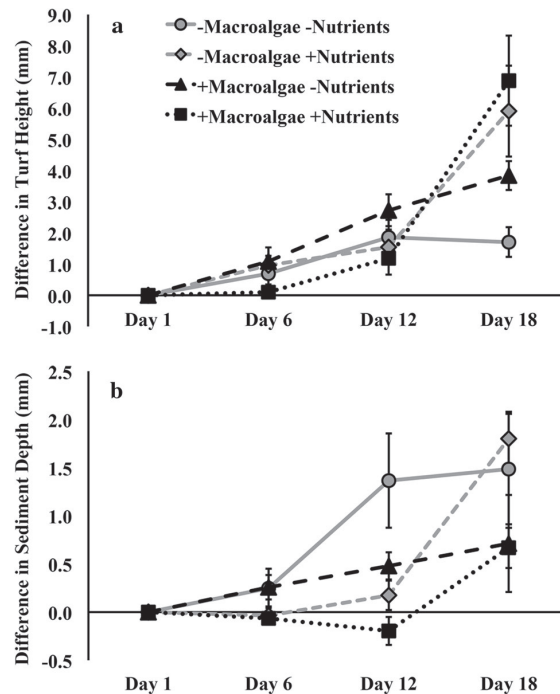


Fig. 1 Difference in turf height (a) and sediment depth (b) (mm mean \pm SE) from day 1 for each time point (days 6, 12, 18)

Fig. 1a). Turf height was not affected by nutrient addition or macroalgal presence until day 18, when both had significant positive effects (day18*nutrients added $t = 5.264$, $df = 68$, $p < 0.0001$; day18*macroalgae present $t = 2.272$, $df = 68$, $p = 0.026$). By day 18, nutrient addition increased algal turf height by 127% compared to turf without nutrient addition, regardless of macroalgal treatment. Macroalgal presence increased algal turf height by 34% compared to the absence of macroalgae, regardless of nutrient treatment.

Nutrients and macroalgae also did not interact to affect sediment depth and were not included in the final model (Table S2). The independent effects of nutrient addition and macroalgal presence on sediment depth also developed over time (Table S2, Fig. 1b). On day 12, nutrient addition significantly and independently decreased sediment depth by 100%, regardless of macroalgal treatment ($t = -3.095$, $df = 68$, $p = 0.003$). However, this effect was transient and by day 18 sediment depth was no longer affected by nutrient addition ($t = 0.481$, $df = 68$, $p = 0.632$). In contrast, macroalgal presence had an independent and significant negative effect on sediment depth on day 12 ($t = -2.093$, $df = 68$, $p = 0.040$) and this effect persisted until and strengthened on day 18 ($t = -3.004$, $df = 68$, $p = 0.004$). Macroalgal presence decreased sediment depth by 79% and 58% on days 12 and 18, respectively,

compared to turf in the absence of macroalgae, regardless of nutrient treatment.

We discovered a novel facilitation between macroalgae and algal turf that may promote shifts from short, healthy turf to a longer, less desirable turf state as we found that macroalgae enhanced turf growth. This facilitation contrasts with theoretical predictions that algae, as primary producers, should compete for shared resources such as space, light, and nutrients (Fong and Paul 2011). One possible explanation for the macroalgal-driven facilitation of algal turf growth is that the associated macroalgae may recycle limiting nutrients (Fong and Paul 2011). Macroalgal presence may have also facilitated algal turf growth through reduction of sediment accumulation. Sediment can inhibit turf growth, in some cases leading to anoxia (Clausing et al. 2014); therefore, in the absence of herbivory, where sediments' protective function is negated (e.g., Bellwood and Fulton 2008; Goatley and Bellwood 2013), less sediment accumulation likely has a positive effect on turf growth. In contrast to our results, two studies in a temperate intertidal zone found negative effects of canopy-forming macroalgae on turf algae (Kim 2002; Kim et al. 2004), most likely due to shading (Kim 2002). Negative effects due to shading were unlikely in our study because our experiment occurred in shallow tropical water where light availability was likely extremely high. Macroalgae vary widely in size, morphology, toughness, and chemical defenses (Fong and Paul 2011), which could also explain why our results differ from those of Kim (2002) and Kim et al. (2004). Although macroalgal presence did not result in sediment-laden algal turfs, which are suggested as an alternative stable state (e.g., Bellwood and Fulton 2008; Goatley and Bellwood 2013; Goatley et al. 2016), it increased algal turf growth and high turf cover is indicative of reef degradation (Smith et al. 2016). Thus, macroalgal facilitation of turf growth could lead to a transition from short, cropped turfs, which are part of healthy coral reef systems, into longer turfs or macroalgae.

