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A View From Both Ends: Shifts in Herbivore Assemblages Impact Top-Down and Bottom-Up Processes on Coral Reefs

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ABSTRACT

A fundamental goal in ecology is to understand the role of consumers in top-down (TD) and bottom-up (BU) processes that affect the functioning of ecosystems. Consumers ingest organic matter and excrete inorganic nutrients, and individual roles are influenced by body size and functional identity. Our study quantifies how alterations to herbivore assemblages affect both TD and BU processes on coral reefs in the South Pacific. We collected empirical data on consumption and nutrient excretion rates from 300 individual herbivorous fishes belonging to five functional groups. Individual-level traits were then scaled to a 13-year time series of fish populations from reefs that have either shifted to algal dominance or remained in the coral state. Large excavating parrotfishes and other herbivores on reefs in the coral state contributed 43% more herbivory and excreted nutrients at a higher ratio of N:P than herbivores on algal-dominated reefs; both processes may benefit coral health. Algal-dominated reefs experienced 56% higher rates of detritivory by large detritivorous fishes that remove detritus from algal surfaces, a process that may facilitate algal dominance. By scaling individual-level traits to population time series, our study provides a framework to quantify how changes to consumer assemblages impact both TD and BU processes across ecosystems undergoing change. Identifying the unique roles of consumers in processes that maintain and reinforce ecosystem states is the key to predicting the importance of shifts in diverse consumer assemblages.

Key words: Herbivory; Consumer-derived nutrients; Functional groups; Consumer assemblages; Ecosystem processes; Coral reefs.

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MANUSCRIPT HIGHLIGHTS

- Herbivore identity and size influence top-down and bottom-up processes.

- Coral and algal-dominated reefs host different herbivore assemblages.
- Herbivores impact ecosystem processes differently across reef states.

INTRODUCTION

Consumers shape the processes that underpin how ecosystems function. From bison grazing in North American grasslands (Frank 2008) to mussel predation by sea stars in the rocky intertidal (Paine 1980), consumers play a critical role in structuring ecosystems through consumptive processes (that is, top-down or TD hereafter; Estes and others 2011; Terborgh 2015). Consumers also contribute to bottom-up processes (BU) via nutrient recycling (that is, nitrogen and phosphorus excretion) that can promote primary production in freshwater (Vanni 2002), terrestrial (McNaughton and others 1997) and marine (Meyer and others 1983; Allgeier and others 2017) ecosystems. Although the extent to which consumers impact TD (Chase 1996; Silliman and Zieman 2001) and BU (Wolf and others 2013; Allgeier and others 2014) processes independently is well known, a remaining challenge is to improve our understanding of how consumers simultaneously influence multiple ecosystem processes (Hunter 2016).

Defining how consumers mediate ecosystem processes requires an understanding of how organisms modify the transfer and storage of nutrients in ecosystems (Bellwood and others 2019). Metabolism is an important governor of TD and BU processes and is strongly influenced by individual traits (for example, body size and behavior) and the environment (Fritschie and Olden 2016). In addition to these individual traits, the density of consumer populations and the diversity within assemblages also impact TD and BU processes (McIntyre and others 2008; Peters and others 2019; Ruttenberg and others 2019). However, anthropogenic forces (for example, overharvesting and habitat modification) are reducing consumer biomass and altering the size structure of consumer populations, leading to changes in how consumers shape ecosystem processes (Estes and others 2011; Ripple and others 2015).

On coral reefs, climate change, overfishing and nutrient pollution are driving shifts in ecosystem state away from coral states toward algal-dominated reefs (Hughes and others 2017). These different reef states can support fundamentally different consumer assemblages, and herbivorous fishes in particular often respond strongly to such changes (Robinson and others 2019). Alterations to communities of herbivorous fishes may impact the dynamics of reef ecosystems as herbivores control algal abundance and clear space for corals via TD processes (Bellwood and others 2004; Hoey and Bellwood 2008) and may promote primary production by providing limiting nutrients via BU processes (Burkepile and others 2013; Allgeier and others 2014).

These key ecosystem processes are also influenced by body size. For example, large parrotfishes often have different diets and feeding rates than smaller individuals of the same species (Adam and others 2018) and have the jaw morphology to erode calcium carbonate reef structure in a process known as bioerosion (Bruggemann and others 1996). Further, small individuals with higher rates of metabolism excrete larger quantities of nutrients per unit of body mass (Brown and others 2004), suggesting that populations with abundant small-sized individuals would exhibit very different nutrient dynamics (for example, differences in nitrogen (N) excretion rates or nitrogen/phosphorus (N:P) ratio) than populations with larger individuals. Thus, alterations to both the community composition and size structure of herbivorous fish communities may have important implications for ecosystem processes on coral reefs.

Changes in herbivore communities have profound effects on coral reefs through TD processes (Carpenter 1988; Ruttenberg and others 2019), but we know far less about the commensurate impacts on BU processes (but see Allgeier and others 2016), and we are not aware of any study that has investigated both processes simultaneously by any group of coral reef fishes. Here, we studied how shifting herbivorous fish assemblages altered TD and BU processes on shallow reefs in Mo'orea, French Polynesia that have either transitioned to algal dominance or remained in a coral state (Schmitt and others 2019). We coupled empirical data on consumption (TD rates) and N and P excretion (BU rates) of herbivorous fishes with a 13-year time series of their populations across reefs in the two ecosystem states. We had three specific objectives: (1) determine how body size influences TD and BU rates across five herbivore functional groups, (2) investigate spatiotemporal changes in their population density, size structure and biomass and (3) evaluate differences in ecosystem processes on reefs in both coral and algal states before, during and after a reef-wide phase shift. By parsing apart multiple consumptive and nutrient recycling pathways, we predicted that larger-sized herbivores on reefs in the coral state would provide more space-clearing TD processes (turf and macroalgal herbivory, bioerosion), while smaller-sized herbivores on algal-dominated reefs would have higher rates of BU processes (N, P excretion) and alter stoichiometry of N:P excretion.

METHODS

Individual Consumption and Excretion Rates

To determine how body size influences TD and BU process rates in five herbivore functional groups in *Objective 1*, we collected empirical data on consumption and excretion rates of eight common herbivorous fish species in Mo'orea, French Polynesia (17°30′ S, 149°50′ W) during the months of May–September in 2016, 2017 and 2018 (Figure S1). Our focal species were *Acanthurus nigrofuscus* (grazer), *Acanthurus triostegus* (grazer), *Zebrasoma scopas* (grazer), *Chlorurus spilurus* (excavator), *Ctenochaetus striatus* (detritivore), *Naso lituratus* (browser), *Scarus oviceps* (scraper) and *Scarus psittacus* (scraper). Overall, this species list comprises 95% of the total herbivore biomass in the back reef habitat recorded by the Mo'orea Coral Reef Long-term Ecological Research (MCR LTER) program (Brooks 2019). Within each functional group, our focal species comprise at least 95% of herbivore biomass with the exception of browsers, which were nearly absent from LTER records for the 13 years covered by the study (Table S1).

