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Processes that promote resilience of coral reef systems: How dynamics of fishing and herbivory alter coral-algal interactions

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# Processes that promote resilience of coral reef systems: How dynamics of fishing and herbivory alter coral-algal interactions

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

by

Dana Toshi Cook

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September 2023

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Holbrook, S.J., Wencélius, J., Dubel, A.K., Adam, T.C., Cook, D.T., Hunter, C.E., Lauer, M., Lester, S.E., Miller, S.D., Rassweiler, A., and Schmitt, R.J. (2022). Spatial covariation in nutrient enrichment and fishing of herbivores in an oceanic coral reef ecosystem. Ecological Applications 32(3): e2515.

Kopecky, K.L., Cook, D.T., Schmitt, R.J., A.C. Stier. (2021). Effects of corallivory and coral colony density on coral growth and survival. Coral Reefs 40: 283-288.

Kamath, A., Pruitt, J.N., Brooks, A.J., Ladd, M.C., Cook, D.T., Gallagher, J.P., Vickers, M.E., Holbrook, S.J. and Schmitt, R.J. (2019). Potential feedback between coral presence and farmerfish collective behavior promotes coral recovery. Oikos 128: 482-492.

### *In Preparation*

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Cook, D.T., Schmitt, R.J., and Holbrook, S.J. Patterns of spatial covariation in herbivore functions on coral reefs: Implications for reef resilience.

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# ABSTRACT

## Processes that promote resilience of coral reef systems: How dynamics of fishing and herbivory alter coral-algal interactions

by

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The worldwide degradation of coral reef systems often is associated with shifts of the benthic community from coral- to macroalgal-dominance. Transitions to macroalgal-dominance, especially those that are maintained by stabilizing feedbacks, can have profound societal implications, prompting considerable interest in the predictability and reversibility of these undesired shifts. Herbivory by fishes is a key ecological process that can prevent an undesired shift to macroalgae and/or facilitate a return to coral-dominance. Herbivorous fishes are harvested in many small-scale fisheries, setting up the potential for fishers to alter coral-macroalgae interactions and the resilience of alternative reef states. However, in this context, macroalgae, herbivorous fishes, and fishing are often considered as monolithic groups despite the potential for substantial, species-specific differences in their influence. For example, macroalgae species vary in traits that influence growth rates, herbivores vary in their dietary preferences, and fishers can differentially target species of herbivorous fishes.

My dissertation research examines the intricacies of these influences in the context of abrupt (non-linear) ecosystem shifts and the resilience of coral reefs. I first applied the competition – palatability paradigm from plant – herbivore theory to assess how the attributes of macroalgae influence their vulnerability to trophic and competitive interactions, and in turn, can strengthen or weaken feedbacks stabilizing a macroalgae state. My second research focus was motivated by the recognition that different functional groups of herbivores play two distinct but complementary roles in controlling macroalgae on coral reefs; grazers can prevent the establishment of macroalgae, but only browsers can remove mature macroalgae. Consequently, I explored how spatial covariation in grazing and browsing rates is linked to the prevention and reversibility of shifts to macroalgae at the local reef scale. Notably, grazing and browsing herbivores have different life history attributes that make them differentially susceptible to overexploitation from fishing. Thus, as a third research focus, I modeled how selective fishing on grazing or browsing herbivores influences the non-linear dynamics of shifts between coral and macroalgae states. My findings provide deeper understanding into key ecological processes and attributes that shape non-linear dynamics of the benthic community on coral reefs and can inform spatially-explicit management strategies to enhance coral resilience in our rapidly changing world.

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# Chapter I: The influence of competition – palatability trade-offs among macroalgae on the reversibility of coral-to-macroalgae regime shifts

## *Introduction*

A regime shift is a persistent, often abrupt transition to a qualitatively different ecosystem state that is maintained by a new set of ecological feedbacks (Hughes 1994, Steneck et al. 2002, Scheffer and Carpenter 2003, Folke et al. 2004, Nystrom et al. 2012). Such wholesale change can have profound societal consequences when the new state provides fewer or less valuable ecosystem goods and services (Graham et al. 2013). This has prompted considerable interest in the reversibility of undesired shifts. In this context, a particularly challenging case is when stabilizing feedbacks strongly reinforce the alternative state because a return to the original community requires those feedbacks to be interrupted, such as by extensive relaxation in underlying ecological drivers, far past the original tipping point, or by a pulse disturbance large enough to trigger a 'state tip' back to the previous state (Suding et al. 2004, Petersen et al. 2008, Rassweiler et al. 2010, Nystrom et al. 2012, Davis 2018, Schmitt et al. 2019, Kopecky et al. 2023). Thus, understanding reversibility requires knowledge of how ecological processes influence the feedbacks that maintain an ecosystem in a given state, which in turn can inform management strategies to reverse undesired regime shifts.

Although regime shifts have occurred in a wide variety of ecosystems (Scheffer and Carpenter 2003, Folke et al. 2004), many have involved some form of vegetation in both terrestrial and aquatic ecosystems (Rassweiler et al. 2010, Hirota et al. 2011, D'Odorico et al. 2012, Gaertner et al. 2014, Guo et al. 2017, Schmitt et al. 2019). There is a rich theoretical and empirical literature on how competitive and trophic interactions shape the dynamics and composition of vegetation based on the notion that plant species trade off the ability to compete and the capacity to withstand herbivory (McCauley and Briand 1979, Holt et al. 1994, Viola et al. 2010). A fundamental tenet in plant-herbivore theory is that a trade-off between competitive ability and palatability arises from the allocation of energy to either faster growth or enhanced defenses (Coley et al. 1985, Simms and Rausher 1987, Herms and Mattson 1992, Pacala and Crawley 1992, Rees et al. 2001). Species that grow faster in the absence of their consumers are believed to do so because of a disproportionate investment in growth over defense, which in turn makes these palatable species more vulnerable to herbivory (Coley et al. 1985, Simms and Rausher 1987, Herms and Mattson 1992, Pacala and Crawley 1992, Rees et al. 2001). Thus, while palatable species can outcompete slower-growing, better defended species when herbivory is sufficiently low, density- or frequency-dependent herbivory can maintain species richness of the plant community, and preferential feeding by herbivores can shift the composition of the community to unpalatable plants (Rees et al. 2001, Viola et al. 2010). As such, the competition – palatability trade-off has been invoked to explain patterns of species composition, coexistence and biodiversity in plant communities (Rees et al 2001, Viola et al. 2010). Here we explore an additional manifestation of the competition – palatability tradeoff by asking how it influences the resilience and reversibility of a regime shift to an undesired vegetated state.

Coral reefs, our study system, provide vast ecosystem goods and services to millions of people (Hughes et al. 2003). Increasingly, reef tracts throughout the global distribution of reef-forming coral have shifted from coral to macroalgae (Gardner et al. 2003, Bruno and Selig 2007, Ledlie et al. 2007, Roff and Mumby 2012, Schmitt et al. 2019) or, in some cases, to another non-coral state (Graham et al. 2014). There is compelling evidence that coral and macroalgae can be alternative stability basins (Mumby et al. 2007, 2013, Steneck et al. 2014, Muthukrishnan et al. 2016, Briggs et al. 2018, Schmitt et al. 2019, 2022, Cook et al. *in review*), although the conditions that give rise to hysteresis in underlying driver – response relationships for these major space holding groups are not well understood (Schmitt et al. 2019, 2022). Hysteresis creates a region of bistability over some range of an underlying driver (e.g., herbivory), and the reversibility of a regime shift is influenced by the magnitude of hysteresis (Suding et al. 2004, Kopeckey et al. 2023). In a model of macroalgae-coral dynamics (Briggs et al. 2018), the magnitude of hysteresis increased with declining vulnerability of the plants to herbivory. The few examples from a variety of coral reef systems collectively suggest an undesired shift to macroalgae might be more readily reversed when the vegetated state is composed of palatable (i.e., highly vulnerable) macroalgae (Bellwood et al. 2006, Muthukrishnan and Fong 2018) (Bellwood et al. 2006, Muthukrishnan and Fong 2018) compared to more heavily defended species (Holbrook et al. 2016, Schmitt et al. 2019, 2022). Thus, the capacity of trophic interactions to reverse a coral to macroalgae state shift is likely influenced by the composition of the vegetated community, which in turn might be shaped by a competition – palatability tradeoff. This knowledge could inform feasible management actions, such as harnessing competition in addition to trophic interactions to interrupt the feedbacks that maintain an undesired vegetated state.

Here we focus on a well-studied lagoon reef system, where bistability of coral and macroalgae has been demonstrated through *in situ* hysteresis and stability experiments (Schmitt et al. 2019, 2022), to understand how herbivory and competition shape resilience of the macroalgae state. Specifically, we sought evidence that: (1) the three main space-holding species of macroalgae in our system trade off competitive ability and palatability; (2) the trade-off influences both the abundance and composition of the macroalgae community on lagoon reefs; and (3) the interplay between competitive and trophic interactions has a predictable effect on the ability of herbivores to reverse a coral-to-macroalgae regime shift.

## ***Methods***

### *Study site and study organisms*

Field work was conducted in the lagoons on the north shore of Moorea, French Polynesia (17°30’ S, 149°50’ W), where a barrier reef ~1 km offshore protects the shallow lagoons from the open ocean. Back reef habitats just inshore of the barrier reef consist mainly of contiguous reef substrate, which then transitions into patch reefs (bommies) surrounded by sand in the mid-lagoon. Mid-lagoon patch reefs are highly variable with respect to cover of coral, macroalgae, cropped turf algae, and other taxa. The shallow fringing reefs adjacent to shore can be separated from the mid-lagoon by deep channels. Water circulation within the lagoon is driven by waves forcing water over the crest of the barrier reef, through the lagoons, and out the passes (Leichter et al. 2013).

Reefs of Moorea typically have high abundances of herbivorous fishes, which are the dominant herbivore in this system (as opposed to sea urchins) (Adam et al. 2011, Holbrook et al. 2016). We focused on the ‘browsing’ functional group of herbivorous fishes as they are the only fishes in the system capable of removing established macroalgae (Han et al. 2016, Gil et al. 2017, Schmitt et al. 2022). Time-series data reveal that disturbed patch reefs can either return to the coral state or transition to a macroalgal state where the brown fucoid *Turbinaria ornata* becomes the dominant space holder (Schmitt et al. 2019, 2022). *Turbinaria* ontogenetically develops structural and chemical defenses (Stiger et al. 2004), becoming resistant to herbivory once the stipes reach 2 cm in length (Davis 2018). Adults can therefore provide an associational refuge to younger life stages, which creates a positive feedback reinforcing the highly resilient *Turbinaria* state (Davis 2018). Although less abundant, two other species of macroalgae frequently co-occur with *Turbinaria* in Moorea – the fucoid *Sargassum pacificum* and the red alga *Amansia rhodantha.* Some existing evidences suggests that herbivorous fishes may prefer *Sargassum* and *Amansia* over *Turbinaria* (Bellwood et al. 2006, Mantyka and Bellwood 2007, Hoey and Bellwood 2009, Chan et al. 2012, Gil et al. 2017), which we explicitly test here.

### *Ranking herbivore preference for focal macroalgae*

To quantify herbivore preference for the 3 space-holding macroalgae (*Turbinaria ornata, Sargassum pacificum, Amansia rhodantha*), we conducted two different assays on reefs in the mid-lagoon. In both cases, three 10-cm long stipes of algae were either exposed to herbivores or placed within an herbivore-exclusion cage (as a handling control) for 48 hrs, after which the amount remaining was quantified. The two types of assays were single species presentations (3 stipes of one species) to measure the amount consumed in the absence of other macroalgae, or mixed species presentations (1 stipe of each of the three species) to quantify herbivore choice when all 3 species were encountered simultaneously. Replicates were affixed to a chain laid on open substrate (lacking coral or macroalgae) on the top of patch reefs (single-species assays exposed to herbivores: N = 7 replicates per species, mixed species assay exposed to herbivores: N = 20 replicates; handling controls: single-species assays: N = 3 replicates per species, mixed species assay: N=10 replicates). Replicates were separated spatially by at least 3 m. Single-species and mixed-species assays were conducted at the same mid-lagoon site one month apart. The damp weight (g) of each stipe was recorded before and after deployment to calculate percent consumption. For single-species assays, the values for the three stipes deployed together were averaged for each replicate and then replicates were averaged for each species and herbivory treatment (exposed to or protected from herbivores). For mixed-species assays, replicate values were averaged for each species and herbivory treatment. The average percent consumption values were used to rank taxa from highest to lowest preference by herbivores, which we operationally consider the palatability rank (which potentially reflects the relative investment in growth vs defense by the three focal taxa).

### *Ranking competitive effects of focal macroalgae*

To assess the relative competitive effect of each alga on the other two species in the absence of herbivorous fishes, we conducted a 6-month-long competition experiment in the mid-lagoon by outplanting the three species alone or paired with a putative competitor (N = 10 replicates per species per treatment) inside fish exclusion cages. Each cages was 20 x 20 x 20 cm and constructed of PCV-coated galvanized 2.5 cm wire mesh. The three pair-wise combinations to quantify growth in the presence of a competitor were: *Turbinaria-Sargassum, Turbinaria-Amansia, Sargassum-Amansia*. To initiate the experiment, reef substrate covered with the target species of macroalgae was collected from the mid-lagoon using a hammer and chisel. To create patches of *Turbinaria*, all other algae were removed so only *Turbinaria* of uniform size (~8.5 cm) and number (4-5 stipes) remained on 5 x 2.5 cm pieces of substrate. The same process was then used to create substrates containing only *Sargassum* or *Amansia.* In addition, all algae were removed from additional pieces to create bare substrate (i.e., containing no algae). Each replicate contained four pieces of substrate;

single species treatments had two with algae of the same species and two bare, and pairwise treatments contained two patches of each species. Substrate patches were glued to 15 x 15 cm terra cotta tiles attached to the bottom of herbivore-exclusion cages (**SI Fig. 1**).

To estimate the initial biomass of algae on each piece of substrate, we measured the length of *Sargassum* or *Turbinaria* stipes and used established species-specific length to biomass relationships. Due to the branching growth form of *Amansia*, we destructively sampled *Amansia* substrates (equivalent to those deployed) and recorded total *Amansia* biomass on each piece (N = 36 replicates); replicate values were averaged to provide an estimate of initial *Amansia* biomass. Cages were deployed in pairs at least 3 m apart and affixed to rebar posts embedded into bare substrate on the tops of patch reefs. After 6 months, cages were retrieved and brought to the laboratory, where the three taxa were damp weighed (g) and the values averaged for each replicate. Replicate values were then averaged for each species and competition treatment. The relative competitive effect (RCE) of a competitor on the growth of a target species was calculated as: $RCE = \frac{B_C - B_A}{B_A} x100$ where $B_C$ is the final biomass of the target species when grown with a competitor, and $B_A$ is the final biomass of the target species when grown alone (see Keddy et al. 2002). $B_C$ and $B_A$ are expressed as the mean of the experimental replicates. Algae were ranked from best to worst interspecific competitor using *RCE* values, where a lower value indicates a larger competitive effect.

### *Exploring the effects of the competition-palatability trade-off on reef state*

A field experiment tested if a competition-palatability trade-off structures the macroalgal assemblage on lagoon patch reefs. To determine whether *Turbinaria,* a heavily defended alga that predominates under ambient levels of herbivory, can be competitively excluded by more palatable species in the absence of herbivorous fishes, we deployed for 2 years experimental patches initially dominated by *Turbinaria* under two herbivory treatments: ambient herbivory (uncaged and fully exposed to browsing fishes) and no herbivory (caged to prevent access by herbivorous fishes). Macroalgae-covered reef substrate dominated by *Turbinaria* were collected from the mid-lagoon, affixed to a tile, and assigned randomly to an herbivory treatment (N = 20 replicates per treatment). All replicates were initially dominated by *Turbinaria*, and they contained small amounts of *Sargassum*, *Amansia* and other, rarer taxa of macroalgae. The footprint of each replicate was 0.2 m$^2$, which approximated the mean size of natural *Turbinaria*-dominated patch reefs in the lagoon (Davis 2016, **SI Table 1**). Replicates were affixed to rebar posts embedded into bare substrate on the tops of patch reefs at the same mid-lagoon site used for herbivory assays and the competition experiment. After 2 years, a period sufficient for several complete population turnovers of *Turbinaria* plants (Davis 2016, Schmitt et al. 2019), replicates were brought back to the lab where they were destructively sampled to identify macroalgae to the lowest taxon possible and damp weighed (g). Two of the fish-exclusion cages were heavily damaged during the deployment, enabling herbivorous fishes access, and were not considered further in the analyses. Replicates were assigned to one of three final community states: unpalatable-dominated (at least 80% of final biomass was *Turbinaria*), palatable-dominated (at least 80% of final biomass was *Amansia* and/or *Sargassum*), and turf/CCA-dominated (i.e., tile lacked macroalgae and was covered by cropped turf and crustose coralline algae).

### *The effect of the trade-off on the provision of coral-invasible space*

The availability of hard substrates that support closely cropped turf algae and/or crustose coralline algae (CCA) that are free of macroalgae is crucial for the establishment and proliferation of coral on a reef (see Schmitt et al. 2022). We thus explored the capacity of herbivores to provide coral-invasible space under conditions of macroalgal dominance based on the ambient level of herbivory and attributes of the macroalgae community (i.e., dominated by *Turbinaria* or by *Amansia/Sargassum*). Macroalgae-covered lagoon substrates were collected using a hammer and chisel, and uniform sizes of substrate were glued to cover the top surface of cement blocks (40 x 20 x 15 cm), creating experimental assemblages of two types: unpalatable macroalgae, dominated by *Turbinaria* (N = 30) or palatable macroalgae, dominated by *Amansia* and *Sargassum* (N = 30) (**SI Fig. 3a**). The experimental assemblages (N = 6 replicates per community type per site) were randomly deployed on the benthos at sites in the lagoon with either *a priori* determined high (N = 2 sites) or low (N = 3 sites) ambient levels of browsing (see chapter 2). For each replicate, the same observer visually estimated the percent cover of palatable algae, unpalatable algae, and exposed hard substrate (turf/CCA) using photographs taken before and at the end of a 10-day long exposure to herbivores. The values for each benthic category were averaged for each site and timepoint (N = 6 replicates per site and timepoint) and then values were averaged for each treatment (i.e., ambient browsing level and initial community state). The mean values for final and initial exposed hard substrate (covered by cropped turf and crustose coralline algae) were used to estimate the provision of coral-invasible space in each treatment. Differences among treatments were assessed using a two-way ANOVA with ambient browsing level, initial community state, and their interaction as factors. Data were arcsine-transformed to meet model assumptions.

## ***Results***

### *Ranking herbivore preference for focal macroalgae*

Herbivory assays captured clear differences in the preferences of herbivores for focal species: *Amansia* was most preferred by herbivores, followed by *Sargassum* and then *Turbinaria* (**Fig. 1**). Biomass losses of algae in deployed cages to exclude fishes were negligible after 48 hrs for all taxa tested (**Fig. 1**), indicating that virtually all biomass loss in treatments exposed to fishes could be attributed to consumption. In single-species assays, herbivores consumed 97 ± 3% (mean ± SE) of *Amansia*, 60 ± 13% of *Sargassum*, and 11 ± 3% of *Turbinaria* (**Fig. 1a**). A Kruskal-Wallis test revealed that consumption significantly differed between all taxa ($\chi^2(2) = 39.586$, $p < 0.001$); pairwise comparisons using Dunn’s test with Benjamini-Hochberg adjustments indicated that consumption significantly differed between *Amansia* and *Sargassum* ($p < 0.01$), *Amansia* and *Turbinaria* ($p < 0.001$), and *Sargassum* and *Turbinaria* ($p < 0.001$). In the mixed species assays, herbivores consumed 61 ± 9% of *Amansia*, 13 ± 5% of *Sargassum*, and 2 ± 1% of *Turbinaria* (**Fig. 1b**) with consumption significantly differing between all taxa (Kruskal-Wallis, $\chi^2(2) = 31.148$, $p < 0.001$). Pairwise comparisons using Dunn’s test with Benjamini-Hochberg adjustments indicated that consumption significantly differed between *Amansia* and *Sargassum* ($p < 0.001$), *Amansia* and *Turbinaria* ($p < 0.001$), and *Sargassum* and *Turbinaria* ($p = 0.01$). Although the average amount of an alga consumed was higher when offered alone than with the other species, the pattern of herbivore preference was consistent in both assays. Thus, based on these assays, the rank order of palatability to herbivores was *Amansia* > *Sargassum* > *Turbinaria*.

### *Ranking competitive effects of focal macroalgae*

Interspecific competition experiments revealed differences in the relative competitive effects (RCEs) of the macroalgae (**Table 1**). Relative to when grown alone, the biomass of *Sargassum* and *Turbinaria* was 51% and 48% lower, respectively, when grown with *Amansia*. *Sargassum* reduced *Turbinaria* biomass by 24% and *Turbinaria* only caused an 18% reduction in *Sargassum.* Interestingly, while *Sargassum* and *Turbinaria* were negatively impacted when *Amansia* was present, *Amansia*'s growth was enhanced in the presence of either of the other taxa. Based on these RCE values, the rank order of interspecific competitive ability was: *Amansia* > *Sargassum* > *Turbinaria.* Thus, these 3 species of algae fit with the competition – palatability trade-off paradigm.