Although our experiment was done in the absence of herbivory, it is useful to consider how this macroalgal facilitation could manifest in natural reef settings in the presence of herbivores. Some research indicates herbivory is reduced near large stands of macroalgae (Hoey and Bellwood 2011); thus, our observed facilitative effect of macroalgae on turfs may also occur in the presence of herbivorous fish. However, some macroalgae are highly palatable and are readily consumed by herbivorous fish. Thus, if herbivorous fish recover (e.g., following a disturbance) and the macroalgae present are highly palatable, the herbivores may readily consume the macroalgae, leaving the underlying turf exposed. This could also result in consumption of the underlying long algal turfs, too, since macroalgal presence reduces sediment accumulation on the

turf and herbivory is higher on turfs with less sediments (Bellwood and Fulton 2008; Goatley and Bellwood 2013). Therefore, the effect of macroalgae on turf algae in the presence of herbivores will likely depend upon the identity of macroalgae present, with palatable macroalgae likely leading to recovery of short algal turfs, but unpalatable and dense macroalgae possibly leading to a positive feedback stabilizing an algal-dominated state.

Our results suggest that either macroalgal presence or nutrient addition may lead to positive feedbacks that further stabilize an algal-dominated state in coral reefs as these factors acted independently to increase algal turf growth. Of these two factors, nutrient addition is more likely to result in a positive feedback because it both increased turf growth and maintained the same amount of sediment accumulation that occurs without added nutrients. Since sediments inhibit herbivore feeding on algal turfs (Bellwood and Fulton 2008; Goatley and Bellwood 2013), this could lead to persistence of an algal-dominated state. Our lack of a significant interaction between nutrients and macroalgal presence on turf growth contradicts a vast literature that finds significant interactions between multiple stressors in coral reef habitats (Burkepile and Hay 2006; Crain et al. 2008; Fong et al. 2018). The lack of interaction may be because we eliminated herbivory as a factor, and it is herbivory that drives many interactions (e.g., Burkepile and Hay 2006). This may suggest that interactions or "ecological surprises" may be reduced on overfished reefs. Therefore, reefs already in transition to an algal-dominated environment due to some disturbance, i.e., overfishing, must be carefully monitored for introduction of nutrients that will only exacerbate algal dominance, since nutrient enrichment allows turfs to overgrow neighboring coral (Vermeij et al. 2010). Furthermore, macroalgal presence alone enhanced algal turf growth, which means the development of a positive feedback cycle is possible since turf is a multispecies assemblage including juvenile macroalgae (Littler and Littler 2013). Similarly, another study found a facilitative effect of one macroalga on another by providing a refuge from herbivory, which allowed the second macroalga to persist and contributed to a shift to an algal-dominated reef (Roff et al. 2015). Coral reefs experiencing macroalgal blooms and/or nutrient inputs are at risk of perpetuating an algal-dominated state on coral reefs through their independent and positive effects on algal turf.

Acknowledgements We thank the government of French Polynesia for permitting this research and the UC Berkeley Richard B. Gump South Pacific Research Station for providing laboratory space and housing. This material is based upon work supported in part by UCLA's Department of Ecology and Evolutionary Biology and Office of Instructional Development, the National Science Foundation Graduate Research Fellowship Program (Sura) under Grant No.

1144087, the National Council for Scientific and Technological Development of Brazil (Turba) under Grant No. 209261/2014-5, the A.R. Wallace Scholarship for International Field and Marine Research (Franco), and the Academic Affairs Commission (Franco).

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states there is no conflict of interest.

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APPENDICES

Chapter 1 Supplement

Supplement for Sura SA, Molina NE, Blumstein D, & Fong P. (2021) Selective consumption of macroalgal species by herbivorous fishes suggests reduced functional complementarity on a fringing reef in Moorea, French Polynesia. Journal of Experimental Marine Biology and Ecology. 536: 151508. doi.org/10.1016/j.jembe.2020.151508.

