

# A budget of algal production and consumption by herbivorous fish in an herbivore fisheries management area, Maui, Hawaii

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**Abstract.** The relative rates of carbon fixed by primary producers vs. consumption by primary consumers shape the community of organisms in ecosystems. On coral reefs, it is important to understand the demography of algae, given known competitive dynamics with reef-building corals. Numerous studies have shown that fleshy algal abundance is enhanced in the absence of top-down control by herbivores on coral reefs. However, fewer studies have quantified and compared rates of production by the benthic fleshy algal community and consumption by herbivores. Here, we estimate a budget for fleshy algal growth and herbivorous fish consumption on a Hawaiian coral reef based upon integration of field-measured and taxonomically specific variables. Data were collected at Kahekili Herbivore Fisheries Management Area, Maui, established in 2009, in which taking of herbivorous fish and urchins is prohibited. Daily algal production was determined by quantifying benthic community composition, standing stock of algal biomass, and growth rates of common algal components. Consumption was determined using distributions of biomass and size classes of herbivorous fish species, consumption rates of herbivores on different algal species, and herbivore bite sizes. Our results show that throughout the first five years of herbivore protection, algal production consistently exceeded the grazing capacity of the herbivorous fish assemblage, but by a diminishing margin since 2010 (consumption 20.8% of production) to the end of the study in 2014 (consumption 67.0% of production). Further, larger size classes of herbivorous fishes in the scraper/excavator herbivore guild contributed more to consumption in later years, which could have additional feedbacks that promote reef-building taxa. Projecting the budget using data from a neighboring decades-long protected herbivorous fish assemblage indicated that the production and consumption budget for Kahekili could become balanced in future with continued management.

**Key words:** algae; coral reef; grazing; herbivory; net primary production; phase shift; productivity.

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## INTRODUCTION

Primary production in ecosystems, be it by grasses and woody plants in temperate landscapes, phytoplankton in freshwater lakes, or

benthic algae on coral reefs, provides the basis of food webs across the planet. Consumers of this primary production, including ungulates in forests and savannahs, zooplankton in lakes, and fishes and urchins on coral reefs, shape these

ecosystems via top-down influence of grazing (Carpenter 1986, Belsky 1992, Shurin et al. 2002). Importantly, changes to top-down control can result in shifts in ecosystem dynamics and to phase shifts. For example, increased top-down influence can shift plant community structure (Ripple and Beschta 2003) or result in desertification of former grasslands (Andrew 1988). In lakes, the absence of top-down control can result in exponential growth of unpalatable phytoplankton (Benndorf et al. 2002). Finally, on coral reefs, removal of herbivores via over-extraction (Friedlander et al. 2007) or disease (Hughes 1994) can lead to phase shifts to fleshy algal-dominated reefs.

To understand the influence of top-down control in an ecosystem or how changes to top-down control may alter systems, it is important to understand net primary production in ecosystems. In temperate forests, using direct measurements of growth of individual plants, identifying allometric relationships, and scaling up these relationships, grazers are estimated to consume 10–50% of primary production (as reviewed in Gower et al. 1999). In African savannas, consumption of grasses by large ungulates, determined by net foliage consumption and ungulate energetic expenditure, was estimated to be 57% of primary production (Coe et al. 1976, Frank et al. 1998). Alteration of grazing populations in these ecosystems, for example through livestock grazing, can alter the portion of primary production that is consumed (Andrew 1988).

On coral reefs, upwards of 100% of the total benthic algal production may be consumed (Wanders 1977, Hatcher 1981, Carpenter 1986, van Rooij et al. 1998), which is believed to be important in allowing corals to maintain a competitive advantage for space over faster growing algae (as reviewed in McCook et al. 2001). Generally, estimates of total herbivory on reefs have been based on extrapolation from detailed observations of a few abundant herbivores (Klumpp and Polunin 1990, Paddack et al. 2006), calculated through estimates of metabolic demands of fishes (van Rooij et al. 1998), or based on consumption of algae on settlement tiles (Wanders 1976, Russ 2003). Production of benthic algal biomass on reefs has been estimated through laboratory measurements of oxygen production (Wanders 1976, Klumpp and Polunin 1990, van

Rooij et al. 1998) and growth of algae *in situ* in the absence of herbivores (Carpenter 1986, Russ 2003, Paddack et al. 2006).

The proportion of benthic algal production consumed by herbivores varies according to the benthic composition of a given reef. On reefs with high coral-cover (>50%) herbivores were estimated to consume upwards of 100% or more of daily algal production (Wanders 1977, Hatcher 1981, Carpenter 1986, van Rooij et al. 1998). On naturally algal-dominated reef flats, site-attached damselfish and blennies combined with roving acanthurids and scarids were estimated to remove between a quarter and over double the daily production (Klumpp and Polunin 1990). Finally, following fleshy (non-calcareous turf and macroalgae) algal phase shifts on low coral-cover reefs (<10%), herbivores were estimated to consume 31–77% of algal production (Paddack et al. 2006). Thus, some of the variability in these estimates likely arises from differences in habitat and the herbivore community living within that habitat.

The balance of production and consumption on a coral reef based upon the herbivore assemblage and algal community could be used to project future trajectories for a given reef. On a reef in which estimates of production and consumption are balanced, in theory benthic community composition would be expected to remain fairly stable. However, if production grossly exceeds consumption there is potential for algal biomass to increase through time. The balance between production and consumption could be indicative of how fleshy algal standing stock on a reef may be increasing, decreasing, or remaining stable, although importantly changes in algal cover on reefs also depend on competition dynamics (McCook et al. 2001). To date, there has not been an examination of how this balance of production and consumption changes through time at a given site. Detailed field-derived rates of algal growth and herbivore assemblage consumption, while inherently variable, are needed to develop reasonable estimates of production–consumption budgets for coral reefs.

Directly increasing herbivore biomass to drive the reversal of phase shifts has been discussed as a management option for coral reefs (Green and Bellwood 2009, Rasher et al. 2013, Jackson et al. 2014). Several studies have shown a negative

relationship between herbivore biomass and macroalgal cover across reefs in the Caribbean and the Pacific (Williams and Polunin 2001, Friedlander et al. 2007, Jouffray et al. 2015). Results from Fiji in shallow-water reefs lend promising support for herbivore management as a tool for coral reef recovery, with higher growth rates of corals and lower macroalgal biomass in protected reefs (Rasher et al. 2012). While there are few examples of such management being put into practice (Jackson et al. 2014), the decline in coral cover and increase in fleshy algal cover as well as fleshy algal blooms on the reef at Kahekili Beach Park on West Maui, Hawaii (Rodgers et al. 2015), led state managers to designate this reef an Herbivore Fisheries Management Area (HFMA) in 2009. This HFMA is the first of its kind in Hawaii. The goal of the Kahekili HFMA (KHFMA) was to promote coral cover by increasing herbivore biomass and consequent grazing pressure. Here, we use a calculated budget of benthic algal production and consumption by herbivorous fish to better understand the ability of the fish assemblage to reduce algal cover at the KHFMA.