Consumption Rates

We used a twofold approach to identify the TD processes provided by each functional group. First, we quantified bite rates by individual fish (n = 134 total fish) on benthic substrates using 20-min focal follows during foraging hours (around 1000–1600; Bruggemann and others 1994), totaling 43 h of focal follows. For each fish, we recorded total length (TL) to the nearest 10 mm and used species-specific scaling parameters to estimate wet mass in grams (Kulbicki and others 2005). From the 20-min follows, we calculated hourly bite rates and multiplied these rates by 10 to create daily bite rates, given that herbivores forage approximately 10 h per day as they do not forage at night (Bruggemann and others 1994). Then, we paired those daily bite rates with bite size power functions specific to each functional group to quantify total carbon (C) consumption rates (mg C d^{-1}) for each individual (similar to van Rooij and others 1998; see Supporting Information). We used a linear model to evaluate how consumption (C) rates scaled with body size (mass in grams) and functional group identity (*consumption rate* ~ *mass x functional group*) and ANOVA to examine differences among functional groups in total C consumption rates. Next, we developed linear models to assess the relationship between consumption rates and individual size for each of the five functional groups separately. Regressions were performed on log-transformed variables to estimate slope, intercept and root-mean-square error (RMSE) for each model. Residuals were visually inspected to ensure assumptions of normality and homoscedasticity.

Second, to quantify specific TD processes we classified the benthic taxa of each bite taken by individual herbivores during focal follows. Targeted benthic taxa were identified and binned by benthic functional group (detritus, epibionts, macroalgae and turf algae/crustose coralline algae or CCA). Bites on macroalgae and turf algae/CCA that did not remove algae were categorized as bites on epibionts, characterized by a 'picking' foraging behavior that was typical of smaller individuals. All bites by detritivorous fishes were classified as bites on detritus, as these fishes typically have minimal impact on the removal of algae (Tebbett and others 2017). We characterized four separate TD processes (consumption of epibionts, detritus, macroalgae and turf) by calculating the average proportion of bites from each diet group within four size classes of each functional group (categorical; 40–89, 90–149, 150–199, 200 + mm TL). We used a Chi-square contingency test (χ^2) to evaluate whether the proportion of bites on different diet items varied across the four size classes within each functional group. To assess the role of detritivorous fishes, we identified the substrate type (macroalgae, turf and sediment) from which each bite of detritus was removed and tested whether the proportion of detritus removed from each substrate varied across three size classes for detritivores (categorical; 40–89, 90–149, 150–199 mm) using a Chi-square test.

Excretion Rates

We measured N and P excretion rates from over 170 herbivorous fishes across a broad size range (N: n = 176, P: n = 171; Table S1), following the methods of Allgeier and others (2015). Individual fish were collected using barrier nets and clove oil and immediately transported back to the University of California (UC) research station in an aerated cooler. We measured excretion rates in individual

Ziploc bags containing a known volume of pre-filtered seawater (using 0.7-µm pore size Gelman GFF) that we incubated for 30 min in a temperate-controlled water bath (25–27.5 °C). Water collected from each bag at the beginning and end of the incubation period was filtered (using 0.45-µm pore size Whatman filters) and immediately placed on ice. Each fish was identified to species, measured for standard length (mm) and weighed for wet mass (g) post-excretion trials in order to limit handling stress. A set of controls ($n = 6$; filtered seawater with no fish) were incubated for the same time period at each sampling event to control for autogenic changes in nutrients.

Samples were analyzed within 12 h for ammonium (NH_4^+) using the methodologies of Taylor and others (2007) or frozen for transport to UC Santa Barbara for soluble reactive phosphorus (PO_4^{3-}) analyses using the ascorbic acid method and colorimetric analyses (APHA 1995). By factoring in bag volume and incubation time for each individual, we calculated hourly excretion rates for each individual fish and multiplied rates by 24 to create daily excretion rates (mg nutrient d^{-1}), given that fishes excrete continuously (Schreck and Moyle 1990) and that other recent work on nutrient cycling has made this same assumption (Burkepile and others 2013; Allgeier and others 2014; Shantz and others 2015).

Similar to consumption (C) models, we evaluated whether nutrient excretion (N and P) rates scaled with body size (mass in grams) and functional group identity using linear models (*excretion rate ~ mass x functional group*) and ANOVA to examine differences among functional groups in nutrient excretion (BU) rates. We developed separate linear models to assess the relationship of N and P excretion rates and individual size for four functional groups (browser functional group excluded due to insufficient sampling). Following visual inspection of residuals, we log-transformed variables and used regressions to estimated slope, intercept and RMSE.

Time Series of Herbivore Populations

In *Objective 2*, we investigated the spatiotemporal changes in biomass, density and size structure of herbivore assemblages using a 13-year time series collected by the MCR LTER program (Carpenter 2019; Brooks 2019). Six sites in the back reef habitat provide the framework to assess changes to herbivore assemblages from data collected annually on individual size and abundance of mobile herbivorous reef fish species within 250-m^2 fixed transects ($n = 3$ transects per site per year; Figure S1). We classified herbivorous reef fish species into five distinct functional groups: browser, detritivore, excavator, grazer and scraper (see Table S1 for complete list of species and classifications) based on common classifications (Green and Bellwood 2009). Sizes and abundances of all individuals were converted to wet mass using species-specific scaling parameters (Kulbicki and others 2005).

To analyze the spatiotemporal dynamics of herbivore functional groups at replicate transects at each of the six sites every year, we: (1) averaged the total biomass of all herbivorous fishes, (2) averaged the biomass of each functional group, (3) summed total abundance of individuals within each functional group and (4) determined the median size of individuals of each functional group. We then classified the six study sites based on the phase shift regime identified by Schmitt and others (2019) where three sites have maintained high abundance of coral over the time series ('coral state'), while the other three sites have seen a decline in coral and subsequent rise in macroalgae ('algal state'). Separate linear mixed-effects models were used to test how (1) total biomass of all herbivores, (2) biomass of each functional group, (3) density of each functional group and (4) median size of individuals within each functional group was driven by ecosystem state, time or the interaction between state and time (fixed effects = state, year and state × year, random effect = site with AR 1 correlated error to account for temporal autocorrelation). To meet normality assumptions, biomass, density and median size data were log-transformed prior to statistical analyses.