### *Exploring the effects of the competition-palatability trade-off on reef state*

Our two-year long field experiment that explored whether a competition-defense trade-off structures the macroalgal assemblage revealed that the persistence of an undesirable state (i.e., dominated by unpalatable macroalgae) or a shift to an alternate state depended on both the strength of herbivory and the competitive dynamics among the macroalgae. Under ambient herbivory conditions, 35% of the initially *Turbinaria*-dominated communities persisted in that state, while 65% lost their cover of macroalgae and were characterized by open substrate covered with cropped turf and crustose coralline algae (**Fig. 2a**). By contrast, in the absence of herbivory, all 20 replicates (100%) switched from *Turbinaria* to a state dominated by palatable macroalgae (e.g., *Amansia* and *Sargassum*) (**Fig. 2b**). The macroalgal communities that persisted under ambient herbivory conditions were completely comprised of unpalatable *Turbinaria* (**Fig. 3a, SI Fig. 2a**), the least preferred, competitively inferior species. Conversely, communities protected from herbivores were all characterized by high cover of palatable taxa (**Fig. 3b**), with the preferred, competitively dominant alga, *Amansia* dominating the biomass in most (13 of 20) replicates (**SI Fig. 2b**). These results are consistent with expectations if the plants trade off competitive ability and vulnerability to herbivores.

### *The effect of the trade-off on the provision of coral-invasible space*

The relationship between browsing level and the resultant provisioning of coral-invasible space depended on the initial composition of the macroalgae community (i.e., dominated by palatable or unpalatable taxa) ($F_{(1, 56)} = 420.138$, $p < 0.0001$; **Fig. 4**, **SI Fig. 3**). For plots initially dominated by palatable macroalgae, final community composition (on day 10) was similar between those subjected to high or to low ambient browsing (**Fig. 4a**). Both were characterized by an almost complete loss of cover of their palatable algae, with resultant exposure of the previously-occupied open hard substrate. By contrast, final community composition for plots initially dominated by unpalatable macroalgae differed significantly between high and low browsing treatments. The degree of removal of unpalatable macroalgae was much higher at high browsing sites than at low browsing sites, with a corresponding greater increase in coral-invasible substrate in the former (Tukey's HSD, $p < 0.0001$; **Fig. 4a**). Overall, the results of the experiment revealed that both browsing level and taxonomic composition of the macroalgal assemblage affected the provisioning of coral-invasible space (i.e., turf/CCA cover). Communities initially dominated by palatable macroalgae subjected to high levels of browsing were the most likely to revert back to the coral (i.e., had the highest provision of coral-invasible substrate), whereas the communities of unpalatable macroalgae subjected to low levels of browsing had an extremely low likelihood of returning to coral because herbivores were not able to remove macroalgae to provide coral-invasible space (**Fig. 5**).

## ***Discussion***

Ecological feedbacks can trap a system in a degraded state (Nystrom et al. 2012), which can make restoration to the original state especially challenging (Bakker and Berendse 1999, Nienhuis et al. 2002, Suding et al. 2004, Peters et al. 2020). Restoration strategies that weaken the feedbacks that maintain a unwanted state can be effective, including for a variety of vegetated systems (Zedler 2000, Holmes 2001, Willems 2001, Suding et al. 2004). However, the limited understanding of the ecological processes that shape the resilience of the vegetated state on coral reefs after a coral-to-macroalgae regime shift hinders the development of feasible restoration strategies for this ecologically and societally important marine ecosystem (Graham et al. 2013). The essential role played by 'browsing' herbivores, the functional group that consumes mature macroalgae, in reversing a shift to vegetation is well-recognized (Bellwood et al. 2006, Han et al. 2016, Burkepile et al. 2020, Cook et al. *in review*). However, current coral reef management efforts focus primarily on means to enhance resilience of the coral state to prevent a shift to macroalgae, rather than on weakening resilience of the vegetated community following a regime shift (Graham et al. 2013). This in part reflects the notion that increasing populations of browsing herbivores to the level needed to bring macroalgae back under control will often be impossible or impractical (Schmitt et al. 2019; Cook et al. *in review*). However, while benthic communities dominated by unpalatable macroalgae appear to be highly resilient to herbivores (Holbrook et al. 2016, Schmitt et al. 2019, 2022), those composed of palatable species appear far more vulnerable at ambient levels of herbivory (Bellwood et al. 2006, Muthukrishnan and Fong 2018). Our findings here confirm that a much lower level of browsing was required to bring macroalgae under control when the assemblage was composed of palatable species. Reduced palatability in plants is typically associated with a greater investment in defense, which characteristically comes at the cost of reduced competitive ability (Coley et al. 1985, Simms and Rausher 1987, Herms and Mattson 1992, Pacala and Crawley 1992, Rees et al. 2001).

Changes in reef state in our study system were underpinned by a competition-palatability trade-off where browsing herbivores preferentially consumed the competitively superior species. For the three main species of space-holding macroalgae in our system, the rank order of vulnerability to herbivory was identical to our estimate of the rank order of competitive ability (*Amansia* > *Sargassum* > *Turbinaria*). This trade-off between competition ability and defense predicted well how variation in browsing pressure resulted in the reduction in macroalgae and conversion to a benthic state that is invasible by coral propagules. Under comparatively high levels of herbivory, the initial *Turbinaria*-dominated, mixed-algae species assemblage in our experimental plots exposed to herbivores either became a monoculture of *Turbinaria*, or the community transitioned into a non-macroalgae state (turf and crustose coralline algae) that coral can colonize. The 2-year duration of the experiment was sufficient for multiple complete turnovers of *Turbinaria* plants (see Schmitt et al. 2019), indicating that these alternative states subjected to the same (relatively high) level of herbivory were self-reinforcing. The extirpation of more palatable algae (*Amansia*, *Sargassum*) from the plots that persisted as monocultures of *Turbinaria* is consistent with preferential consumption of more palatable species by browsers.

In contrast to the alternative outcomes when plots were exposed to browsers, all 20 of the experimental plots protected from herbivores underwent a dramatic shift from initial domination by *Turbinaria* to assemblages comprised almost entirely of palatable macroalgae. After 2-years, the most abundant species on herbivore-exclusion plots shifted from *Turbinaria* to *Amansia*, the superior competitor that is most vulnerable to herbivory. *Sargassum*, which was ranked intermediate in both competitive ability and palatability, was the next most common constituent, whereas the initially dominant alga, *Turbinaria*, was scarce or absent in all no-herbivory replicates. These results conform with two expectations from a competition – palatability trade off: preferential feeding by herbivores can shift the composition of the plant community to highly unpalatable species, and reductions in herbivory can shift the community to highly palatable species.

The empirical relationship we observed between palatability and reversibility of a shift to macroalgae suggests that variation in vulnerability to consumers influences the existence and magnitude of hysteresis in the relationship between herbivory and abundance of macroalgae. This was shown theoretically in a model of macroalgae-coral dynamics based on our study system (Briggs et al. 2018), and arose from the influence of stage-structure on plant-herbivore interactions. Some but not all macroalgae show dramatic ontogenetic increases in resistant to herbivory to become highly unpalatable when they reach a size or developmental threshold (Davis 2016). Models have shown that this type of stage-structure can produce and widen hysteresis in underlying driver-response relationships (Scheffer et al. 2001), including the relationship between herbivory and macroalgal abundance on coral reefs (Briggs et al. 2018, Rassweiler et al. 2022, Kopecky et al. 2023, Cook et al. *in review*). In the system we explored, a strong stabilizing feedback that maintains the *Turbinaria* state under levels of browsing that eliminate more palatable algae arises from the associational defense that vulnerable, early developmental stages of *Turbinaria* gain from the canopy of highly unpalatable adults (Davis 2018). Unlike newly recruited *Turbinaria*, adult plants are exceptionally tough and spiny, and have a high phenolic content that further deters herbivory (Stiger et al. 2004, Stewart 2006). As a consequence, dense patches of adults function as a physical barrier to consumers (Bittick et al. 2010, Davis 2018). This refuge effect of unpalatable adults protecting more vulnerable life stages until they grow to become defended sets up a positive feedback that enables patches of *Turbinaria* to self-replicate (Davis 2018). This suggests that coral-to macroalgae regime shifts that are especially challenging to reverse occur when environmental conditions favor highly unpalatable species that promote defense-based, self-reinforcing feedbacks. Indeed, coral and macroalgae may not represent alternative basins of attraction when the vegetated state is composed of highly palatable species.

The observed competition-palatability trade-off provides two pathways by which the strong positive feedback that maintains the *Turbinaria* state can be interrupted. The traditional pathway that managers typically consider is to strengthen trophic interactions such that browsing pressure eventually becomes sufficiently great. The establishment of Marine Protected Areas (MPAs) is one such action that can result in the build-up of herbivore biomass on reefs (McClanahan 1994, Roberts 1995) and the subsequent reduction of macroalgae (Mumby et al. 2021). This approach often is impractical (Schmitt et al. 2019). A less appreciated approach may be to reduce the strength of trophic interactions to the point where competitive interactions shifts the plant assemblage to highly palatable species that lack defense-based, self-reinforcing feedbacks; such assemblages subsequently can be rapidly eliminated with relatively small increases in herbivory, as demonstrated by a long-term experiment reported by Bellwood et al. (2006). These researchers excluded large fishes for 3 years from 25 $m^2$ experimental plots that initially had almost no macroalgae ($< 0.1$ kg $m^{-2}$), which resulted in an order of magnitude increase in macroalgae biomass ($> 5$ kg $m^{-2}$), primarily palatable *Sargassum*; subsequent re-exposure of the plots to fishes lead to the elimination of *Sargassum* within 8 weeks under the ambient level of browsing (Bellwood et al. 2006). This suggests that management actions that harness competitive interactions rather than enhancing browser biomass could be a viable strategy provided it can be scaled in space and time. In this context, rotational closures where intense fishing of browsers in a location is alternated temporally with a complete ban to first protect and then expose macroalgae from consumers may be an alternative approach to fixed MPAs.

Effective restoration strategies are an urgent priority to resolve a growing environmental problem in many ecosystems, how to reverse an undesirable regime shift. Our results reveal it is possible to interrupt feedbacks reinforcing an undesirable state by harnessing natural biotic interactions, at least at small spatial scales. The relationship between competitive ability and palatability for primary producers yields valuable insight into the processes that regulate alternate stable states. Specifically, management should consider trophic interactions between herbivores and primary producers in light of the attributes of primary producers.

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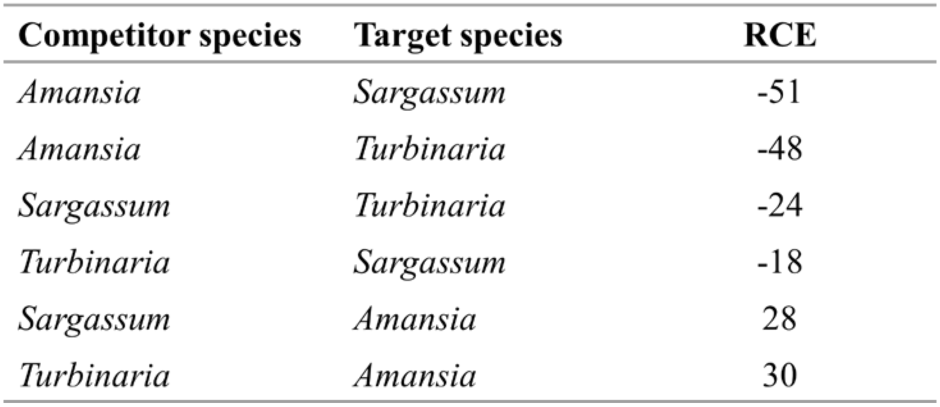
## *Tables*

**Table 1.** The effect of a competitor species on the growth of a target species. Relative competitive effect (RCE) is expressed as percent reduction or increase in the biomass of the target species.



| Competitor species | Target species | RCE |
|---|---|---|
| *Amansia* | *Sargassum* | -51 |
| *Amansia* | *Turbinaria* | -48 |
| *Sargassum* | *Turbinaria* | -24 |
| *Turbinaria* | *Sargassum* | -18 |
| *Sargassum* | *Amansia* | 28 |
| *Turbinaria* | *Amansia* | 30 |

## *Figures*

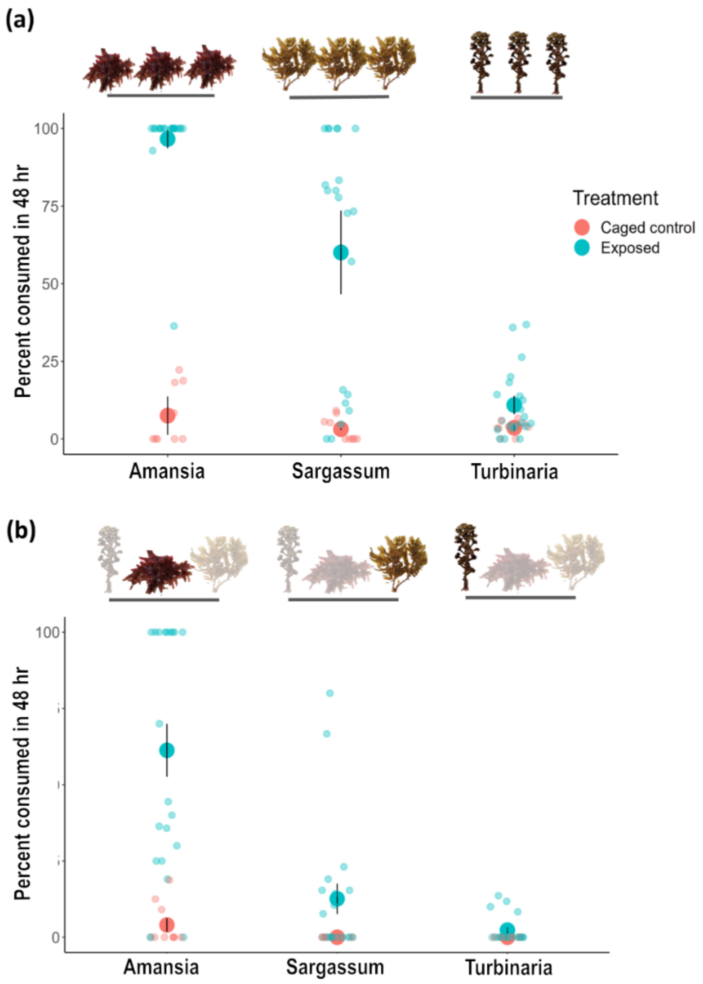


**Figure 1.** Average percent consumption of *Amansia*, *Sargassum*, and *Turbinaria* by herbivores from **a)** single-species assays and **b)** mixed species assays. Macroalgae were either exposed to herbivores (denoted in blue; single-species assays: N = 7 replicates per species; mixed species assays: N = 20 replicates) or protected from herbivores by cages (denoted in red; single-species assays: N = 3 replicates per species; mixed species assays: N = 10 replicates). Shown are means (± SE) in percent consumption of each taxa (large colored dots) and percent consumption for each replicate (small colored dots) after 48 hours.

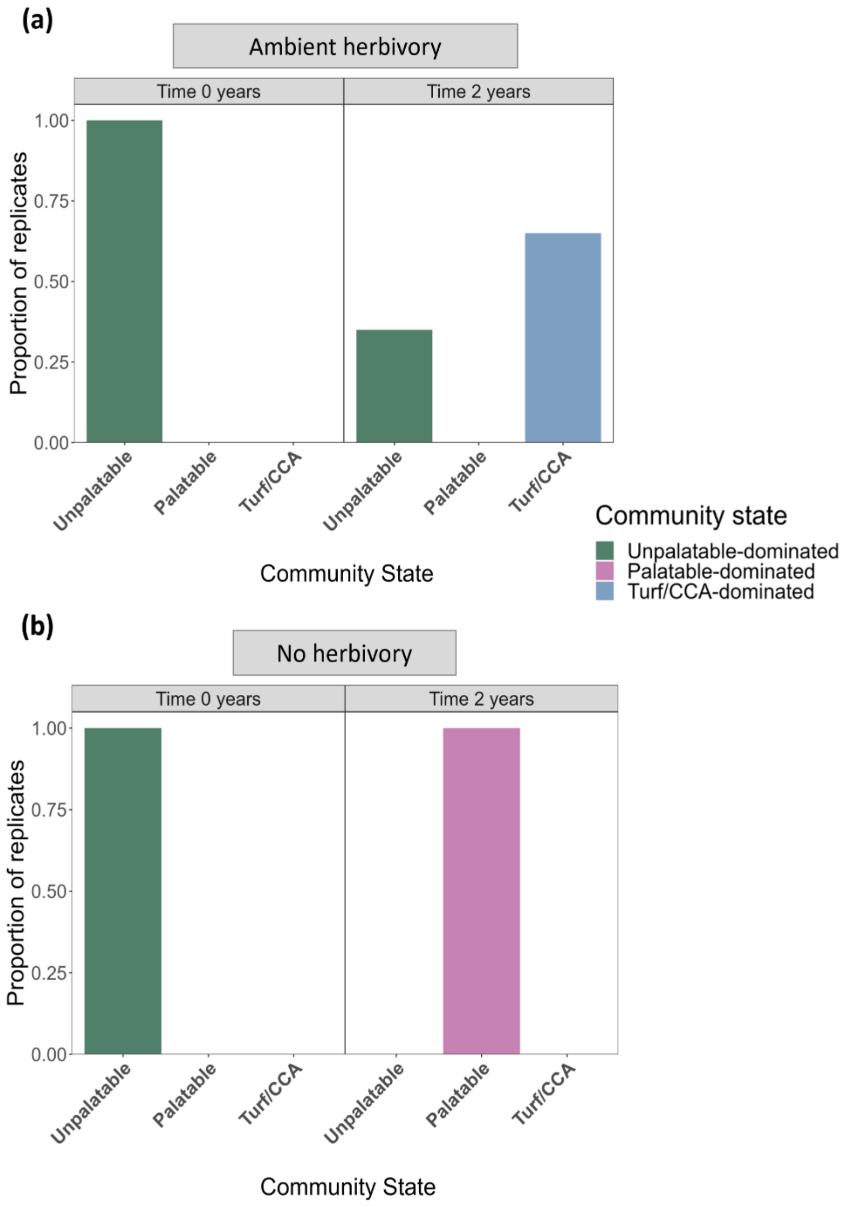


**Figure 2.** The proportion of *Turbinaria*-dominated communities that persisted in an unpalatable-dominated state (green) or shifted to an alternative community state (i.e., palatable-dominated (pink) or turf/CCA-dominated (blue)) after two years under **a)** ambient herbivory or **b)** no herbivory conditions.

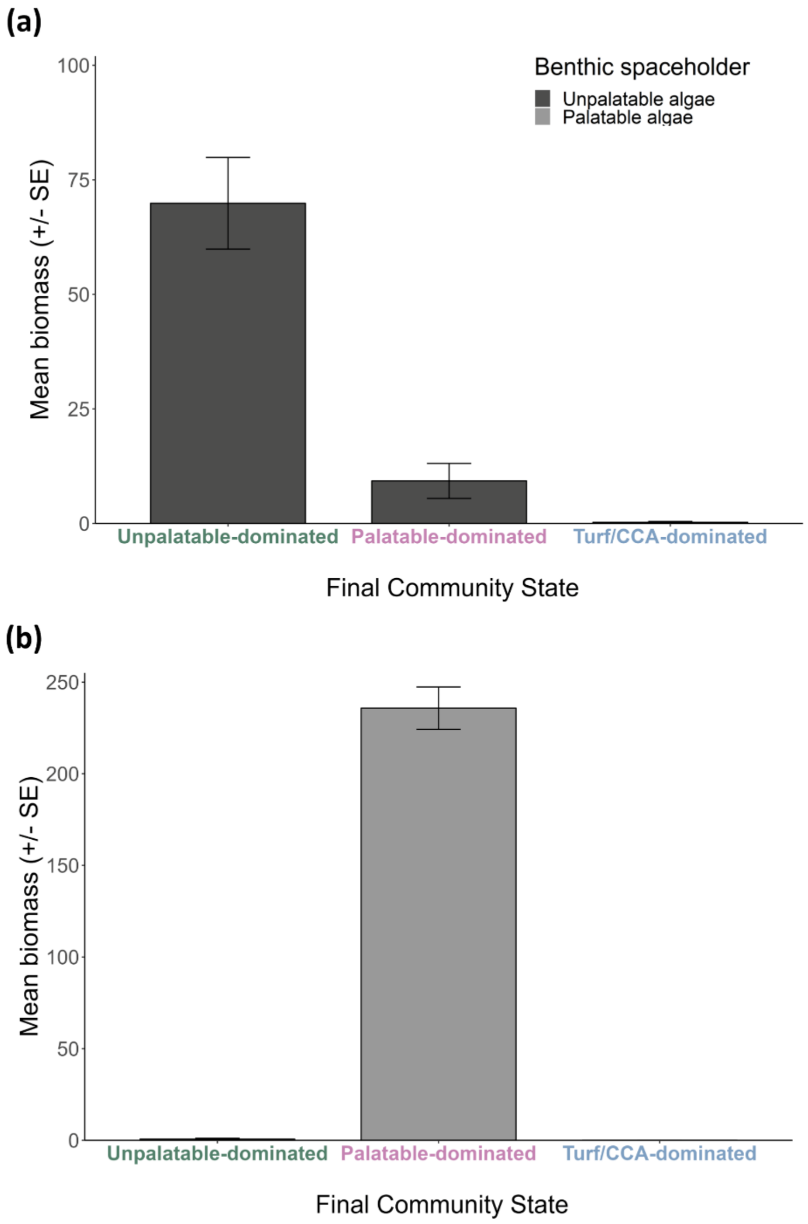
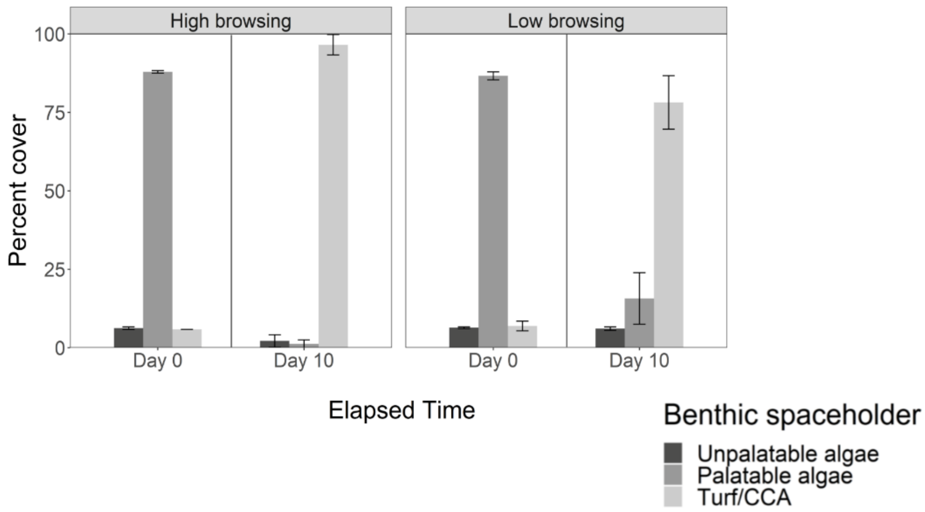


**Figure 3.** The biomass of **a)** unpalatable macroalgae (*Turbinaria*) and **b)** palatable macroalgae (*Amansia* and *Sargassum*) in each of the three possible final community states: unpalatable-dominated, palatable-dominated, and turf/CCA-dominated. Shown are mean biomasses (± SE) of unpalatable (dark grey) and palatable algae (light grey) at the end of the two-year long field experiment.