The major components of this study were fourfold. First, we quantified herbivore consumption and algal production based on observational surveys and experimentation. Second, we tracked these rates through time from before the inception of an herbivore-specific fisheries management area to five years into herbivore protection in order to quantify community-level changes in algal growth and consumption over the duration of protected status. Next, through modeling production and consumption through time, we quantified the proportion of algal production consumed by the KHFMA herbivore assemblage to assess the amount of production consumed by the herbivorous fish assemblage. Finally, we calculated production and consumption using herbivore biomass from a nearby marine protected area that has been fully closed for 40 yr to understand how a future herbivore assemblage may impact the KHFMA benthic community.

## METHODS

### *Study area and overview*

All data were collected at the KHFMA on West Maui, Hawaii, in relatively shallow (2–10 m deep) fringing reef habitat (shallow aggregated

reef in Williams et al. 2016). Algal growth and consumption by herbivores were determined through analysis of benthic community composition, standing stock of algae, growth rates of dominant algal species, abundance and biomass of herbivorous fish species, the species-specific consumption rates of herbivores on different algal species, and the bite size of herbivores. These data were collected through a series of field and laboratory experiments as well as semi-annual monitoring surveys at KHFMA as described below.

### *Benthic community composition*

Benthic cover was determined from surveys conducted twice a year from 2008 to 2014 by the NOAA Coral Reef Ecosystem Program and Hawaii Division of Aquatic Resources (DAR) (Williams et al. 2016). These surveys were conducted across the ~1 km<sup>2</sup> area of KHFMA and included ~20–50 transects per survey. Photoquadrats (~1 m<sup>2</sup>) were taken every meter along each 25-m transect. Photographs were analyzed using the image analysis software PhotoGrid 1.0 in which 15–100 points were superimposed on the image in a stratified random fashion and benthic cover was identified to genus for corals and macroalgae or functional group for turf algae, crustose coralline algae, and cyanobacteria.

### *Algal standing biomass*

Standing stock of macroalgae was determined by removing all fleshy algae inside eight 0.6 × 0.85 m quadrats placed haphazardly on the shallow aggregate reef at 5–8 m depth. Algae were collected by hand using blunt metal tools and razor blades, separated by species in the laboratory, wet-weighed, dried in the oven at 60°C for 24 h, and dry-weighed. Prior to the removal of macroalgae, photoquadrats were taken of the area and canopy heights were measured using a ruler. Benthic cover was then related to wet and dry standing stock biomass estimates within each quadrat.

To determine standing stock of mixed-assemblage turf algae, areas of turf covering dead massive *Porites* colonies were scraped off the calcium carbonate in situ and vacuumed into a bag using a marine battery and a bilge pump (Appendix S1: Fig. S1). A known area of turf was scraped using a razor blade, and tubing on the intake end of the

pump was held adjacent to this area to capture all material removed. Tubing on the outgoing end of the pump was connected to a polyvinyl chloride (PVC) canister capped with Nitex mesh to catch all scraped material. Samples were transferred from Nitex mesh to filter paper in the laboratory and then decalcified for 24 h with 5% HCl to remove carbonate material. Samples were then filtered on pre-weighed Whatman Grade 1 qualitative cellulose ash-free filters, dried at 60°C for 24 h, and their dry weight recorded and normalized to the size of the scraped area.

#### Algal growth rates

To determine in situ growth rates of common macroalgal species, samples were first collected from the KHFMA and transported to a small field station in Lahaina in plastic bags of seawater. Samples were spun gently 20 times in a salad spinner, blotted with a paper towel, and weighed to obtain an initial wet weight (3–5 g). All samples were then placed in mesh pockets and stored overnight in ambient seawater aerated with bubblers. Samples were deployed on the reef at KHFMA the following morning by placing them in small cylindrical cages constructed out of 1 cm diameter clear plastic mesh and galvanized wire frame. Algae were deployed at 10-m intervals along a 150-m transect at depths of 2 and 8 m. Cages were attached to ropes, which were staked into the limestone substrate, and small floats were used to elevate samples off the benthos. After 4–7 d, algae were removed from cages and transported via labeled plastic bags to the laboratory to obtain final wet weight. Changes in weight were used to determine proportional algal growth rates over the period of deployment ( $\text{change in weight} \times \text{initial weight}^{-1} \times \text{time}^{-1}$ ). Macroalgal species assessed here included the most common species found on the reef as follows: *Acanthophora spicifera* (red, non-native blooming species;  $n = 9$ ), *Ulva lactuca* (green, native blooming species;  $n = 10$ ), *Amansia glomerata* (red, native species;  $n = 10$ ), and *Tricleocarpa fragilis* (red, native species;  $n = 10$ ).

To determine growth rates of turf algae, plots that were cleared to quantify standing stock were caged with standard hardware 2.54 cm diameter vinyl-coated chicken wire preventing urchins with tests larger than 2.54 cm and fishes >5 cm from grazing inside. Turf samples were allowed to grow for 7–60 d ( $n = 22$ ) and then resampled using the

vacuum method as mentioned above, decalcified, and dried using the methods described above.

#### Herbivore abundance and biomass

Surveys to quantify herbivorous fish abundance and biomass were conducted twice per year by the NOAA Coral Reef Ecosystem Program and Hawaii Division of Aquatic Resources (Williams et al. 2016). In this study, ~20–50 25-m transects were sampled haphazardly in the shallow aggregate reef habitat inside the KHFMA. Fish densities of all observed species were estimated by visual strip transect along each transect line. On the outward-bound leg, fish >15 cm, within a 4 m wide belt centered on the diver, were recorded. On the return leg, fishes <15 cm were recorded within a 2 m wide belt. Fish sizes were estimated in 5-cm bins. Biomass was calculated using established species-specific conversion factors taken largely from FishBase (Froese and Pauly 2016).

Herbivores were categorized as grazers, scrapers, or browsers (Green and Bellwood 2009, Edwards et al. 2014). Detritivores were not included in the consumption calculation as their impact in removal of algal biomass is considered minimal or not well quantified (Choat et al. 2002, Tebbett et al. 2017), and by excluding them, estimates of consumption err on the side of conservative.

