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Understanding the role of herbivorous fishes in top-down and bottom-up processes
on coral reefs

A thesis submitted in partial satisfaction of the
requirements for the degree Master of Arts in Ecology,

Evolution & Marine Biology

by

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September 2019

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September 2019

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Katrina Sky Munsterman

Dedication

I would like to dedicate this work to my good friend and colleague, Umi. May you forever be playing your accordion in the sky.

Acknowledgements

One of the most important things that I learned during my Master's degree is that science takes a community, and I am forever grateful for the community that has supported me along my journey at UC Santa Barbara. First and foremost, I want to thank my amazing committee members. I have had the pleasure of working on collaborative projects with each member of my committee. Thank you to Erika Eliason for being such a positive force and for teaching me so much about fish physiology and anatomy during our late-night dissections in the lab. I am so lucky to have had the opportunity to work with Jenn Caselle and her amazing team in Palmyra Atoll (solo chub forever!). Despite being across the country, adding Jake Allgeier to my committee was a no-brainer. Jake has been one of my biggest mentors in science since we met 4 years ago to work on project Pipi Poisson and I can't wait to work with him over the next five years in my PhD. And lastly, Deron Burkepile provided me with so many opportunities and eye-opening experiences since I joined the Pile as a lab manager 4 years ago. Thank you for supporting my wild endeavors and believing in me through and through. I want to thank the Pile, an amazing lab group of diverse personalities and skill sets. Thank you for the endless constructive feedback, the support during the rough times, and all of the fun memories.

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Abstract

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A foundational goal in ecology is to understand the top-down and bottom-up forces that regulate communities. By ingesting organic matter and excreting inorganic nutrients, consumers play a critical role in multiple pathways that influence ecosystem function. As ecosystems change under the threat of anthropogenic stressors, understanding the impacts to consumer assemblages is crucial, though few studies have quantified how alterations to consumers affect multiple ecosystem processes. In this study, we used a 13-year time series from coral reefs in the South Pacific that have either undergone shifts to algal dominance or remained in the coral state in order to scale individual-level processes to herbivorous fish populations in the different reef states. By collecting empirical data on organismal traits to partition various top-down and bottom-up functions, we emphasize the importance of understanding the different processes that consumers can influence. We show that reefs in the coral state host large-bodied parrotfishes that contribute up to 50% more space-clearing herbivory (turf and macroalgae), 88% higher rates of bioerosion, and excrete a higher ratio of N:P. In contrast, reefs that have undergone

transitions to algal states are characterized by abundant detritivorous fishes and small-bodied parrotfishes that influence 56% more detritivory and 29% higher rates of herbivory on epibionts rather than turf or macroalgae. By scaling individual traits to ecosystem processes, our study highlights multiple consumer-mediated mechanisms that may alter ecosystem function. Ultimately, our results provide a better understanding of how changes to ecosystem state impact top-down and bottom-up functions with direct implications for ecosystem recovery and resilience.

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Introduction

Across disparate ecosystems, consumers help shape the processes that underpin ecosystem function. From bison grazing in North American grasslands (Frank, 2008) to mussel predation by seastars in the rocky intertidal (Paine, 1980), consumers play a critical role in structuring ecosystems through consumptive processes (also known as top-down processes or TD hereafter; Estes et al., 2011; Terborgh, 2015).

Consumers also fuel bottom-up processes (BU) via excretion of nutrients (Allgeier, Burkepile, & Layman, 2017; Vanni 2002). Studies from both terrestrial and aquatic ecosystems, including grazing mammals in Africa and migratory fishes on Caribbean reefs, highlight how nutrient cycling by animals can enhance primary production (McNaughton, Banyikwa, & McNaughton, 1997; Meyer, Schultz, & Helfman, 1983).

While we may know how and to what extent consumers impact either TD (Chase, 1996; Silliman & Zieman, 2001) or BU (Allgeier, Layman, Mumby, & Rosemond, 2014; McIntyre et al., 2008b; Wolf, Doughty, & Malhi, 2013) processes, few studies have shown how consumer assemblages simultaneously impact both TD and BU. By scaling individual level-traits to consumer populations, our study takes a novel approach to understand how changes to diverse consumer assemblages impact ecosystem processes.

Anthropogenic impacts such as overharvesting and habitat degradation are fundamentally altering consumer assemblages (Essington, Beaudreau, & Wiedenmann, 2006; Estes et al., 2011; Jackson et al., 2001), which modifies consumer-mediated TD and BU processes. For example, large-scale wildfires in the

Serengeti decimated ungulate populations and decreased grazing, which led to increased plant biomass and subsequently more frequent fires (Holdo, Holt, & Fryxell, 2009). In pelagic regions of the world's oceans, industrial whaling led to reductions in consumer-mediated nutrient dynamics as whales are known to create a nutrient vector between oligotrophic surface waters and nutrient-rich depths, a concept known as the 'whale pump' (Roman et al., 2014). In addition to reducing consumer abundance, anthropogenic impacts often alter size structures of consumer populations (Dayton, Tegner, Edwards, & Riser, 1998; Ripple et al., 2014; Sandin et al., 2008). In the Gulf of Maine, increased harvesting by humans resulted in declines in medium size classes of blue mussels (*Mytilus edulis*), a foundational species known to influence productivity of intertidal habitats (Sorte et al., 2017). Owing to metabolic and physiological constraints, shifts in size structure further complicate ecosystem scaling (Fritschie & Olden, 2016). As humans rapidly reshape ecosystems, understanding how changes to consumer populations affects ecosystem function is imperative.

Under the stressors of climate change, overfishing, nutrient pollution, and sedimentation, coral reefs are among some of the most threatened ecosystems globally (Bellwood, Hughes, Folke, & Nyström, 2004; Hughes et al., 2017). These anthropogenic forces are driving a decline in corals on many reefs worldwide, resulting in shifts away from coral-dominated reefs (Donovan et al., 2018; Jouffray et al., 2019; Norström, Nyström, Lokrantz, & Folke, 2009). Once reefs lose their foundational coral species, they can become dominated by fast-growing algae

(McManus & Polsenberg, 2004; Rogers & Miller, 2006). However, algal-dominated states often do not support the same consumer assemblages and shifts in state often result in dramatic losses to species richness and diversity, especially in fish communities (Halford & Caley, 2009; Holbrook, Brooks, Schmitt, & Stewart, 2008; Robinson, Wilson, Jennings, & Graham, 2019). While the potential impacts of alterations to consumer communities on TD processes have been well studied on coral reefs (Carpenter, 1988; Terence P. Hughes et al., 2007; Kuempel & Altieri, 2017), we know far less about the commensurate impacts to BU processes (but see Allgeier, Valdivia, Cox, & Layman, 2016; Layman, Allgeier, Rosemond, Dahlgren, & Yeager, 2011) and no study that we are aware of has investigated both TD and BU effects simultaneously.

Herbivorous fishes comprise a large proportion of consumer biomass in many reef systems (Han, Adam, Schmitt, Brooks, & Holbrook, 2016; Robinson, Wilson, Jennings, & Graham, 2019). In order to sustain their daily functions on low nutrient algal diets, herbivores often have fast metabolisms (Schindler & Eby, 1997).

Combined, these abundant consumers with high metabolic rates often strongly influence fundamental ecosystem processes (Hatcher, 1981). Herbivores play an important role in controlling algal abundance and clearing space for corals via two key TD processes, herbivory and bioerosion (Bellwood, Hughes, & Folke, 2004; Hoey & Bellwood, 2008; Hughes et al., 2007). While there is substantial evidence that reef fishes fuel BU processes on reefs (Allgeier et al., 2014), most studies focus on aggregations of higher trophic levels (i.e., predators) on nutrient dynamics (Meyer

& Schultz, 1985; Shantz, Ladd, Schrack, & Burkepile, 2015). Lesser known is the role that herbivorous fishes play in BU processes on reefs. By recycling nitrogen (N) and phosphorus (P) in their daily excretions, herbivores may also promote primary production (Burkepile et al., 2013) and deliver nutrients at an optimal ratio (N:P) for coral growth (Allgeier, Layman, Mumby, & Rosemond, 2014; Meyer, Schultz, & Helfman, 1983). Few studies have scaled individual-level traits of diverse herbivore assemblages to ecosystem-level TD functions (but see Kelly et al., 2017; Ruttenberg, Adam, Duran, & Burkepile, 2019), and none have estimated BU processes. As humans alter fundamental herbivore communities, understanding the role of herbivores in TD and BU processes is of high importance for coral reef conservation.

Here, we investigated how associated shifts in benthic communities and herbivorous fish assemblages have impacted key ecosystem processes. In Moorea, French Polynesia, patch reefs in the shallow lagoon habitat exist in multiple ecosystem states, with some reefs shifting to algal states and others remaining coral-covered (Schmitt, Holbrook, Davis, Brooks, & Adam, 2019). These reefs provide an experimental framework to study how changes to consumer assemblages following benthic phase shifts impact fundamental TD and BU processes. As such, we aimed to: (1) determine herbivore size and taxon-specific differences in various TD and BU processes, (2) estimate TD and BU rates given spatial and temporal changes in population size structure, and (3) evaluate how changes in herbivore communities influence ecosystem processes across coral and algal states. To do this, we (1)

collected empirical data on foraging behaviors (TD rates) and N and P production (BU rates) by multiple herbivorous fish species, (2) modelled these data to 13 years of time series data on herbivore populations encompassing 22,159 individuals, and (3) assessed how critical TD and BU functions changed before, during, and after an algal phase shift compared to adjacent coral-dominated reefs. We hypothesized that algal-shifted reefs would create novel herbivore assemblages that would not provide critical space-clearing TD functions (turf and macroalgal herbivory, bioerosion) and excrete fewer nutrients in BU functions (N, P) compared to coral-dominated reefs.