**(a)** Initial community state: palatable-dominated



**(b)** Initial community state: unpalatable-dominated

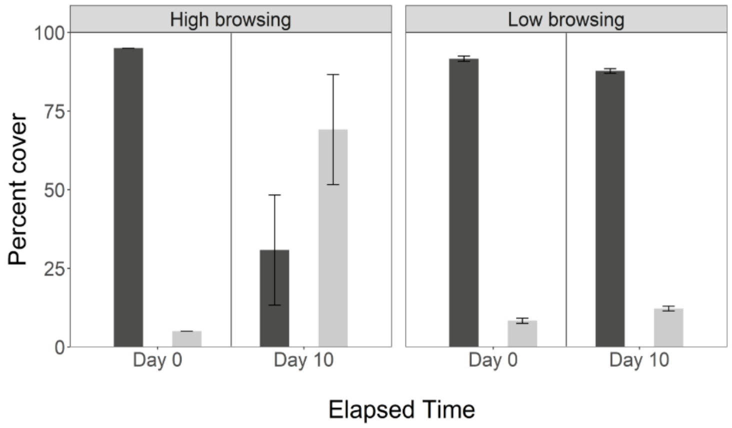


**Figure 4.** Change in percent cover (mean ± SE) of benthic spaceholders in communities initially dominated by **a)** palatable algae and **b)** unpalatable algae at either high or low browsing sites after 10 days of exposure to herbivores.

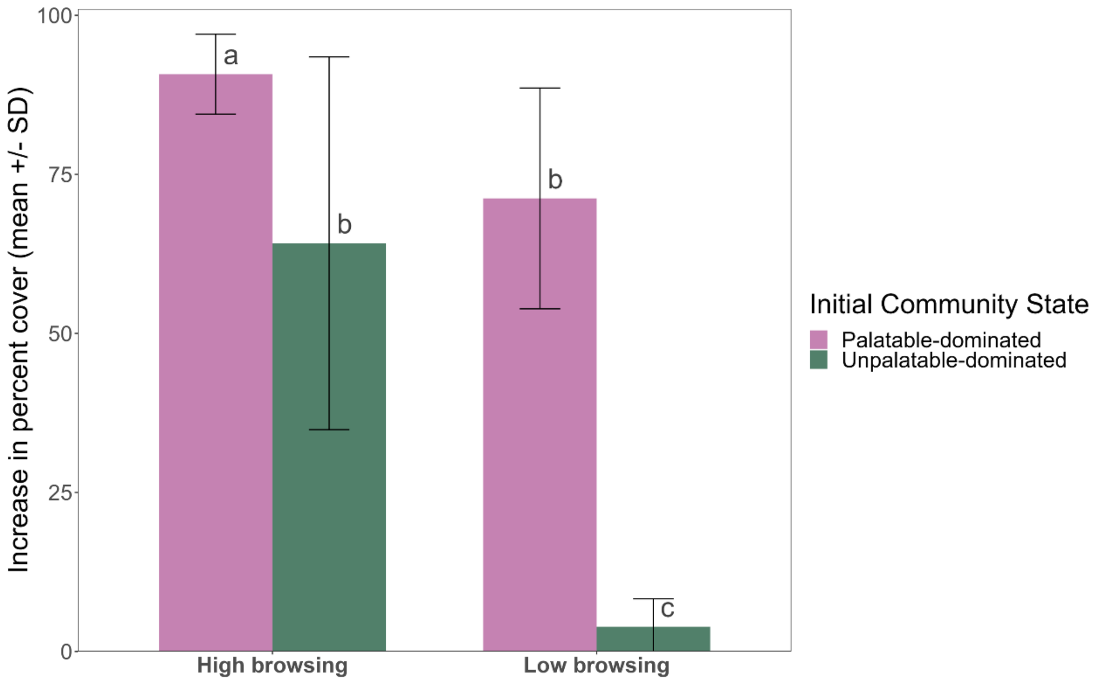
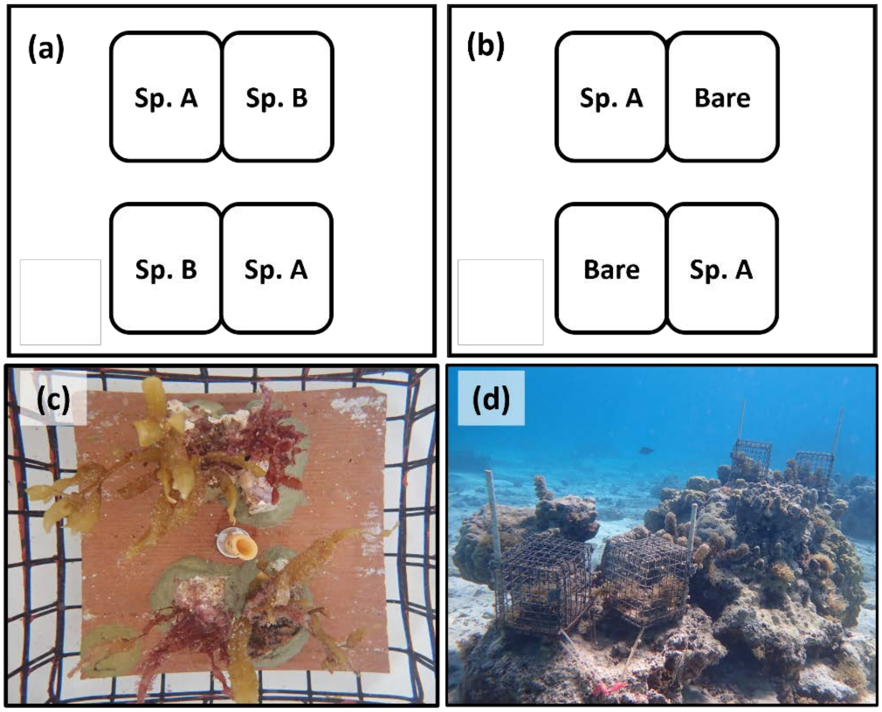


**Figure 5.** Increase in coral invasible space (i.e., dominated by turf/CCA) within communities initially dominated by palatable algae (pink) or unpalatable algae (green). Shown is the increase in percent cover (mean ± SD) of coral-invasible space for each initial community state at high or low browsing sites after 10 days of exposure to herbivores.

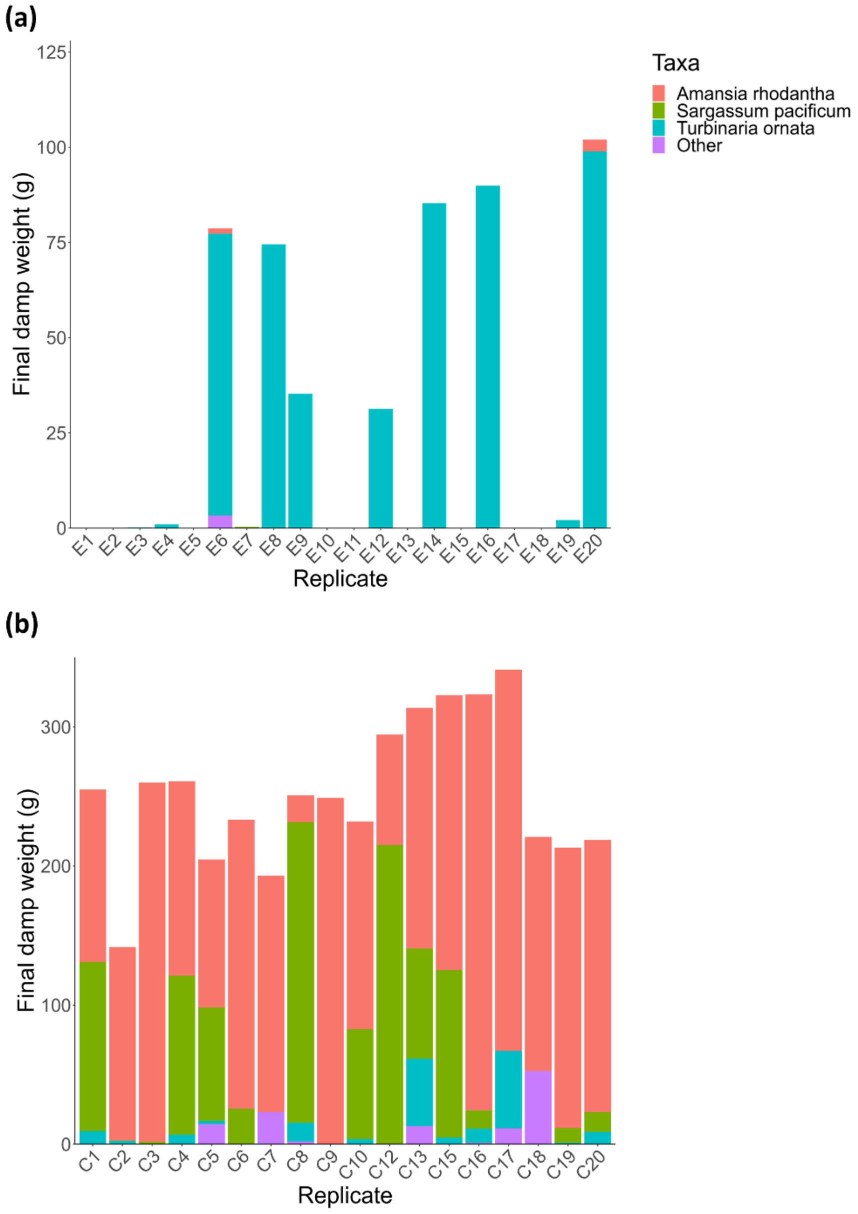
## *Supplementary Information*

**Supplemental Table 1.** Footprint ($m^2$) of *Turbinaria*-dominated patch reefs in the lagoon of Moorea, French Polynesia.

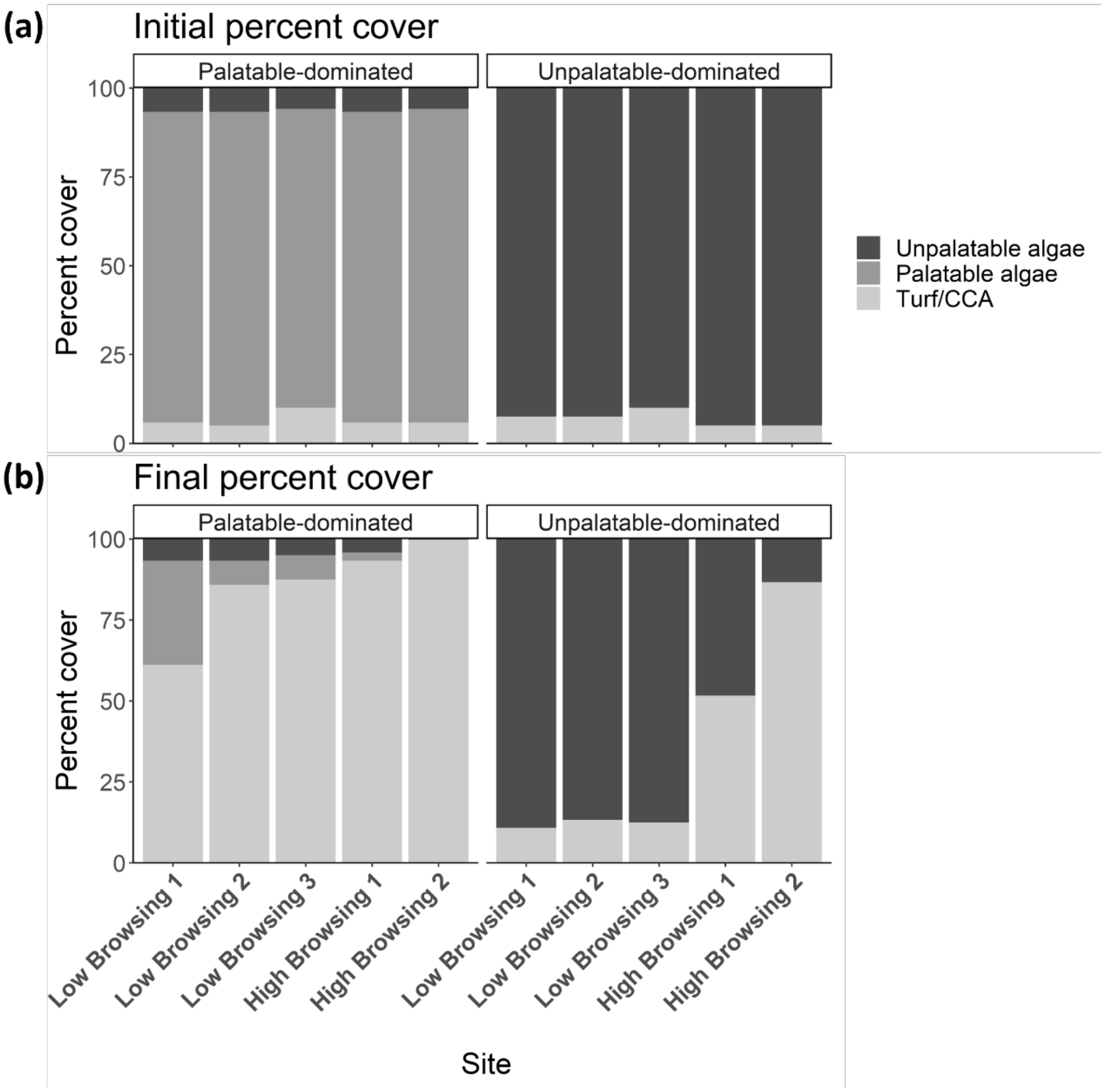
| **Location** | **Year** | **N** | **Median patch size ($m^2$)** | **Standard Deviation** |
|---|---|---|---|---|
| North Shore lagoon | 2021 | 100 | 0.03 | 0.12 |



**Supplemental Figure 1.** Schematic of interspecific competition experiment for **a)** competition treatment and **b)** no competition treatment. Photos of **c)** *Sargassum-Amansia* treatment before deployment and **d)** deployed cages affixed to bare substrate on the tops of patch reefs.



**Supplemental Figure 2.** Final composition and biomass of communities initially dominated by *Turbinaria* after two years under **a)** ambient herbivory and **b)** no herbivory conditions. Shown is total damp weight (g) of algae in each replicate (N = 20 exposed to herbivores, N = 20 protected from herbivores) colored by taxa.



**Supplemental Figure 3.** (a) Initial and (b) final mean percent cover (N = 6 replicates per community state and site) of each benthic spaceholder in communities initially dominated by palatable or unpalatable algae after 10 days of exposure to herbivores. Sites either had high (N = 2 sites) or low ambient levels of browsing (N = 3 sites).

# Chapter II: Patterns of spatial covariation in herbivore functions on coral reefs: Implications for reef resilience

## *Introduction*

A major focus in ecology is to understand the complex dynamics of ecosystems that simultaneously are being buffeted by rapidly changing disturbance regimes and by more slowly changing environmental drivers (Conversi et al. 2015, Cowles et al. 2021, Zinnert et al. 2021, Reed et al. 2022). Of considerable interest are abrupt transitions between qualitatively different ecosystem states (Scheffer and Carpenter 2003, Petraitis 2013, Conversi et al. 2015), which can be challenging to anticipate (Hastings and Wysham 2010, Boettiger and Batt 2020) and problematic to reverse (Suding et al. 2004, Mumby et al. 2013, Schmitt et al. 2019). The consequences to society of such shifts can be profound if an alternative community state provides either fewer or qualitatively different ecosystem services (Suding and Hobbs 2009, Miller et al. 2011, Mumby et al. 2013). This adds urgency to the need to better understand the processes that influence transitions between alternative, self-reinforcing states (regime shifts) (Conversi et al. 2015). In general, shifts in state can occur when the magnitude of a perturbation overwhelms the internal resilience of a system, which itself can be eroded when key biological processes are altered by human activities or natural events (Elmqvist et al. 2003, Folke et al. 2004). Resolving links between state shifts, biological processes, and ecosystem resilience can inform management strategies intended to maintain desired ecosystem states during this era of unprecedented human impact on the environment (Mcleod et al. 2019).

Thresholds in driver – response relationships are a source of non-linear dynamics in ecological systems. Incremental changes in an underlying driver can result in little change in the ecosystem until a critical value is crossed, after which the system's structure and/or functions transition abruptly to a qualitatively different state (Holling 1973, Groffman et al. 2006, Holbrook et al. 2008, Briggs et al. 2018, Schmitt et al. 2019). In cases where the fundamental relationship between the driver and ecological response does not change from before to after a shift, the system can readily revert to the original state with a small relaxation in the parameter value back across the original threshold (i.e., non-linear tracking) (Gunderson 2000, Scheffer et al. 2001, Walker et al. 2006, Bestelmeyer et al. 2011). A more complex dynamic arises when hysteresis exists in the driver-response relationship, which creates a region of state space where bistability of alternative states is possible over some range of parameter values (Scheffer et al. 2001, Scheffer and Carpenter 2003, Petraitis 2013). In this situation, reversal of a transition requires a much greater relaxation of the driver past the original tipping point and through the region of bistability (Scheffer et al. 2001); this lag can render such a regime shift impractical or impossible to reverse. Further, hysteresis adds another source of non-linear behavior by creating a second pathway between alternative regimes; ecosystems that lie within a region of bistability are vulnerable to 'state tipping' where a sufficiently large disturbance alone can flip the system to the alternative basin of attraction without any change in an underlying parameter and irrespective of the system's proximity to a tipping point (Scheffer et al. 2001, Beisner et al. 2003, Schmitt et al. 2019, 2022, Boettiger and Batt 2020).

One method to anticipate an abrupt shift has been to use statistical signals in the dynamical behavior of a system as an early warning indicator (EWI) that the system is approaching a tipping point (Scheffer et al. 2009, Hastings and Wysham 2010, Dakos et al. 2015, Titus and Watson 2020, Boettiger and Batt 2020). While useful in certain circumstances (see Bestelmeyer et al. 2011, Dakos et al. 2015), among the limitations of an EWI approach is that it cannot warn of state tipping from a large environmental shock (Lenton 2013), highlighting the need for additional tools to help predict vulnerabilities to and reversibility of transitions to an alternative state (Pace et al. 2015). Here we explore the extent to which knowledge of spatial patterns of top-down control of macroalgae on coral reefs can provide spatially-explicit insight into resilience of the benthic community in a Pacific island reef system where coral and macroalgae can be alternative basins of attraction (Schmitt et al. 2019, 2022).

Coral reefs are being degraded worldwide by local and global stressors and acute disturbances (Hughes et al. 2007, Lough et al. 2018, Sully et al. 2019). Declines in coral cover frequently have been accompanied by concomitant increases in macroalgae (coral-algae ‘phase shifts’) (McManus and Polsenberg 2004, Roff and Mumby 2012, Adam et al. 2021). Macroalgae generally are superior competitors to coral and can preclude a return to a coral-dominated state (Hughes et al. 2007, Schmitt et al. 2022).  Top-down control of macroalgae is widely recognized as a crucial biological process that can influence shifts between coral and macroalgae (Hughes et al. 2007, Ledlie et al. 2007, Cheal et al. 2010, Adam et al. 2011, 2015, Holbrook et al. 2016, Schmitt et al. 2019, 2022). In this context, herbivorous fishes on coral reefs have two distinct functions (Bellwood et al. 2004, Green and Bellwood 2009, Burkepile and Hay 2010, Cheal et al. 2010, Han et al. 2016, Burkepile et al. 2020), which we operationally term ‘grazing’ and ‘browsing’ (e.g., Han et al. 2016). Following a massive coral mortality event, grazing herbivores that consume endolithic and filamentous algae *prevent* the establishment of macroalgae by consuming their early developmental stages on the disturbed substrate, thereby maintaining the reef surface in a condition (cropped turf) that can be colonized by coral (Birrell et al. 2005, Cheal et al. 2010, Graham et al. 2013, Han et al. 2016, Robinson et al. 2020, Adam et al. 2022, Schmitt et al. 2022). However, if macroalgae become established, they subsequently can be removed by species of browsing herbivores that consume mature macroalgae (Cheal et al. 2010, Graham et al. 2013, Han et al. 2016). Thus, browsers, but not grazers, play a critical role in *reversing* coral-to-macroalgae state shifts (Bellwood et al. 2006).