#### Herbivore grazing rates

Grazing rates were quantified for all observed species of protected herbivores at the KHFMA (acanthurids, scarids, and kyphosids, the last of which were not recorded on surveys at the reef during the course of this study). Grazing rates were determined using timed behavioral observations (Bellwood and Choat 1990, Hamilton et al. 2014, Kelly et al. 2016). Briefly, divers followed at least 10 and up to 60 individuals of each herbivorous fish species. Observations were made between 2 and 10 m depth in the shallow aggregate reef habitat. Divers recorded number of bites and type of substrate consumed by each fish during 3- to 5-min timed swims, allowing for multiple grazing forays. Divers terminated observations if fish behavior was altered by diver presence. Substratum type of bites was recorded to the finest taxonomic classification possible through field identification. Macroalgae were identified to genus while turf algae, crustose



coralline algae, and other groups were identified to functional group.

### Herbivore bite size

Laboratory experiments were conducted to calculate the weight of algae removed per bite by representative acanthurids and scarids of varying sizes. Bite size data collection was conducted at the Maui Ocean Center using fish on display at the aquarium. *Ulva lactuca* was used in these experiments because of low error in calculating wet weight for that species and its high degree of palatability. *Ulva lactuca* fragments were weighed initially and lowered into aquariums housing target fish species using fishing line. The number of bites taken by a single fish on a piece of algae was recorded. After grazing, the remaining algal tissue was removed from the tank and wet-weighted as described above. Bite size per species and size class were calculated from the change in weight of the algal specimen divided by the number of bites taken by the herbivore. These bite rate data were only used in this calculation to estimate biomass of algae removed per bite and not as bite rate data in the overall consumption calculation.

Literature values for bite size of herbivore species in this study were also used when available for various acanthurid and scarid species. Data were either taken directly from previous studies as measurements of algal biomass removed per bite (Klumpp and Polunin 1990) or were extrapolated from recorded values of scarid grazing scar area (Ong and Holland 2010) and combined with experimental turf standing stock data in this study to determine algal biomass removed per bite of a given species and size class.

Herbivore total length (TL; cm) was plotted against bite size (BS; g of algae removed per bite), and a power function was used to describe the relationship between these two factors, roughly following the allometric increase in body size by length of fishes (Huxley and Tesissier 1936, Zgliczynski and Sandin 2017). Because bite-sized data were not available for all species and size classes of fishes, the relationship between herbivore size and BS was estimated at family level (acanthurid or scarid) given gross mouth morphological similarities. This estimate further assumes that the same biomass of algae was removed for a bite on turf algae or macroalgae.

### Overall fish consumption

In calculating total fish consumption for a given year on the reef, we used a bootstrapping approach to combine the multiple sources of uncertainty that contribute to the total algal consumption estimate. For a given type of fish (e.g., trophic group, size class), the mean algal consumption is a function of the fish biomass density sample ( $D$ :  $\text{g}_F/\text{m}^2$ ) and the fish grazing capability ( $K$ :  $\text{g}_A \cdot \text{g}_F^{-1} \cdot \text{day}^{-1}$ ).  $K$  is a function of the estimated fish bite rates ( $R$ : bites/day), the corresponding BS ( $S$ :  $\text{g}_A/\text{bite}$ ), and species biomass ( $F$ :  $\text{g}_F$ ). As explained above, the BS and fish biomass were both calculated using the fish TL associated with the BS. Thus, we can write  $K$  as:

$$K = \frac{R \times S}{F}.$$

The bootstrapping procedure involved generating series of length  $\beta$  ( $=10^4$ ) of values of  $D$  and  $K$ , randomly resampled with replacement from survey and experimental data, and noted as  $D^*$  and  $K^*$ , respectively. Hence, the  $b$ th sampled mean,  $a_b$ , can be written as:

$$a_b = \frac{1}{n} \left( \sum_{i=1}^n D_i^* \right) \times \frac{1}{m} \left( \sum_{j=1}^m K_j^* \right),$$

where  $b \in [1, \beta]$ ,  $n$  is the length of the fish biomass density sample,  $D$ , and  $m$  the length of the fish grazing capability sample,  $K$ . By repeating this process  $\beta$  times, we obtained a distribution of estimated means from which a global estimated mean and 95% confidence interval were calculated. Following this procedure, we calculated mean annual fish consumption at KHFMA for each year between 2008 and 2014.

### Overall algal production

We calculated overall algal production in a similar manner to consumption using a bootstrapping approach. For a given type of algae (e.g., turf or macroalgae), the overall algal growth is a function of the algal growth rate ( $G$ :  $\text{g}/\text{day}$ ) and the algal benthic cover ( $C$ : %). Because we used a bootstrapping procedure, we did not directly use our sample set, but rather a series, of length  $\beta$ , of data randomly resampled with replacement, and, respectively, noted  $G^*$  and  $C^*$ . Hence, the  $b$ th sampled mean,  $c_b$ , can be written as:

$$c_b = \frac{1}{n} \left( \sum_{i=1}^n G_i^* \right) \times \frac{1}{m} \left( \sum_{j=1}^m C_j^* \right),$$

where  $b \in [1, \beta]$ ,  $n$  the number of algal growth rate samples, and  $m$  the number of algal benthic cover samples. By repeating this process  $\beta$  times, we obtained a distribution of estimated means from which a global estimated mean, noted  $A$ , and its 95% confidence interval were calculated. Following this procedure, we calculated mean annual algal production at KHFMA from 2008 to 2014.

Finally, using the bootstrapped data of  $\beta$  samples for both consumption and production we created a new distribution of net production (production remaining after herbivorous fish consumption). As with the above distributions, we obtained a global estimated mean of net production from this new distribution and determined its 95% confidence interval via quantiles generated by the bootstrap. Following this procedure, we calculated mean annual net production at KHFMA from 2008 to 2014.

To project potential future herbivore assemblage scenarios after many more years of herbivore management at the KHFMA, we calculated the net production at the KHFMA using KHFMA benthic data from 2014 and herbivore assemblage data in 2014 from Molokini Marine Life Conservation District (MLCD) just offshore of Maui that was closed to all fishing in 1977. Regular benthic and fish biomass data are collected as part DAR's long-term monitoring program (Sparks et al. 2015). Using the herbivorous fish assemblage data from Molokini, we compared the consumption estimates to the current benthic algal biomass production estimates from KHFMA to determine whether such a long-term protected herbivore population has the capacity to consume the algal production at the KHFMA.

## RESULTS

### Benthic community composition

Over the course of this study (2008–2014), the reef was comprised primarily of turf algae (41.2–53.8%) and hard coral (34.0–37.3%), as well as crustose coralline algae (CCA) (0.3–9.2%), macroalgae (1.3–4.7%), cyanobacteria (0.01–1.4%), and other substrata including sand and other invertebrates (<10%; Fig. 1). CCA increased between 2008 and 2014 from 0.3% to 9.2% ( $t$  test,  $p < 0.001$ )

and turf decreased between 2008 and 2014 from 53.8% to 41.2% ( $t$  test,  $p < 0.001$ ). Coral cover and macroalgal cover did not significantly change over this time period ( $t$  test,  $p = 0.840$  and  $p = 0.467$ , respectively).