Methods

Study location and benthic dynamics

Fieldwork was conducted in Moorea, French Polynesia (17°30' S, 149°50' W) during the months of May through August in 2016 – 2018. Moorea is an inhabited high volcanic island in the South Pacific Ocean. The 60 km perimeter of the island is surrounded by a barrier reef, enclosing a lagoon with patch reefs of average 5 – 7 m water depth. Field data were collected at multiple lagoon sites and samples were processed on shore at the University of California Berkeley Richard B. Gump Biological Station in Cook's Bay of Moorea (Fig. 1). The Moorea Coral Reef Long Term Ecological Research (MCR LTER) has been collecting data on patterns of lagoon benthic dynamics using in situ measurements at six long-term ecological research sites since 2006 (Carpenter, 2019). At each site, five permanent 10 m long transects are surveyed using 0.25 m² quadrats. Major benthic taxa (e.g., coral, macroalgae, turf, crustose coralline algae or CCA) were identified to genus or

species (n = 10 quadrats per transect) for percent cover estimates. We classified benthic communities into four functional groups: 1) turf/CCA (mixed assemblage of filamentous algae, microalgae, cyanobacteria, damselfish turf and CCA – all substrates that can be overgrown by benthic competitors), 2) live coral (all species of hermatypic corals), 3) macroalgae (all species), and 4) other (includes sand, coral rubble, soft coral, sponges, etc.).

The MCR LTER reef fish surveys are conducted on SCUBA during the same time each year at six long-term sites (Brooks, 2019; Fig. 1). Mobile reef fish taxa were identified to species, total length estimated to nearest 1 cm, and abundances were recorded on replicate 5 x 50 m permanent transects. Total length of each individual herbivore was converted to biomass using published species-specific scaling parameters (Kulbicki, Guillemot, & Amand, 2005).

Two families of herbivores, Kyphosidae and Siganidae, were excluded from this study due to rarity on the reef (0% and 1.09% of total herbivore biomass). Our study examines the role of mobile herbivores in ecosystem processes, therefore we excluded herbivorous invertebrates and territorial damselfishes (*Stegastes* farmer fish). In addition, large schools (> 60 individuals) of *Acanthurus triostegus* were removed from all analyses because time series surveys do not adequately sample highly aggregated schools of fishes (Han, Schmitt, Brooks, & Holbrook, 2016). Additional details concerning the sampling protocol and data for time series datasets can be viewed at mcr.lternet.edu/data.

Foraging behavior of herbivorous fishes

To assess the role of a diverse herbivore assemblage on TD and BU processes, we classified herbivores into five distinct functional groups based on Green and Bellwood (2009): browser, detritivore, grazer, scraper, or excavator (see Table 1 for complete list of species and classifications). In order to get bite rate estimates, we characterized the foraging behavior of 8 species of herbivorous fishes that account for 96.5% of the total herbivore biomass in the lagoon of Moorea: *Acanthurus nigrofuscus* (grazer), *Acanthurus triostegus* (grazer), *Chlorurus spilurus* (excavator), *Ctenochaetus striatus* (detritivore), *Naso lituratus* (browser), *Scarus oviceps* (scraper), *Scarus psittacus* (scraper), and *Zebrasoma scopas* (grazer). At least 8 individuals of each species were followed for 20-minute intervals in order to record bites taken on benthic substrate, totaling 38 hours of focal follows (see Table 2 for details on sample size and size range). For each individual, we identified the species, estimated the total length to the nearest cm, and recorded the phase (for sexually dimorphic species). Food items targeted by herbivores were identified to the lowest taxonomic level possible in the field and binned by benthic functional group (epibionts, turf/CCA, macroalgae, and detritus). All bites on macroalgae and turf that did not lead to removal of algae were categorized as bites on epibionts (e.g., small crustaceans, algae, cyanobacteria, etc.). Detritivores are often excluded from herbivore grazing estimates because they have minimal impact on the removal of algal biomass (Choat, Clements, & Robbins, 2002; Tebbett, Goatley, & Bellwood, 2017). Therefore, all bites by detritivorous fish were categorized as bites on 'detritus'. If at any point during the 20-minute follow the individual fish appeared to

be influenced by the observer (e.g., fish ceased to eat for extended period of time, starting swimming erratically, turned around to look the observer, etc.), the trial was aborted. Focal follows lasting longer than 15 minutes were included in the analyses. In order to control for diel variation in foraging behavior, we followed focal individuals during peak grazing hours (1000 – 1600; Bruggemann, Kuyper, & Breeman, 1994).

Top-down models

In order to allow us to scale up individual-level bite rates to relative carbon (C) consumption at the population level, empirical bite rate data were multiplied by bite size power functions to investigate the relationship between consumption rate (g C) and body size (mass) for each of the five functional groups. Bite size power functions were calculated based on the allometric relationship between fish size (biomass; w) and C consumption (van Rooij, Videler, & Bruggemann, 1998):

$$C \text{ intake} = 0.0342 \times w^{0.816}$$

Regressions on consumption data were performed on log-transformed variables to estimate slope, intercept, and root mean square error (RMSE) for each functional group model (Table 2). Residuals were visually inspected to ensure assumption of normality and homoscedasticity. Outliers in the bite rate data that differed more than an order of magnitude from other datapoints were omitted from TD models ($n = 13$ of 128 follows) in an effort to further minimize the potential effect of observers on fish foraging.

Excretion trials

To understand the role of herbivores in BU processes, we captured individual herbivores from the lagoon using barrier nets and clove oil, and immediately transported fish back to the research station in an aerated cooler. Each fish was identified to species, measured for standard length and weighed for wet mass (post excretion trial in order to limit handling stress). We collected excretion data from the same 8 species described above (plus an additional 5 species that are much less abundant on the reef: *Acanthurus nigricans* (grazer), *Acanthurus olivaceus* (detritivore), *Acanthurus pyroferus* (grazer), *Naso vlamingii* (browser), and *Scarus globiceps* (scraper); see Table 1 for details) covering a broad total size range (0.6 – 398.9 g body mass; see Table 2 for details). We measured excretions following the methodologies of Schaus et al. (1997), as modified by Whiles, Huryn, Taylor, and Reeve (2009). Individual fish were placed in Ziploc bag containing a known volume of pre-filtered seawater (using 0.7 μm pore size Gelman GFF) and incubated for 30 minutes to obtain excretion rates ($\mu\text{mol nutrient h}^{-1}$). We based trial periods on recommendations from previous studies (Whiles, Huryn, Taylor, & Reeve, 2009; Allgeier, Wenger, Rosemond, Schindler, & Layman, 2015) and our own experimental time trials, by which we measured excretion every 10 minutes over the course of 60 – 90 minutes in order to determine when excretions asymptote relative to time ($n = 16$, 8 species). A set of controls (typically $n = 6$; filtered seawater with no fish) were incubated for the same time period at each sampling event. All fishes and controls were kept at a constant temperature during the trial (25 – 27.5°C).

We extracted seawater samples from each bag, filtered with 0.45 μm pore size Whatman filters, and immediately placed on ice. Samples were analyzed within 12 hours for ammonium (NH_4^+) using the methodologies of Taylor et al. (2007), or frozen for transport to University of California Santa Barbara (UCSB) for soluble reactive phosphorus analyses (PO_4^-) using the ascorbic acid method and colorimetric analyses (Apha, 1995).

Bottom-up models

Similar to TD models, empirical excretion data (N, P) were used to develop generalized linear models to assess the relationship between excretion ($\mu\text{mol N, P}$) and body size (mass) for each herbivore functional group. Linear regressions on excretion data were performed on log-transformed variables to estimate slopes and intercepts (Table 2), similar to Peters, Reed, & Burkepile (2019). Residuals were visually inspected, and outliers (high nutrient values) caused by possible nutrient contamination were removed from models ($n = 5$ for N and $n = 14$ for P).

In some cases, we adjusted models to increase sample size and size range within the different herbivore functional group models. Due to low sample size of browser individuals ($n = 2$), grazer (also from family Acanthuridae) excretion data were pooled in order to develop browser excretion models (N, P). Given that browsers are quite rare, potential under- or overestimations of nutrient excretion in these browser models likely minimally impact our estimates of nutrient budgets on the reef. Because we lacked a sufficient size range of small scrapers, we included data from

small excavators (< 80 g) in the scraper excretion models (N, P). Both belonging to tribe Scarinae, scrapers and excavators have similar diets at small sizes and likely excrete similar rates and ratios of N and P.

Ecosystem processes by herbivorous fish communities

We used a 13-year time series on reef fish populations in Moorea (described above) in order to assess how changes in herbivore populations might influence TD and BU processes. In order to estimate consumption rates (g C individual⁻¹ hr⁻¹) for each individual in the time series dataset, individual linear models on C consumption for each functional group were applied to time series data based on individual mass and functional identity. Bite rates on different diet items (detritus, epibionts, macroalgae, turf) were averaged within fish size bins (40 – 89, 90 – 149, 150 – 199, 200+ mm) for each functional group. Bite proportions were multiplied by total C ingested in order to estimate consumption rates of each diet item. Bioerosion estimates were calculated based on a polynomial regression of the proportion of bites on turf producing bite scars for excavators larger than 150 mm (Yarlett, Perry, Wilson, & Philpot, 2018). All rates were multiplied by 10 to obtain areal consumption estimates per day (g C m⁻² d⁻¹), making the assumption that herbivores are grazing for approximately 10 hours per day (Bruggemann, Kessel, Rooij, & Breeman, 1996).

To estimate the contribution of the herbivore community to nutrient cycling, per capita and areal excretion rates were calculated using linear models of N and P excretion and applied to the time series using the same sampling procedures

described above. Values were multiplied by 24 to estimate areal excretion (N,P) per day ($\mu\text{mol m}^{-2} \text{d}^{-1}$). The potential overestimation of excretion rates is mitigated by the fact that we measured excretion estimates from non-active fishes and perpetuate model error through the scaled data. Finally, areal estimates of N excretion were divided by P in order to calculate community level N:P molar ratios.

For all models, prediction uncertainty was propagated into our final estimates using a Monte Carlo procedure similar to Peters, Reed, and Burkepile (2019). We calculated mean estimates for each individual based on 1000 iterations of simulated model coefficients and 95% confidence intervals. Monte Carlo iterations and modeling procedures were performed using the *arm* package (Gelman & Hill, 2007) in R (R Core Team 2019).