Time Series of Top-Down and Bottom-Up Processes

For *Objective 3*, we evaluated differences in TD and BU ecosystem processes by generating a 13-year time series of consumption and nutrient excretion rates at six long-term back reef sites (Figure S1). To do this, we estimated daily consumption rates (mg C d^{-1}) for each individual herbivorous fish in the MCR LTER time series ($n = 22{,}437$ individuals) using linear models of C consumption (from *Objective 1*) based on individual mass and functional identity. We incorporated differences in foraging behavior by applying multiple TD processes in the time series based on functional identity and size. To do this, the proportions of size-specific bites on detritus, epibionts, macroalgae and turf were multiplied by total C ingested for each individual to estimate C consumption rates of each diet item (see Supporting Information for more details). Additionally, we estimated bioerosion rates by excavating parrotfishes (only those > 150 mm TL) using a polynomial regression of the proportion of bites on turf algae that produce bite scars (Yarlett and others 2018).

Similarly, we estimated daily N and P nutrient excretion rates (mg nutrient d^{-1}) for each individual fish in the MCR LTER time series ($n = 21{,}958$ individuals; browser functional group excluded due to lack of empirical data on excretion) using linear models of N and P excretion (from *Objective 1*) according to individual mass and functional identity. For all models, we propagated model prediction uncertainty into our final consumption and excretion rate estimates by using simulated model coefficients and their 95% confidence intervals to calculate consumption and excretion rates 1,000 times for each individual. The Monte Carlo iterations and modeling procedures were performed using the *arm* package in R (Gelman and Hill 2006).

By modeling individual rates to consumer populations over space and time, we may be underestimating subtle shifts in consumer-mediated processes due to spatiotemporal changes in feeding behavior, diet quality and resource availability. Herbivore diets can depend somewhat on algal productivity and benthic composition (Fox and Bellwood 2007), although studies have found feeding preferences to be consistent over space and time (Chong-Seng and others 2014; Hamilton and others 2014). Our data suggest there is little impact of resource availability on bite rates and patterns in herbivore diet appear to be quite consistent across space (see Supporting Information Figure S2, Table S2). Importantly, feeding behavior is consistent enough that herbivores are often classified into functional groups that are used widely across the literature (Green and Bellwood 2009). Although this approach makes simplifying assumptions, it allows for robust comparisons of TD and BU processes over space and time and has been used extensively in coral reef ecology (Bellwood and others 2012; Allgeier and others 2016; Ruttenberg and others 2019; Cinner and others 2020).

To test for changes in TD and BU processes in coral and algal states before, during and after a reef-wide phase shift, we categorized data into three distinct periods: 'pre'-algal-shift (2006–2008), 'during' algal-shift (2009–2014), and 'post'-algal-shift (2015–2018) which coincide with state transitions of benthic cover (Schmitt and others 2019). TD and BU rates for individual fishes were summed within each transect to obtain areal TD and BU daily rates for the entire herbivore assemblage (mg C m^{-2} d^{-1}; mg N, P m^{-2} d^{-1}). Prior to statistical tests, areal TD and BU rates were summed across replicate transects ($n = 3$ transects) and averaged for each site ($n = 3$ sites) within each state ($n = 2$ states) and time period ($n = 3$ time periods). All data were log-transformed to meet normality assumptions.

We evaluated changes in site-level N:P molar ratios by converting each areal N and P estimates to moles and dividing the sum of N by the sum of P. Ratios were averaged across sites within each state and time period, and data were log-transformed to meet normality assumptions. We used mixed-effect models to test how each TD process (turf herbivory, macroalgal herbivory, bioerosion, detritivory and epibiont consumption) and BU process (N excretion, P excretion, N:P ratio) was affected by ecosystem state, time period or the interaction between ecosystem state and time period (fixed effects = state, period and state × period, random effect = site). Assumptions of normality and homoscedasticity were assessed through visual inspection of model residuals. All linear mixed-effects models were run in the *nlme* package in R (Pinheiro and others 2017). All data analyses were performed in R (R Core Team 2019), and all figures were created using R *ggplot2* package (Wickham and Chang 2016).

RESULTS

Individual Consumption and Excretion Rates

Consumption Rates

Individual body size and functional identity collectively explained 54% of the variation in the carbon (C) consumption data (Figure 1A), which is to be expected given that we used allometric relationships between size and C removed per bite to calculate total C consumption per individual. There were no differences in total C consumption among functional groups (ANOVA: $F_4 = 0.61$, $P = 0.65$; Table S3). In separate linear models, total C consumption (mg C d^{-1}) increased with body size (g) for all five functional groups ($P < 0.05$ scrapers and browsers, and $P < 0.001$ detritivores and excavators; Table S4), although the pattern for grazers was less strong ($P = 0.09$).

Some functional groups exhibited ontogenetic shifts in diet across body size, while others did not. The proportion of bites on different diet items varied across size of excavators (Chi-square:

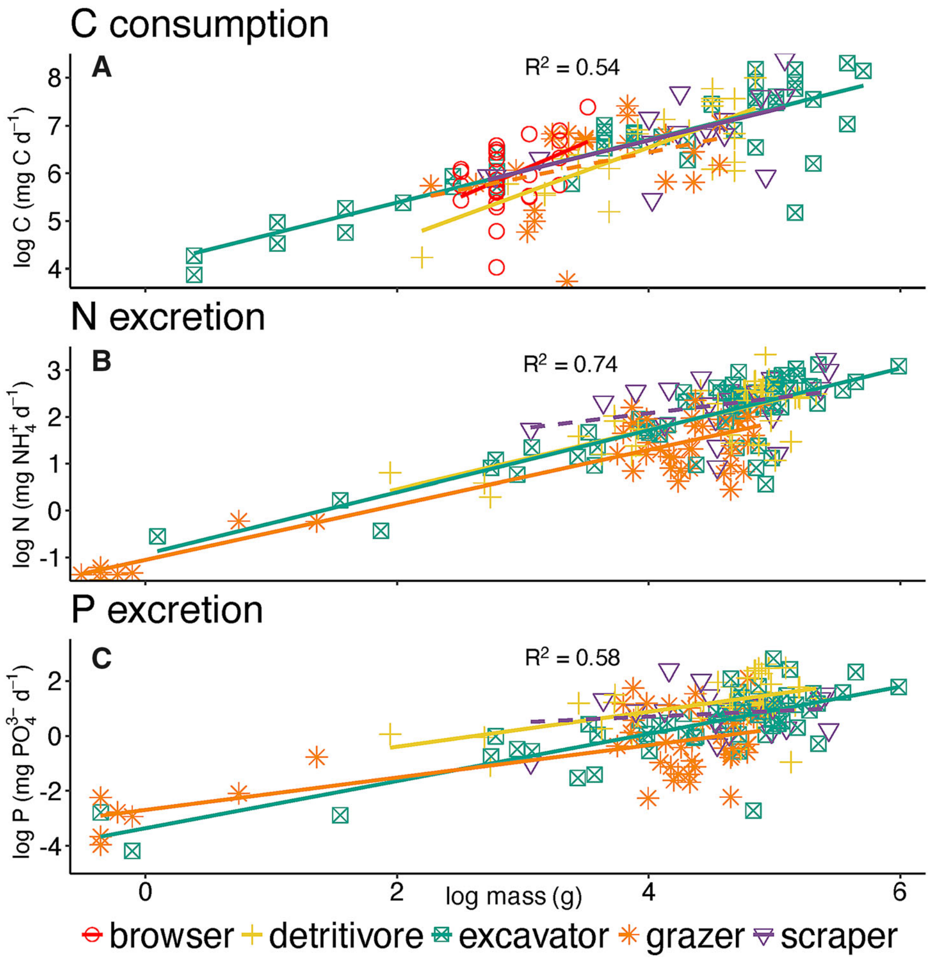

Figure 1. Linear models for top-down and bottom-up processes by functional group. Log–log linear relationship between body size (grams) and rates for top-down processes (**A**) C consumption mg C d^{-1} and bottom-up processes, (**B**) N excretion mg NH_4^+ d^{-1} and (**C**) P excretion mg PO_4^{3-} d^{-1}. Note differences in y-axis scale for plots. Adjusted R^2 values are from linear models (*consumption or excretion rate ~ mass x functional group*). Each line represents a separate linear model for each functional group. Dashed lines represent functional group models with $P > 0.05$. Browsers are not included in bottom-up processes due to limited sample size. For individual linear model parameters and statistics, see Table S4.

$\chi^2(6) = 1384.9$, $P < 0.001$) with the smallest individuals (< 90 mm) consuming 98% epibionts, whereas larger sizes targeted turf algae (Figure S3). Grazers also changed diet with size ($\chi^2(4) = 271.1$, $P < 0.001$) with individuals smaller than 90 mm consuming about 95% turf and little macroalgae, while the largest grazers consumed about 20% macroalgae. Scrapers did not shift diets across size ($\chi^2(2) = 3.91$, $P = 0.14$). Independent of size, browsers ate proportionately more macroalgae than the other functional groups, with about 30% of bites coming from macroalgae and 70% from turf algae ($\chi^2(2) = 0.66$, $P = 0.72$). Detritivorous fishes consumed detritus from a variety of different substrates that varied across size classes ($\chi^2(4) = 22.3$, $P < 0.001$) with the largest detritivores (> 150 mm) more likely to remove detritus from macroalgae (9.4% of bites) than small detritivores (0.9% of bites; Figure S3).

Excretion Rates

BU processes (N excretion: mg NH_4^+ d^{-1}; P excretion: mg PO_4^{3-} d^{-1}) were predicted by individual body size and functional identity, collectively explaining 74% (N) and 58% (P) of the variation (Figure 1B, C). Nutrient excretion (N, P) differed among the functional groups (ANOVA: N functional group: $F_3 = 44.19$, $P < 0.001$; P functional group: $F_3 = 13.01$, $P < 0.001$; Table S3). N and P excretion increased with size of detritivores, excavators and grazers ($P < 0.001$ for all individual models; Table S4). However, size was unrelated to

N or P excretion in scrapers (N excretion: $P = 0.17$, P excretion: $P = 0.53$).

Time Series of Herbivore Populations

Between 2009 and 2014, three back reef sites that underwent a phase shift had large increases in macroalgae and declines in corals, while three others remained in a coral state with little macroalgae (Schmitt and others 2019; Figure 2A, B). Despite these differences in benthic community composition, total herbivore biomass increased significantly over the study period in both states (year: $F_{12,48} = 9.13$, $P < 0.001$; Figure 2C, D; Table S5). Temporal increases in total herbivore biomass were driven by 3 dominant functional groups that make up 83% of the total herbivore biomass: detritivores (year: $F_{12,48} = 2.28$, $P = 0.02$), scrapers (year: $F_{12,48} = 7.0$, $P < 0.001$) and excavators (year: $F_{12,48} = 9.09$, $P < 0.001$). Excavator biomass was greatest in the coral state in later years (year × state interaction: $F_{12,48} = 2.59$, $P < 0.01$) and represented as much as 37.6% of total herbivore biomass on reefs in the coral state in 2015. There was also a trend for higher scraper biomass in the coral state compared to the algal state (state × year interaction: $F_{12,48} = 1.82$, $P = 0.07$).

Temporal increases in detritivore biomass were driven mostly by increases in the size of detritivores over time (year: $F_{12,48} = 12.9$, $P < 0.001$; Figure 3A). Across both algal and coral states, detritivores doubled in size from a median size of 87.5 mm in 2006 to 175 mm in 2015, but actually decreased in abundance over the study period (year: $F_{12,48} = 1.97$, $P = 0.05$; Figure S4). In contrast, excavators were on average 40% smaller in the algal state than coral state in later years, 2015–2018 (state × year interaction: $F_{12,48} = 2.02$, $P = 0.04$; Figure 3B). Across both states, excavators