### Algal standing biomass

For ease of calculation with differing percent cover of algae across the reef, algal standing biomass was reported assuming 100% coverage of a given area by these algal groups. Therefore, macroalgal standing biomass was 51.5 g dry wt/m<sup>2</sup> (SE = 17.9), and turf algal standing biomass was 79.0 g dry wt/m<sup>2</sup> (SE = 11.8; Table 1). The majority of standing biomass of macroalgae was *Amansia glomerata*, which accounted for 38.0 g dry wt/m<sup>2</sup> (SE = 12.4).

### Algal growth rates

Growth rates (g [g<sup>-1</sup> algae]·day<sup>-1</sup>, and mean [±SE]) for turf algae and four species of macroalgae were measured in situ at the KHFMA (Fig. 2). Turf algae had the fastest growth rate at 0.0708 (±0.0163), which was variable (Appendix S1: Fig. S2). The growth rates of macroalgal species were as follows: *Ulva lactuca* at 0.0341 (±0.0051),

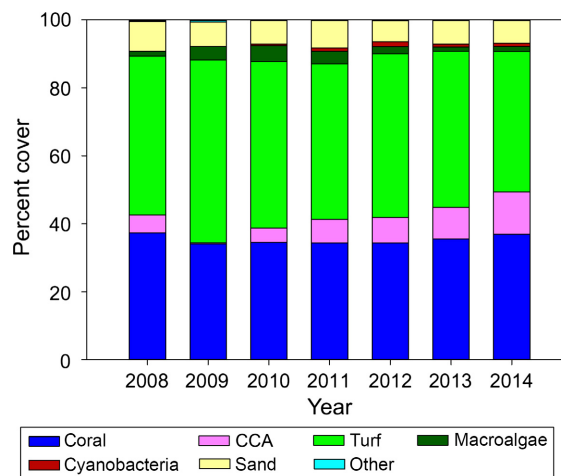


Fig. 1. Benthic community composition through time across all survey years. Turf and macroalgae cover for each season and year are used in the calculation of algal production. The 2009 surveys were completed a month after the Kahekili Herbivore Fisheries Management Area was legally established, but before signage or enforcement.  $n = 42$  (2008), 23 (2009), 21 (2010), 54 (2011), 40 (2012), 39 (2013), 40 (2014) per year.

Table 1. Growth rate, standing biomass, and average percent cover of algae measured at the Kahekili Herbivore Fisheries Management Area.

Species	Growth rate (g dry wt·m <sup>-2</sup> ·day <sup>-1</sup> ) (±SE)	Standing biomass† (g dry wt/m <sup>2</sup> ) (±SE)	Average percent cover (across all years)
Turf algae			
Mixed	0.0708 (±0.0164)	78.98 (±11.83)	46.9
Macroalgae			
All	...	51.49 (±17.92)	4.0
<i>Amansia glomerata</i>	0.0093 (±0.0021)	38.02 (±12.36)	0.9
<i>Tricleocarpa fragilis</i>	0.0003 (±0.0046)	<0.1	<0.1
<i>Acanthophora spicifera</i>	0.0229 (±0.0099)	<0.1	<0.1
<i>Ulva lactuca</i>	0.0341 (±0.0051)	<0.1	<0.1

Note: Data are averages for each measurement across all years and seasons of the study (2008–2014).

† Standing biomass assumes 100% coverage of given alga in a square meter.

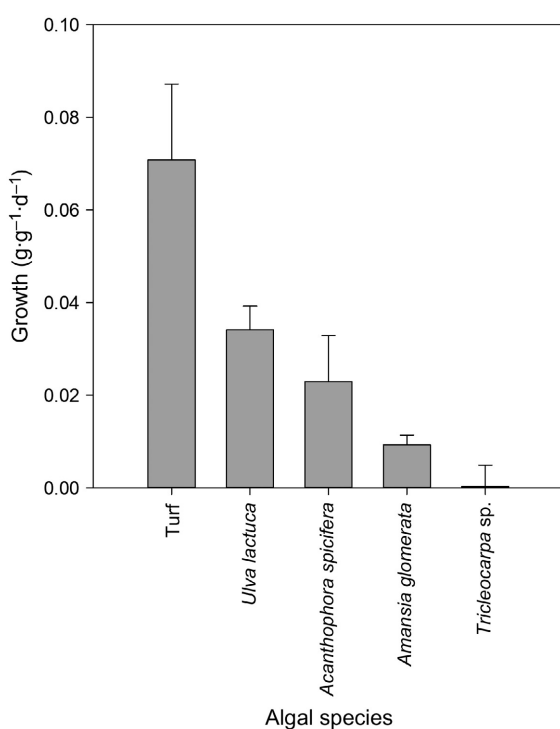


Fig. 2. Growth rates of turf algae and four species of macroalgae (g dry wt·g<sup>-1</sup> algae·day<sup>-1</sup>) at the Kahekili Herbivore Fisheries Management Area. Bars are SE. Turf algae,  $n = 22$ ; *Ulva lactuca*,  $n = 10$ ; *Acanthophora spicifera*,  $n = 9$ ; *Amansia glomerata*,  $n = 10$ ; *Tricleocarpa sp.*,  $n = 10$ ).

*Acanthophora spicifera* at 0.0229 (±0.0099), *Amansia glomerata* at 0.0093 (±0.0021), and *Tricleocarpa fragilis* at 0.0003 (±0.0046). Raw data from algal growth experiments, as opposed to means, are used in the calculation of algal growth below.

### Herbivore biomass

Total herbivore biomass fluctuated throughout the duration of the study (Fig. 3) with the highest biomass occurring in 2014 (19.7 g/m<sup>2</sup> ± 2.1 SE). Total herbivore biomass declined between 2009 (16.4 g/m<sup>2</sup> ± 2.4 SE; when the HFMA was designated) and 2010 (9.4 g/m<sup>2</sup> ± 1.1 SE). However, when considering the feeding guilds separately (Appendix S1: Table S2), scraper and grazer biomass increased from 2010 to 2014 while browser biomass fluctuated but remained lower than both scrapers and grazers through all years. While grazer biomass showed an increasing trend from 2010, there were more smaller-bodied fishes that make up this biomass than in 2008 and 2009 (Fig. 4). For scrapers, the increase in biomass from 2008 to 2014 was the result of more biomass in the larger size classes. Browser biomass remained low throughout the study years but with all size classes present in the last three years of the study.

### Herbivore grazing rates

Herbivore grazing rates varied across species of herbivores as well as for turf algae and macroalgae (Fig. 5). Grazer species had an overall higher grazing rate (with the exception of *Zebrasoma flavescens*) than scraper species, and both had higher average bite rates than all browser species.