Ethics and animal care statement

The capture and handling of fish for this project were approved in a protocol from the University of California Santa Barbara's Institutional Animal Care and Use Committee (IACUC #915 2016 – 2019). Permits for fieldwork in French Polynesia were issued by the Haut-Commissariat de la République en Polynésie Française (Protocole d'Accueil 2016 – 2017, 2017 – 2018 to DEB).

Data analyses

Benthic community dynamics

In order to establish the experimental framework of this study, we measured temporal changes in benthic state across the six long-term research sites in the lagoon. Given a priori knowledge of the benthic dynamics in the lagoon of Moorea (Schmitt, Holbrook, Davis, Brooks, & Adam, 2019), we classified sites into two distinct ecosystem states: 'algal state' characterized by high abundances of algae, and 'coral state' characterized by high coral cover. Percent cover was averaged across all quadrats within each site in each year and data was logit transformed to meet model assumptions. After assigning ecosystem states, separate linear mixed-effects models were used to assess changes in the percent cover of each benthic community type (turf/CCA, macroalgae, and coral) spanning from 2007 – 2018 (2006 was excluded due to inconsistencies in data collection; fixed effect = year, random effect = site with AR 1 correlated errors). Post hoc Tukey's tests were used to reveal temporal changes in percent cover of each benthic space holder.

Herbivore population dynamics: biomass, abundance, and size structure

To assess changes in both total herbivore biomass and the biomass of each functional group in algal and coral states, we averaged log-transformed biomass across transects at each site and year. A linear mixed-effects model was used to test the interaction between year and ecosystem state on biomass (fixed effects = year, state, and year \times state, random effect = site with AR 1 correlated errors). We evaluated differences in abundance and median size of each functional group at the

site level using the same mixed models with log-transformed data. When biomass, size, or abundance differed significantly across state or time, Tukey's test was used to test the interactions. In order to get population estimates of herbivores capable of bioerosion processes, we examined large excavators (> 150 mm) in additional models using the same methods described above.

Ecosystem processes

We examined how changes to herbivore populations impact ecosystem processes by comparing community-level TD and BU functions during distinct time periods. For this purpose, we categorized time series data into three periods: "pre" algal-shift (2006 – 2008), "mid" algal-shift (2009 – 2014), and "post" algal-shift (2015 – 2018) that coincide with dramatic changes in benthic cover. For consistency in analyses, we binned time periods at sites in the algal and coral states in the same manner. In order to test the differences in various TD and BU functions across states, we used Welch's two-sample t tests of unequal variances within each time period. Prior to statistical tests, areal TD and BU rates were averaged across sites and years within each state and time period, and data were log-transformed.

All linear mixed-effects models were done in the *nlme* package in R (Pinheiro, Bates, DebRoy, & Sarkar, 2011), and post-hoc tests were calculated using *emmeans* package (Lenth, 2018). All data analyses were performed in R (R Core Team, 2019) and figures were created using R *ggplot2* package (Wickham & Chang, 2016).

Results

Benthic community dynamics

At sites in the lagoon that transitioned to abundant algae during the time series (i.e., 'algal state'), coral cover declined over time ($F_{11,22} = 5.26$, $P < 0.001$; Fig. 2), while macroalgae increased ($F_{11,22} = 6.40$, $P < 0.001$). In 2012, macroalgae surpassed coral cover and remained above coral cover for the duration of the time series, reaching a high of 34% in 2016. Live coral cover remained at ~5% cover since 2015 (post hoc Tukey's test, $P < 0.001$). Turf remained ~45% cover over the entire 13-year time series with no differences over time ($F_{11,22} = 0.94$, $P = 0.52$). In contrast, at sites that have not have transitioned to algal dominance (i.e., 'coral state'), coral cover was ~25% with no differences over time ($F_{11,22} = 0.87$, $P = 0.57$) and macroalgae cover was consistently low (~3%; $F_{11,22} = 2.0$, $P = 0.08$). Turf cover declined over time on reefs in the coral state ($F_{11,22} = 9.1$, $P < 0.001$).

Herbivore population dynamics

Total herbivore biomass increased significantly over the study period in both coral and algal states (year: $F_{12,48} = 9.18$, $P < 0.001$; Fig. 3). Increases in total herbivore biomass were driven by three functional groups: detritivores (year: $F_{12,48} = 2.28$, $P = 0.02$), scrapers (year: $F_{12,48} = 7.0$, $P < 0.001$), and excavators (year: $F_{12,48} = 9.09$, $P < 0.0001$). The two other functional groups (grazers and browsers) contributed less than one-fifth of total herbivore biomass in the lagoon. Grazers showed no change in biomass during the 13-year times series. Notably, grazer biomass was on average 2.5 times higher in algal state compared to coral state (state: $F_{1,4} = 15.23$, $P = 0.01$).

Lastly, browser biomass remained consistently low, around $0.14 \pm 0.1 \text{ g m}^{-2}$ ($\pm \text{SE}$) over the study period in both states.

Higher detritivore biomass was driven mostly by increases in average total length of individuals (year: $F_{12,48} = 12.9$, $P < 0.001$; Fig. 4). Across both algal and coral states, detritivores doubled in size from a mean of 87.5 mm in 2006 to 175 mm in 2015 (post hoc Tukey's test, $P < 0.001$ for both). Interestingly, detritivores actually decreased in abundance over time at both coral and algal states (year: $F_{12,48} = 1.9$, $P = 0.05$). Scraper biomass increased via total abundance (year: $F_{12,48} = 16.97$, $P < 0.001$). In the algal state, there were differences in the size structure of scrapers through time, with a decline in average size from 140 mm in 2006 to 80 mm in 2012 (post hoc Tukey's test, $P = 0.09$).

Excavators showed higher biomass in the coral state than algal (year \times state interaction: $F_{12,48} = 2.59$, $P < 0.01$, Fig. 3), with biomass as high as $17.6 \pm 0.6 \text{ g m}^{-2}$ ($\pm \text{SE}$) at coral states in 2015. Excavators tended to be about 45% smaller in algal states than coral states in later years (year \times state interaction: $F_{12,48} = 2.02$, $P = 0.04$; Fig. 4). These differences were driven by decreases in body size to an average 45 mm total length in 2013 at algal states (post hoc Tukey's test, $P < 0.01$). Small excavators were also more abundant (year: $F_{12,48} = 6.8$, $P < 0.001$), with significant increases in density at algal states between 2010 and 2012 (post hoc Tukey's test, $P < 0.01$) and continuing through subsequent years (2013 – 2018; post hoc Tukey's test, $P < 0.001$ for each). Additionally, there was an increase in biomass of large

excavators (> 150 mm) in coral states compared to algal (year × state interaction: $F_{12,48} = 3.59$, $P < 0.001$). Increases in biomass were driven by increases in average body size of large excavators (year × state interaction: $F_{12,33} = 3.59$, $P = 0.03$).

Individual patterns in top-down functions

Functional group identity and body size determined the strength of top-down processes of individual herbivores. The diet of both excavators and scrapers changed across ontogeny, with smallest size classes (< 90mm) targeting protein-rich epibionts (Fig. 5) while larger size classes targeted algal turf. Independent of size, browsers removed the most macroalgae, around 30% of their diet, but surprisingly 70% of their bites were from algal turf. In general, most herbivores targeted turf algae, making up around 88% of diets of herbivores larger than 150 mm.

Detritivorous fishes fed off of a variety of different substrates including algae, sediments, and bare rock, regardless of size, however, we assumed that all of these bites removed detritus.

Linear regressions of TD processes revealed a positive relationship between body size (g) and total C consumption rate (g C hr⁻¹) for each functional group ($P = 0.05$ browsers, $P = 0.06$ grazers, and $P < 0.001$ all other functional groups; Fig. 6a).

Excavators removed greater rates of C compared to all other functional groups and detritivores removed the least (Table 2).

Individual patterns in nutrient recycling

Linear regressions of N excretion ($\mu\text{mol NH}_4^+$ hr⁻¹) and body size (g) also showed a positive relationship across functional groups ($P < 0.0001$ all functional groups; Fig. 6b). Overall, functional group models explained 68% of the variance in N excretion rates. Scaling coefficients were similar across functional groups, however grazers excreted less N than other functional groups (Table 2). Similar to N excretion, P excretion ($\mu\text{mol PO}_4$ hr⁻¹) scaled positively with body size with an average R^2 value of 0.57 ($P < 0.0001$ all functional groups; Fig. 6c). In general, detritivores excreted more P than other functional groups (Table 2).

Ecosystem processes

During the pre- and mid-periods, there were few differences in all five TD processes (turf herbivory, macroalgae herbivory, bioerosion, detritivory, and epibiont herbivory) at the community level between the algal and coral states (Fig. 7a – e). Once the benthic communities diverged in years after the algal shift, we saw dissimilarities in various herbivory rates between algal and coral states. Herbivory of turf algae was 49% higher in the coral state than algal during the post period ($t = -2.4$, $P = 0.03$; 317 ± 69 mg C m⁻² removed vs. 191 ± 19 , respectively; Fig. 7a). Macroalgal herbivory was 44% greater at coral than algal states in later years ($t = -2.4$, $P = 0.03$; Fig. 7b). Additionally, bioerosion rates by large excavators were 88% higher at coral states ($t = -3.1$, $P = 0.005$; Fig. 7c), with rates as high as 56 ± 17 mg C m⁻² per day. In contrast, detritivory rates were significantly greater in algal states compared to coral in the post period ($t = 2.7$, $P = 0.01$; Fig. 7d). On average, 119 ± 9 (\pm SE) mg C

m⁻² of detrital material was removed per day on algal covered reefs, a 56% difference from coral states. Lastly, epibiont herbivory was 29% higher in algal states during the post period ($t = 2.2$, $P = 0.04$; Fig. 7e).

Unlike TD processes, N and P excretion rates did not differ between coral and algal states during any time period (N excretion $t = -0.59$, $P = 0.6$; Fig. 8a; P excretion $t = 0.73$, $P = 0.5$; Fig. 8b), but did show increases over time. Interestingly, average community-level N:P molar ratio of excretion was 17% higher in coral states during the post period ($t = -2.6$, $P = 0.01$; Fig. 8c). The average N:P molar ratio at coral states was 6.8 ± 0.1 while the N:P ratio of excretion at algal states was 5.7 ± 0.2 .