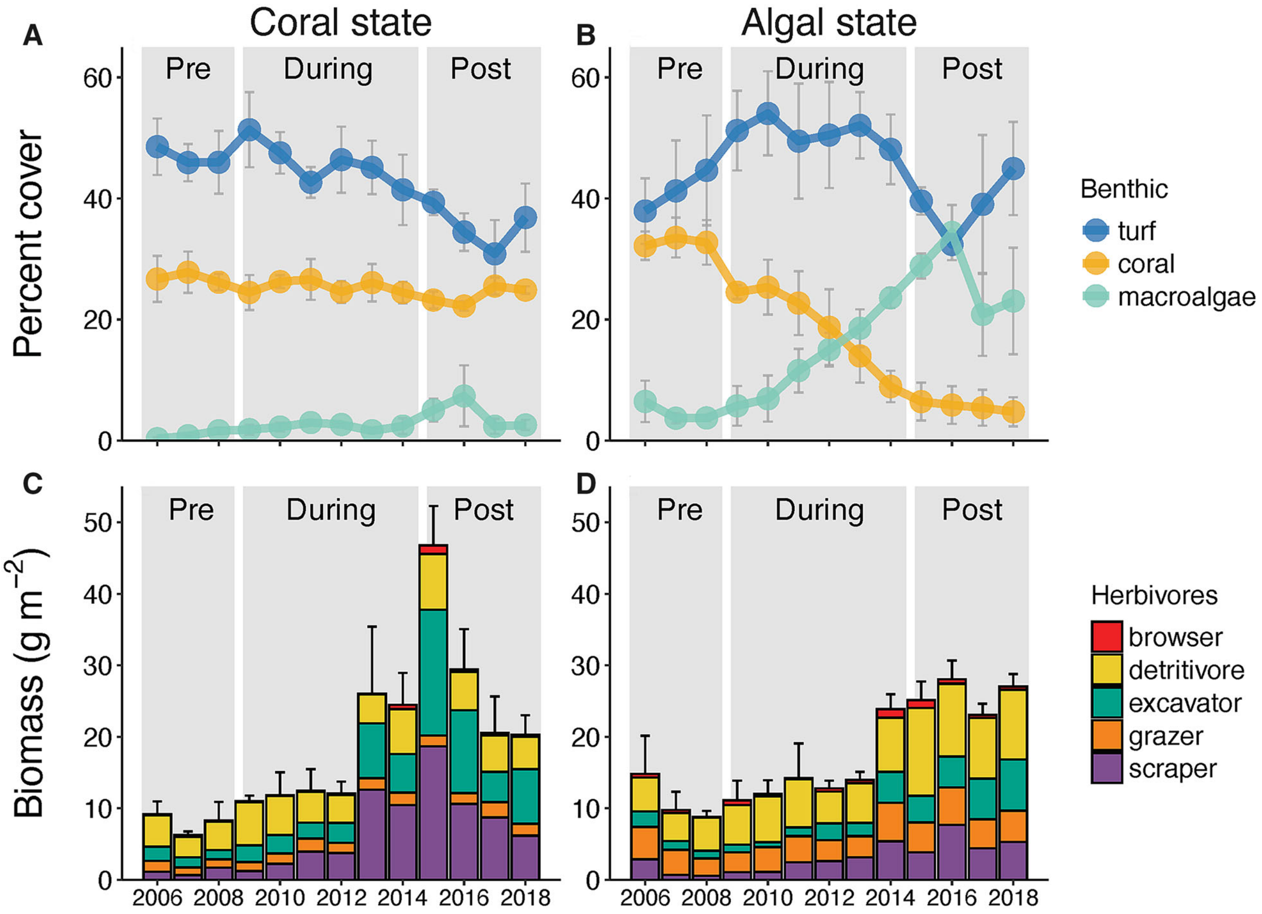

Figure 2. Benthic cover and herbivore biomass dynamics. Percent cover data (mean ± SE) of turf algae/CCA, live coral and macroalgae at reefs in the **A** coral state and **B** algal state at six long-term back reef sites from 2006 to 2018 ($n = 3$ sites for each state). Dynamics of total herbivore biomass (mean ± SE) and the contribution of each herbivore functional group across the **C** coral and **D** algal states from 2006 to 2018 ($n = 3$ sites for each state). Gray-shaded areas indicate 'pre'- (2006–2008), 'during'- (2009–2014) and 'post' (2015–2018)-state change periods.

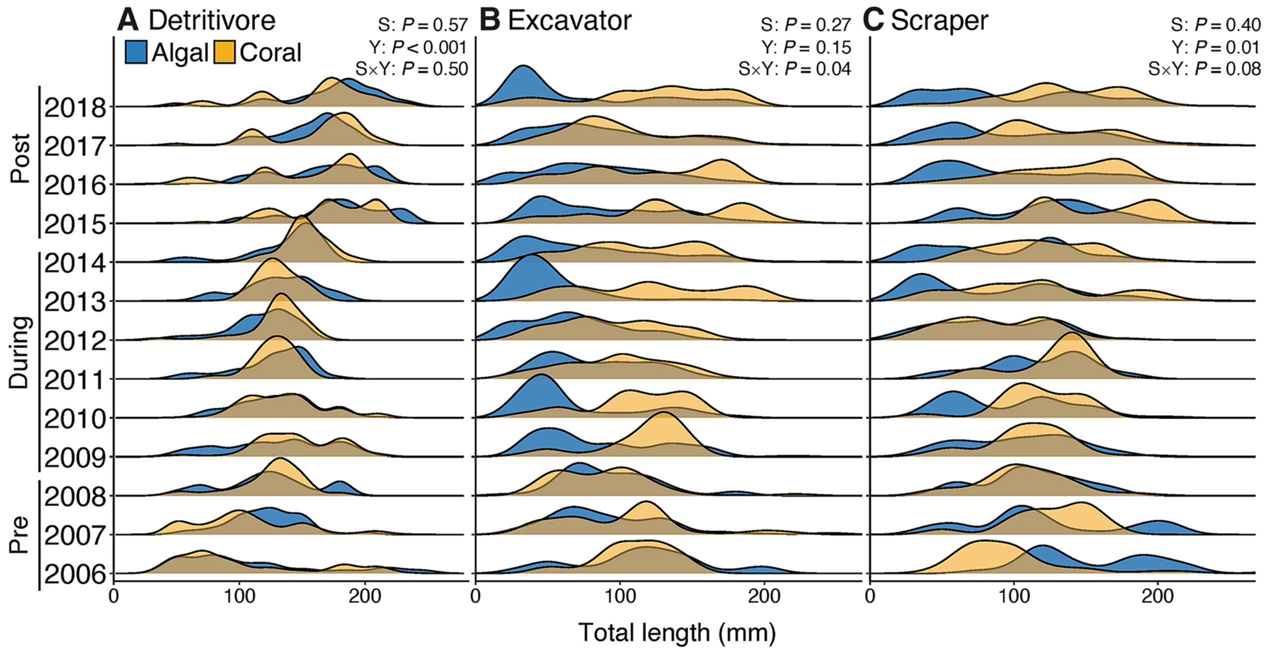

Figure 3. Size structure of herbivore populations. Size-frequency distributions for body size (total length in mm) of dominant functional groups **A** detritivore, **B** excavator, **C** scraper from 2006 to 2018 at algal (blue) and coral (orange) long-term back reef sites. Plots show relative population abundances over time, with most recent years at the top. *P* values from results of linear mixed-effects models used to test the interaction between year and ecosystem state on median total length for each functional group (fixed effects = state (S), year (Y), and state × year (S × Y), random effect = site; see Table S5).

became more abundant over time (year: $F_{12,48} = 6.8$, $P < 0.001$; Figure S4). Scraper biomass increased over time as a result of increases in abundance (year: $F_{12,48} = 16.98$, $P < 0.001$; Figure S4). Scrapers tended to decrease in size on reefs in the algal state (state × year interaction: $F_{12,47} = 1.76$, $P = 0.08$; Figure 3C), with median size decreasing from 140 mm in 2006 to 80 mm in 2012, where it remained for subsequent years.