Table S1. Generalized linear mixed-effects models (GLMM) for two models that best predicted the number of bites fish took on macroalgae: a) number of bites ~ macroalgae + fish species, and b) number of bites ~ macroalgae + fish functional group. For a) the reference groups for the intercept are *Acanthophora spicifera* (macroalgae) and *Acanthurus nigrofuscus* (fish species). For b) the reference groups for the intercept are *Acanthophora spicifera* (macroalgae) and Browser (fish functional group). For both models, there were 201 fish visits, resulting in 1407 data points (one data point for each of seven macroalgal species for each fish visit). Asterisks indicate the following: * <0.05 ; ** <0.01 ; *** <0.001 .

| a) | Value Estimate | Standard Error | z-value | p-value |
|-------------------------------|----------------|----------------|---------|-----------|
| (Intercept) | -0.851 | 0.392 | -2.169 | 0.030* |
| <i>Dictyota sp.</i> | -0.274 | 0.331 | -0.826 | 0.409 |
| <i>Galaxaura sp.</i> | -1.370 | 0.438 | -3.128 | 0.002** |
| <i>Halimeda sp.</i> | -2.207 | 0.523 | -4.216 | <0.001*** |
| <i>Padina boryana</i> | 3.559 | 0.342 | 10.419 | <0.001*** |
| <i>Sargassum mangarevense</i> | 2.219 | 0.338 | 6.574 | <0.001*** |
| <i>Turbinaria ornata</i> | -1.070 | 0.414 | -2.583 | 0.009** |
| <i>Balistapus undulatus</i> | 0.347 | 0.380 | 0.914 | 0.361 |
| <i>Calotomus carolinus</i> | -1.877 | 0.369 | -5.089 | <0.001*** |
| <i>Chlorurus sordidus</i> | 0.076 | 0.618 | 0.123 | 0.902 |
| <i>Ctenochaetus striatus</i> | 1.231 | 0.479 | 2.571 | 0.010* |
| <i>Naso lituratus</i> | -1.585 | 0.353 | -4.485 | <0.001*** |
| <i>Naso unicornis</i> | -1.962 | 0.525 | -3.735 | <0.001*** |

b)

| | Value Estimate | Standard Error | z-value | p-value |
|----------------------------------|---------------------------|---------------------------|----------------|----------------|
| (Intercept) | -2.561 | 0.300 | -8.553 | <0.001*** |
| <i>Dictyota sp.</i> | -0.263 | 0.330 | -0.796 | 0.426 |
| <i>Galaxaura sp.</i> | -1.184 | 0.420 | -2.817 | 0.005** |
| <i>Halimeda sp.</i> | -2.021 | 0.502 | -4.026 | <0.001*** |
| <i>Padina boryana</i> | 3.540 | 0.340 | 10.409 | <0.001*** |
| <i>Sargassum mangarevense</i> | 2.184 | 0.338 | 6.465 | <0.001*** |
| <i>Turbinaria ornata</i> | -1.066 | 0.411 | -2.592 | 0.009** |
| Grazer / Detritivore | 2.168 | 0.309 | 7.006 | <0.001*** |
| Scraper / Small Excavator | 1.785 | 0.563 | 3.169 | 0.002** |
| Unclassified | 2.034 | 0.296 | 6.881 | <0.001*** |

Chapter 2 Supplement

| Table S1. Equations for the basic model adapted from van de Leemput et al. 2016, with the state variables and parameters listed below. | | | |
|---|--|---|------------------|
| $S = 1 - C - A$ | | $\frac{dA}{dt} = (i_A + b_A A)S - \frac{g_A A H}{g_A \eta_A A + 1}$ | |
| $\frac{dC}{dt} = (i_C + b_C C)S(1 - \alpha_A A) - d_C C$ | | $\frac{dH}{dt} = rH(1 - \frac{H}{(1 - \sigma) + \sigma C}) - fH$ | |
| State Variables: | | Initial Condition Values: | |
| S = unoccupied space C = coral cover A = algal cover H = herbivore proportion | | S0 = 0.15 C0 = 0.75 A0 = 0.1 H0 = 0.9 | |
| Parameters (<i>units not specified by van de Leemput et al. 2016</i>): | | Values: | |
| <i>i</i> | import of propagules | $i_C = 0.05$ | $i_A = 0.05$ |
| <i>b</i> | expansion of existing adults (which is proportional to existing cover) | $b_C = 0.3$ | $b_A = 0.8$ |
| <i>d</i> | mortality of coral (constant decay rate) | $d_C = 0.1$ | |
| <i>g</i> | mortality of algae (constant grazing rate per herbivore) | | $g_A = 1$ |
| <i>r</i> | growth rate of herbivores | $r = 1$ | |
| <i>f</i> | herbivore mortality (constant fishing pressure) | $f = 0.1$ | |
| <i>η</i> | algal handling time of herbivores | | $\eta_A = 1$ |
| <i>α</i> | competition effect of algae on coral recruitment and growth | | $\alpha_A = 0.5$ |
| <i>σ</i> | strength of relationship between coral cover and herbivore carrying capacity | $\sigma = 0.6$ | |