It has been posited that hysteresis in the herbivory – macroalgae (driver-response) relationship may arise from disparity between the two functional groups of herbivores that control forward versus backward shifts in coral-macroalgae state changes (Schmitt et al. 2022), a notion that modeling of the system has supported (Cook et al. *in review*). Evidence suggests there often can be inequality in the biomass of grazers and browsers on tropical reefs, both at local reef tract (Adam et al. 2014, Han et al. 2016, Schmitt et al. 2022) and larger scales (Cheal et al. 2010, Edwards et al. 2014, Rassweiler et al. 2020). For example, persistent shifts to macroalgae on the Great Barrier Reef have been correlated with low abundances of browsing fishes (Cheal et al. 2010). Thus, the spatial pattern of covariation in herbivore grazing and browsing functions might provide insight into both the vulnerability of a reef to a coral-to-macroalgae state shift as well as the potential for such a shift to be reversed.

The lagoon patch reefs of Moorea, French Polynesia, provide an ideal model system to explore spatial variation in herbivory functions and the potential consequences of that spatial pattern to coral resilience at the local patch reef scale. Experimental studies suggest coral and macroalgae on the patch reefs can be alternative basins of attraction (Schmitt et al. 2019, 2022), and time-series data and other process studies show that herbivory is essential to coral recovery following mass mortality events (Adam et al. 2011, Holbrook et al. 2016, Schmitt et al. 2019). In general, prior research and management approaches have focused primarily on the maintenance of coral dominance to prevent a shift to macroalgae, and less on the reversibility of such a shift to re-establish coral dominance (Bellwood et al. 2006, Graham et al. 2013). Here we address that information deficit by exploring patterns and environmental correlates of spatial covariation in grazing and browsing functions of herbivorous fishes, and relate those patterns to both the vulnerability and potential reversibility of a patch reef to a coral-macroalgae phase shift. Our findings have considerable relevance to the development of spatially-explicit management actions to enhance resilience of coral.

## ***Methods***

### *Study site*

This study was conducted in the shallow lagoons of Moorea, French Polynesia (17°30’ S, 149°50’ W). A barrier reef ~ 1 km offshore protects the lagoons from the open ocean except for 2 to 4 breaks produced by deep reef passes on each of the 3 sides of the island. Back reef habitats shoreward of the barrier reef are characterized by a short band of contiguous reef substrate that then transitions into patch reefs (bommies) surrounded by sand in the mid-lagoon. Mid-lagoon reefs are highly variable with respect to cover of coral, macroalgae, cropped turf algae, and other taxa. Directly adjacent to shore are shallow fringing reefs that can be separated from the mid-lagoon by deep channels. Water circulation within the lagoon is driven by waves forcing water over the crest of the barrier reef, through the lagoons, and out the passes (Leichter et al. 2013). Hydrodynamic circulation patterns, along with terrestrial run-off, concentrate nutrient enrichment at passes, bays, and beneath major watersheds (Adam et al. 2021).

Along Moorea’s north shore, we selected twenty sites spread across the four lagoons that are divided by three reef passes (**Fig. 1a, b**). Ten sites were located on the fringing reef, and ten were in the mid-lagoon. At each site we quantified rates of grazing and browsing, as well as biomass and taxonomic composition of the herbivorous fish community, benthic community composition, productivity of algal turf and of macroalgae, and nutrient enrichment. To determine the distance of each site from geographic features of interest (e.g., the barrier reef crest, deep water channels), we used spatial data layers produced from a previous study (Holbrook et al. 2022) that mapped the inner edge of the reef crest and the coastline based on LiDAR-based digital elevation maps (Collin et al. 2018), as well as satellite imagery provided by Google Earth Pro (Version 7.3.6.9345). For each site, we calculated the minimum distance from the reef crest using the ‘sf’ package in R (version 4.1.1). Then, we used the ruler tool in Google Earth Pro to measure the minimum distance between a site and its nearest deep-water channel, which was visually classified by having deep blue color (as opposed to visible reef substrate or sand) and being located within the lagoon.

### *Quantifying spatial patterns in herbivory*

We deployed assays to quantify levels of both grazing on algal turf and browsing on macroalgae at the 20 sites. For grazing, we exposed uniform pieces of turf-covered reef substrate to herbivores for 3 h between the hours of 10:00 and 16:00. Turf offerings consisted of 7 x 7 $cm^2$ pieces of dead coral rubble covered by highly palatable turf (e.g., *Polysiphonia* spp.) that were collected from gardens in the lagoon that were cultivated by farming damselfish (*Stegastes* spp.). Each of these was fastened to a rack constructed of PCV-coated galvanized wire mesh that was affixed to open substrate (i.e., lacking coral or macroalgae) on the tops of patch reefs (N = 5 replicates per site). Racks at each site were placed at least 5 m apart. The percent of turf that was consumed was estimated after 3 h by the same observer (see Davis 2018, Schmitt et al. 2022). Two trials of the grazing assay were conducted two weeks apart and all replicates at each site were pooled (N = 10 replicates per site) and then averaged to obtain the percent turf consumed, which we used as an estimate of grazing intensity. Simultaneously, we conducted browsing assays using macroalgae offerings. We attached two 15 cm-long pieces of the palatable brown macroalga, *Sargassum pacificum,* to a rack using clothes pins to hold them upright and deployed them as described above (N = 5 replicates per site). Lengths of *Sargassum* pieces were measured after 24 h (see Davis 2018) to determine the percent consumed; values for the two fronds deployed together were averaged for each replicate. Three trials of browsing assays were conducted two to three weeks apart and all replicates were pooled (N = 15 replicates per site) and averaged for each site to calculate the percent consumption, our estimate of browsing intensity. To explore spatial patterns of herbivory we created maps of grazing and browsing estimates from the twenty sites using the ‘sf’ package in R (version 4.1.1). Covariation between grazing and browsing across sites was determined using Pearson’s correlation coefficient.

*Quantifying herbivorous fish communities and benthic composition*

The assemblage of herbivorous fishes at each site was characterized using visual surveys in which an observer swam a timed transect, counting and visually estimating total lengths (TLs) of mobile herbivorous fishes ≥ 10 cm TL in a 5 m wide swath. The observer towed an inflatable float behind them with a Garmin GPSMap 78 handheld GPS (Olathe, Kansas, USA) to geo-reference fish counts and provide an estimate of the area covered by the survey (Miller et al. 2023). TLs were used to estimate biomass using published species-specific relationships, and species were assigned to functional groups (Brooks 2019). Based on the fish biomass estimates and the area covered by the survey, we calculated biomass per unit area, expressed as g/m$^2$ of grazers and browsers.

Benthic composition was quantified along 50 m x 1 m long transects (N = 3 transects per site), in which the substratum was recorded at every 0.5 m (101 points per transect, 303 points per site). Substratum categories consisted of live scleractinian corals and macroalgae identified to genus, ‘other sessile invertebrates’ (mainly giant clams and sea cucumbers), rubble, sand, and three categories of turf: (1) turf inundated with sediment (hereafter ‘sedimented turf’), (2) turf growing within farmerfish (*Stegastes nigricans*) gardens (hereafter ‘*Stegastes* turf’), and (3) closely cropped turf without sediment and located outside of a *Stegastes* garden (hereafter ‘turf’). The number of points for each substratum category was divided by the total 303 points per site and multiplied by 100 to estimate percent cover.

### *Quantifying the nutrient environment and algal productivity*

The waters surrounding Moorea are highly oligotrophic, so we used the nitrogen tissue content of a common macroalga, *Turbinaria ornata,* as a proxy for the local nutrient environment during a period of up to three months prior to *Turbinaria* collection (Adam et al. 2021, Holbrook et al. 2022). *Turbinaria* responds to N pulses by storing surplus N (Schaffelke 1999) and N tissue content can provide a time-integrated measure of N availability (Atkinson and Smith 1983, Fong et al. 1994, Shantz et al. 2015). In June of 2017, a total of 10 *Turbinaria* stipes were randomly collected at each site and transported damp to the laboratory, where 10 florets were removed from each stipe 5 cm from the tip. Samples were dried in a drying for 4 days at 60° C. Total N content was determined via elemental analysis using a CHN Carlo-Erba elemental analyzer (NA1500) at the University of Georgia Center for Applied Isotope Studies.

The productivity of turf was measured by allowing turf to colonize and grow for 21 days on 2.5 $cm^2$ unglazed terra cotta tiles in herbivore-exclusion cages (N = 8 caged tiles per site). Herbivore exclusion cages were 10 x 10 x10 cm galvanized mesh, with mesh size of 2.5cm. After the deployment period, tiles were brought to the lab, and turf was removed and processed to obtain ash-free dry weight (AFDW). The mean value of AFDW for each site provided an estimate of turf productivity (g accumulated 3 $wk^{-1}$). Macroalgal productivity was quantified by allowing juvenile *Turbinaria,* and other colonizing macroalgae, to grow protected from herbivores for 8 weeks. We collected reef substratum with attached juvenile *Turbinaria* from the mid-lagoon and removed all other algae so only juvenile *Turbinaria* (≤ 3 cm length) of uniform size and density remained. The substrates containing *Turbinaria* were attached to the bottom of herbivore-exclusion cages at each site (N = 8 per caged replicates per site). After two months, *Turbinaria* and any other colonizing macroalgae were removed and damp weighed. Weights of replicates were pooled at a given site to provide an estimate of macroalgal productivity (g accumulated 8 wk$^{-1}$).

### *Relationships between spatial variation in herbivory, herbivore biomass, and environmental attributes*

We used regression analyses to test whether the among-site variation in grazing or browsing could be predicted from the biomass of grazing or browsing fishes as estimated from our fish counts. This analysis was conducted using the full set of twenty sites. We then utilized principal component analysis (PCA) to explore the degree to which environmental factors could explain observed spatial patterns in browsing and grazing, specifically, the 'hot spots' (high grazing or browsing activity) and 'cold spots' (low activity) in the lagoon. A subset of sites that reflected the highest (hot spots) and lowest (cold spots) levels in one of the herbivory processes was selected for this analysis, utilizing an additional criterion that the level of the second herbivory process was similar among the group. To explore variation in grazing we chose sites that exhibited the highest or lowest grazing, but that had similar (low) levels of browsing. This selection process resulted in five high grazing sites (i.e., grazing hot spots) and three low grazing sites (i.e., grazing cold spots) (**Fig. 2** bottom right and left corners). The full range of browsing only occurred among sites with moderate to high levels of grazing. Four high browsing sites (i.e., browsing hot spots) and five low browsing sites (i.e., browsing cold spots), all of which had high levels of grazing were chosen for analysis (**Fig. 2** right top and bottom corners).

Explanatory variables for the PCA analyses included both spatial factors as well as variables that reflected the amount and productivity of the food resources of the fishes and therefore could reflect the intensity of browsing or grazing. Location in the lagoon can be important predictors of fish spatial patterns of abundance and activity, and each site's distance from the reef crest and from deep water were included as predictor variables. The amounts of algal cover and productivity impact the distribution and feeding behavior of herbivorous fishes (Tootell and Steele 2016). For example, turf can vary in palatability or accessibility to grazing herbivores due to sediment load (Bellwood and Fulton 2008, Goatley and Bellwood 2012) or whether it is guarded by territorial farming damselfish (*Stegastes* spp.), with sedimented turf and turf within farmerfish gardens comprising less preferred feeding substrates than unsedimented and undefended turf. Therefore, turf productivity and cover of different types of turf (turf, sedimented turf, turf inside *Stegastes* gardens) were included in the PCA for grazing, and cover and productivity of macroalgae for browsing. The analysis was based on a correlation matrix of these data.

### *Predicting variation in herbivore biomass using environmental attributes*

To explore whether environmental attributes associated with hot spots and cold spots in herbivory also predict variation in the biomass of herbivores, we utilized the best subset selection approach, which is an exploratory model building regression analysis. Using predictor variables from the grazing PCA analysis, we utilized the R package "leaps" (Version 3.1) to test all possible combinations of predictors in a multiple linear regression to explain variation in grazer biomass, and then selected the best model according to lowest

AIC score with the R package “AICcmodavg” (Version 2.3). The same procedure was done for browsers using predictors from the browsing PCA.

### *Linking spatial variation in herbivory to the resilience of coral*

Because of a general lack of data that link browsing intensity and reversibility of state shifts to macroalgae, we explored this relationship using a field experiment. Macroalgae-dominated communities were exposed to herbivores along a natural gradient in browsing intensity to evaluate whether reversal potential was related to variation in browsing. The gradient in browsing was established by selecting five of the original twenty sites that represented the range in observed browsing intensity based on short-term herbivory assays described above. At each site, we deployed macroalgae communities that mimicked patch reefs that had undergone a shift to macroalgal dominance. Each community was constructed by chiseling off reef substrate with attached *Turbinaria*, which was then assembled into a community that reflected the size and density of macroalgae-dominated patch reefs within the lagoon. This assemblage was then epoxied to a cinderblock and the density of adult *Turbinaria* stipes recorded. The cinderblock macroalgal community (N = 6 replicates per site) was then deployed at a depth within 2-5 m and left exposed to herbivores for 10 days. At the end of the experiment, final adult *Turbinaria* density was recorded. The percent change in density of adult *Turbinaria* was calculated for each replicate using the equation *(Final – Initial) / Initial x 100*. Replicate values were then averaged for each site and used as a proxy for reversibility of a coral-to-macroalgae state shift.

Lastly, we were interested in whether environmental features associated with variation in browsing were also good predictors of reversibility. Covariation between reversibility and distance from deep water (log-transformed) for the five sites was determined using Pearson's correlation coefficient.

## ***Results***

### *Patterns of spatial variation in rates of grazing and browsing*

Short-term herbivory assays captured high spatial variation in herbivory rates across the lagoon reef system (**Fig. 1**). Of the sites examined, many had moderate to high levels of grazing, and only a few had low levels of grazing activity (**Fig. 1a, c**). By contrast, many sites were characterized by low or moderate levels of browsing, with few having high browsing activity (**Fig. 1b, d**). We first explored patterns in grazing and browsing along two spatial gradients: 1) alongshore (west to east along the north shore), and 2) cross-shore between two major reef habitats – fringing reefs and mid-lagoon reefs. No alongshore trend was apparent in either grazing or browsing **(Fig. 1c, d)**. However, grazing – but not browsing – differed between habitats; grazing was higher on mid-lagoon reefs than fringing reefs (grazing: $t_{(11)} = 2.5$, $p < 0.05$), browsing: Wilcoxon's test = 48, $p = 0.9$) (**SI Fig. 1**).

Grazing and browsing rates were not spatially correlated with each other across the twenty sites (Pearson's $r = 0.36$, $p = 0.12$). Despite this lack of concordance, a striking spatial pattern was apparent (**Fig. 2**). Sites clustered into three of the four possible herbivory regimes (i.e., the orthogonal combinations of high and low rates of grazing and browsing), which were: 1) low grazing-low browsing, 2) high grazing-low browsing, and 3) high grazing-high browsing (**Fig. 2**). None of the sites were characterized by low grazing but high levels of browsing (**Fig. 2**).

### *Relationships between spatial variation in herbivory, herbivore biomass, and environmental attributes*

The PCA analyses revealed that grazing ‘hot’ and ‘cold’ spots (i.e., high and low rates respectively) separated in ordination space along both axes PC1 and PC2, with cumulative proportion of variance explained = 0.71 (**Fig. 3a**). Loading revealed that spatial variation in grazing was related to turf productivity, cover of different categories of turf, and geographic location. Grazing hot spots were characterized by high productivity and cover of turf as well as increased distance away from deep water drop-offs and closer proximity to the reef crest. Conversely, grazing cold spots were associated with turf containing high sediment loads, high cover of turf algae gardens defended by farmerfish (*Stegastes*), increased distance from the reef crest and closer proximity to deep water drop-offs.

By comparison with grazing, the PCA for browsing revealed that hot and cold spots separated almost entirely along PC2, which was associated with geographic location (**Fig. 3b**; cumulative proportion of variance explained for Axes 1 and 2 = 0.84). Loadings revealed that browsing hot spots tended to be further from the reef crest and closer to deep water drop-offs, whereas cold spots were generally the converse - at sites closer to the reef crest and farther from deep water.

Patterns of grazing were associated with differences in the composition of turf communities between the mid-lagoon and fringing reef habitats. Mid-lagoon sites, which consistently had high grazing rates, were characterized by high cover of cropped turf that contained little or no sediment (Wilcoxon’s test = 21, *p* = 0.03, **SI Fig. 2a**). Fringing reefs, which supported generally lower and spatially more variable levels of grazing, were characterized by higher cover of turf with high sediment loads ($t_{(3)} = 2.7$, $p = 0.008$, **SI Fig. 2b**) and turf gardens defended by *Stegastes* ($t_{(3)} = 2.5$, $p = 0.02$, **SI Fig. 2c**).

We did not find the observed spatial variation in our measured rates of grazing or browsing were correlated with our visually-based estimates of herbivore biomass among the sites (**SI Fig. 3**). Neither the among-site variation in the measured rate of grazing (Pearson's $r = 0.21$, $p = 0.37$, **SI Fig. 3a**) or browsing (Pearson's $r = -0.24$, $p = 0.3$, **SI Fig. 3b**) was related to the estimated local biomass of grazers or browsers, respectively.

### *Predicting variation in herbivore biomass using environmental attributes*

Despite the fact that herbivore biomass and herbivory rates were not strongly correlated, spatial variation in the biomass of each herbivore group did map onto the same major environmental variables relating to the spatial patterns in grazing and browsing as revealed by our PCA analyses (**SI Table 1**). An AIC-based model selection approach indicated that variation in grazer biomass across the twenty sites was best predicted by turf productivity and, more weakly, cover of sedimented turf, which together explained 24% of the among-site variation in grazer biomass ($F_{(2, 7)} = 3.96$, $p = 0.04$). The best model for browsers revealed that variation in macroalgal productivity and distance from the reef crest were the best combination of predictors, which together explained 36% of variation in browser biomass ($F_{(2, 17)} = 6.28$, $p = 0.009$).

### *Linking spatial variation in herbivory to the resilience of coral*

Our experiment revealed that spatial variation in reversibility was strongly related to browsing intensity based on short-term estimates. We found that the capacity of browsing herbivores to remove late successional communities of macroalgae increased along a gradient in browsing (**Fig. 4a**). After 10 days, the average density of adult *Turbinaria* within experimental communities in low browsing areas either did not change or decreased by only 6% (**Fig. 4a**). This implies reefs in areas with low browsing capacity are vulnerable to remaining trapped in a macroalgae-dominated state (**Fig. 4b** yellow and red quadrants). By contrast, herbivores in the high browsing site removed 84 ± 9% (mean ± SE) of *Turbinaria* and in some plots completely removed macroalgal communities, suggesting high potential for reversibility if a shift were to occur (**Fig. 4b** tan and green quadrants). We found that reversibility significantly increased with closer proximity to deep water (Pearson's $r = 0.89$, $p = 0.044$, **SI Fig. 4**), which paralleled the pattern observed for spatial variation in browsing intensity revealed by our short-term assays (**Fig. 3b**).

## *Discussion*

Grazers and browsers are critical for preventing and reversing state shifts on coral reefs, respectively, and there is concerning evidence that small-scale fisheries may disproportionately reduce browser biomass relative to grazers. Given the posited implications of such a disparity in functional impact of these two herbivore groups for coral-to-macroalgae state shifts (Cheal et al. 2010, Schmitt et al. 2022, Cook et al. *in review*) it is crucial to better understand spatial patterns of grazing and browsing and how variation in these processes impacts the resilience of coral. Here, we investigated spatial variation in grazing and browsing, identified key environmental factors contributing to that variation, and assessed how covariation in these distinct herbivory processes may influence resilience of the coral state in a system where coral and macroalgae have been demonstrated experimentally to be alternative basins of attraction under certain environmental conditions (Schmitt et al. 2019, 2022).

Our study revealed high spatial variation in herbivory rates across lagoon reefs with different patterns emerging for grazing and browsing. Grazing hot spots were more common across lagoons than browsing hot spots, which likely reflects the disparity in species richness and abundance of grazers and browsers in Moorea. Although we did not detect alongshore or cross-shore gradients in browsing, we found grazing varied between fringing and mid-lagoon reef habitats that differ in distance from shore. Rates of grazing were consistently high on mid-lagoon reefs but variable on fringing reefs. This decline in grazing impact across a reef gradient has been observed in other coral reef systems (Fox and Bellwood 2007) and has been attributed to the effect of territorial fishes such as farming damselfish that defend turf gardens (Ceccarelli et al. 2005), increased rates of sedimentation in nearshore habitats (Goatley and Bellwood 2012), and increasing productivity of algae with distance from shore (Klumpp and McKinnon 1992). In our case all three hypotheses are supported; compared to mid-lagoon reefs, fringing reefs had higher cover of *Stegastes* turf and sedimented turf as well as lower turf productivity. Therefore, in our system fringing reefs appear to be less attractive foraging habitats for grazers due to the quality and accessibility of algal turfs.