Grazer and browser functional groups did not respond to changes in benthic cover within reef states. The biomass of grazers remained unchanged over the 13-year period (year: $F_{12,48} = 0.57$, $P = 0.86$); however, their biomass was on average 2.5 times higher in the algal state compared to coral state, with this difference preceding changes in ecosystem state (state: $F_{1,4} = 15.23$, $P = 0.02$). Grazers were also more abundant in the algal state (state: $F_{1,4} = 21.56$, $P < 0.01$; Figure S4) and increased in median size during the study period (year: $F_{12,48} = 3.9$, $P < 0.01$). Browsers were essentially absent from reefs during the 13-year time series with an average biomass of 0.41 ± 0.06 g m^{-2} (± SE) across all sites.

Time Series of Top-Down and Bottom-Up Processes

We modeled individual TD and BU process rates to fish populations across six back reef sites in Mo'orea over 13 years to evaluate spatiotemporal changes in ecosystem processes. We found few differences in TD processes between coral and algal states before reefs became dominated by algae (pre- and during periods; Figure 4). Once the benthic phase shift occurred (post-period), turf algal herbivory was 43% higher in the coral state than algal state (269.8 ± 57.2 mg C m^{-2} d^{-1} (± SE) removed vs. 174.5 ± 10.6, respectively; state × period interaction: $F_{2,68} = 3.75$, $P = 0.03$; Figure 4A; Table S6). Macroalgal herbivory increased over time (period: $F_{2,68} = 17.40$, $P < 0.001$; Figure 4B), as average rates across all reefs nearly tripled from an average 3.7 ± 0.9 mg C m^{-2} d^{-1} before the phase shift (pre-period) to 11.1 ± 1.5 mg C m^{-2} d^{-1} in later years (post-period). There was some evidence that bioerosion was higher in the coral state (41.7 ± 12.5 mg C m^{-2} d^{-1}) than the algal state (16.3 ± 3.4 mg C m^{-2} d^{-1}) after the phase shift; however, the interaction strength is weak due to high variability (state × period interaction:

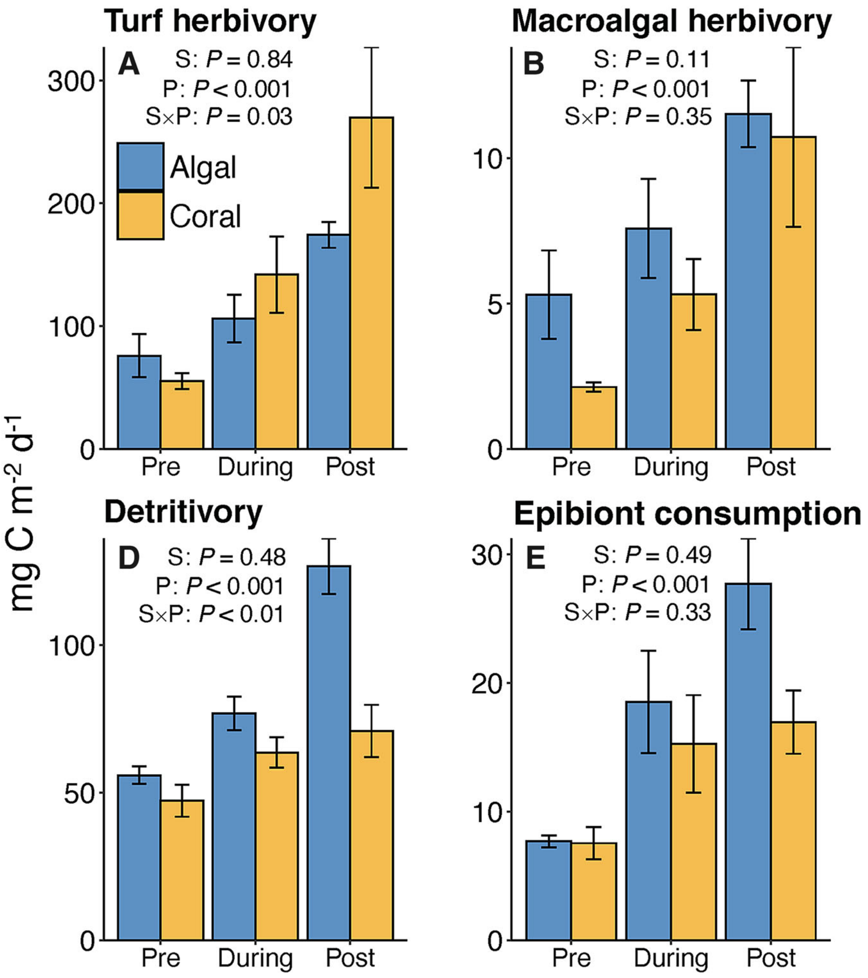

Figure 4. Top-down ecosystem processes. Top-down rates (mg C m^{-2} d^{-1}) (mean ± SE) summed across all individuals and binned into discrete time periods: 'pre'- (2006–2008), 'during'- (2009–2014), and 'post' (2015–2018)-ecosystem state shift. Mean differences between algal (blue) and coral (orange) states across three distinct time periods were tested using mixed-effects models (fixed effects = state (S), period (P) and state × period (S × P), random effect = site) with *P* values shown for each model (see Table S6).

$F_{2,68} = 2.24$, $P = 0.11$). After the phase shift, detritivores on algal-dominated reefs removed 126.6 ± 9.5 mg C m^{-2} d^{-1} of detritus (post-period), a 56% higher rate of detritivory compared to reefs in the coral state during the same time (state × period interaction: $F_{2,68} = 6.52$, $P < 0.01$; Figure 4D). Lastly, epibiont consumption increased over time (period: $F_{2,68} = 18.08$, $P < 0.001$; Figure 4E) as average rates across all reefs were nearly 3 times higher in the post-period (22.3 ± 2.8 mg C m^{-2} d^{-1}) compared to before the phase shift (pre-period; 7.6 ± 0.6 mg C m^{-2} d^{-1}).

Unlike TD processes, N and P excretion rates did not differ between states during any time period but increased over time (N period: $F_{2,68} = 47.09$, $P < 0.001$; P period: $F_{2,68} = 45.03$, $P < 0.001$; Table S7). Across all reefs, average N excretion rates were 2.7 times higher in the post-period (2.4 ± 0.2 mg NH_4^+ m^{-2} d^{-1}; Figure 5A) compared to the pre-period (0.91 ± 0.07 mg NH_4^+ m^{-2} d^{-1}), whereas P excretion rates were 2.4 times higher after the phase shift (0.68 ± 0.05 mg PO_4^{3-} m^{-2} d^{-1} post-period vs. 0.28 ± 0.02 pre-period; Figure 5B). The average N:P molar ratio of excretion was 11% higher on reefs in the coral state during the post-shift period (state × period interaction: $F_{2,68} = 8.70$, $P < 0.001$; Figure 5C). In the post-shift period, the average N:P molar ratio of excretion in the coral state was 6.6 (± 0.1), whereas the N:P ratio in the algal state was 5.9 (± 0.1).