Discussion

Consumers play a critical role in the TD (Estes et al., 2011; Terborgh, 2015) and BU (Allgeier, Burkepile, & Layman, 2017; Vanni, 2002) processes that impact the functioning of disparate ecosystems. By scaling process rates by herbivorous fishes to 13 years of data collected on coral reefs in French Polynesia, we provide evidence that changes to consumer assemblages impact both TD and BU functions simultaneously. Reefs in the coral state host large-bodied parrotfishes that contribute up to 50% more space-clearing herbivory (turf and macroalgae) and 88% higher rates of bioerosion than reefs that have transitioned to algal domination. In contrast, reefs that became dominated by algae over time experienced an increase in the abundance of small parrotfishes and an increase in the individual body size of detritivorous fishes. These shifts in size structure contribute 29% higher rates of

epibiont herbivory and 56% higher rates of detritivory. Although BU rates (N,P) scaled similarly across states, the molar ratio N:P excretion appears higher in the coral state. Ultimately, our work suggests that altered herbivore populations in the algal state provide functions (detritivory and epibiont herbivory) that may not facilitate coral recovery. These results provide a better understanding of how changes to ecosystem state impact essential TD and BU functions via consumer-mediated pathways, with direct implications for ecosystem recovery and resilience.

Ecosystem state differentially impacts functional groups

Consumers respond to ecosystem change in a multitude of ways, often resulting in novel community assemblages (Lurgi, López, & Montoya, 2012). On coral reefs, herbivores are often the first to respond to changes in benthic cover (Adam et al., 2011; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Robinson, Wilson, Jennings, & Graham, 2019; Rogers, Blanchard, & Mumby, 2018). However, herbivore assemblages are made up of a diversity of taxa that are not all alike in their contribution to TD and BU functions (Green & Bellwood, 2009; Bellwood, Hughes, Folke, & Nyström, 2004). In the lagoon of Moorea, we found a differential response in the size structure of particular herbivore functional groups to changes in algal cover. While temporal increases in total herbivore biomass led to increases in all TD and BU processes, exploring population effects (via changes to size structure) helped us tease apart the key functional groups that influence various TD and BU functions.

Removal of macroalgae is an important consumptive process that prevents macroalgal accumulation and reverses algal phase shifts (Hoey & Bellwood, 2011). Browsers are a key functional group responsible for macroalgal herbivory on reefs across the Indo-Pacific (Chong-Seng, Nash, Bellwood, & Graham, 2014; Edwards et al., 2014; Rasher, Hoey, & Hay, 2013). Throughout the lagoon of Moorea, the dominant browsers, *Naso* spp., makes up less than 0.5% of total herbivore biomass, likely due to high fishing pressure on these targeted species (Rassweiler et al., 2019). Compared to a study from the Great Barrier Reef, algal and coral-dominated reefs in Moorea show 89% and 93% lower rates of macroalgal herbivory due to the low abundance of browsers (Chong-Seng, Nash, Bellwood, & Graham, 2014). Interestingly, browser biomass has been historically low across both coral and algal states, implying that the lack of browser biomass is not the only factor driving phase shifts at sites that have transitioned to algal domination. In addition to the effects of missing functional groups, excess nutrients linked to denser human populations and agricultural production have likely led to the decline in coral and the rise in algae at certain sites in Moorea (T.C. Adam, unpublished data).

Among the most interesting response to increases in algal cover was the two-fold increase in detritivore biomass driven by increases in individual body size at sites that have transitioned to abundant algae. Detritivores are typically long-lived species with limited annual reproduction events (Choat & Robertson, 2002; Ochavillo, Tofaeono, Sabater, & Trip, 2011). *Ctenochaetus striatus*, the species that accounts for 97% of detritivore biomass throughout the lagoon, can live up to 40 years in

systems with low predation pressure (Choat & Robertson, 2002; Davis, Carlson, Bradley, Warner, & Caselle, 2017). Fishers in Moorea strongly avoid catching this species because they can be ciguatoxic and their sale is banned in French Polynesia (Rassweiler et al., 2019; Walter, 1968). With their comb-like mouthparts, detritivores provide a different TD function than other herbivorous fishes (Choat, Clements, & Robbins, 2002; Nelson & Wilkins, 1988; Tebbett, Goatley, & Bellwood, 2017). By brushing macroalgae, turf, and other benthic substrates of detritus, detritivores may in fact facilitate algal growth (Crossman, Choat, Clements, Hardy, & McConochie, 2001) and potentially influence algal proliferation in an algal state.

Our study suggests that detritivores play an important role in P recycling on coral reefs. While most herbivores excrete high ratios of N:P due to protein-rich diets (Allgeier, Layman, Mumby, & Burkepile, 2014; Burkepile et al., 2013; Schindler & Eby, 1997), our results show that detritivores excrete 72% higher mass-specific rates of P than any other functional group. Some potential explanations for this novel finding may be a P-rich detritus diet, low P body tissue content (K.S. Munsterman, unpublished data), and slow growth (Choat & Robertson, 2002) that leads to slower accumulation of body P over time (Sterner & Elser, 2002). By recycling high rates of biologically-available P, detritivores appear to be key P recyclers, a common phenomenon found in freshwater systems (McIntyre et al., 2008a; Small, Pringle, Pyron, & Duff, 2011; Vanni, 2002). Similar to detritivore aggregations in deep freshwater runs that accrue sediments in the Amazon, detritivores in Moorea seem to inhabit areas with higher abundances of detritus such as reefs that have

transitioned to high algal cover. As a result, their presence drives slightly higher community-level P excretion rates and significantly lower N:P excretion ratios on algal-shifted reefs, which may positively influence algal growth. While P is also important for coral health (Ezzat, Maguer, Grover, & Ferrier-Pagès, 2016), the fact that detritivores excrete P in areas that have shifted to abundant algae likely doesn't allow for coral recovery in these coral-depauperate areas.

In contrast to body size increases in detritivores, parrotfish biomass increased in the algal state due to three-fold increases in the abundance of small-bodied scrapers and excavators. A study by Han, Adam, Schmitt, Brooks, and Holbrook (2016) suggests that the increases in parrotfish populations in Moorea were due to particularly large recruitment events in later years (e.g., 2010, 2013, 2018), a reasonable explanation given that parrotfishes have indeterminate growth patterns with opportunistic episodes of rapid growth following increased food resources (Choat, Axe, & Lou, 1996). As many reef systems become algal dominated, shifts to smaller size structures of herbivores is becoming more prevalent (Han, Adam, Schmitt, Brooks, & Holbrook, 2016; Robinson, Wilson, Jennings, & Graham, 2019). However, only a few recent studies highlight the emergent role of small-bodied herbivores on TD processes (Cernohorsky, McClanahan, Babu, & Horsák, 2015; Fong, Frazier, Tompkins-Cook, Muthukrishnan, & Fong, 2016; Kuempel & Altieri, 2017), and many others exclude herbivores of this size altogether in TD grazing estimates (Gil & Hein, 2017; Kelly et al., 2017).

The role of body size in driving ecosystem processes

Central to understanding the role of consumers in driving ecosystem processes is incorporating the effect of body size in TD and BU pathways (Fritschie & Olden, 2016). Individual body size is linked to differences in physiology and metabolic rates both across species (Ohlberger, 2013) as well as within species over ontogeny (Chen, 2002). Thus, body size is a key determinant used to assess differences in consumer-mediated processes (Atkinson, Capps, Rugenski, & Vanni, 2017).

Fundamental to our findings is that we incorporated these organism traits in how we scaled the time series data to account for intrinsic differences across a broad size range of fishes. Our empirical data show strong relationships between function and body size within each of the five herbivore functional groups and reveal the various roles provided by diverse consumer body sizes.

Parrotfish have strong ontogenetic shifts in diet (Bonaldo & Bellwood, 2008; Chen, 2002) in addition to differences in jaw morphology and function (Choat & Clements, 1993) that impact body size differences in the functional roles they provide. In order to capture the functional differences and contributions to different TD processes across their size range, we implement a novel approach that incorporates shifts in ontogeny in scaling rates to meaningful population estimates. Young parrotfish with high metabolic rates target protein-rich epibionts to meet energetic requirements, providing an alternative TD function on reefs that is not akin to space-clearing turf and macroalgal herbivory. In fact, by removing epibionts from macroalgae and turf algae, these abundant small parrotfish may actually facilitate algal growth (Eich et

al., 2019; Fricke, Titlyanova, Nugues, & Bischof, 2011). However, future experiments are needed to test the extent to which epibiont herbivory influences algal persistence.

While most studies focus on the TD functions provided by consumers, small-bodied herbivores in particular may contribute substantially to BU processes due to their high metabolic demands. Small fishes require N for opportunistic growth and P for bone and scale production (Schindler & Eby, 1997), and have steeper mass-scaling at early ontogenetic stages (Barneche & Allen, 2018). Owing to their N-rich epibiont diets and P-limited body stoichiometry, our data show that abundant small parrotfishes excrete higher ratios of N:P. The ammonium they excrete, the main form of nitrogen recycled by marine fishes (Meyer, Schultz, & Helfman, 1983), is rapidly acquired by primary producers (Mulholland & Lomas, 2008). Interestingly, schooling young parrotfishes shelter within dense macroalgal stands to feed on epibionts of the common macroalgae, *Turbinaria ornata* (K.S. Munsterman, personal observation), excreting high ratios of N:P in close proximity to fast-growing primary producers. Exploring the differential role of small-bodied consumers on the flow of nutrients and energy in appears to be an area ripe for future research. Given their high metabolic rates and often high abundances, considering the TD and BU functions provided by small herbivores is critical for accurately scaling individual level functions to larger-scale ecosystem processes.