Methods

Basic Model Analyses

Recreating Figure 3e from van de Leemput et al. (2016)

We used the model equations, initial conditions, and parameter values (Table S1) from van de Leemput et al. (2016) to reconstruct their model. We tested our model by replicating their Figure 3e. To recreate this figure, we examined the model for hysteresis by using simulations of increasing and decreasing fishing pressure and determining the tipping points where the coral reef system switches from one stable state to another. Specifically, for the “forward” simulations, we increased fishing pressure from 0 – 1 in 0.005 increments, and for the “reverse” simulations, we decreased fishing pressure from 1 – 0 in 0.005 increments. We ran each simulation for 1000 years to ensure the system reached equilibrium. For each fishing pressure, we used the end conditions for the state variables from the previous fishing pressure as the initial conditions for the next fishing pressure.

Testing for bistability of the basic model

Because we are also interested in bistability, we wanted to determine what levels of fishing pressure cause bistability in the basic model. Bistability in our model is indicated by the final coral cover being split between coral dominated (>0.6 coral cover) and algal dominated (<0.2 coral cover) equilibrium states for the same level of fishing pressure, but dependent upon initial coral cover conditions. To test for bistability, we ran the model for 1000 years with 100 different initial coral covers (0 – 1 in increments of 0.01) and 100 different fishing pressures (0 – 1 in increments of 0.01), using the initial conditions and parameter values from van de Leemput et al. (2016) and listed in Table S1.

Expanded Model Analyses

Justification for expanded model parameter values

Our 5 Assumptions:

1. No handling time for turf algae ($\eta_T = 0$).

Justification: We assume no handling time for turf algae because turf algae are highly productive, consumed by many herbivores, and lack physical and chemical defenses, commonly found in macroalgae, that reduce herbivory (Littler et al. 1983, Steneck and Dethier 1994).

2. Expansion of existing macroalgae is slower than expansion of turf algae ($b_M < b_T$).

Justification: We assume expansion is slower for macroalgae compared to turf algae because turf algae are highly productive (Carpenter 1985, Hatcher 1988, Klumpp and McKinnon 1992) and typically have higher productivity than macroalgae (e.g. Littler et al. 1983, Steneck and Dethier 1994).

3. No importation of macroalgal propagules because it grows from turf ($i_M = 0$).

Justification: We assume there is no importation of macroalgal propagules because we define turf algae as sparse to thick mats containing an assemblage of fast-growing filamentous algae and juvenile macroalgae that are cropped short by herbivores (Littler and Littler 2011a). Thus, macroalgae, which are an assemblage of erect, fleshy algae typically > 2 cm tall (Littler and Littler 2011b), grow from turf algae as represented in our model.

4. Mortality of turf due to herbivory is higher than mortality of macroalgae due to herbivory ($g_T > g_M$).

Note: In our model mortality of turf and macroalgae refers to reductions in their benthic cover because their populations are modeled as proportions of benthic space.

Justification: We assume higher mortality due to herbivory for turf algae compared to macroalgae because macroalgae often have chemical and/or physical defenses, which reduce herbivory (Fong and Paul 2011). Functional form models also predict that turf algae are more susceptible to herbivory than macroalgae (Littler et al. 1983, Steneck and Dethier 1994).

5. Competitive effect of macroalgae on coral is higher than competitive effect of turf on coral ($\alpha_M > \alpha_T$).

Justification: We make this assumption because the settlement of coral larvae may or may not be reduced by turf algae, depending on the type of turf and presence or absence of sediment trapped by the turf (Fong and Paul 2011). In contrast, macroalgae is predominantly thought to inhibit settlement of coral larvae (McCook et al. 2001, Fong and Paul 2011). Furthermore, macroalgae has more mechanisms than turf (filamentous) algae to out-compete coral, including allelopathy, overgrowth, shading, and abrasion (McCook et al. 2001).