### Herbivore bite size

Experimental and literature values for acanthurid and scarid bite sizes resulted in the following relationships between fish TL (cm) and BS (g of algae removed per bite). Acanthurid BS was defined (Appendix S1: Fig. S4A) as follows:

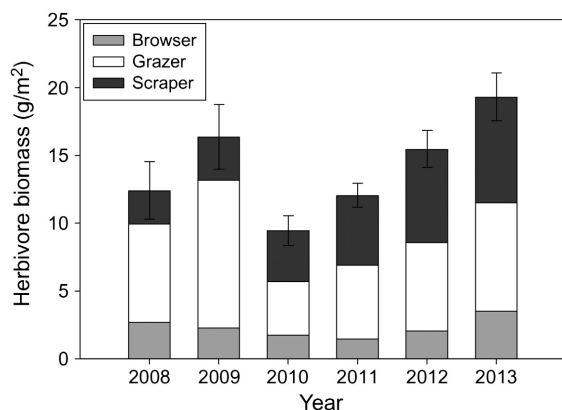


Fig. 3. Fish biomass through time across all survey years. Bars are SE for total herbivore biomass. The 2009 surveys were completed a month after the Kahekili Herbivore Fisheries Management Area was legally established, but before signage or enforcement.  $n = 42$  (2008), 23 (2009), 21 (2010), 54 (2011), 40 (2012), 39 (2013), 40 (2014) per year.

$$BS = 4 \times 10^{-8} \times (TL)^{3.3307} \quad (R^2 = 0.641).$$

Scarid BS was defined (Appendix S1: Fig. S4B) as follows:

$$BS = 5 \times 10^{-10} \times (TL)^{4.3744} \quad (R^2 = 0.831).$$

These equations defined bite size on both turf and macroalgae for these groups.

#### Overall algal growth and fish consumption budget

Based upon our modeled estimates, benthic algal biomass production (turf and macroalgae) was consistently greater than consumption of algal biomass by herbivorous fishes throughout the length of the study (Fig. 6A). Production ranged from the lowest mean value of  $1.9 \text{ g dry wt} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  in 2008 to the highest mean value of  $2.8 \text{ g dry wt} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  in 2012. Consumption ranged from a low mean value of  $0.5 \text{ g dry wt} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  in 2010 to a high mean value of  $1.7 \text{ g dry wt} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  in 2014. At any given time point, the lowest amount of production consumed by the herbivore assemblage was 20.8% in 2010 and the greatest amount of mean production consumed was 67.0% in 2014. In comparison with other studies with calculated production and consumption, these values lie within the breadth of values found on other reefs (Table 2; Appendix S1: Fig. S3). Throughout the years of

analysis at the KHFMA, mean net production (gross production—consumption) was  $>0$ , although not significantly so in 2008 and 2014 (95% CI included 0; Fig. 6B). However, if we used the Molokini Shoal herbivorous fish assemblage biomass data (including species-specific biomass and size classes of fishes) and compare grazing rates of this assemblage to algal biomass production at KHFMA in 2014 (Appendix S1: Table S1), mean net algal production is  $<0$  (Fig. 6B). This exercise showed that it is possible with existing Hawaiian herbivore assemblages to balance the consumption/production budget on KHFMA reefs.

Estimated total consumption rates by different size classes within each herbivore guild varied across years for both turf (Appendix S1: Fig. S5) and macroalgae (Appendix S1: Fig. S6) as a result of changes in abundance of size classes. There was a shift in the size class distribution for the scrapers such that the upper three size classes removed the most turf biomass in 2012 and 2013 (Appendix S1: Fig. S5). Mid-sized grazers removed the most turf biomass in early years, but over the last three years, the smaller size classes removed the greatest daily biomass of turf algae. Based upon our calculations, browsers removed very little turf biomass overall. In terms of macroalgal consumption, our data suggest that browser size classes fairly evenly removed macroalgal biomass (Appendix S1: Fig. S6). Small grazers also appeared important in macroalgal removal. Scrapers removed very little macroalgal biomass overall, and all size classes contributed equally.

## DISCUSSION

Our study assessed the balance of fleshy algal production and herbivorous fish consumption of algae through time at an HFMA. We used a novel approach to assess the potential changes in reef function as a result of herbivore protection by asking whether herbivorous fish consumption has increased in the HFMA through time. Over the first five years of the HFMA designation, we found that mean algal production continued to exceed herbivorous fish consumption; however, the magnitude of difference decreased from 2010 until 2014. When the fish assemblage data from Molokini MLCD were used in the model, mean net production was less than zero. These findings