Small consumers contribute uniquely to specific processes, but it is impossible to ignore the disproportionate role of large consumers in TD and BU functions (Estes et al., 2011; Forbes et al., 2019; Ripple et al., 2014). On coral reefs, large parrotfish with developed beak-like jaws are able to remove substantially more material per bite than small individuals, creating a non-linear relationship between body size and TD function (Bellwood & Choat, 1990; Lokrantz, Nyström, Thyresson, & Johansson, 2008). On Moorean reefs in the coral state, large parrotfishes contribute nearly 50% more turf and macroalgal herbivory (Fig. 9), space-clearing functions that control algal abundance (Bellwood, Hughes, & Folke, 2004; Hoey & Bellwood, 2008). Additionally, large excavators erode more of the calcium carbonate structure of reefs in the coral state (Fig. 9). Known as bioerosion, this TD process promotes coral settlement and growth (Bruggemann, van Kessel, van Rooij, & Breeman, 1996). Large individuals in the coral state also supply a large proportion of areal nutrient excretion rates (N, P) and excrete nutrients at a ratio (N:P) within an optimal range for coral health (6.8 molar ratio; Allgeier, Layman, Mumby, & Rosemond 2014).

Notably, these large parrotfishes (> 150 mm) are often targeted by local spearfishers (Rassweiler et al., 2019). Using our empirical data, we estimated the functional compensation required from the loss of large individuals from a population. A simple calculation reveals that by removing one 250 mm excavating parrotfish (i.e., *Chlorurus spilurus*) from the reef, ten small (100 mm) parrotfish would be needed to offset the losses to space-clearing (turf and macroalgal herbivory). In contrast, no number of small excavators can compensate for the loss of bioerosion function as

only large excavators can perform this process. In terms of compensation for BU processes, nine 100 mm parrotfish would be necessary to excrete equal rates of P as one 250 mm individual and seven 100 mm parrotfish required to compensate for N excretion. Our results highlight not only the role of different taxa but also the significant role of different body sizes within taxa for various ecological processes. Through scaling individual traits to populations across ecosystem states, we show that diversity both across and within taxa matters for ecosystem function.

Conclusion

Humans are altering consumer assemblages through direct forces including overharvesting (Essington, Beaudreau, & Wiedenmann, 2006) and indirect forces that cause habitat degradation (Haddad et al., 2015). These alterations to consumer populations likely impact both TD and BU forces in most ecosystems. Our novel approach investigates both TD and BU effects to gain a more comprehensive understanding of ecosystem functioning. While many studies have shown how state shifts impact the community structure of consumers (Adam et al., 2011; Donovan et al., 2018; Laliberte & Ripple, 2004; Ripple et al., 2015), we go one step further to identify how these shifts extrapolate out to ecosystem processes. By partitioning TD and BU functions into various pathways, we show the importance of taking a more holistic view to understanding the different processes that consumers can influence. Our work stresses the significance of using empirical data of organism traits to scale to consumer populations. Identifying the unique roles of consumers in TD and BU processes that maintain and reinforce ecosystem states is the key to predicting

when and why shifts to diverse consumer assemblages matter. Thus, our study provides a framework that can be used to quantify how changes to consumer communities impact both TD and BU functions in threatened ecosystems.

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Tables

Table 1. **Categorization of herbivore functional groups.** Includes percent of each species within each functional group from MCR LTER time series data in backreef habitat. Two families, Kyphosidae and Siganidae, excluded from browser functional group (see Methods).

Functional	Description	Family	Species	Percent
browser	feed on macroalgae and associated epibionts	Acanthuridae	<i>Naso lituratus</i> <i>Naso unicornis</i> <i>Zebrasoma velifer</i>	47.5% 13.8% 15%
		Scaridae	<i>Leptoscarus vaigiensis</i> <i>Calotomus carolinus</i>	19.5% 4.2%
detritivore	feed on detritus and decaying algal material	Acanthuridae	<i>Ctenochaetus binotatus</i> <i>Ctenochaetus flavicauda</i> <i>Ctenochaetus striatus</i> <i>Acanthurus olivaceus</i>	2.8% 0.02% 96.9% 0.2%
excavator	feed on epilithic algal turfs and macroalgae, removing large amounts of calcium carbonate	Scaridae	<i>Chlorurus frontalis</i> <i>Cetoscarus ocellatus</i> <i>Chlorurus microrhinos</i> <i>Chlorurus spilurus</i>	0.3% 0.1% 0.1% 99.5%
grazer	feed on epilithic algal turfs without removing any reef structure	Acanthuridae	<i>Acanthurus guttatus</i> <i>Acanthurus lineatus</i> <i>Acanthurus nigricans</i> <i>Acanthurus nigricauda</i> <i>Acanthurus nigrofuscus</i> <i>Acanthurus nigros</i> <i>Acanthurus pyroferus</i> <i>Acanthurus triostegus</i> <i>Zebrasoma scopas</i>	0.9% 0.3% 0.4% 1.1% 26.8% 0.1% 0.8% 19% 50.6%

scraper	feed on epilithic algal turfs, macroalgae, and remove small amounts of reef structure	Scaridae	<i>Scarus altipinnis</i> <i>Scarus forsteni</i> <i>Scarus frenatus</i> <i>Scarus ghobban</i> <i>Scarus globiceps</i> <i>Scarus niger</i> <i>Scarus oviceps</i> <i>Scarus psittacus</i> <i>Scarus rubroviolaceus</i> <i>Scarus schlegeli</i>	0.7% 0.2% 0.5% 0.3% 1.3% 1% 11.8% 83% 0.4% 0.8%
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Table 2. **Functional group top-down and bottom-up models.** Model coefficients (a = intercept, b = slope), R_2 and P values for log-log linear regressions TD (g C h⁻¹) and BU rates ($\mu\text{mol nutrient h}^{-1}$) vs. body mass (g) for n individuals from 5 herbivore functional groups with body size range. The root mean square error (RMSE) is used to predict model uncertainty in our per capita estimates. Asterisks denote models altered to increase sample size and/or size range.

Top-down

functional	n	size range (g)	a	b	R_2	RMSE	P
browser	25	12-27	-5.29	0.74	0.15	0.46	0.05
detritivore	22	9-127	-6.55	0.96	0.63	0.58	< 0.001
excavator	32	1.5-265	-3.35	0.76	0.94	0.31	< 0.001
grazer	22	9-96	-4.57	0.47	0.16	0.64	0.06
scraper	14	15-161	-5.37	0.75	0.73	0.47	< 0.001

Bottom-up

nitrogen

functional	n	size range (g)	a	b	R_2	RMSE	P
browser*	52	0.6-133	-0.23	0.59	0.79	0.51	< 0.001
detritivore	44	7-206	0.10	0.61	0.48	0.48	< 0.001
excavator	61	1-399	-0.08	0.66	0.65	0.50	< 0.001
grazer	50	0.6-133	-0.22	0.59	0.81	0.49	< 0.001
scraper*	41	1-229	0.09	0.65	0.65	0.52	< 0.001

phosphorus

functional	n	size range (g)	a	b	R_2	RMSE	P
browser*	46	0.6-133	-2.87	0.67	0.58	0.99	< 0.001
detritivore	41	7-207	-1.66	0.72	0.44	0.64	< 0.001
excavator	57	0.7-399	-2.81	0.81	0.64	0.64	< 0.001
grazer	44	0.6-133	-2.86	0.66	0.58	1.00	< 0.001
scraper*	37	0.7-229	-2.50	0.72	0.61	0.67	< 0.001

Figures

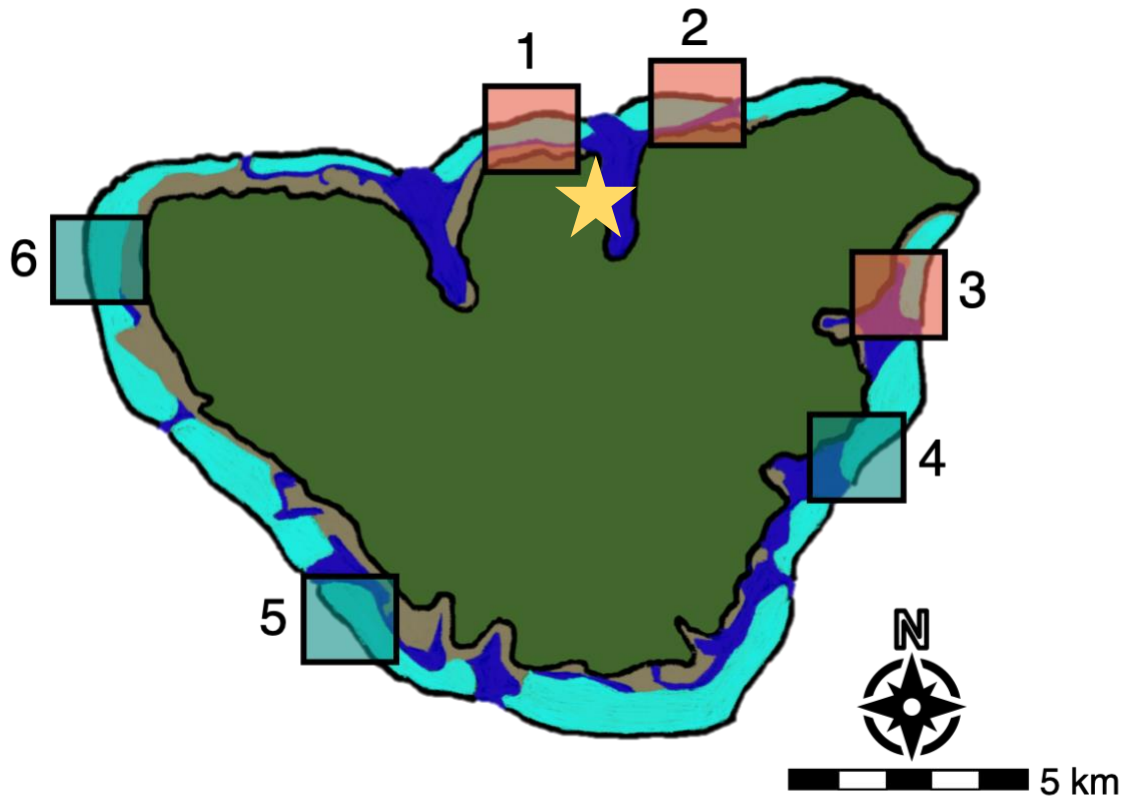


Figure 1. **Map of Moorea, French Polynesia.** Field data was collected from multiple back reef sites (indicated by light blue water surrounding island) and samples processed at the University of California Berkeley Richard B. Gump Biological Station (depicted with a star). Squares show the six long term back reef research sites with site labels. Site categorized as the 'algal state' (1 – 3) denoted in red and sites in 'coral state' (4 – 6) in teal.