By contrast, characteristics related to the macroalgae community did not appear to explain variation in browsing. Instead, browsing was most influenced by distance from deep water. This relationship between browsing and deep water may not be universal on coral reefs, but in this case, it is likely driven by local fishing dynamics. In Moorea and generally in French Polynesia, browsers such as *Naso* (unicornfish) are highly prized for their taste and market value (Nassiri et al. 2021). Although *Naso* are typically difficult to catch and demonstrate fearful behavior of humans – further indicative of the high fishing pressure they face – fishers in Moorea show high selectivity for them (Rassweiler et al. 2020). Free-diving spearfishers report targeting browsers on reefs near deep water as they believe it provides a spatial refuge for the fish.

We found that estimates of herbivore biomass derived from diver surveys were poor predictors of herbivory rate. This decoupling between herbivore biomass and functional impact can occur for various reasons. The grazers and browsers investigated in our study are mainly comprised of highly mobile herbivores, and therefore may not be counted in visual censuses where they feed (Fox and Bellwood 2014). Further, as mentioned previously, fearful behavior in response to human presence by some herbivorous fishes can result in low biomass estimates in diver surveys (Gotanda et al. 2009), which we observed in this study for browsers, which are highly prized by local spearfishers (Rassweiler et al. 2022, Cook et al. *in review*). Another potential explanation is related to the functional dilution of herbivores as the cover of algae increases, which may result in low herbivory estimates even in areas with high herbivore biomass. Consequently, caution should be exercised when linking measures of abundance to functional impact. Therefore, we propose that monitoring both herbivore biomass *and* rates of algal removal may be the most effective method to evaluate the status of vulnerable reefs, as grazing and browsing assays are relatively rapid and cost-effective, and appear to provide reliable assessments of key trophic processes associated with coral reef resilience (Chong-Seng et al. 2014, Nash et al. 2016). Estimating the two types of herbivory processes, in addition to standing biomass of herbivores, provides a direct measure of the influence of the complementary guilds of herbivores on ecosystem functioning and reef resilience (Goatley et al. 2016, Cook et al. *in review*).

Our results indicate grazing and browsing were spatially variable and not strongly correlated with each other across sites. Experimental work and time-series data demonstrate that reductions in grazing can lead to the proliferation of macroalgae on reefs (Holbrook et al. 2016, Schmitt et al. 2019, 2022), and that browsing may be linked to the likelihood of reversing a coral-to-macroalgae state shift (Bellwood et al. 2006, Cheal et al. 2010). It follows that sites with low levels of grazing and browsing are likely vulnerable to shifting to and remaining trapped in a macroalgae-dominated state. By contrast, sites with high levels of both herbivory processes may be resilient due to high prevention and reversal potential. Sites characterized by high grazing and low browsing probably have moderate resilience: establishment of macroalgae is unlikely, but so is recovery of the coral state should a shift occur (i.e., a coral-macroalgae ‘phase shift’ rather than a regime shift). Interestingly, our surveys revealed that sites were not evenly distributed among these four possible herbivory regimes. There was a complete lack of low grazing-high browsing sites, which may not be surprising given the lower ratio of browsers to grazers generally in Moorea. Only 15% and 20% of sites fell into low grazing-low browsing and high grazing-high browsing regimes, respectively, whereas the majority of sites (65%) were characterized by high grazing and low browsing.

The observed pattern of spatial covariation in grazing and browsing functions could be shaped in part by patterns and preferences of fishers in the small-scale fishery of Moorea (Rassweiler et al. 2020, 2022, Holbrook et al. 2022) that, coupled with different life histories that make browsers more susceptible to overfishing (Cook et al. *in review*), can influence both overall biomass of herbivorous fishes and the disparity between grazers and browsers. In systems such as in Moorea where browsers are target species, the first component of resilience to be weakened through fishing is likely to be the reversibility of a coral-to-macroalgae state shift (i.e., system moves from green to yellow box in **Fig. 4b**). As fishing intensity continues to increase, the ability of the herbivore community to prevent a shift to macroalgae will subsequently be eroded (i.e., system moves from yellow to red box in **Fig. 4b**), and the system will remain trapped in the macroalgae state. This trajectory of reef degradation could represent the future for reefs worldwide that support small-scale fisheries in which herbivores are target species (Cheal et al. 2010, Edwards et al. 2014). However, knowledge of spatial covariation in herbivore functions could provide a useful template for spatially-explicit management actions tailored to local conditions.

Our results indicate there likely will not be a single strategy to preserve grazing and browsing functions on reefs. Management goals will require different strategies based on key environmental factors and human pressures influencing each herbivory process. For example, managers may need to mitigate sedimentation caused by certain land-use practices to preserve grazing, while limiting fishing may be a better strategy to enhance browsing capacity. Managers may also need to apply strategies in different reef areas since grazing and browsing hot spots do not necessarily coincide in the same locations. One factor we found important in predicting the biomass of grazing and browsing herbivores alike was algal productivity, which itself can be influenced by bottom-up forcing (nutrient enrichment) (Adam et al. 2021, Holbrook et al. 2022). Therefore, management could support grazers and browsers simultaneously by mitigating stressors or disturbances that alter algal productivity in ways that affect top-down control. Finally, management practices historically have focused on means to preserve grazing functions on coral reefs to prevent coral-to-macroalgae state shifts, which is a reasonable priority given the potential challenges in reversing such a shift.  However, the frequency and intensity of disturbances to coral reefs that alone can trigger state tipping are predicted to increase (Hughes et al. 2017). As such, greater attention should be given to enhance protection of browsers and their functional impact to reefs. To that end, our study suggests that understanding spatial covariation in grazing and browsing functions can help better target management actions to enhance resilience of coral.

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## *Figures*

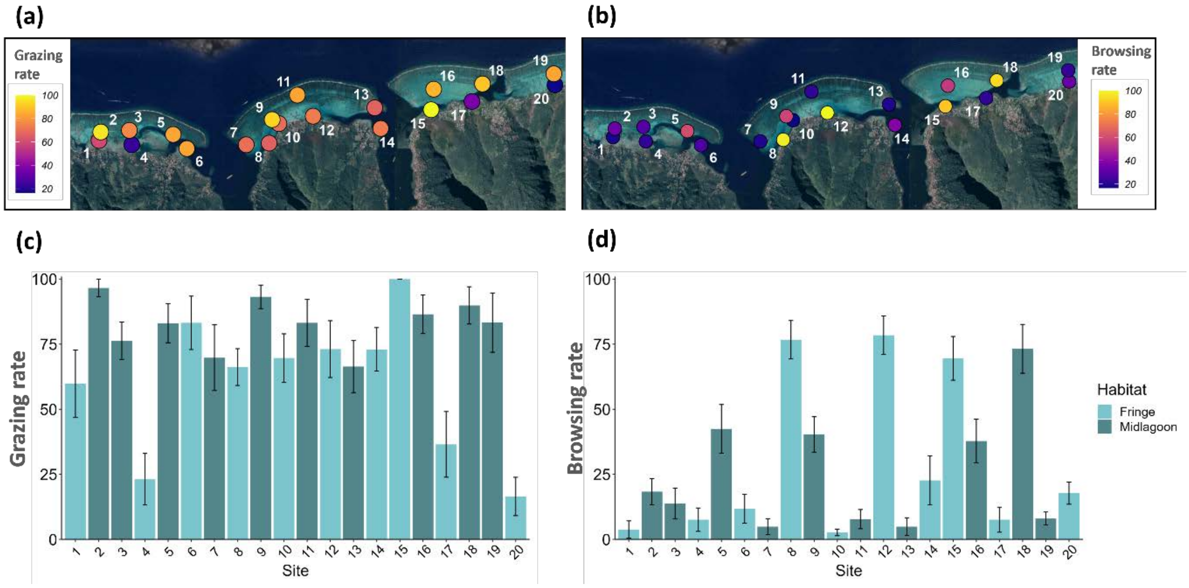


**Figure 1.** Maps showing percent consumption (mean ± SE) of **a)** turf assays after 3 hr (N = 10 replicates per site) (i.e., grazing rate) and **b)** macroalgae assays after 24 hr (N = 15 replicates per site) (i.e., browsing rate) across the twenty sites. Yellow denotes high rates of herbivory and blue indicates low rates. Barplots show the same rates of **c)** grazing and **d)** browsing at the twenty sites sorted from west to east. Bars are colored according to reef habitat.

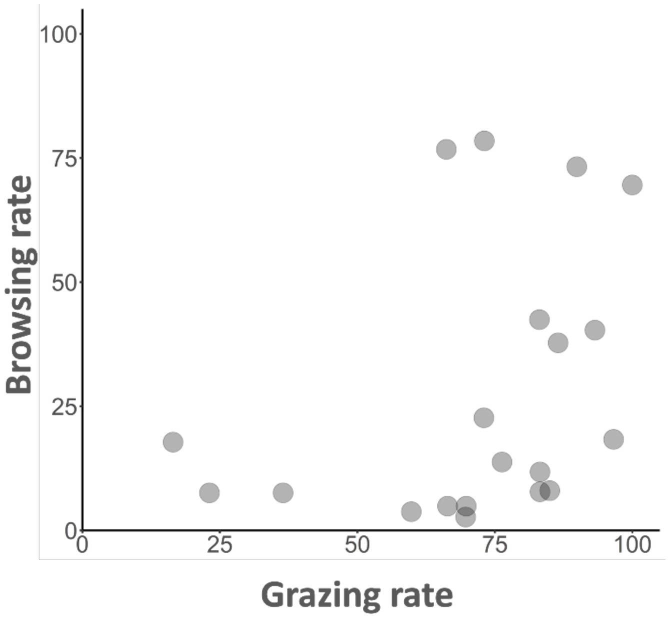


**Figure 2.** Spatial covariation between grazing and browsing rates across the twenty sites. Values are the same site averages shown in Fig. 1.

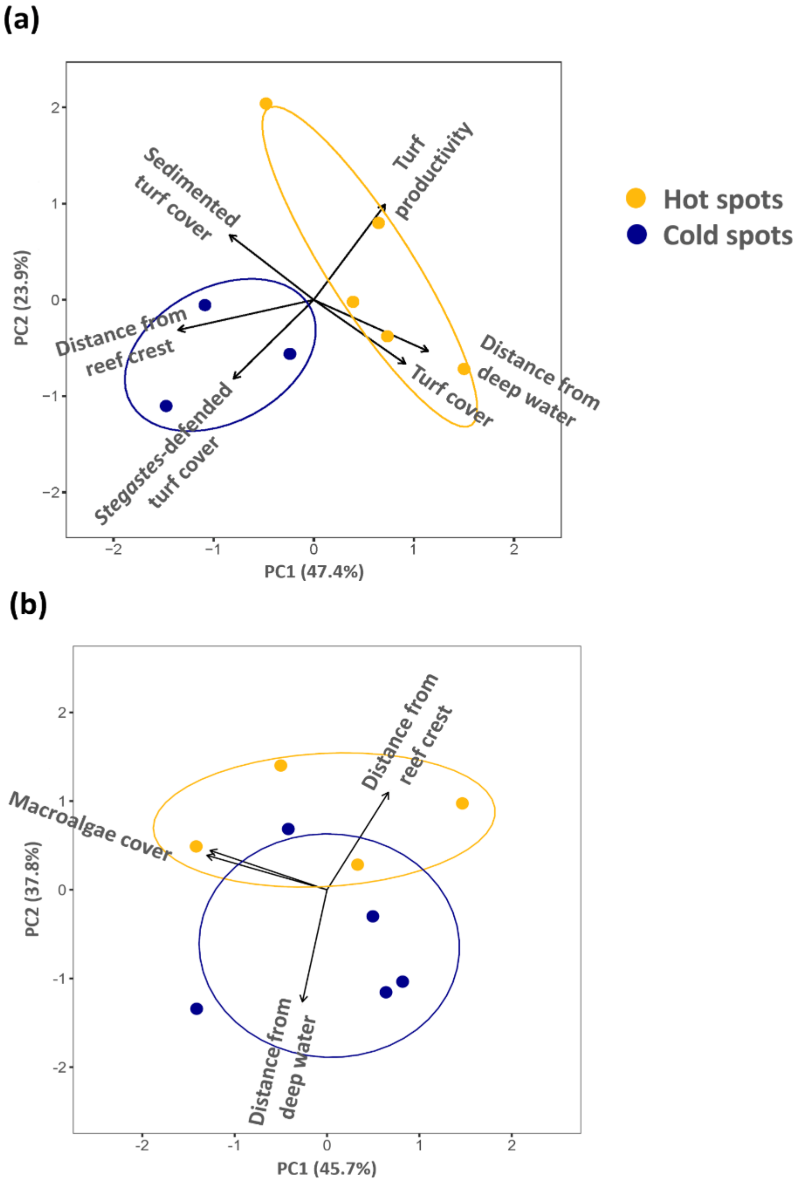


**Figure 3.** Principal component analysis showing the relationships between spatial variation in **a)** grazing and **b)** browsing with environmental attributes at hot and cold spots (i.e., sites with high or low herbivory rates). Yellow circles: hot spots in grazing (N = 5 hot spots) or browsing (N = 4 hot spots). Blue circles: cold spots in grazing (N = 3 cold spots) or browsing (N = 5 cold spots).

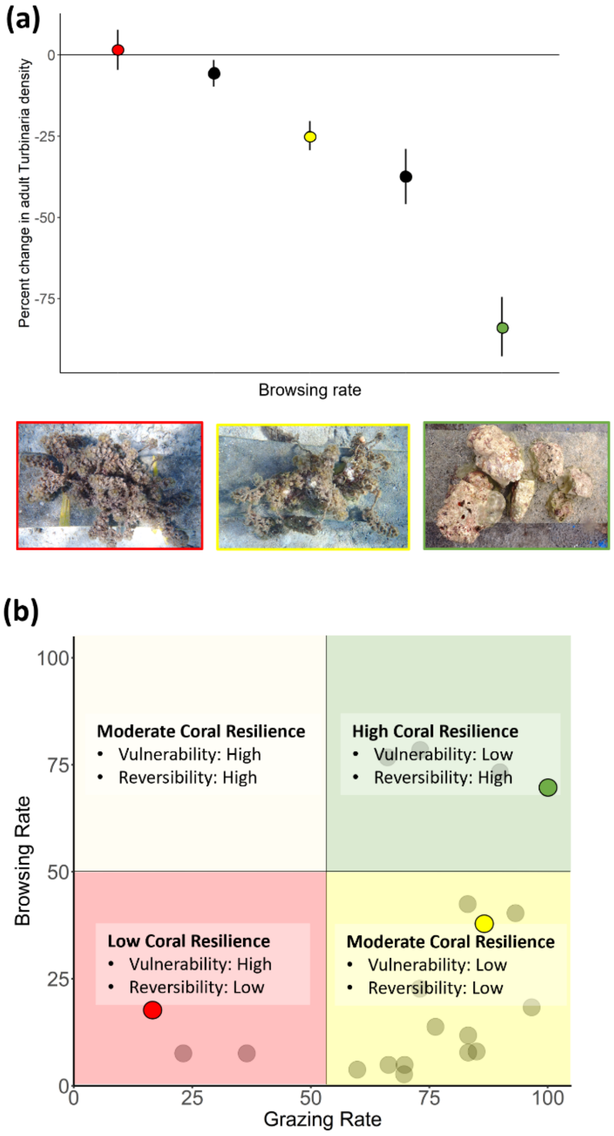
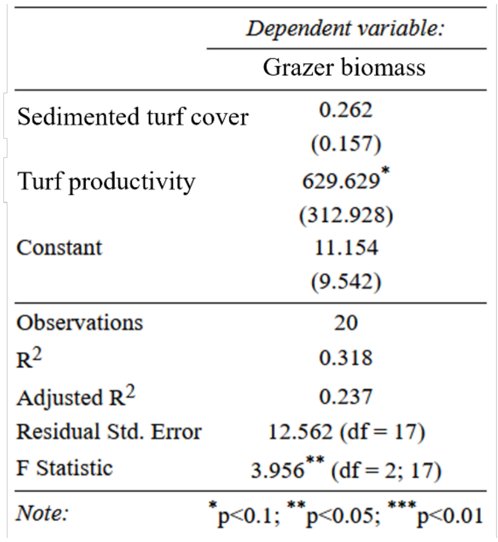


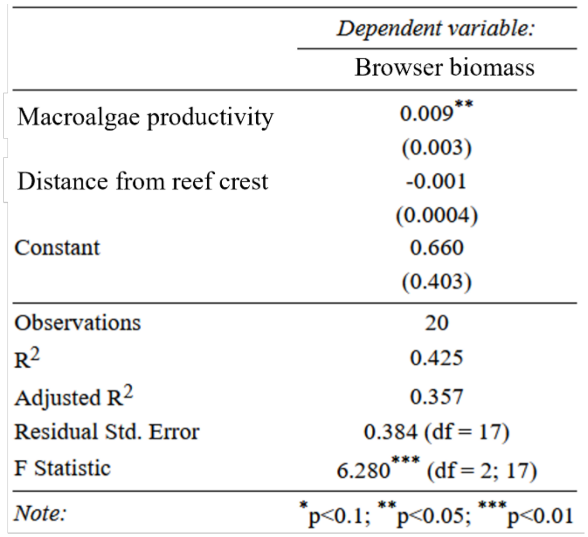
**Figure 4. a)** Percent change (mean ± SE) in adult *Turbinaria* density within macroalgal communities (N = 6 plots per site) along a gradient in ambient browsing level (based on short-term browsing assays). Three of the sites were chosen from the original set of twenty sites. Their location on panel b is noted using the same color. **b)** Conceptual framework linking variation in herbivory to vulnerability to and reversibility of coral-to-macroalgae state shifts. Vulnerability to shifting to macroalgae is tied to grazing level; sites with low grazing are highly vulnerable to shifting to macroalgae (tan and red quadrants) and those with high grazing will likely remain in a cropped turf state (green and yellow quadrants). Reversibility of a coral-to-macroalgae shift is tied to browsing level; if macroalgae establish, sites with low browsing are likely to remain in a macroalgae state (i.e., low reversibility – yellow and red quadrants) and sites with high browsing could return to the coral state (i.e., high reversibility – tan and green quadrants).

## *Supplementary Information*

**Supplemental Table 1.** Summary statistics for multiple linear regressions predicting variation in the biomass of grazers (left) and browsers (right).