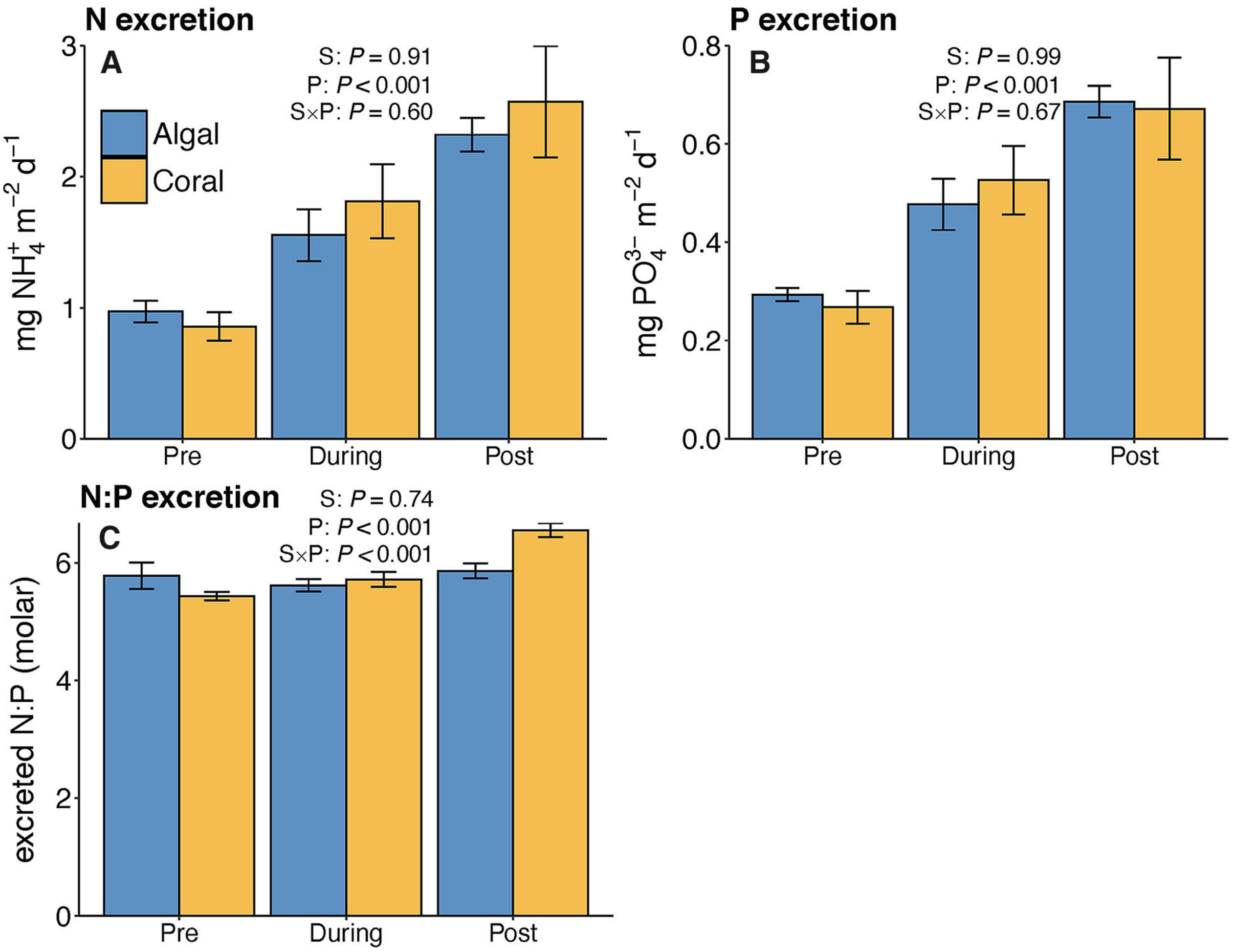

Figure 5. Bottom-up ecosystem processes. Bottom-up rates (mg nutrient m^{-2} d^{-1}) (mean ± SE) summed across all individuals and binned into discrete time periods: 'pre'- (2006–2008), 'during'- (2009–2014) and 'post' (2015–2018)-ecosystem state shift. N: P excretion shows average community N: P molar ratio. Mean differences between algal (blue) and coral (orange) states across three distinct time periods were tested using mixed-effects models (fixed effects = state (S), period (P) and state × period (S × P), random effect = site) with *P* values shown for each model (see Table S7).

DISCUSSION

Consumers play a critical role in the top-down (TD; Estes and others 2011; Terborgh 2015) and bottom-up (BU; Vanni 2002; Allgeier and others 2017) processes that impact the functioning of ecosystems. By developing a 13-year time series on herbivore-mediated TD and BU rates on reefs in French Polynesia, we provide evidence that changes to composition, density and size structure of consumer assemblages can impact both TD and BU processes simultaneously. Reefs in the coral state hosted large-bodied parrotfishes and other herbivores that collectively grazed 43% more turf algae than reefs than algal-dominated reefs, which experienced increases in small-bodied parrotfishes that graze in a fundamentally different way than do their larger conspecifics. In addition, detritivorous fishes increased in size over time, leading to 56% higher detritivory rates on reefs in the algal state. Excretion of N and P was comparable across ecosystem states, as rates increased with general increases in herbivore biomass. However, the molar ratio of N:P excretion was lower on algal-dominated reefs likely due to changes in the composition of herbivore communities. Our work suggests that changes to herbivore assemblages following shifts to degraded algal states may fundamentally alter multiple ecosystem processes that drive community dynamics and likely impact the resilience of reefs.

Ontogenetic Shifts in Diet Impact TD and BU Processes

Our data reveal the importance of body size for how consumers mediate TD and BU processes. For example, changes in size of excavating parrotfishes affected TD processes because of the strong ontogenetic shifts in diet that we observed. These shifts in parrotfish diets are found in other studies (Bellwood 1988; Chen 2002) and are often attributed to differences in jaw morphology and function. Further, we provide evidence that young parrotfishes with high mass-specific 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. By removing epibionts from macroalgae and turf algae, these abundant small parrotfishes may actually facilitate algal growth (Eich and others 2019). Thus, if smaller parrotfishes become more abundant on reefs, they may, counterintuitively, act as positive feedbacks on abundant macroalgae by removing epibionts from their surfaces.