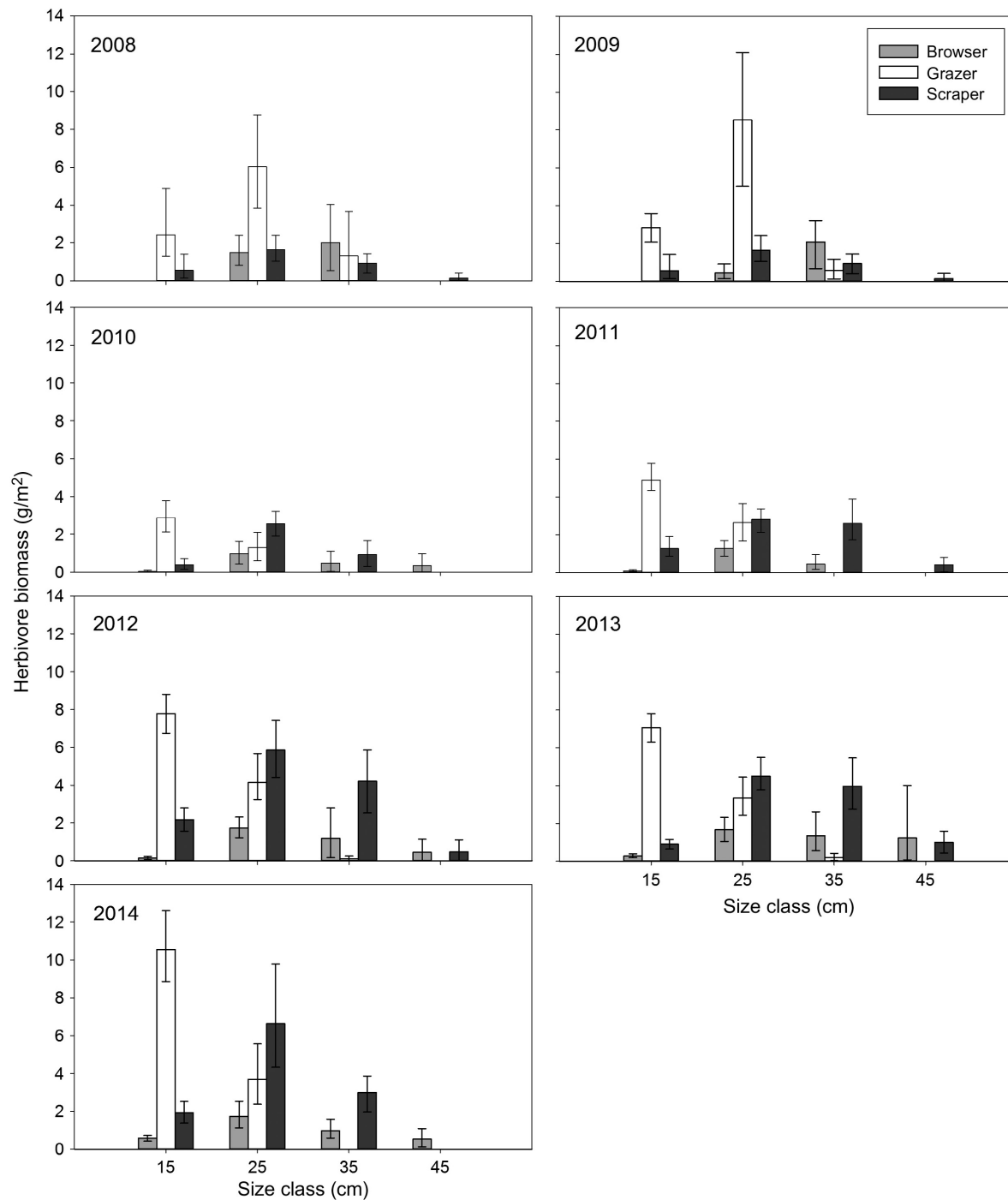


Fig. 4. Herbivore biomass per year broken into guilds and size classes. Bars are 95% confidence intervals. 2009 surveys were completed a month after the Kahekili Herbivore Fisheries Management Area was legally established, but before signage or enforcement.

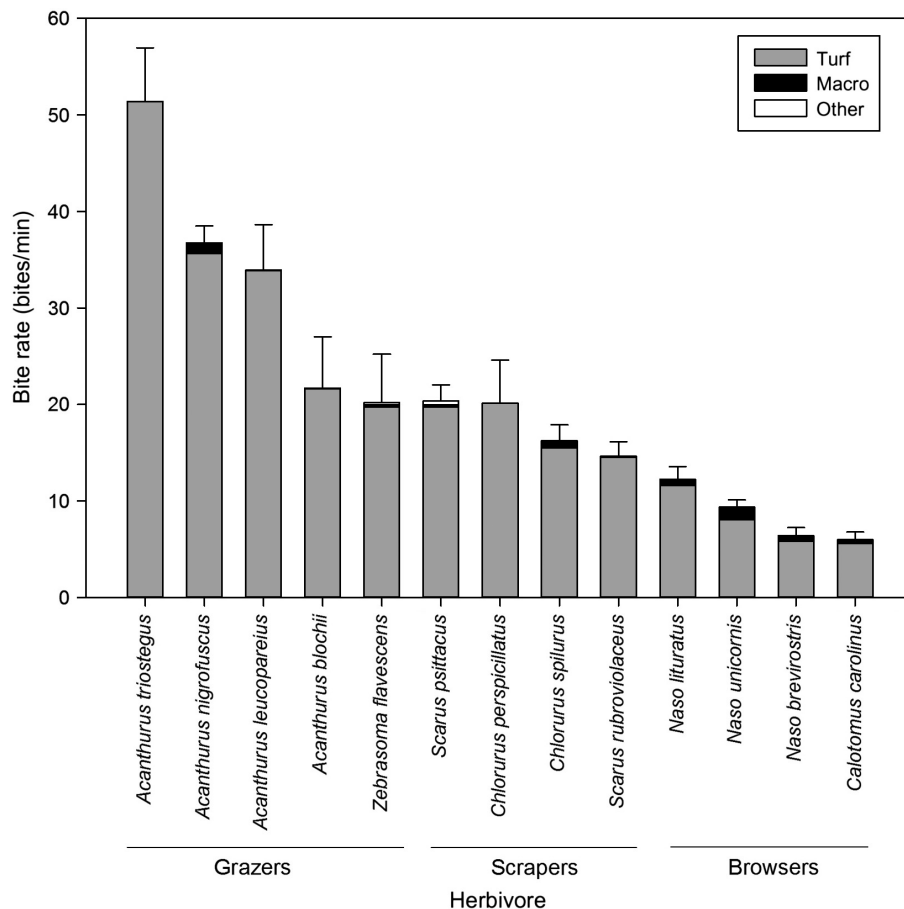


Fig. 5. Herbivore species mean bite rates on turf algae, macroalgae, and other substrates. Bars are SE.  $n = 10\text{--}64$ .

suggest that with further increases in fish abundance and biomass within the KHFMA to a level observed on long-term well-protected nearby reefs in Hawaii, consumption by the herbivorous fish assemblage could balance production at the reef.

In addition to small increases in consumption by the herbivorous fish assemblage through time, the composition of the major contributors to consumption shifted. Importantly, in the later years of the study, larger fishes from the scraper/excavator guild contributed more to consumption, particularly of turf algae, as a result of their increase in density in the fish assemblage (Appendix S1: Fig. S5). By scraping turf off the reef and exposing bare limestone, these fishes are known to promote crustose coralline algae (Belliveau and Paul 2002, Smith et al. 2010), an important reef builder (Smith et al. 2016) and substrate for coral larvae settlement (Price 2010,

O'Leary et al. 2012). Bonaldo and Bellwood (2009) have further demonstrated differences in bite impact across species within this guild and the subsequent importance of these differences in maintaining algae and sediment-free space on the reef. Therefore, the contributions of scrapers to grazing are not only important for the consumed biomass of fleshy benthic algae, but also for the broader "ecological fate" of each bite (Kelly et al. 2016) in opening space for recruitment by reef builders.