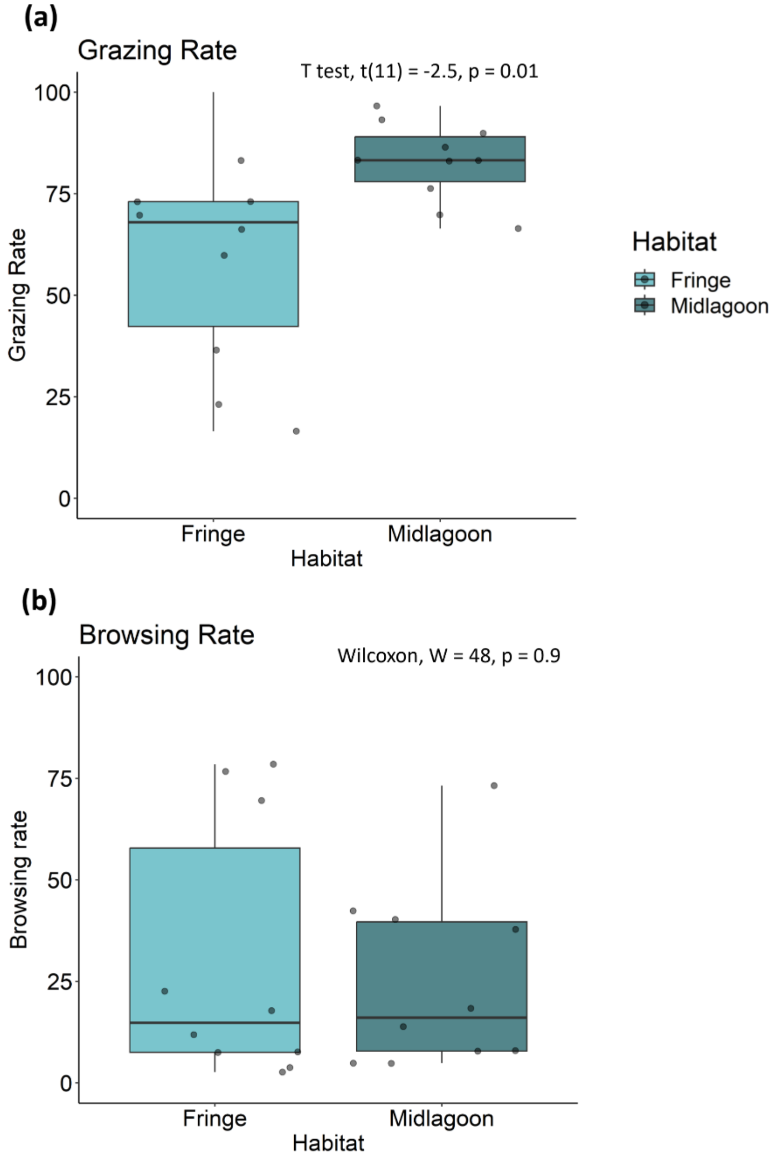


| | *Dependent variable:* |
|---|---|
| | Grazer biomass |
| Sedimented turf cover | 0.262 |
| | (0.157) |
| Turf productivity | 629.629$^{*}$ |
| | (312.928) |
| Constant | 11.154 |
| | (9.542) |
| Observations | 20 |
| $R^2$ | 0.318 |
| Adjusted $R^2$ | 0.237 |
| Residual Std. Error | 12.562 (df = 17) |
| F Statistic | 3.956$^{**}$ (df = 2; 17) |
| *Note:* | $^{*}$p<0.1; $^{**}$p<0.05; $^{***}$p<0.01 |

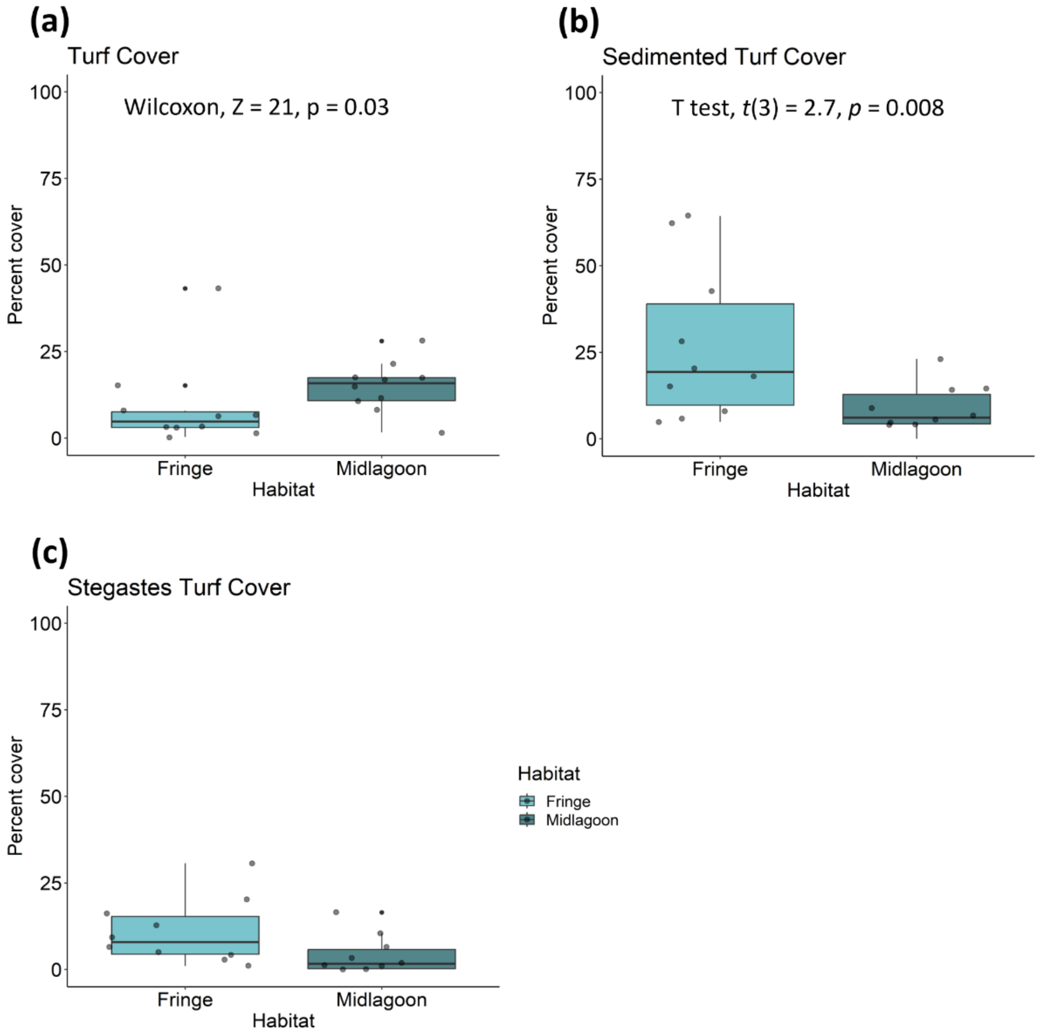


| | *Dependent variable:* |
|---|---|
| | Browser biomass |
| Macroalgae productivity | 0.009$^{**}$ |
| | (0.003) |
| Distance from reef crest | -0.001 |
| | (0.0004) |
| Constant | 0.660 |
| | (0.403) |
| Observations | 20 |
| $R^2$ | 0.425 |
| Adjusted $R^2$ | 0.357 |
| Residual Std. Error | 0.384 (df = 17) |
| F Statistic | 6.280$^{***}$ (df = 2; 17) |
| *Note:* | $^{*}$p<0.1; $^{**}$p<0.05; $^{***}$p<0.01 |

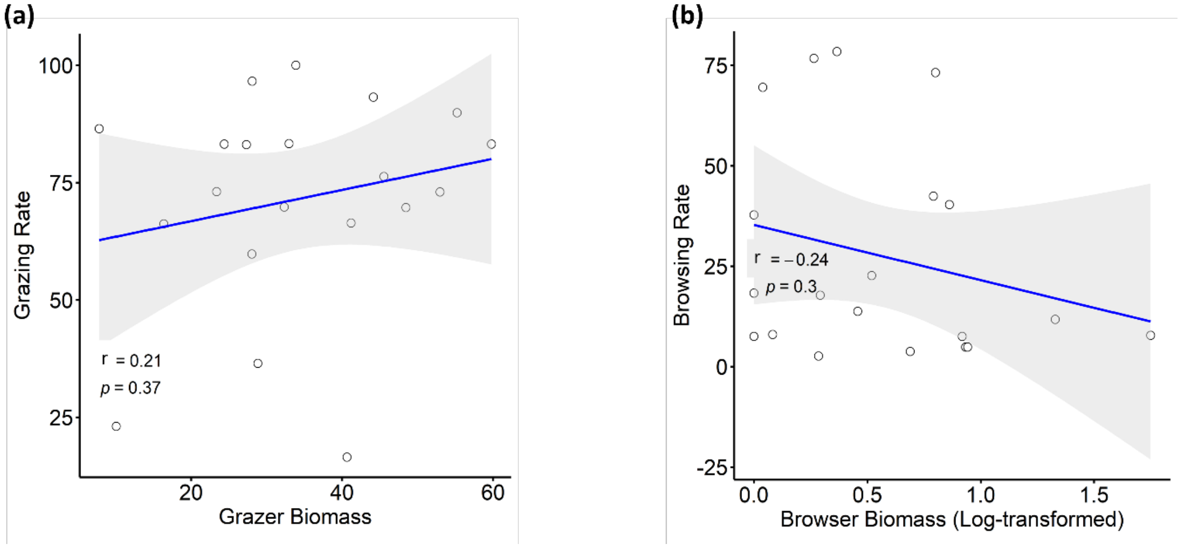
**Supplemental Table 2.** Statistics for principal component analyses (PCAs) that explore the degree to which environmental factors explain observed spatial patterns in grazing (top) and browsing (bottom)**.**



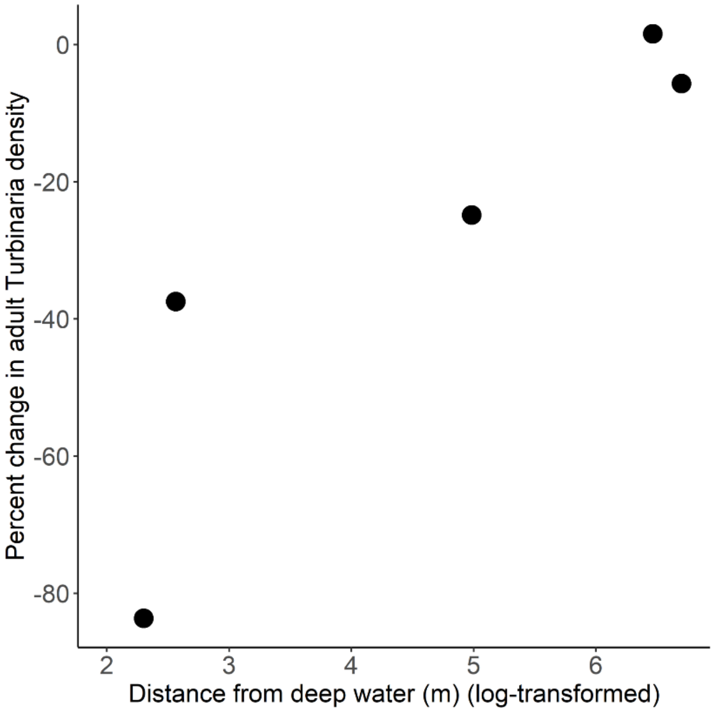
**Supplemental Figure 1.** Boxplots showing rates of **a)** grazing and **b)** browsing at the twenty sites grouped by habitat (N = 10 sites per habitat). Black lines within boxes are medians in grazing or browsing. Lower and upper box boundaries are 25th and 75th percentiles, respectively. Grey circles indicate the average rate of grazing or browsing at a site.



**Supplemental Figure 2.** Boxplots showing differences in turf community composition between mid-lagoon and fringing reef habitats (N = 10 sites per habitat). Cover of three types of turf are shown: **a)** turf, **b)** sedimented turf, and **c)** *Stegastes* turf. Grey circles indicate the average percent cover of turf at a site.



**Supplemental Figure 3.** Relationships between **a)** grazing rate and grazer biomass and **b)** browsing rate and browser biomass at the twenty sites. Circles are site averages of herbivore biomass and grazing or browsing rates.



**Supplemental Figure 4.** Relationship between removal of macroalgae communities (i.e., reversibility of coral-to-macroalgae state shifts) and distance from deep water (log-transformed).

# Chapter III: Modeling the effects of selectively fishing key functional groups of herbivores on coral resilience

## *Abstract*

Mounting evidence suggests that fishing can be a major driver of coral-to-macroalgae regime shifts on tropical reefs. In many small-scale coral reef fisheries, fishers target herbivorous fishes, which can weaken coral resilience via reduced herbivory on macroalgae that then outcompete corals. Previous models that explored the effects of harvesting herbivores revealed hysteresis in the herbivory-benthic state relationship that results in bistability of coral- and macroalgae-dominated states over some levels of fishing pressure, which has been supported by empirical evidence. However, past models have not accounted for the functional differences among herbivores or how fisher selectivity for different herbivore functional groups may alter benthic dynamics and resilience. Here we use a dynamic model that links differential fishing on two key herbivore functional groups to the outcome of competitive dynamics between coral and macroalgae. We show that reef state not only depends on the level of fishing, but also the types of herbivores targeted by fishers. Selectively fishing browsing herbivores that are capable of consuming mature macroalgae (e.g., unicornfish) increases precariousness of the coral state by moving the system close to the coral-to-macroalgae tipping point. By contrast, selectively harvesting grazing herbivores that are only capable of preventing macroalgae from becoming established (e.g., parrotfishes) can increase catch yields substantially more before the tipping point is reached. However, this lower precariousness with increasing fishing effort comes at the cost of increasing the range of fishing effort over which coral and macroalgae are bistable; increasing hysteresis makes a regime shift triggered by a disturbance more difficult

or impractical to reverse. Our results suggest that management strategies for small-scale coral reef fisheries should consider how functional differences among harvested herbivores coupled with fisher selectivity influence benthic dynamics in light of the trade-off between tipping point precariousness and coral recovery dynamics following large disturbances.

## *Introduction*

Regime shifts are abrupt ecosystem transitions to an alternate community state in which a different assemblage of organisms (Hughes, 1994; Steneck et al., 2002; Scheffer & Carpenter, 2003; Petraitis et al., 2009) is maintained by a new set of ecological feedbacks (Folke et al., 2004; Nyström et al., 2012). The new state could be considered undesirable if fewer ecosystem services (e.g., biodiversity or fish stocks) are provided (Graham et al., 2013), leading researchers to explore the predictability and reversibility of regime shifts (Scheffer et al., 2001; Suding et al., 2004; Bestelmeyer et al., 2011; Graham et al., 2013). Regime shifts can occur in two ways. First, a chronic change in an underlying driver can move the system past a tipping point and into an alternative basin of attraction. When the system is close to a tipping point (i.e., high ‘precariousness’ *sensu* Walker et al., 2004), an incremental change in the driver can trigger a large, abrupt reorganization of the community. A much larger relaxation in the underlying driver may be required to restore the system to its original state than the change that initially caused the shift (i.e., hysteresis) (Suding et al., 2004; Blackwood et al., 2012; Briggs et al., 2018), which makes reversing a regime shift difficult. Second, hysteresis in the driver-response relationship creates a region of state space where alternative ecosystem states can coexist (bistability), making it possible for a sufficiently large disturbance to flip the system into an alternative basin of attraction with no change in the underlying driver (Schmitt et al., 2019, 2022). Human activity can reduce resilience by weakening the stabilizing feedbacks that maintain an ecosystem state, increasing the system’s vulnerability to a regime shift from less intense disturbances (Donovan et al., 2020; Reed et al., 2022; Sguotti et al., 2022).

Regime shifts appear to be common in marine systems (Beaugrand, 2004; Bestelmeyer et al., 2011; Conversi et al., 2015; Schmitt et al., 2019; Reed et al., 2022; Sguotti et al., 2022). Fishing has been identified as a powerful top-down driver that can promote them (Shears & Babcock, 2002; Steneck et al., 2004; Guidetti & Sala, 2007; Pershing et al., 2015), including the well-known shifts from coral to macroalgae on tropical reefs (McClanahan & Shafir, 1990; Hughes, 1994). In many small-scale fisheries on coral reefs, fishers target herbivorous fishes that contribute to resilience by controlling algal competitors of coral (Burkepile & Hay, 2006; Rasher & Hay, 2010; Poore et al., 2012; Bozec et al., 2016; Adam et al., 2022). As a result, there is a widely recognized need for proper management of small-scale reef fisheries (Bellwood et al., 2004; Mumby, 2006; Green & Bellwood, 2009; Graham et al., 2013; Adam et al., 2015; Leenhardt et al., 2016). In this context, a potentially critical aspect is how harvesting different types of herbivorous fishes might alter resilience and promote coral-to-macroalgae regime shifts.

Species of herbivores targeted in small-scale coral reef fisheries do not constitute an ecologically uniform group, but vary in the way they feed and/or in the types of algae they consume, which influences whether and how they contribute to the resilience of the coral state (Green & Bellwood, 2009; Adam et al., 2015; Han et al., 2016). Two broad categories of roving herbivorous fishes on coral reefs play different but complementary roles in controlling algae. One group, which we operationally term ‘grazers,’ includes fishes that graze, crop, scrape or excavate endolithic and filamentous algae (hereafter ‘turf’), as well as early developmental stages of macroalgae. By keeping denuded reef surfaces in an early algal successional stage (i.e., cropped turf) that can be colonized by either corals or macroalgae (Birrell et al., 2005; Schmitt et al., 2022) grazers can *prevent* regime shifts to macroalgae (Han et al., 2016; Robinson et al., 2020; Adam et al., 2022; Schmitt et al., 2022). By contrast, ‘browsers’ consume mature macroalgae, and therefore are critical for removing macroalgae that impede coral settlement and overgrow established coral colonies (Han et al., 2016; Schmitt et al., 2022) (**Fig. 1** inset). Thus, browsers, but not grazers, play a critical role in *reversing* coral-to-macroalgae regime shifts.

In addition to playing different ecological roles, the life history attributes of the two herbivore functional groups differ in ways that influence how they may be affected by fishing (Reynolds et al., 2001). It is well known that herbivorous fishes responsible for preventing macroalgae from becoming established (i.e., grazers) are both functionally and demographically different from the species that remove mature macroalgae (i.e., browsers) (Green & Bellwood, 2009; Adam et al., 2015). The grazing functional group is typified by various species of parrotfishes (Scaridae), which have relatively fast life history traits (e.g., rapid body growth, early age of reproduction) that confer resilience to overfishing (Reynolds et al., 2001). By contrast, unicornfishes (*Naso* spp.) that epitomize browsers in the Indo-Pacific, have slower life history traits, making them relatively more vulnerable (Ford et al., 2016).

In some small-scale coral reef fisheries, parrotfishes and unicornfishes can comprise more than 50% of the catch biomass (Rassweiler et al., 2020), but they are not necessarily targeted equally. Fishers often display strong taxonomic selectivity based on cultural or economic values (Bejarano Chavarro et al., 2014; Leenhardt et al., 2016; Rassweiler et al., 2020). For example, the price of unicornfishes, which are highly prized for their flavor, was the greatest for reef fish harvested in Moorea, French Polynesia, averaging 2-3 times that of equivalent parrotfishes (Nassiri et al., 2021). Thus, high fishery value combined with slow life histories predispose unicornfishes to overexploitation compared to parrotfishes (Nash et al., 2013; Edwards et al., 2014; Taylor et al., 2014a; Ford et al., 2016) and may contribute to the disproportionately lower biomass of browsers relative to grazers that is often observed on coral reefs with small-scale fisheries (Cheal et al., 2010; Edwards et al., 2014).

Several existing models have explored how variation in herbivory (related inversely to fishing pressure) can result in abrupt regime transitions between coral and macroalgae (Mumby et al., 2007; Blackwood et al., 2012; Briggs et al., 2018). However, these models generally treat herbivores as a monolithic group, leaving unexplored how the interaction between fisher selectivity and the functional roles of harvested herbivores influences resilience. This knowledge gap hinders the development of management strategies for small-scale fisheries aiming to sustain reef resilience while ensuring food and economic security. To address this gap, we use a dynamic model that simulates the differential harvest (fisher selectivity) of the two major herbivore groups, which have different diets and life histories, linked to the competitive dynamics of key benthic space holders (i.e., coral, turf, and macroalgae). Our main objective is to explore how fisher selectivity coupled with changes in catch alters the precariousness and reversibility of a coral-to-macroalgae regime shift. Our model is broadly grounded by the coral reef system of Moorea, French Polynesia, where there is detailed knowledge of the dynamics of the reef community (Adam et al., 2011, 2014, 2022; Han et al., 2016; Holbrook et al., 2016, 2018, 2022; Schmitt et al., 2019, 2022) and the small-scale reef fishery and fisher behavior (Leenhardt et al., 2016; Rassweiler et al., 2020, 2022; Nassiri et al., 2021; Holbrook et al., 2022; Lauer et al., 2022).

## *Methods*

### *Evidence for fisher selectivity*

We explored patterns of selectivity for key herbivorous fish groups in the small-scale fishery of Moorea, French Polynesia (17º30’S, 149 º50’W). Moorea is a high volcanic island surrounded by shallow lagoons enclosed by a barrier reef located ~1 km offshore. The island is home to an active small-scale reef fishery where over half of the adult population fishes, with most households having at least one member engaged in the fishery (Leenhardt et al., 2016; Rassweiler et al., 2020). The preferred method of fishing is free-dive spearfishing, which allows fishers to be highly selective in their catch by visually assessing each fish before harvesting it. Herbivores in Moorea are held as prized symbols of culture and identity. While more than 40 genera of fishes are caught, grazing parrotfishes and browsing unicornfishes make up 50% of biomass of the catch (Leenhardt et al., 2016; Rassweiler et al., 2020).

We assessed the relative importance of herbivores to the catch using data gathered during a market survey (Holbrook et al., 2017). As a centralized fish market no longer exists in Moorea, most fish sold from the local fishery are strung up at stands along the roadside. These were visited and photographed during peak hours for fish sale activity in 2014 and 2015 (details in Rassweiler et al., 2020). Photographed fish were later counted, identified to the lowest taxonomic resolution possible, and assigned a trophic level and functional group based on published references (Brooks & Adam, 2019). The proportional abundances of major fish groups (browsing and grazing herbivores, benthic carnivores, and planktivores) in the catch were then calculated using the total number of fish caught in both years.

We next investigated how abundances of fish on the reef and selectivity by fishers could influence the composition of the catch. First, we developed a conceptual model illustrating patterns of fishing selectivity based on the relative biomass of fish on the reef and in the catch through a series of simulations in R (version 4.1.1). If, for instance, there are two fish guilds – parrotfish ($P$) and unicornfish ($U$) – we hypothesized that fishers might have some preference, $\sigma$, for one guild of fish, and that fishing effort, $f$, would be split between the two guilds accordingly. Thus, the total fish caught is given by:

$$Total\ Catch = \sigma fP + (1-\sigma)fU \tag{1}$$

From this equation, we can compute the relative proportion of catch that comes from parrotfish ($\sigma fP / (\sigma fP + (1-\sigma)fU)$), compared to the proportion of the fish population comprised of parrotfish ($P / (U + P)$) (**Fig. 2a**).

We compared patterns of selectivity for three fish taxonomic groups (using reef biomass abundance and catch data replotted from **Fig. 5** in Rassweiler et al. (2020)) to the modelled selectivity relationships. The fish taxonomic groups were either important to the fishery – grazing parrotfishes (Scaridae) and browsing unicornfishes (*Naso* spp.) – or highly abundant on the reef (surgeonfishes in the genera *Acanthurus* and *Ctenochaetus*). Biomass data on reef fishes were obtained from the Moorea Coral Reef Long Term Ecological Research site and from the Service d'Observatoire CORAIL PGEM monitoring programs, and catch data were derived from roadside surveys (as described above) conducted around the island during a subset of years in 2007-2015 (for more detail, see Rassweiler et al., 2020).