Supplement Figures

Figure S1. Hysteresis plot from van de Leemput et al. (2016) (panel a), and our recreation of it using their equations, initial conditions, and parameter values coded in R (panel b). Blue, red, and green lines represent herbivores, coral, and algae, respectively.

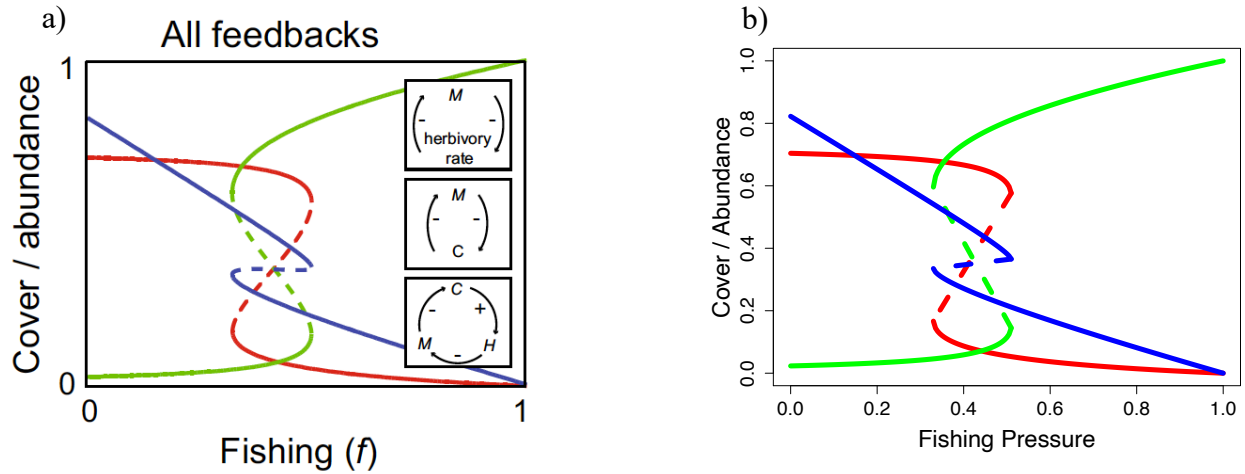


Figure S2. Bistability plot of basic model for a range of fishing pressures and initial coral cover values at the start of a simulation. Each simulation of the model was run for 1000 years.

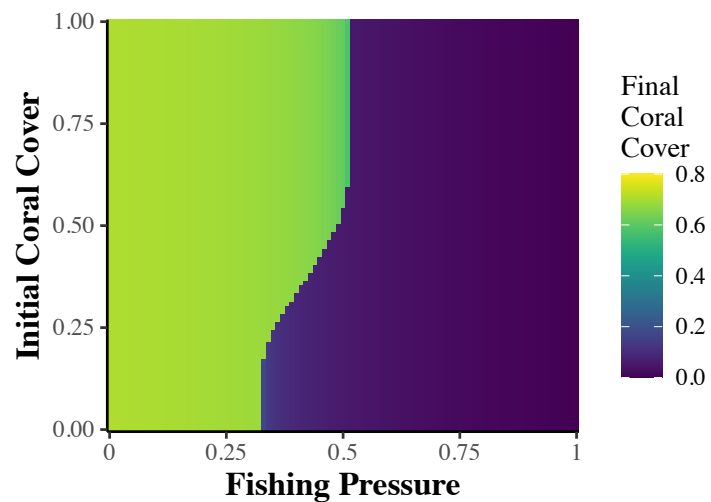


Figure S3. Heatmaps showing how the initial abundance of grazer and browser herbivorous fish affect the final coral cover after 1000 years for fishing pressures ranging from 0 to 0.7 (rows) and for initial generalist abundances set to 0, 0.2, or 0.4 (columns). Other initial conditions include $C_0 = 0.15$, $T_0 = 0.1$, and $M_0 = 0$.