Similar to excavators, grazers increasingly fed on macroalgae at larger sizes (> 150 mm), although turf was still their primary target. Browsers consistently fed on macroalgae, but turf algae represented a surprisingly large portion of their diets. Notably, our time series data of TD processes demonstrates how a lack of large grazers in conjunction with the absence of browsers led to macroalgal herbivory rates that are substantially lower than studies from other reefs (Chong-Seng and others 2014). It is well known that removing erect macroalgae on reefs is key for reversing algal-dominated states (Burkepile and Hay 2011). Thus, pairing size-dependent TD processes with population dynamics conveys how shifts in herbivore assemblages may impair key processes that are important for the resilience of coral reefs.

Theoretically, shifts in size to small-bodied populations will contribute substantially to BU processes due to higher mass-specific excretion rates at early ontogenetic stages (Brown and others 2004). Small fishes require N for protein synthesis and P for bone, scale and RNA production (Schindler and Eby 1997); thus, their role in nutrient recycling reflects these stoichiometric constraints. Additionally, small fishes may excrete nutrients at different spatial scales than large individuals (Hall and others 2007). Schooling young parrotfishes (< 90 mm) that shelter within and feed on N-rich epibionts of the common macroalga, *Turbinaria ornata* (K.S. Munsterman, personal observation), excrete some of the highest ratios of N:P in close proximity to fast-growing primary producers. Therefore, the observed shift in size structure to abundant small parrotfishes on algal-dominated reefs may help reinforce macroalgal proliferation via both TD and BU processes. These findings support previous research from coral-depauperate Caribbean reefs which reported that the combination of decreased herbivory but sustained N-rich nutrient supply by fishes enhanced macroalgal cover (Burkepile and others 2013). Together, these data reinforce the importance of disentangling context-dependent mechanisms that may act as positive feedbacks on algae once corals become rare.

The Unique Role of Detritivores on Degraded Reefs

Among our most interesting findings was the twofold increase in the size of detritivorous fishes at sites that transitioned to abundant algal cover and the ensuing effects on TD and BU processes. Excess detritus, often a product of increases in productive turf and macroalgae (Wilson and others 2003), likely influenced the population dynamics of detritivores as reefs saw a rise in algae. Detritivores provide a different TD function than other herbivores by using their brush-like mouths to sweep macroalgae, turf algae and sediment substrates of detritus (Tebbett and others 2017). We found that small detritivores (< 90 mm) mostly eat detritus from turf algae, while larger detritivores (> 150 mm) are likely to remove more detritus from macroalgae. Their removal of detritus may, in fact, facilitate algal growth (Crossman and others 2001) and influence the accumulation of macroalgae in an algal-dominated state. Long-life spans (up to 40 years in these systems; Choat and Robertson 2002) and low predation pressure (Davis and others 2017) of these large-bodied detritivores likely drove their proliferation over time, which may have further reinforced algal dominance via the distinctive TD function they provide.

Our study also highlights the important role that detritivores play in potential P recycling on coral reefs. Although most herbivores excrete high ratios of N:P due to P-deficient diets (Burkepile and others 2013; Allgeier and others 2014), our results show that detritivores excrete P at higher rates than most other functional groups. Some potential explanations for this novel finding may be a P-rich diet of detritus, low P body tissue content (K.S. Munsterman, unpublished data) and slow growth leading to slower accumulation of body P over time (Choat and Robertson 2002). In our study, detritivores appear to be potentially key P recyclers, a phenomenon also found in freshwater systems (Vanni 2002; McIntyre and others 2008) but currently unreported from marine systems. The increase in size of detritivores was responsible for estimated changes to BU processes, namely a decline in N:P ratio on reefs in the algal state in later years. The N:P ratio of 5.9 supplied by fishes on algal-dominated reefs is pushing a lower limit in the ratio of N:P that may no longer benefit corals (Allgeier and others 2014).

Disproportionate Effect of Large-Bodied Parrotfishes

Although our study demonstrates that increases in fishes of small sizes may have important implications for TD and BU processes, it is impossible to ignore the disproportionate role of larger consumers on ecosystem function (Estes and others 2011; Ripple and others 2015). On coral reefs, large parrotfish (scrapers and excavators > 150 mm) with well-developed jaws are able to remove substantially more material per bite than small individuals, creating a nonlinear relationship between size and TD function (Lokrantz and others 2008). On Mo'orean reefs, large parrotfishes contributed to higher rates of turf herbivory and large excavators in particular led to 88% higher bioerosion rates on reefs in the coral state compared to reefs that shifted to an algal-dominated state. Unlike epibiont consumption or detritivory, both of these TD processes are known to be important for controlling algal abundance and promoting coral settlement (Bruggemann and others 1996; Bellwood and others 2004). Additionally, large parrotfishes on reefs in the coral state during the post-period supplied a large proportion (47% N, 40% P) of community-level nutrient excretion at a higher ratio of N:P. The higher average N:P ratio (9.4 ± 1.5) excreted by large parrotfishes may be closer to the optimal range for coral health (5–20; Allgeier and others 2014). The TD and BU processes provided by large parrotfishes in our study highlight the need to integrate ecosystem processes with population dynamics when considering how to manage the small-scale fisheries of these highly targeted herbivore species.

CONCLUSION

Animals play important roles in most ecosystems via both top-down and bottom-up processes. For example, ungulate herbivores in terrestrial ecosystems can impact primary production both via their consumption of grasses (Frank and others 1998) and recycling of nutrients (McNaughton and others 1997). Similarly, fishes in freshwater streams are key for both recycling limited nutrients (Vanni 2002; McIntyre and others 2008) and controlling the abundance of benthic algae (Power 1990). Yet despite the numerous studies assessing how consumers control ecosystem processes, our study is unique in evaluating how the same consumer assemblages impact both TD and BU processes simultaneously. Other studies focus on how TD or BU forces vary either over space (Wolf and others 2013; Allgeier and others 2016) or time (Peters and others 2019), but our work uses a 13-year time series of consumer populations dynamics to show how both TD and BU processes can potentially change in response to state shifts in the ecosystem.

By partitioning out TD and BU processes, we show the importance of taking a holistic view to understanding the different processes that consumers influence. Our work stresses the significance of integrating empirical data on individual traits and consumer populations to scale up to ecosystem function. Identifying the unique roles of consumers in TD and BU processes that maintain and reinforce ecosystem states is the key to predicting when and how shifts to diverse consumer assemblages matter. Thus, our study provides a framework that can be used to quantify how changes to consumer assemblages impact both TD and BU processes across changing ecosystems.

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DATA AVAILABILITY

Archived data were available in the Moorea Coral Reef LTER database at http://mcrlter.msi.ucsb.edu/cgi-bin/showDataset.cgi?docid=knb-lter-mcr.2010.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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