### *Modeling effects of fisher selectivity*

To investigate the effects of differentially harvesting herbivore functional groups on coral-macroalgae dynamics, we built upon the dynamic model developed by Briggs et al. (2018) which simulates the fraction of a reef occupied through time by key classes of benthic space holders: coral I, immature macroalgae (*I*), mature macroalgae (*M*), and turf algae (*T*) where $C + I + M + T = 1$ (**Fig. 3**). It is assumed that any open space is immediately colonized by turf. Coral and immature macroalgae recruit to turf via open recruitment from outside sources at rates $\varphi_C$ and $\varphi_I$, respectively. Coral, immature, and mature macroalgae can laterally overgrow turf at rates $g_C$, $g_I$, and $g_M$, respectively. We assume mature macroalgae overgrow coral but at a slower rate than they overgrow turf ($\gamma g_M$, where $\gamma \leq 1$) due to coral defenses. Immature macroalgae graduate into a mature stage at maturation rate $\omega$. Coral, immature macroalgae, and mature macroalgae die at natural mortality rates $d_C$, $d_I$, and $d_M$, respectively.

$$\frac{dC}{dt} = \varphi_C T + g_C CT - d_C C - \gamma g_M MC \tag{2}$$

$$\frac{dI}{dt} = \varphi_I T + rMT + g_I IT - d_I I - \omega I - \alpha PI - \alpha UI \tag{3}$$

$$\frac{dM}{dt} = \omega I + g_M MT + \gamma g_M MC - d_M M - \zeta \alpha UM \tag{4}$$

We extended the Briggs et al. (2018) model by introducing two classes of herbivorous fish – grazing parrotfish (*P*) and browsing unicornfish (*U*) – as dynamic state variables. Although unicornfish consume macroalgae, data from behavioral surveys of foraging fish on Moorea reveal that they also feed on turf algae (**SI Fig. 1**). In our model, populations of parrotfish and unicornfish increase based on consumption of algal resources and grow logistically to carrying capacity *K*. Because we are most interested in the effects of varying total fishing effort and fisher selectivity, for simplicity, we assumed that all fish types consume turf and immature macroalgae at a common per capita feeding rate $\alpha$ and convert food into new biomass with conversion efficiency *e*. Relative to turf and immature macroalgae, unicornfish consume mature macroalgae at a reduced rate ($\zeta\alpha$, where $\zeta \leq 1$) due to structural and chemical defenses many macroalgae develop against herbivores as adults (Stiger et al., 2004; Davis, 2018). Fish are removed through fishing at total fishing effort rate *f* (where *f* ranges from 0 to 1). Fishers can show differential selectivity for fish through the parrotfish selectivity term $\sigma$, which allocates a proportion of the total fishing effort onto parrotfish and the remainder onto unicornfish ($1 - \sigma$). If fishers show the same selectivity for parrotfish and unicornfish, then $\sigma = 0.5$ and fishing effort is split equally. The biomass of parrotfish and unicornfish removed each year will depend on the value of $\sigma$ and fish biomass. For instance, if $\sigma = 0$, then no parrotfish are removed by fishers, and all effort is allocated towards harvesting unicornfish. Differences in life history between fish are accounted for by the parrotfish scalar multiplier $\rho$, which describes how much faster parrotfish increase their population biomass relative to unicornfish.

$$\frac{dP}{dt} = [\rho(e\alpha T + e\alpha I)]P\left(1 - \frac{P}{K}\right) - f\sigma P \tag{5}$$

$$\frac{dU}{dt} = (e\alpha T + e\alpha I + \zeta e\alpha M)U\left(1 - \frac{U}{K}\right) - f(1 - \sigma)U \tag{6}$$

We parameterized the model with ranges of values published by Fung et al. (2011), which were derived using empirical studies of reef systems not impacted by anthropogenic stressors (e.g., overfishing or nutrification) and default values based on Briggs et al. (2018) but modified to account for the introduction of herbivores as dynamic state variables (Table 1). We defined ranges and default values for new parameters and state variables based on empirical studies conducted in reef systems like those used by Fung et al. (2011) (Appendix S1: Table S1).

### *Model analysis*

We first performed a local sensitivity analysis to test the influence of key parameters on the equilibrium states of the system. Our analysis focused on the effects of two key parameters: total fishing effort ($f$) and fishing selectivity ($\sigma$). First, we explored how variation in total fishing effort influences equilibrium values of coral and macroalgae cover by using bifurcation diagrams, which show how a model output changes with respect to a parameter. We tested for the existence of bistability and hysteresis by running simulations under two initial conditions: 1) high coral and low macroalgae cover, and 2) low coral and high macroalgae cover. Following Briggs et al. (2018), we quantified the region of bistability (i.e., the range in parameter values where coral- and macroalgae-dominated states are both possible) and the associated degree of hysteresis. We defined two critical thresholds in total fishing effort on each bifurcation diagram: $crit_M$ is the lowest level of fishing for which a macroalgae-dominated state exists and $crit_C$ is the highest level of fishing for which a coral-dominated state exists. If $crit_C - crit_M > 0$, then hysteresis in the system is possible, and a larger difference between critical threshold values correlates to a wider region of bistability and a higher degree of hysteresis. We then explored how fishing selectivity alters critical thresholds and state shift dynamics by comparing $crit_C$ and $crit_M$ under various scenarios of selectivity: equal selectivity of parrotfish and unicornfish ($\sigma = 0.5$) or selectivity of one over the other ($\sigma \neq 0.5$). Finally, we explored how selectivity interacts with total fishing effort to change critical thresholds and reef state (i.e., dominated by coral or by macroalgae) at equilibrium.

## ***Results***

### *Evidence for fisher selectivity*

Data obtained during market surveys revealed that herbivores comprise a major component of the catch in Moorea's local-scale reef fishery. They made up over half of the total fish in market surveys conducted in 2014 and 2015, representing a slightly larger proportion of the catch than benthic carnivores and planktivores combined (**Fig. 1**). Browsers comprised just under a third of the herbivores caught, and the remainder consisted of grazers (mainly parrotfish) that primarily consume turf. The inset on **Fig. 1** shows the possible interaction web that arises from fishers harvesting browsing and grazing herbivores.

We observed strongly contrasting patterns of selectivity for different herbivorous fishes, in that only certain taxa were disproportionately caught relative to their abundance on the reef (**Fig. 2**). *Acanthurus* and *Ctenochaetus* – surgeonfishes that crop turf and/or consume detritus – are some of the more abundant taxa on the reef. However they were consistently strongly under-represented in the catch, which suggests fishers preferentially harvest other taxa (**Fig. 2b**). Compared with surgeonfishes, Scaridae (parrotfish; grazers) biomass showed weak selectivity, as the catch was roughly proportionate to their biomass in the environment. This implies that fishers mostly catch parrotfish as they encounter them on the reef and do not necessarily seek them out. Most notably, fishers displayed a strong positive selectivity for *Naso* (unicornfish; browsers), which comprised relatively modest amounts of biomass on the reef. For example, at a time when *Naso* represented about a fifth of the fishable biomass on the reef they comprised over half of the herbivore catch (**Fig. 2b**).

### *Modeling effects of fisher selectivity on promoting alternative stable states*

Consistent with other models (Mumby et al., 2007; Fung et al., 2011; Blackwood et al., 2012; Briggs et al., 2018, Gil et al. 2020), our model predicts bistability between alternate stable states dominated by either coral or macroalgae (**Fig. 4**) that arises from hysteresis in the relationship between fishing intensity (or herbivory) and macroalgal cover (or coral cover). Critical thresholds in total fishing effort represent tipping points between stable states (**Figs. 4** and **5**) and reflect the amount of herbivory required to either maintain corals by controlling macroalgae (i.e., below $crit_C$ or dashed line in **Figs. 4** and **5**) or allow macroalgae to escape control and dominate (i.e., above $crit_M$ or solid line in **Figs. 4** and **5**). Increasing total fishing effort ($f$) and/or the selectivity for unicornfish over parrotfish ($\sigma$) promote dominance by macroalgae and increase the likelihood of a coral-to-macroalgae regime shift triggered by fishing (**Fig. 5**).

### *Modeling effects of fisher selectivity on resistance to and reversibility of a regime shift*

The tipping point in total fishing effort at which a shift from coral- to macroalgal-dominance is triggered ($crit_C$) depends on the pattern of fisher selectivity (**Fig. 4**). When fishers selectively harvested unicornfish over parrotfish, the tipping point occurred at the lowest total fishing effort (**Fig. 4** top panels, **Fig. 5**). By contrast, a much higher fishing effort was needed to tip the system from coral- to macroalgal-dominance when parrotfish were targeted over unicornfish (**Fig. 4** bottom panels, **Fig. 5**). Thus, our model indicates that the coral state is most resistant to a fishing-induced regime shift when fishers show high selectivity for parrotfish. This is because the system can withstand a higher total fishing effort before crossing the tipping point to macroalgae (**Figs. 4** and **5**). Conversely, targeting unicornfish substantially increases the precariousness of the coral state. For example, at a low level of total fishing effort, an incremental increase in fishing moves the system close to the tipping point to macroalgae (**Fig. 4** top panels), which is not the case if parrotfish are targeted (**Fig. 4** bottom panels).

Once the tipping point from coral to macroalgae is crossed, the equilibrium cover of macroalgae can vary depending on the level of herbivory (or fishing effort). For instance, the maximum level of coral cover at equilibrium does not vary with respect to the type of selectivity, whereas the maximum equilibrium cover for macroalgae increases with increasing fishing effort. Further, the highest level of macroalgal cover is achieved when fishers selectively harvest unicornfish, while targeting parrotfish yields the lowest macroalgal cover. This is because targeting parrotfish lowers the fishing effort directed toward unicornfish, leading to higher unicornfish populations and increased browsing on both mature and immature macroalgae.

In addition to altering resistance of the coral state to fishing, our model reveals that fisher preference can also influence the degree of hysteresis, that is the width of the region of total fishing effort ($f$) over which coral and macroalgae are bistable (**Fig. 4**). The narrowest region of bistability occurs when unicornfish are selectively harvested, while the widest region is produced by fishers preferentially targeting parrotfish (grey regions, **Fig. 4**). Reversing a regime shift from macroalgae to coral requires relaxation in fishing effort below

$crit_M$. Thus, restoring the system back to the coral state would demand a much greater reduction in fishing when fishers preferentially harvested parrotfishes (grey region, **Fig. 4** bottom panels) instead of unicornfish (grey region, **Fig. 4** top panels).

Additionally, when alternative stable states exist in the system, a sufficiently large coral-killing disturbance can flip the system from coral to macroalgae without any change in total fishing effort; selectively fishing parrotfishes increases the vulnerability of the system to a disturbance-induced regime shift because of the greater region of state space where coral and macroalgae are bistable.

### *Discussion*

Fishing often generates a cascade of indirect effects that can alter community structure, ecosystem function, and resilience. Lagged responses between trophic levels (e.g., herbivores and primary producers) can create nonlinear community dynamics by promoting thresholds and tipping points (Salomon et al., 2009), potentially triggering an abrupt regime shift to a degraded state (Frank et al., 2005; Österblom et al., 2007; Rassweiler et al., 2022). Our model reveals that resilience of corals on coral reefs is not only affected by the intensity at which fishers harvest herbivores, but also by the type of herbivore that is targeted. Specifically, our model predicts that harvester preference for browsing unicornfish over grazing parrotfishes may leave Moorea coral reefs more prone to transitions to the macroalgal state.

Like previous models of benthic dynamics on coral reefs (Mumby et al., 2007; Fung et al., 2011; Blackwood et al., 2012; Bozec et al., 2016; Briggs et al., 2018, Gil et al., 2020), our model predicts that there is a range in herbivory over which coral- and macroalgae-dominated states can be bistable. Such regions of bistability arise from different forward and return paths of consumer and resource populations – that is when the underlying driver-response relationship changes from before to after a state shift, which is diagnostic of a hysteretic system (Salomon et al., 2009; Bestelmeyer et al., 2011; Briggs et al., 2018; Schmitt et al., 2019, 2022). If a coral-to-macroalgae regime shift occurs, a return to the coral state will require a large reduction in fishing effort, well below the original tipping point, to allow for a sufficiently high build-up of herbivory to extirpate established macroalgae. This has profound management implications. Food and economic security are typical drivers of small-scale reef fisheries (Leenhardt et al., 2016); therefore, an inherent tension exists between maximizing fish yields and minimizing adverse effects on coral resilience (Bozec et al., 2016). Management policies that lower the precariousness of the system by maintaining fishing effort well below the threshold that triggers a shift to macroalgae may come at the cost of reduced fish yields. Our model gives insight into how fisher behavior might be harnessed to better optimize strategies to maintain coral resilience while maximizing catch.

Grazing herbivorous fishes responsible for preventing macroalgae from becoming established are generally both functionally and demographically different from the browsing species that remove mature macroalgae once they have proliferated (Green & Bellwood, 2009; Adam et al., 2015). For example, among the ecologically most important taxa in the grazer functional group are scraping and excavating parrotfishes (family Scaridae, often in the genera *Scarus* and *Chlorurus*), which can show substantial rapid increases in biomass after large, coral-killing disturbances generate large amounts of new turf-covered reef habitat (Gilmour et al., 2013; Adam et al., 2014; Han et al., 2016). These rapid individual and population-level responses of parrotfishes to augmented food resources can be attributed to fast rates of body growth, early age of reproductive maturity, and short life-spans (~5-6 yrs.) (Choat et al., 1996; Taylor et al., 2014b). Browsers are a less speciose group than grazers (Holbrook et al., 2016) and are exemplified in the Indo-Pacific by unicornfishes in the genus *Naso* (Hoey & Bellwood, 2009, 2010; Michael et al., 2013). Compared to grazing parrotfishes, browsing unicornfishes grow much slower, reach reproductive maturity at an older age, and can live longer (Choat et al., 1996; Taylor et al., 2014a). The different dietary and life history traits likely explain why, after a large disturbance that resets the benthic assemblage to early successional stages of algae, rapid biomass responses have been observed for grazers but not browsers (Adam et al., 2014; Han et al., 2016; Rassweiler et al., 2020). Our model reflects these functional differences in its construction by (1) allowing parrotfish to grow at more rapid rates, and (2) partitioning the feeding niches of these fishes to allow browsers to also consume macroalgae. This parameterization reduced competition between the fish in our model: model runs with only one species of fish (i.e., initializing the simulation with parrotfish or unicornfish set to 0) resulted in equilibrium population sizes of the remaining fish that were at most 9% greater than that species' population size in the two-fish simulation. In contrast, fishing had a large effect on fish population sizes, with parrotfish decreasing by up to 15% and unicornfish driven extinct at the highest levels of fishing we studied.

Our model revealed that resistance of the coral state to increasing fishing effort depended on the pattern of fisher selectivity between grazing parrotfish and browsing unicornfish. The coral state was most resistant to the harvesting of herbivores when fishers preferentially targeted parrotfish due to the high level of fishing effort associated with the tipping point to macroalgae. By contrast, the tipping point to macroalgae was reached at a far lower fishing effort when fishers selectively harvested unicornfish over parrotfish. As a result, when coral is the only stability domain in the environment (i.e., at low fishing intensities), a given increase in fishing moves the system much closer to the tipping point to macroalgae when fishers selectively harvest browsers rather than grazers. This difference in how the same incremental increase in fishing effort alters the precariousness of the system to a regime shift implies there can be management strategies based on fisher selectivity patterns that balance the conflicting demands of enhancing food security and maintaining coral resilience. In systems like Moorea where fishers selectively target browsers, a potential management strategy suggested by our results would be to reduce fishing effort on unicornfish. This could result in reduced vulnerability to a fishing-induced regime shift.

Our model also revealed that the region of bistability (i.e., the degree of hysteresis) was inversely related to the degree of resistance arising from a fisher selectivity scheme. This has two important management implications. First, when the ambient level of fishing falls within the region of bistability (i.e., between the critical thresholds), a sufficiently large coral-killing disturbance (e.g., bleaching event, cyclone) can flip the system from the coral to the macroalgae stability domain without any change in fishing effort. Thus, our model showed that, relative to selectively targeting grazing parrotfish, preferentially harvesting browsing unicornfish increased the precariousness of the system to a fishing-induced regime shift. However, this also resulted in a much smaller region of bistability, thereby conferring a relatively lower risk of a disturbance-induced regime shift. Second, the degree of hysteresis influences the reversibility of a regime shift, regardless of whether it was triggered by a large disturbance or overfishing. Hence, the wider region of coral-macroalgae bistability that arose when fishers selectively harvested parrotfish over unicornfish means that after a regime shift, more relaxation in fishing effort will be required to restore the system back to the coral-dominated state. This implies that a general trade-off may exist between fisher selectivity schemes that enhance catch while minimizing a system’s precariousness to overfishing and those that minimize disturbance-induced regime shifts and are less challenging to reverse.

Solutions to balance conflicting small-scale fishery management goals will also depend in part on how the herbivores’ functional role in contributing to resilience (i.e., grazing vs. browsing) maps onto life history traits that influence their vulnerability to overexploitation. With respect to grazing fishes that typically have fast life history traits, Taylor et al. (2014b) were able to predict the sensitivity of parrotfish to exploitation using length- and age-based traits that can be measured and tracked readily by resource managers. Further, Shantz et al. (2020) found that fishing in the Caribbean resulted in the extirpation of large-bodied parrotfishes, skewing populations towards younger, smaller individuals that were not able to keep macroalgae suppressed. These simple metrics may not be as useful for browsers with slow life history traits such as *Naso* that do not show as strong a relationship between body size and age (Choat & Robertson, 2002). Effective management strategies for maintaining the crucial ecological role of ‘slow’ browsers such as *Naso* are likely to involve severe limitations on fishing, including heavily reduced take or even outright bans (Ford et al., 2016).

Fishing along with nutrient pollution from land use practices that harm coral and promote macroalgae (Donovan et al., 2020; Burkepile et al., 2020; Adam et al., 2021, Holbrook et al., 2022) are major local stressors that threaten the resilience of corals. Such local stressors are occurring as the disturbance regime of coral reefs is changing due to increases in the frequency and severity of thermal stress events that cause mass bleaching of corals (Hughes et al., 2017) and possible increases in the intensity of powerful storms as ocean waters warm (Trenberth, 2005). These two major sources of disturbance themselves may promote dissimilar post-disturbance dynamics on coral reefs (Kopeckey et al., 2023). Stressors associated with global climate change place a premium on effectively reducing the adverse effects of local human activities (Bellwood et al., 2004). More effective management of small-scale fisheries in which herbivores are targeted species is an urgent priority to enhance both catch sustainability and coral resilience.

Clearly there is not a single template for managing small-scale coral reef fisheries to optimize food and economic security without undermining reef resilience. Resource managers will need to consider the costs and benefits of different strategies contextualized by the details of the local social-ecological system. Our results suggest that management strategies for small-scale reef fisheries should consider the nexus between the functional differences among harvested herbivores and selectivity by fishers in shaping benthic dynamics in light of the trade-offs between precariousness, disturbance dynamics, and reversibility of regime shifts.