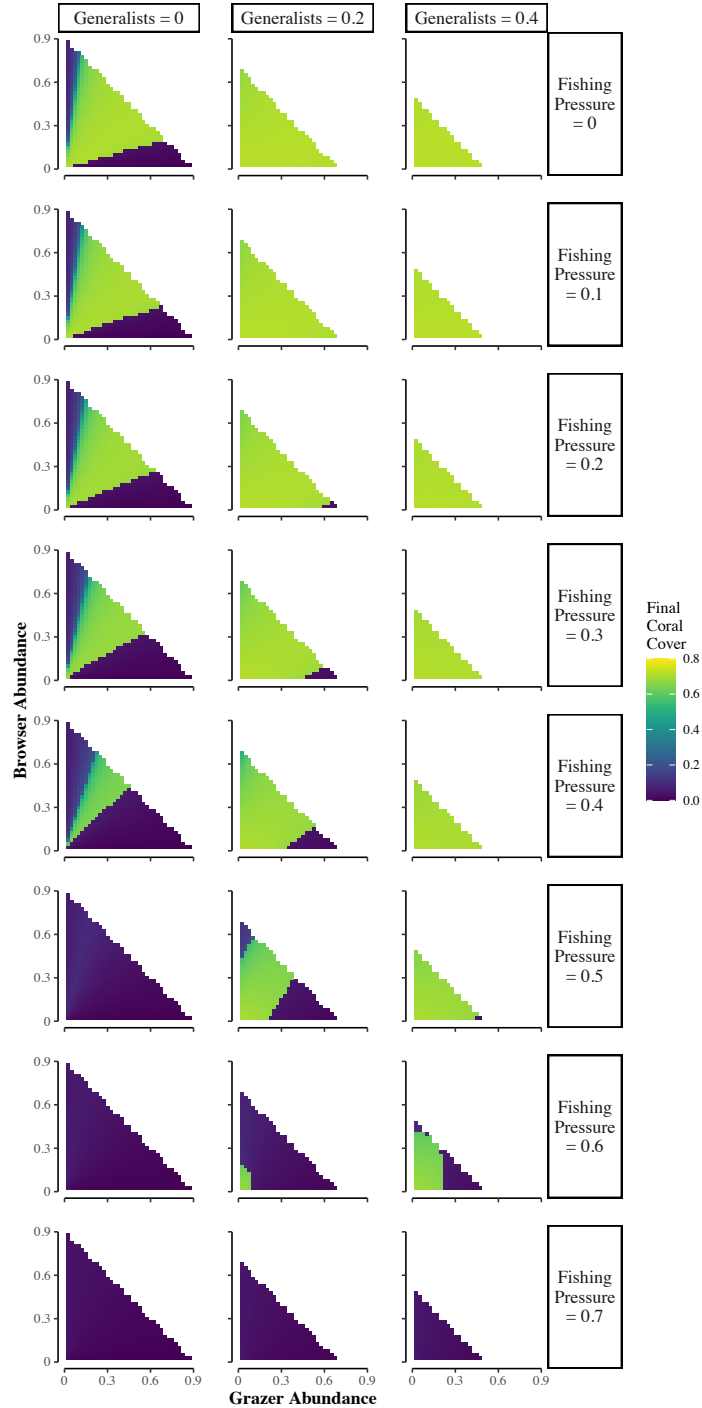


Figure S4. Heatmaps showing how the initial cover of turf and macroalgae affects the final coral cover after 1000 years for fishing pressures ranging from 0 to 0.7 (rows) and for initial coral covers set to 0.15, 0.35, 0.55, and 0.75 (columns). Initial herbivore abundances each set to 0.3.