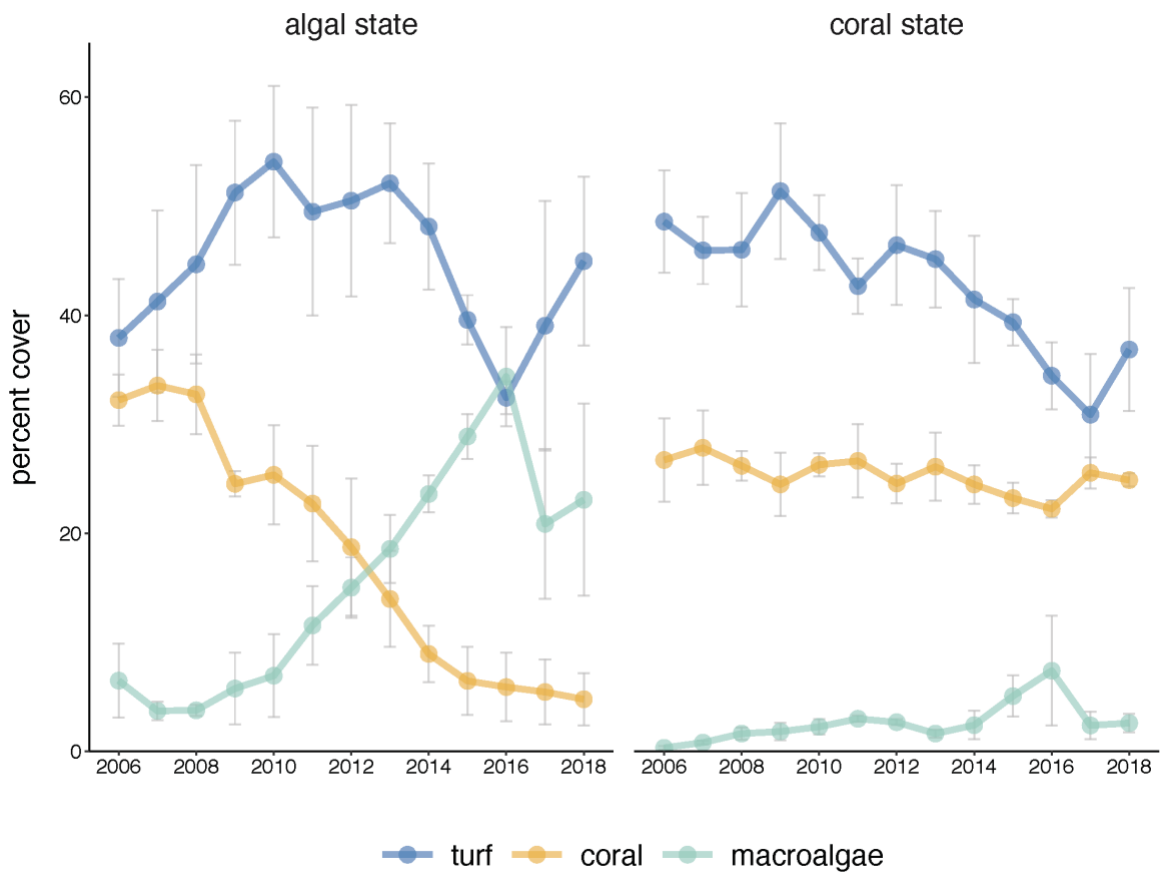


Figure 2. **Back reef benthic dynamics.** Percent cover data (mean \pm SE) of turf algae/CCA, live coral, and macroalgae at sites in the algal state and coral state in the lagoon back reef habitat from 2006 to 2018 (n = 3 sites for each state).

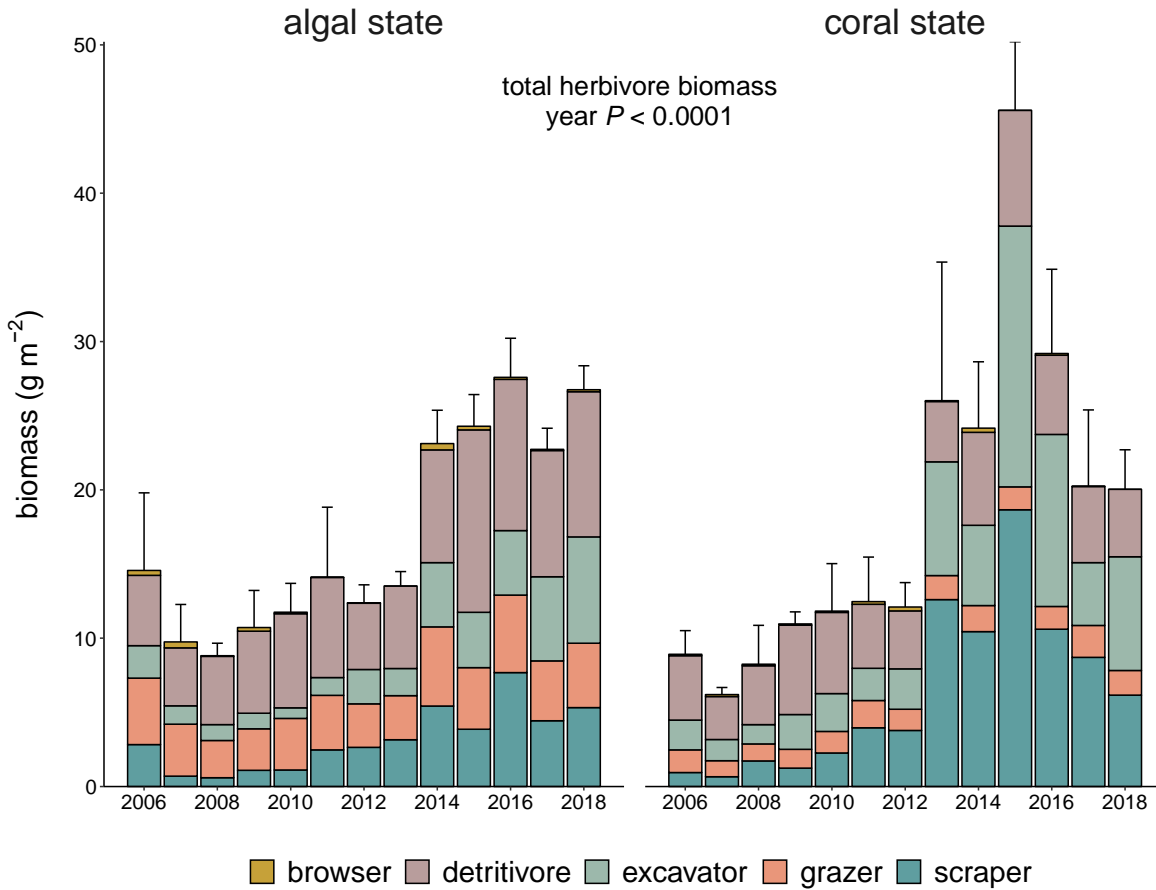


Figure 3. **Herbivore biomass by functional group.** Dynamics of total herbivore biomass (mean \pm SE) and the contribution of each herbivore functional group across the algal and coral states from 2006 to 2018 ($n = 3$ sites for each state).

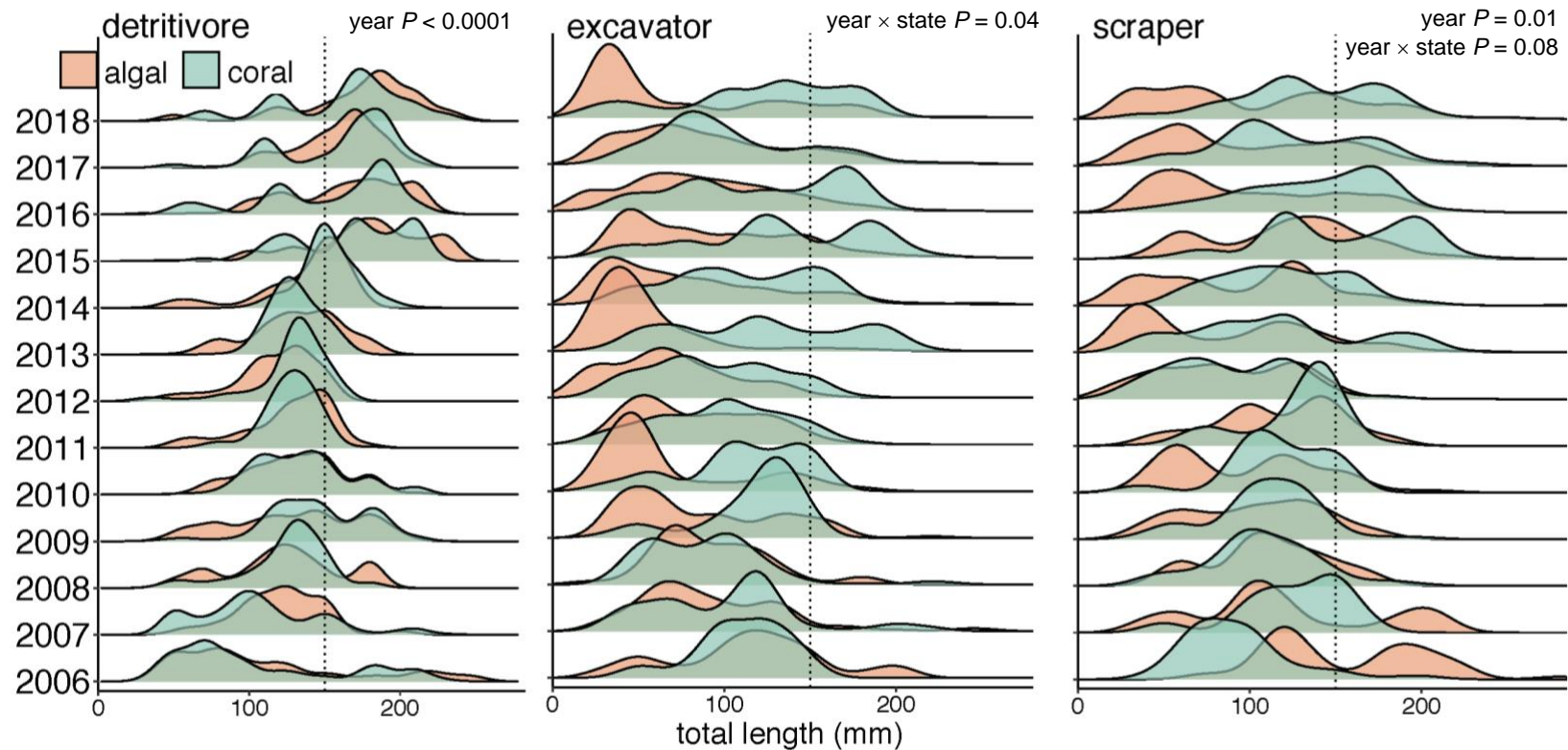


Figure 4. **Population size structure.** Kernel density body size estimates (total length in mm) of dominant functional groups (detritivore, excavator, scraper) from 2006 to 2018 at algal and coral states. Most recent years are at the top. Dashed vertical line denotes ‘larger’ individual size of 150 mm, which coincides with the unofficial and unregulated spearfishing size limit (Rassweiler et al., 2019).