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## *Tables*

**Table 1.** Variables and parameters, their descriptions, units, and values.

| Symbol | Description | Default value (range) |
|---|---|---|
| **Variables** | | |
| $C$ | Fraction of space occupied by coral | |
| $I$ | Fraction of space occupied by immature macroalgae | |
| $M$ | Fraction of space occupied by mature macroalgae | |
| $U$ | Unicornfish population | |
| $P$ | Parrotfish population | |
| **Parameters** | | |
| $\varphi_C$ | Open recruitment rate of corals | 0.001 (0 to 0.05) $y^{-1}$ |
| $\varphi_I$ | Open recruitment rate of macroalgae | 0.0001 (0 to 0.05) $y^{-1}$ |
| $g_C$ | Rate at which corals overgrow turf | 0.1 (0 to 0.2) $y^{-1}$ |
| $g_I$ | Rate at which immature macroalgae overgrow turf | 0.6 ($g_C$ to ($g_C$ + 1)) $y^{-1}$ |
| $g_M$ | Rate at which mature macroalgae overgrow turf | 0.6 ($g_C$ to ($g_C$ + 1)) $y^{-1}$ |
| $\gamma$ | Scaling constant to slow overgrowth of corals by mature macroalgae | 0.5 (0 to 1) |
| $r$ | Local production of vulnerable macroalgae by mature stage | 0.5 ($g_C$ to ($g_C$ + 1)) $y^{-1}$ |
| $d_C$ | Natural mortality rate for corals | 0.05 (0 to 0.1) $y^{-1}$ |
| $d_I$ | Natural mortality rate for immature macroalgae | 0.5 (0 to 12) $y^{-1}$ |
| $d_M$ | Natural mortality rate for mature macroalgae | 0.3 ($d_C$ to ($d_C$ + 1)) $y^{-1}$ |
| $\alpha$ | Herbivory rate | 10 (5 to 15) $y^{-1}$ |
| $\omega$ | Maturation rate of immature macroalgae into the mature stage | 2 (0 to 12) $y^{-1}$ |
| $\zeta$ | Scaling constant to reduce herbivory on mature macroalgae | 0.2 (0 to 0.8) |
| $K$ | Fish carrying capacity | 0.2 kg $m^{-2}$ |
| $\rho$ | Parrotfish scalar multiplier | 4 |
| $f$ | Total fishing effort | Varies (0 to 0.15) $y^{-1}$ |
| $\sigma$ | Fishing effort allocated onto parrotfish | Varies (0 to 1) |
| $e$ | Conversion efficiency of algae to fish | 0.02 |

*Figures*

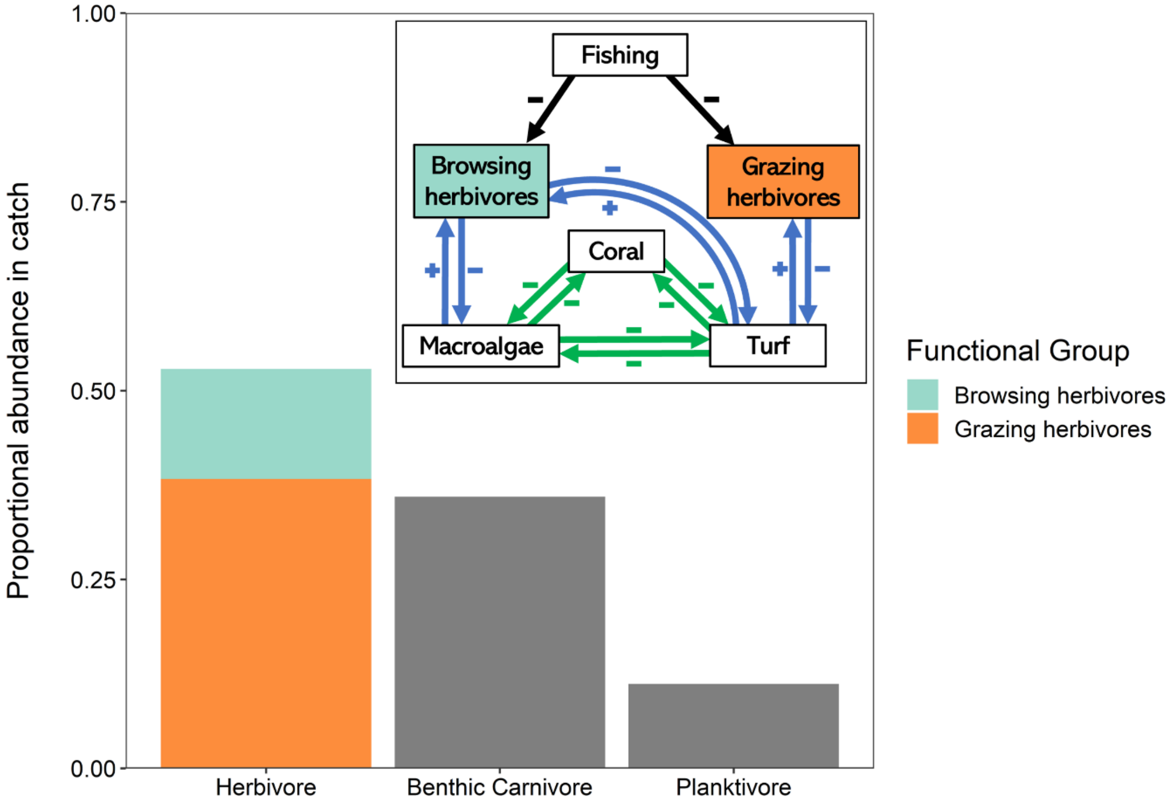


**Figure 1.** Taxonomic composition of the catch based on market surveys done in Moorea in 2014 and 2015. The proportional abundance of fish (pooled for both years) is shown by trophic level (i.e., herbivores, benthic carnivores, and planktivores). Herbivores are split into functional groups (i.e., browsing and grazing herbivores) and denoted by color. Inset: Conceptual diagram of interactions between fishing, key herbivore functional groups, and benthic space holders. Arrows are color-coded to depict different interaction types: black denotes human effects, blue denotes trophic interactions, and green denotes competition for space.

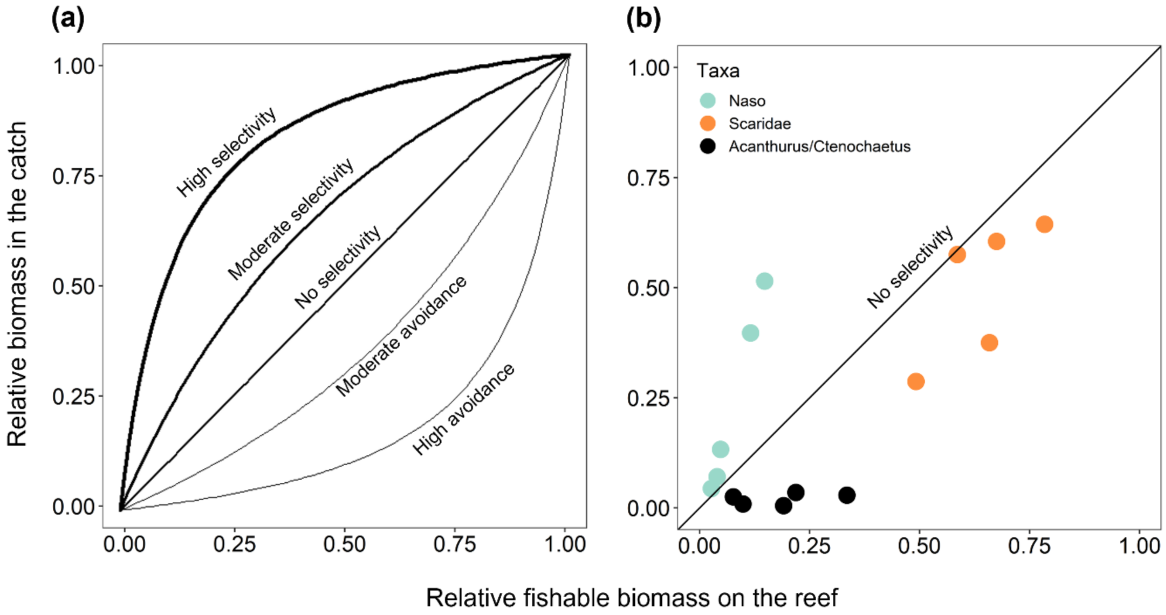


**Figure 2. a)** Conceptual diagram showing a range of selectivity patterns that can arise as a function of fish abundance on the reef and biomass in the catch. **b)** Relative biomass of three taxonomic groups [surgeonfish (*Acanthurus/Ctenochaetus*), parrotfish (Scaridae), and unicornfish (*Naso*)] on the reef and in the catch based on market surveys on Moorea over 5 years (2007, 2008, 2012, 2014, 2015). Each point represents a year. Data are re-plotted from Fig. 5 in Rassweiler et al. (2020).

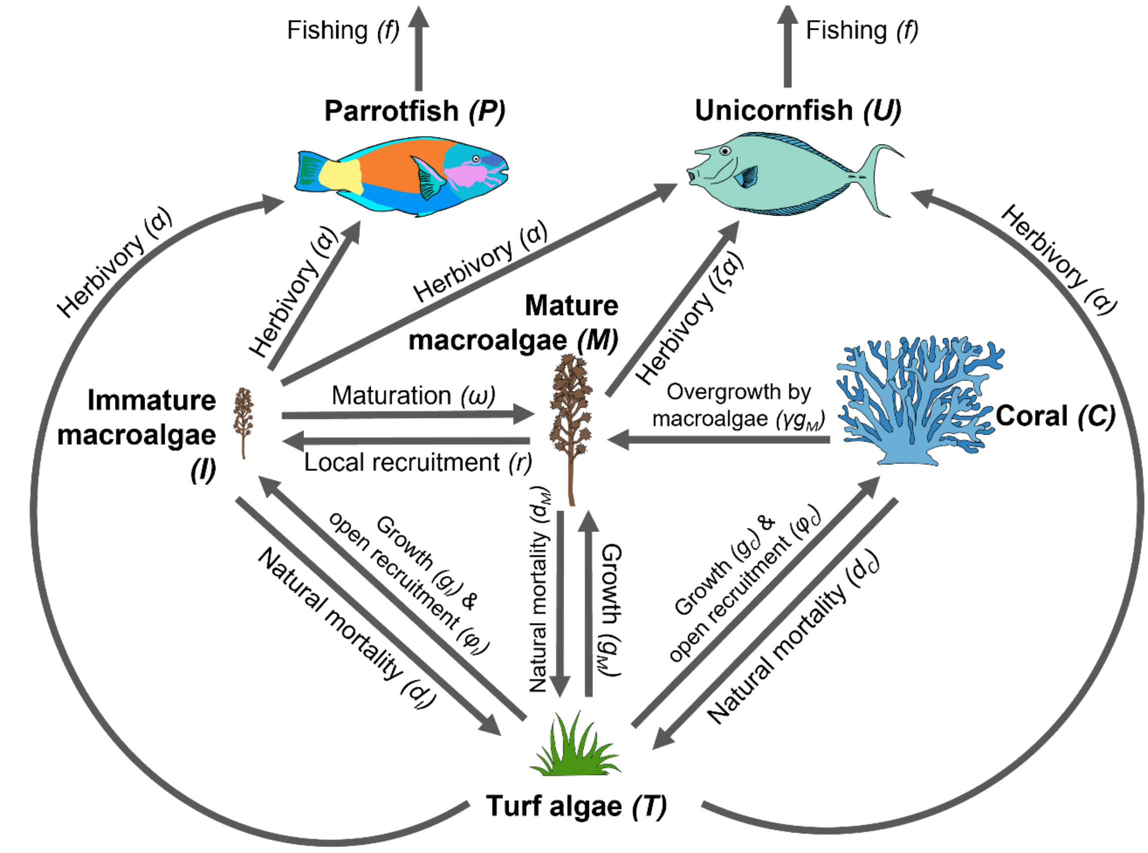


**Figure 3.** An illustrative diagram of the model system showing variables and parameters that describe their interactions and the transfer of occupation of space or biomass (black arrows).

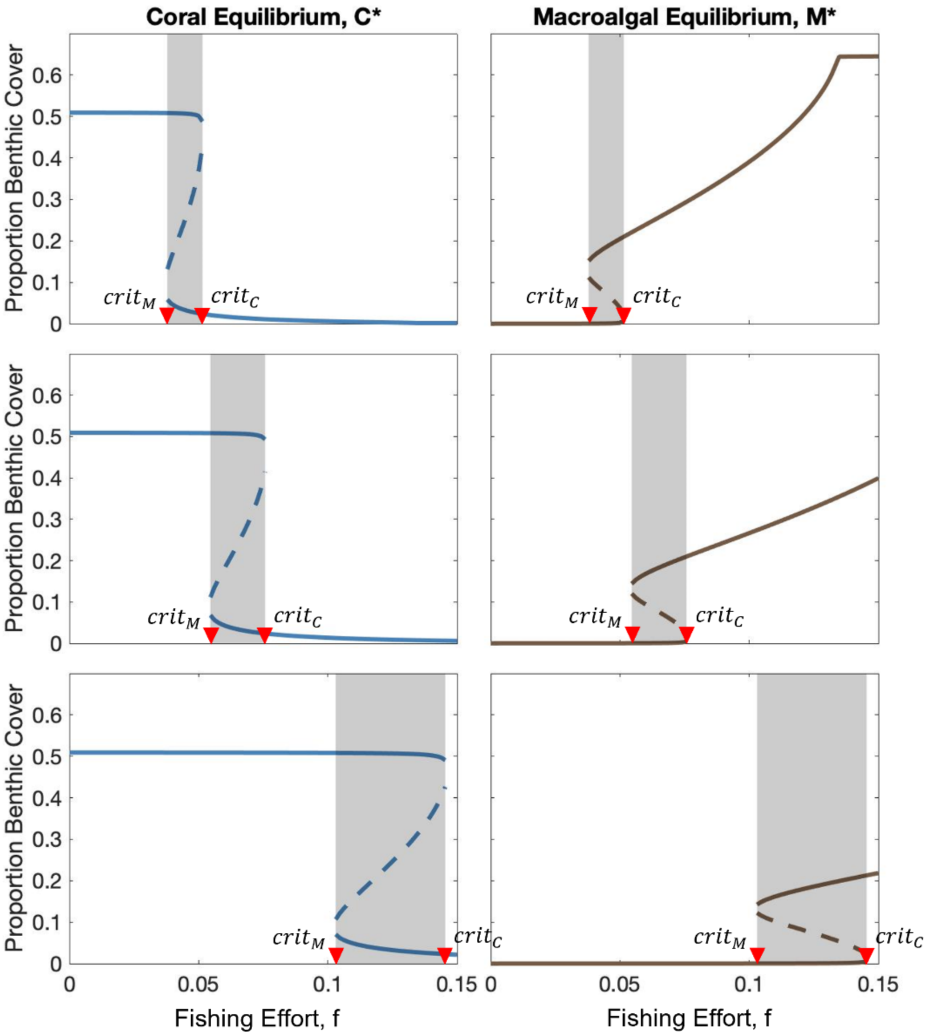


**Figure 4.** Bifurcation diagrams showing how the equilibrium cover of coral and macroalgae changes as a function of total fishing effort. Panels depict simulations under different selectivity scenarios: high unicornfish selectivity ($\sigma = 0.25$, top), equal selectivity for the two herbivore groups ($\sigma = 0.5$, middle), and high parrotfish selectivity ($\sigma = 0.75$, bottom). Solid lines indicate stable equilibria, dashed lines indicate unstable equilibria, and shaded regions depict the region of bistability. Red triangles indicate critical fishing thresholds $crit_C$ and $crit_M$.

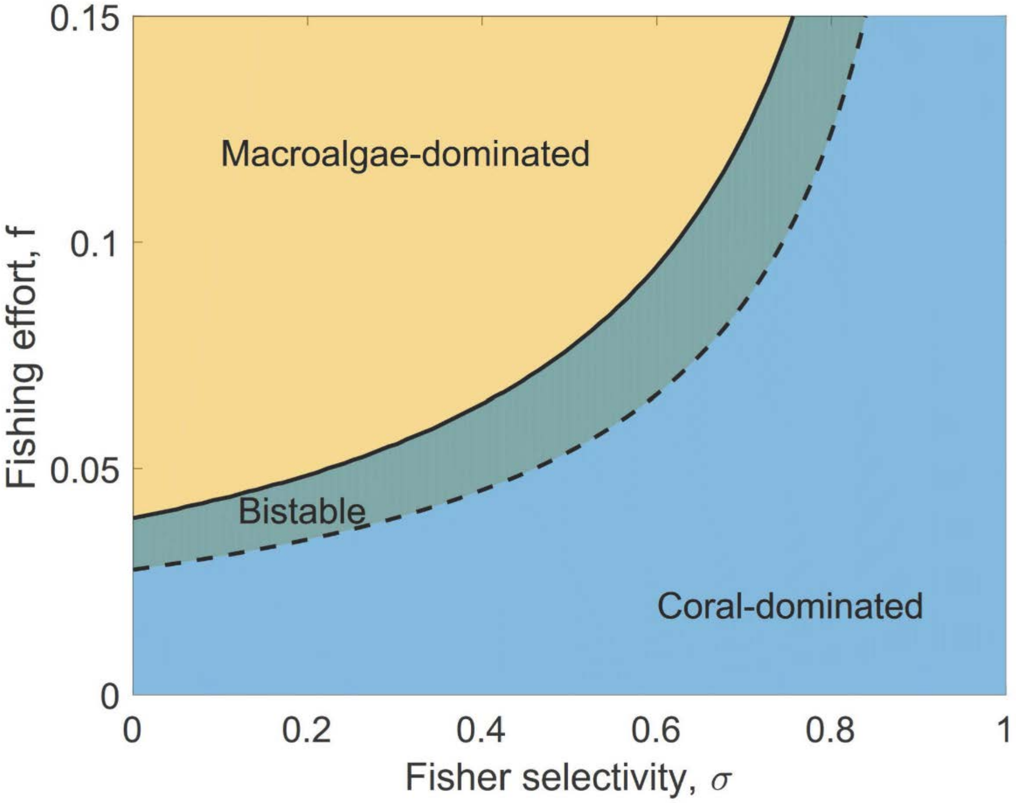


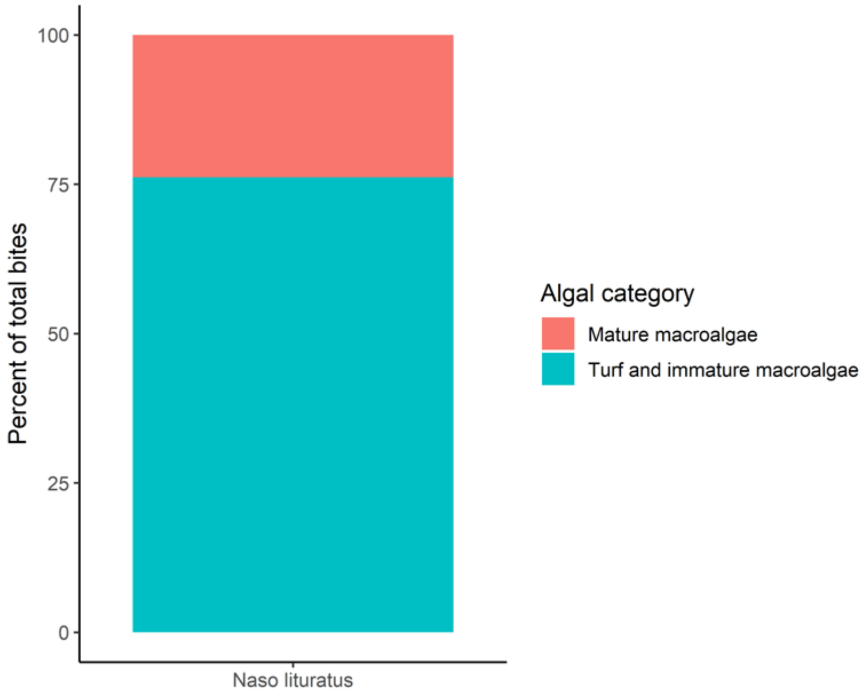
**Figure 5.** Operating diagram showing the region of reef stability as a function of fisher selectivity (x-axis) and fishing effort (y-axis). The solid line represents $crit_C$, the maximum fishing effort at which a coral-dominated state exists, and the dashed line shows $crit_M$, the minimum fishing effort at which a macroalgae-dominated state exists. Regions are colored based on the possibility of macroalgae states (yellow), coral states (blue), or bistability (green). As fishers' preference for parrotfish increases, the amount of fishing pressure a reef can tolerate while remaining in a coral-dominated state also increases.

## ***Supplementary Information***

**Supplemental Table 1.** Details on the parameterization of state variables and parameters added or modified from the Briggs et al. (2018) foundational model.

| | |
|---|---|
| $A$, herbivory rate | We use the default value and range for herbivory rate used by (Fung et al., 2011), which is from the set of parameter values used by Briggs et al. (2018). See Fung et al. (2011) for more detail on how herbivory rate was parameterized. In this study, we are interested in how the differential feeding strategies and diets of herbivores (and not differences in feeding rates) interact with fishing to affect coral resilience. Thus, for simplicity, we assume both groups of herbivores feed on each type of algae at the same rate. |
| $Z$, scaling constant to reduce herbivory on mature macroalgae | Davis (2018) showed that herbivory on *Turbinaria* – a common macroalga on reefs in Moorea and what we based the macroalgae in our model upon – significantly declines as algae increase in size and age. On reefs with relatively low biomass of browsing herbivores, Davis (2018) found ≥ 97% of mature *Turbinaria* survived after being exposed to herbivores for 7 days. Therefore, we set the lower bound of $\zeta$ to be 0. To determine the upper bound of herbivory on mature *Turbinaria*, we used herbivory data (Cook, *unpublished*) collected from a reef near study sites used by Davis (2018) and where relatively high abundances of browsers had been observed (Cook, *personal observation*). We exposed plots of *Turbinaria*-dominated communities to browsing herbivores and found 84 ± 9.1% (mean ± SE) of mature *Turbinaria* was consumed from plots (n=6) in 24 h$^{-1}$. Therefore, we set the upper bound of $\zeta$ to 0.8. Our default value of 0.2 falls within these field observations. |
| $K$, fish carrying capacity | A global assessment by Edwards et al. (2014) showed fishing strongly influences the biomass of herbivores on coral reefs. The highest recorded value of herbivore biomass found by Edwards et al. is 0.175 kg m$^{-2}$ on unfished reefs in the Seychelles. Therefore, we set $K$ to be 0.2 kg m$^{-2}$. For simplicity, we assume both groups of herbivores have the same carrying capacity. |

| | |
|---|---|
| *P*, parrotfish scalar multiplier | To determine how much faster parrotfish grow relative to unicornfish, we compared the growth coefficients (which describe how fast a fish reaches its maximum length) for two common species of grazing parrotfish (*Chlorurus sordidus* and *Scarus 105sittacus*) with that of a browsing unicornfish (*Naso unicornis*). The growth coefficient of *Naso unicornis* is 0.22 $yr^{-1}$ (Taylor et al., 2014a) and 0.95 and 0.91 $yr^{-1}$ for *C. sordidus* and *S. 105sittacus,* respectively (Taylor & Choat, 2014b). Therefore, *C. sordidus* and *S. 105sittacus* reach their maximum length 4.1 – 4.3 times faster than *N. unicornis* and thus we set $\rho = 4$. |
| *E*, conversion efficiency of algae to fish | There are few studies on the conversion efficiency of coral reef herbivores. Therefore, we use the transfer efficiency (i.e., the fraction of production passing from one trophic level to the next) of *Sparisoma viride*, a common herbivore on Caribbean reefs that feeds on both turf and macroalgae. Van Rooij et al. (1998) estimated that on shallow coral reefs *S. viride* convert only 2% of the energy they gain through consumption of algal resources to somatic and gametic production (i.e., new biomass). Therefore, we set $e = 0.02$. |



**Supplemental Figure 1.** Percent of total bites (n = 2094) taken on mature macroalgae and combined turf and immature macroalgae by *Naso lituratus* (n = 19) during 20-minute follows by a snorkeler. Fish follows were conducted on a midlagoon reef in Moorea, French Polynesia in 2017.

### *Supplemental References*

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