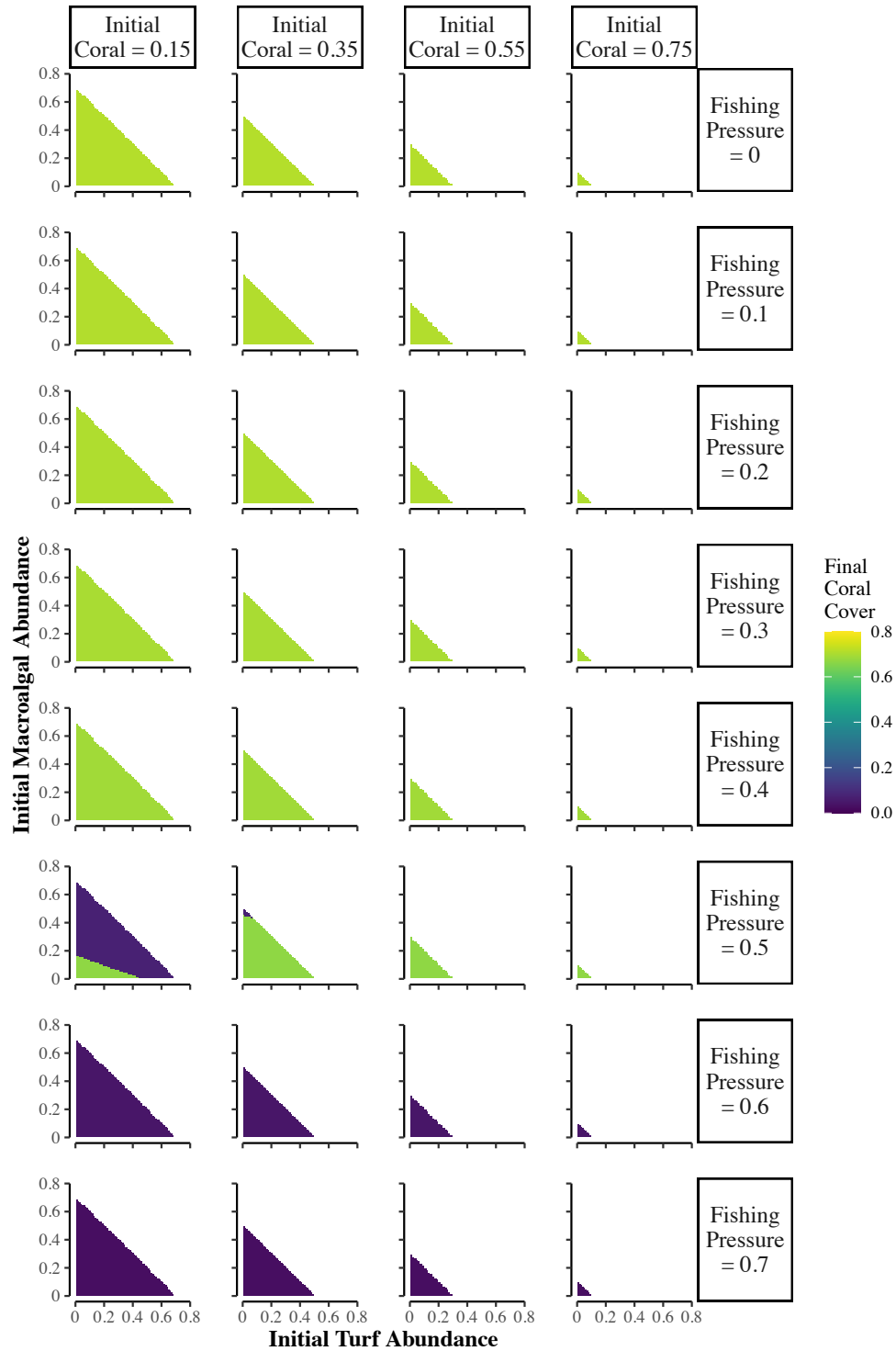
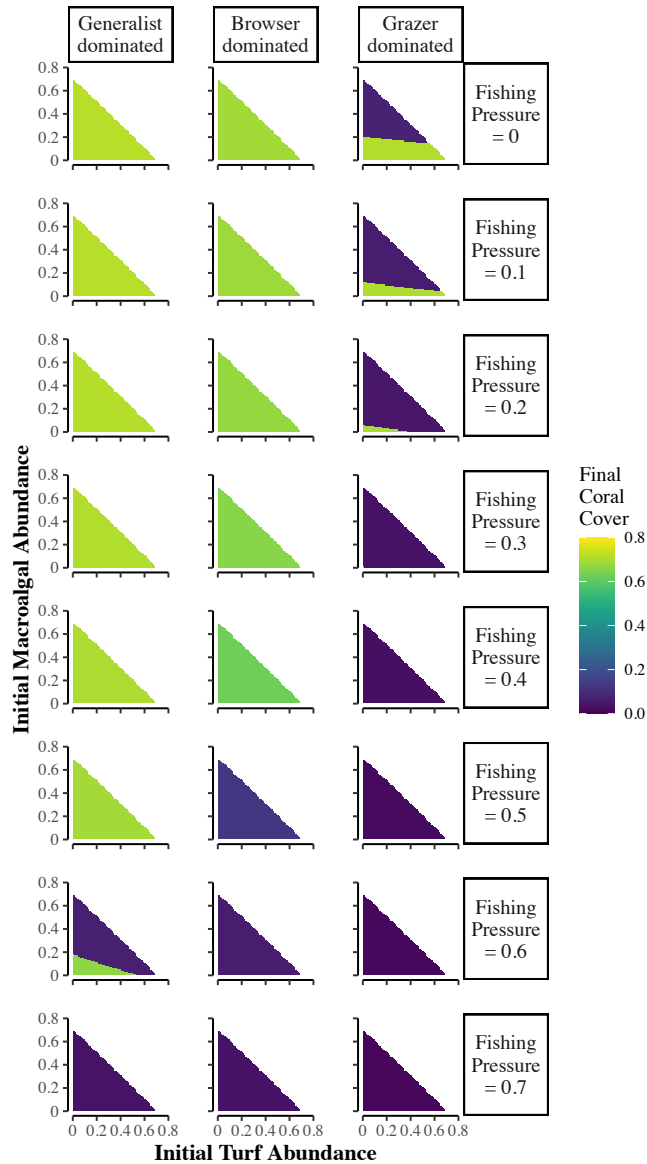