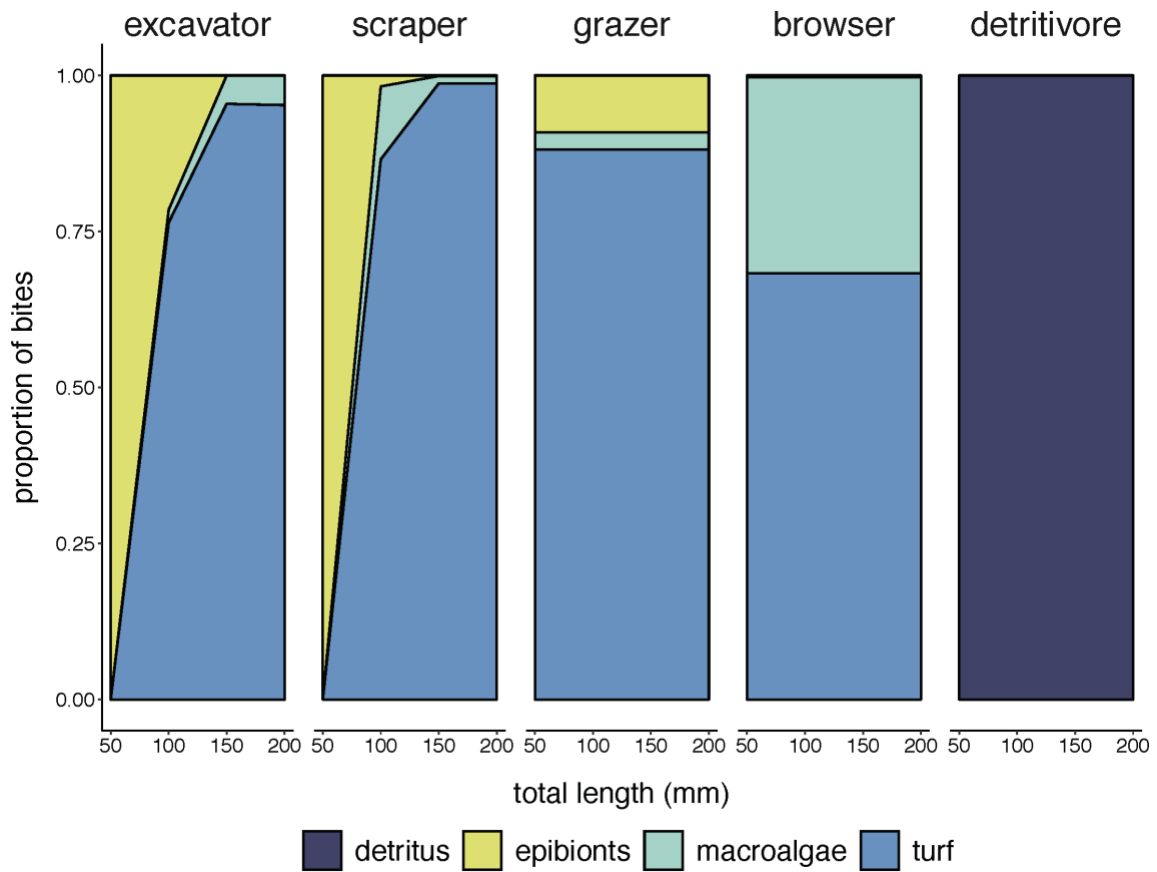


Figure 5. **Top-down organismal traits: diet proportions.** Diet items targeted for each functional group averaged across body size gradient ($n = 14 - 32$ per functional group). 'Detritus' includes all bites taken on sediment and detrital material. 'Epibionts' includes algae and animal organisms living on turf algae and macroalgae.

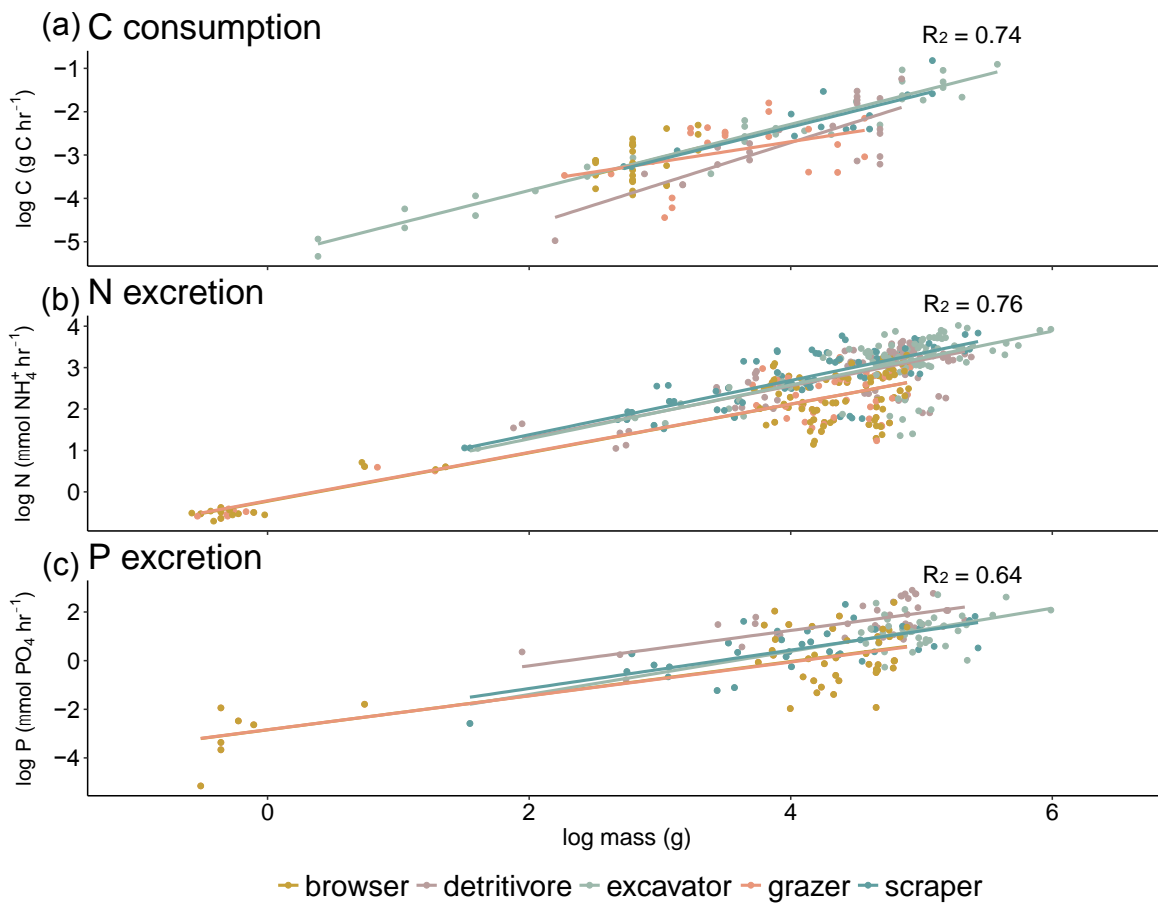


Figure 6. Top-down and bottom-up organismal traits: body size regressions.

Log-log linear relationship between body size and rates for TD (C consumption g C hr^{-1} ; a) and BU (N excretion $\text{NH}_4^+ \text{hr}^{-1}$; b; P excretion $\text{PO}_4 \text{hr}^{-1}$; c) processes. Values show adjusted R_2 values of overall model. Each line represents a separate model for each functional group for each rate process. For individual linear model parameters and statistics, see Table 2.