In contrast to the scrapers, browsers played a larger role in consumption of macroalgae than turf algae, though they removed more turf biomass than macroalgal biomass (Appendix S1: Figs. S5, S6) per observations of their feeding (Fig. 5). Grazers of the two smallest size classes played important roles in turf and macroalgal removal, likely a result of their high bite rates,

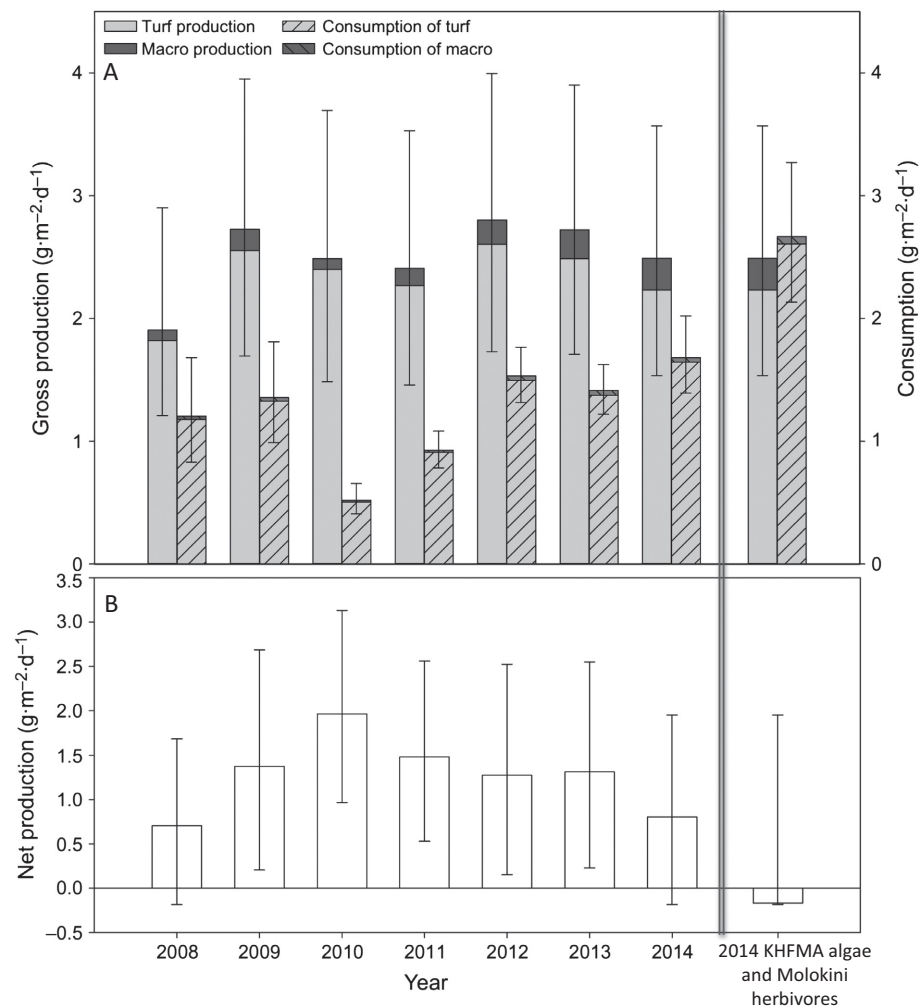


Fig. 6. (A) Estimated growth (solid bars) of macroalgae and turf algae ( $\text{g dry wt} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) and consumption (hashed bars) of macroalgae and turf algae ( $\text{g dry wt} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) by the herbivore assemblage from 2008 to 2014 and, after the black vertical line, using the herbivorous fish assemblage of Molokini Shoal reef. (B) Estimated net production of the algal community after accounting for consumption by the herbivores. Protection of Kahekili as an Herbivore Fisheries Management Area occurred in summer 2009. (C) Molokini's herbivorous fish assemblage can be used as a proxy for Kahekili in potential future years. Bars are 95% confidence intervals.

which exceeded those of both browsers and scrapers (Fig. 5). While the two smallest grazer size classes removed the most turf biomass of all fishes, their bites remove algal filaments without exposing bare limestone as those of scrapers do. The “ecological fate” of a bite from a small grazer is therefore to maintain productive turf algae. Thus, while our model focused on removal of algal biomass, there are additional dynamics to consider in how the herbivore assemblage shapes not just removal of fleshy algae but also what

will occupy the space from where a bite was taken.

Integrating the impact of all herbivores, we saw a higher proportion of algae consumed by the herbivorous fish assemblage in 2014 (67.0%) as compared to just after designated an HFMA in 2010 (20.8%; Fig. 6B). There were two important benthic responses to this increased grazing. First, there was an increase in CCA from 2008 to 2014 from 0.3% to 9.2% (see Williams et al. 2016 for further details). Secondly, turf algae cover

Table 2. Comparison across studies that have measured benthic fleshy algal production and consumption by herbivores.

Study	Location	Mean production rate (g c·m <sup>-2</sup> ·day <sup>-1</sup> )	Mean consumption rate (g c·m <sup>-2</sup> ·day <sup>-1</sup> )	Percentage of production consumed
Hawaii				
This study	Maui	0.63–0.68	0.34–0.42	20.8–67.0
Caribbean				
Paddock et al. (2006)	Florida Keys	1.05	0.34–0.76	31–77
van Rooij et al. (1998)	Bonaire	1.46–1.86	1.74	101
Carpenter (1986)	St. Croix	1.58–3.11	2.5	97
Kopp et al. (2010)	Guadeloupe	0.35–0.95	0.1–0.7	27–200
Great Barrier Reef				
Russ (2003)	Myrmdon	0.2–1.8	0.2–2.1	38–100
Klump and Polunin (1990)	Davies	1.11–2.51	0.57–1.13	42–72
Hatcher (1981)	One Tree Reef	0.61–0.97	0.40–0.79	61–290

Note: For comparison to other studies, dry weight calculations in this study were converted to g C by assuming g C = 0.25 × g dry wt algae.

declined from 53.8% to 41.2% over this same period. That said, the magnitude of these two changes did not match the magnitude of the change in proportion of production consumed. We believe two factors were at play here. First, increasing grazing intensity on the reef may have resulted in increased productivity of fleshy algae, particularly turf algae (on reefs: Carpenter 1986, in grasslands: Westlake 1963, McNaughton 1979), which could have delayed a corresponding change in turf algae cover. Secondly, the functional group “turf algae” is a very broad category and a relatively small change in cover might have under-represented a potentially larger change in turf biomass if turfs were more heavily cropped turfs on average. Turf height was not examined in this study but could serve as a helpful metric in future work (as in Harris et al. 2015). A dynamic model in future studies utilizing the in situ rates provided in this study would further illuminate benthic response to increased grazing pressure.