Figure S5. Heatmaps showing how the initial cover of turf and macroalgae affects final coral cover after 1000 years for fishing pressures from 0 to 0.7 (rows) and for initial herbivore abundances set to 1 of 3 scenarios (columns): 1) **high generalists**: generalists = 0.6, grazers = 0.15, browsers = 0.15; 2) **high browsers**: browsers = 0.6, generalists = 0.15, grazers = 0.15; or 3) **high grazers**: grazers = 0.6, generalists = 0.15, browsers = 0.15. Total initial benthic cover is restricted to ≤ 0.85 , and initial coral cover (C_0) = 0.15; therefore, the amount of unoccupied space changes for each combination of initial turf and macroalgae abundance.



Chapter 3 Supplement

Supplement for 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.

doi:10.1007/s00338-019-01793-w

Table S1. Linear mixed model of minimum adequate model for difference in turf height.

| | Value | Standard Error | df | t-value | p-value |
|----------------------------------|--------|----------------|----|---------|-------------------|
| (Intercept) | 0.994 | 0.577 | 68 | 1.722 | 0.090 |
| Day 12 | 1.165 | 0.616 | 68 | 1.892 | 0.063 |
| Day 18 | 0.995 | 0.621 | 68 | 1.693 | 0.114 |
| Day 6*Nutrients Added | -0.340 | 0.672 | 68 | -0.506 | 0.615 |
| Day 12*Nutrients Added | -0.914 | 0.672 | 68 | -1.359 | 0.179 |
| Day 18*Nutrients Added | 3.628 | 0.689 | 68 | 5.264 | <0.0001 |
| Day 6*Macroalgae Present | -0.217 | 0.672 | 68 | -0.323 | 0.747 |
| Day 12*Macroalgae Present | 0.270 | 0.672 | 68 | 0.402 | 0.689 |
| Day 18*Macroalgae Present | 1.566 | 0.689 | 68 | 2.272 | 0.026 |

Table S2. Linear mixed model of minimum adequate model for difference in sediment depth.

| | Value | Standard Error | df | t-value | p-value |
|----------------------------------|--------|----------------|----|---------|------------------|
| (Intercept) | 0.257 | 0.260 | 68 | 0.988 | 0.327 |
| Day 12 | 0.982 | 0.304 | 68 | 3.233 | 0.002 |
| Day 18 | 1.310 | 0.306 | 68 | 4.282 | <0.001 |
| Day 6*Nutrients Added | -0.303 | 0.303 | 68 | -0.9998 | 0.321 |
| Day 12*Nutrients Added | -0.939 | 0.303 | 68 | -3.095 | 0.003 |
| Day 18*Nutrients Added | 0.150 | 0.312 | 68 | 0.481 | 0.632 |
| Day 6*Macroalgae Present | -0.009 | 0.303 | 68 | -0.030 | 0.976 |
| Day 12*Macroalgae Present | -0.635 | 0.303 | 68 | -2.093 | 0.040 |
| Day 18*Macroalgae Present | -0.937 | 0.312 | 68 | -3.004 | 0.004 |