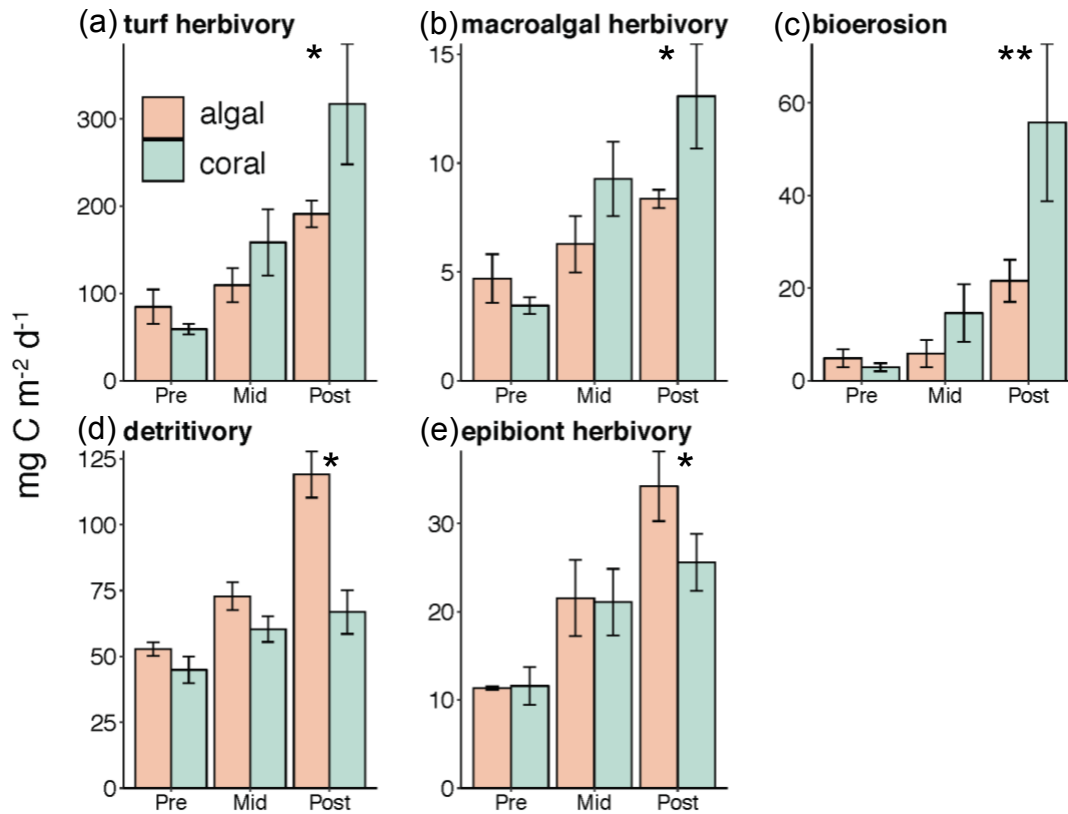


Figure 7. **Top-down ecosystem processes.** Modelled areal (mean \pm SE) top-down rates (mg C m⁻² d⁻¹; a-e) summed across all individuals in time series and binned into discrete time periods: “Pre” algal shift (2006 – 2008), “Mid” (2009 – 2014), and “Post” (2015 – 2018). Identical period bins used for coral state. Mean differences between algal and coral states for each time period were tested using pairwise t tests (* $P < 0.05$, ** $P < 0.01$).

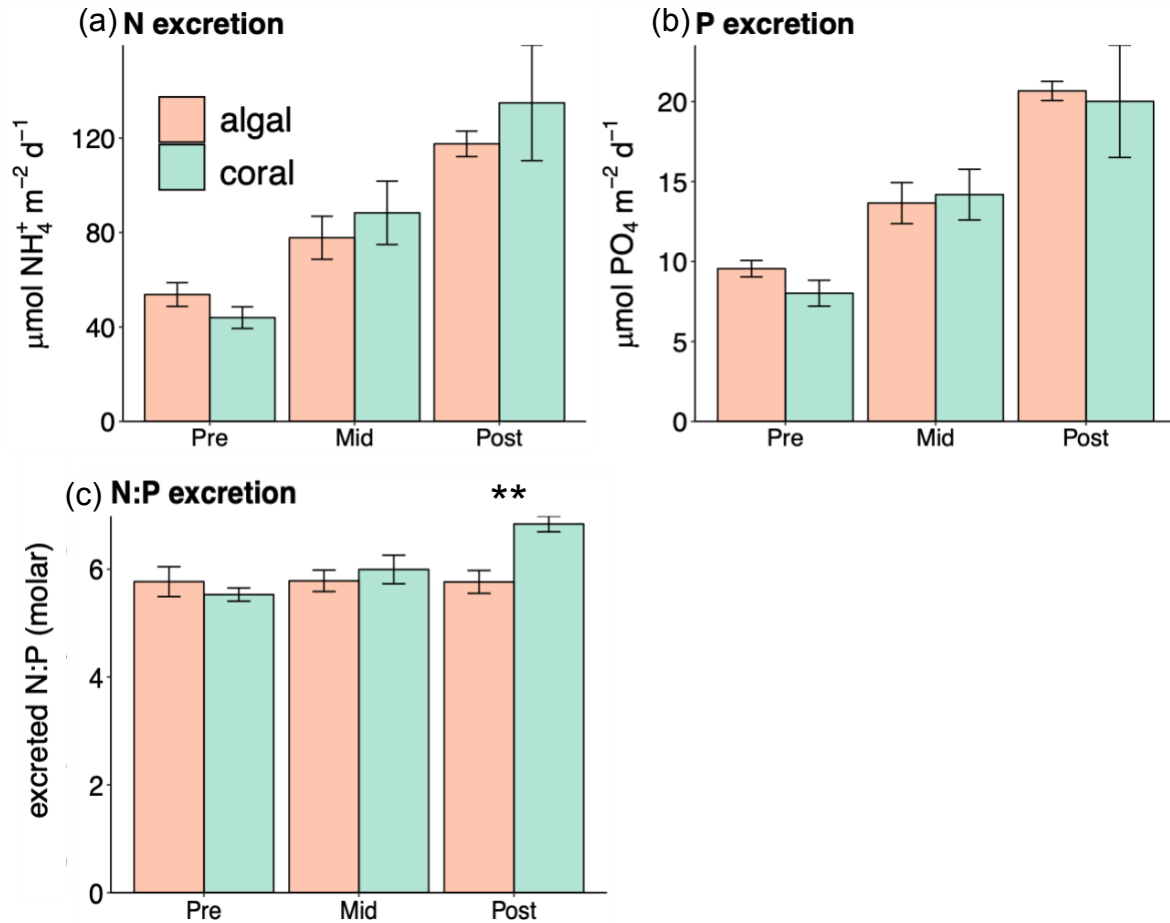


Figure 8. **Bottom-up ecosystem processes.** Modelled areal (mean \pm SE) bottom-up rates (μmol - nutrient $\text{m}^{-2} \text{d}^{-1}$; a-c) summed across all individuals in time series dataset. N:P excretion shows average community N:P molar ratio. Time series binned into discrete time periods, similar to Fig. 7. Mean differences between algal and coral states for each time period were tested using pairwise t tests (* $P < 0.05$, ** $P < 0.01$).

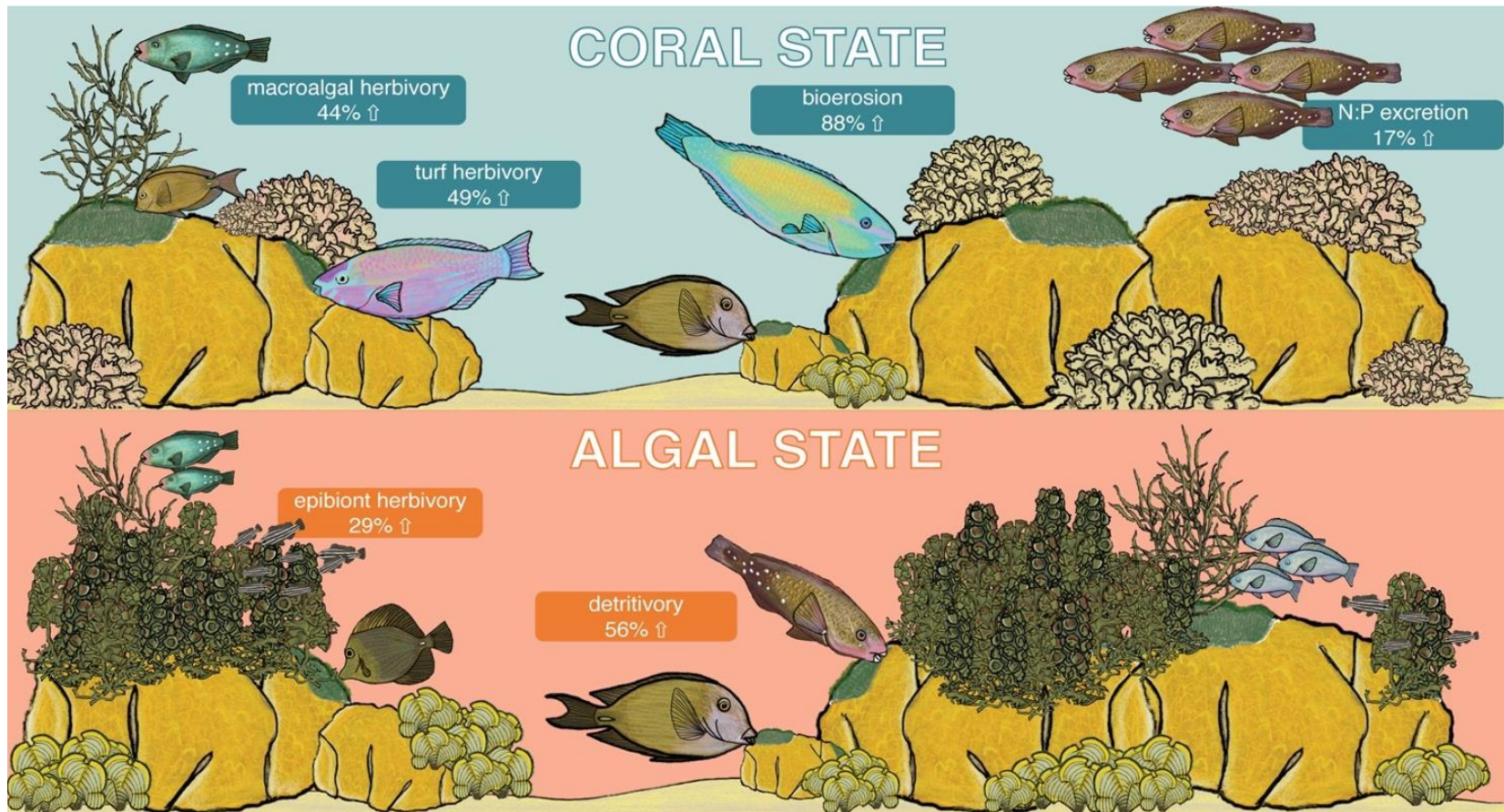


Figure 9. **Top-down and bottom-up processes in coral vs. algal states.** Conceptual diagram depicting differences in functional assemblages, size structures, benthic communities, and TD and BU rates and ratios during the post period (2015 – 2018). Percentages show percent differences between coral and algal states.