Importantly, some of the production not consumed in our model would undoubtedly have been converted to detritus (Hatcher 1990), exported off the reef (Hamner and Hauri 1981), or consumed by other organisms. The sea urchin assemblage is known to be major a contributor to algal grazing on reefs (Ogden and Lobel 1978, Mumby 2006, Sandin and McNamara 2012), but urchin grazing was not assessed here. Sea urchins have also been shown to exhibit species-specific preferences for different algal species and

functional groups (Stimson et al. 2007, Lewis et al., *unpublished data*), though their influence relative to herbivorous fishes can certainly vary (McClanahan et al. 1996). Further, our grazing budget considers only herbivores observed on the reef within the fish families protected by the KHFMA. The impact of some species from these families (e.g., *Ctenochaetus strigosus* and *Acanthurus olivaceus*) is still debated (Marshall and Mumby 2012, Tebbett et al. 2017), as these species are often classified as detritivores but are known to also remove some algal filaments (Choat et al. 2002, Kelly et al. 2016). These species likely have interesting non-linear impacts on fleshy algal dynamics via reduced algal shading by removal of detritus, which may increase algal productivity, as well as contributing to turf algal grazing via incidental consumption of algal filaments. In the interest of being conservative in our approach to estimating consumption, since a “balanced budget” of production and consumption would signal success of the HFMA management, and given the uncertainty in the impact of *C. strigosus* and *A. olivaceus*, we have excluded these species from the analysis. We also did not include territorial damselfishes or omnivorous fishes, including triggerfish such as *Melichthys niger*, one of the more abundant triggerfishes within the KHFMA (Williams et al. 2016) and known to consume benthic algae in some contexts. While these species were not within the goal of this study (given that the management measures do not provide explicit protection for



these taxa), further research is needed to better understand their ecological role on reefs including the KHFMA.

Other studies that have calculated production and consumption on reefs through a variety of methods and on a variety of reef types have seen similar results to those reported here in proportion to benthic cover and herbivorous fish biomass (Table 2; Appendix S1: Table S3). On reefs with <10% coral and high algal cover in the Florida Keys, mean production was two times our estimates from KHFMA (1.05 vs. 0.48–0.70; Paddack et al. 2006), while KHFMA has three times the amount of coral cover and proportionally less fleshy algae. Meanwhile, herbivore fish biomass in the Florida Keys sites was 3–10 times that of the KHFMA and mean consumption rates were equivalent to 1.5 times the KHFMA rates, perhaps a result of different species and size class distributions within the herbivore communities. On high coral-cover reefs in the Caribbean (Wanders 1976, Carpenter 1986), production was 3–5 times that of the KHFMA despite having a smaller proportion of the benthos being covered by algae. These patterns are likely the result of higher growth rates of algae in the Caribbean (Roff and Mumby 2012) as well as the potential for high growth rates of algae subjected to intense grazing (Westlake 1963).

Consumption patterns on other reefs intuitively also vary with herbivore biomass, though herbivore community composition invariably can and does alter this relationship. Our estimates of total consumption by the herbivore community of benthic fleshy algal production were on the low end of the spectrum when comparing to other studies (Table 2; Appendix S1: Table S3). However, total fish biomass at the KHFMA was also on the low end of biomass estimates of these other studies, which in many cases were no-take areas or remote reefs, and consumption in this study was proportional to biomass as compared to other studies (Appendix S1: Fig. S3). Placing the KHFMA in a global context, both total herbivore biomass and biomass of individual herbivore guilds in 2014 were similar to the global mean for each of these metrics at fisheries accessible coral reefs (global mean = 20.5 g/m<sup>2</sup>; scraper = 9.5 g/m<sup>2</sup>; browser = 2.0 g/m<sup>2</sup>; grazer = 17.5 g/m<sup>2</sup>; Edwards et al. 2014). This level of herbivore biomass remains less than half the biomass found on reefs not

accessible to fishing in the Main Hawaiian Islands (MHI; ~40 g/m<sup>2</sup>; Edwards et al. 2014). On low coral-cover reefs (<10%), even a return of herbivore biomass to historically equivalent populations may not be enough to reverse phase shifts given the high algal standing stock now present on many reefs (Paddack et al. 2006). With >30% coral cover, after 5 yr of herbivore protection KHFMA was already showing signs of declining consistent with herbivore control on net algal production (Fig. 6B). These patterns are corroborated by recent findings showing an increasing cover of CCA and decreasing cover of turf algae (Williams et al. 2016). Thus, if herbivorous fish biomass becomes more similar to other Hawaiian protected areas such as the Molokini MLCD, consumption will likely become sufficient to control algal production and ultimately reduce algal standing stock (Fig. 6C).

There are important assumptions and caveats in using data from Molokini MLCD in this study. Importantly, this offshore reef is not exposed to the same nutrient and sediment loading that the nearshore KHFMA reef experiences (Dailer et al. 2010, Swarzenski et al. 2012) and benthic community composition differs (Rodgers et al. 2015). However, the use of Molokini herbivorous fish biomass is intended to provide an example of potential herbivore biomass for the KHFMA using a nearby reef with long-term protection. While fish biomass at the KHFMA in recent years has appeared to asymptote in the last two years (Williams et al. 2016), this is largely understood to be a result of poaching within the KHFMA, rather than indicating that the carrying capacity of the reef has been reached. Therefore, from an ecological standpoint, parrotfishes and surgeonfishes at KHFMA are probably not limited by the system itself, but rather by ongoing harvesting. That being said, it likely will not be possible for the KHFMA herbivore biomass to substantially increase beyond current levels without a meaningful reduction in the levels of poaching.

Given that herbivores consumed 67% of algal production in 2014 within the KHFMA (Fig. 6B), we suggest that herbivorous fish biomass will need to continue to increase to reduce algal biomass and ultimately reduce algal cover. Reefs in the MHI that are not accessible to fishing with herbivore biomass of 40 g/m<sup>2</sup> (Edwards et al. 2014) may be reasonable medium-term goals for

herbivore biomass at KHFMA with continued herbivore management into the future. The results of the production–consumption budget for the KHFMA calculated with the 2014 herbivore assemblage data from the Molokini MLCD support this, providing a potential future scenario for the KHFMA using an ecosystem that has been protected for decades.

Our approach here incorporates functional roles of benthic cover and the fish assemblage, and by projecting fish biomass into the future, provides support for the potential of herbivore protection in balancing production and consumption within the KHFMA. By using these rates, we may be able to begin estimating how many and what type of herbivores are needed to elicit strong top-down control on algal communities. While herbivore management is currently promoted as a strategy to reduce algal overgrowth of corals, we need more tools to be able to predict management and set targets for the herbivore assemblages. These targets will be directly related to the benthic community structure of a given reef community and the production of the algal community.

Across terrestrial and marine ecosystems, a mass balance calculation for primary production and consumption by grazers can inform management efforts as to the deficit or excess in grazing in a system and provide a target window for ecosystem restoration. For coral reefs, the KHFMA and other herbivore protected areas around the world provide a unique new opportunity to manage a key ecosystem service, grazing, without completely eliminating fishing and have shown exciting positive results thus far. It is our hope that the framework provided in this study is used in other locations to begin to understand and estimate how many and what types of herbivorous fishes are needed to control algal abundance on a given reef. Herbivore management is an approach that can be used for both maintaining healthy reef ecosystems as well as for restoration and should be used more broadly for reef conservation.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1899/full>