ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems

Mae Rennick[1] | Bartholomew P. DiFiore[1] | Joseph Curtis[1] | Daniel C. Reed[2] | Adrian C. Stier[1,2]

[1]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California, USA

[2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California, USA

Correspondence
Mae Rennick
Email: maerennick@ucsb.edu

Abstract

Herbivores can reach extraordinary abundances in many ecosystems. When herbivore abundance is high, heavy grazing can severely defoliate primary producers and, in some cases, even drive ecosystem to undergo regime shifts from a high productivity state to a denuded, low productivity state. While the phenomenon of herbivore-driven regime shifts is well documented, we only partially understand the mechanisms underlying these events. Here, we combine herbivory experiments with 21 years of long-term monitoring data of kelp forest ecosystems to test the hypothesis that herbivores drive regime shifts when herbivory exceeds primary production. To test this hypothesis, we quantified how the foraging habits of an important group of marine herbivores—sea urchins—change with increases in sea urchin biomass and trigger regime shifts to a foundation species, giant kelp (*Macrocystis pyrifera*). Using experiments, we quantified how the grazing capacity of urchins increases as urchin biomass increases, then we combined these estimates of urchin grazing capacity with estimates of kelp production to predict when and where urchin grazing capacity exceeded kelp production. When grazing capacity exceeded kelp production, sea urchins caused a 50-fold reduction in giant kelp biomass. Our findings support the hypothesis that the balance between herbivory and production underlies herbivore-driven regime shifts in Southern California kelp forests and provides insight into when and where urchins are likely to force regime shifts in kelp forest ecosystems.

KEYWORDS
consumption, density dependence, detritus, ecosystem transition, herbivore, kelp

INTRODUCTION

Intense foraging by primary consumers can fundamentally alter the structure and function of communities

Mae Rennick and Bartholomew P. DiFiore contributed equally to this manuscript.

(Silliman et al., 2013). For instance, outbreaks of herbivorous insects can defoliate forests across thousands of square kilometers (Kautz et al., 2016), grazing by ungulates can denude landscapes (Hopcraft et al., 2010), and predation by sea stars can lead to widespread mortality of reef building corals (Holbrook et al., 2018). In extreme cases, consumers can eliminate the dominant primary

https://onlinelibrary.wiley.com/r/ecy

producers in a community, reducing productivity and leaving only producers that are resistant to foraging (Augustine & McNaughton, 1998). Consumer-driven changes in community structure are often persistent, such that even when consumer abundance decreases, the community remains in an alternative state (Schröder et al., 2005). Yet, high consumer density does not always trigger alternative ecosystem states. Some locations can support high biomass of consumers, while others undergo rapid shifts at relatively low consumer biomass. The mechanism underlying variability in when and where consumers drive shifts into alternative community states remains an active area of research. Resolving this context dependency is critical to understanding ecosystem tipping points and to avoid crossing biological thresholds to alternative states that provide fewer services to people and nature.

In principle, consumer-driven shifts to alternative states occur when consumption exceeds resource production. Predicting when and where consumption exceeds production requires an understanding of how consumer foraging behavior and per-capita consumption rates shift with consumer density. The relationship between consumer density and per-capita consumption can take three plausible forms (Klemmer et al., 2012). First, increases in consumer density can have no effect on per-capita consumption, such that the collective consumption rate of a population increases linearly with consumer density (Reice, 1991). Second, interference or competition among consumers as consumer density increases can cause per-capita consumption to decline. At the population-scale, competition can cause consumption to increase at a decelerating rate with density, because competition is weaker at low densities and stronger at high densities (Arditi & Ginzburg, 1989; Brook & Bradshaw, 2006; Little et al., 2020). Finally, facilitation among consumers can cause per-capita consumption to increase as consumer density increases. In this case, the collective consumption rate of a group might accelerate exponentially or sigmoidally with consumer density (McKie et al., 2009; Sommer, 1992). When the relationship between consumer density and per-capita consumption is constant or positive, there is a higher probability that increases in consumer density will cause large reductions in primary producers because consumers are not limited by intraspecific competition. However, the extent to which constant or positive increases in foraging with consumer density are common in consumer-driven disturbances remains unclear, particularly in ecosystems that are prone to alternative states.

Here, we quantify how the relationship between consumer biomass and consumer foraging rates drives when and where kelp forest ecosystems undergo shifts to alternative states. Temperate rocky reefs characterized by kelp, a group of canopy-forming brown macroalgae that form productive subtidal "forests," are known to experience abrupt changes from kelp-dominated communities to communities with little to no kelp (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015). An important factor causing such state shifts is intensive grazing by sea urchins, which has been linked to massive declines in kelp abundance and the formation of urchin-dominated states, known as urchin barrens, that can persist for decades (Lawrence, 1975; Sala et al., 1998; Spindel et al., 2021). Urchin barrens occur on shallow rocky reefs worldwide and are characterized by herbivore-resistant algal species (Ling & Johnson, 2009) that display lower net primary productivity and biodiversity than kelp-dominated sites (Steneck et al., 2002). In theory, kelp deforestation should result when the consumption rate of an urchin population exceeds kelp production. Increases in the consumption rate can occur due to increases in urchin density, such as when top-down control by urchin predators is reduced or urchin recruitment to a site is high. Alternatively, kelp production can vary independently of urchins due to temperature (Wernberg et al., 2016), wave disturbance (Dayton & Tegner, 1984; Reed et al., 2011), and nutrient availability (Bell et al., 2015). Across temperate rocky reefs, kelp abundance can be high even when urchin abundance is high and changes in urchin abundance do not result in proportional declines in kelp (Ling et al., 2015), suggesting that when and where urchins deforest kelp communities depends on the balance between kelp production and how much kelp urchins consume at a given urchin biomass.

One long-standing hypothesis for why urchin populations switch from coexisting with kelp to deforesting kelp is a shift in foraging behavior (Harrold & Reed, 1985). Urchins are notably omnivorous, foraging on kelp, pieces of kelp detached from the substrate (e.g., detritus), other algal species, invertebrates (e.g., salps or tubeworms, Duggins, 1981; Spindel et al., 2021), or calcareous reef structures (Rasher et al., 2020). The leading hypothesis is that urchins passively forage on kelp detritus until a change in kelp production causes urchins to actively graze canopy-forming kelps attached to the substrate (from this point forwards "standing" kelp, *sensu* Kriegisch et al., 2019). However, variation in urchin foraging rates with changes in urchin biomass could interact with shifts in the availability of detritus to result in kelp deforestation. For instance, if urchin foraging rates are invariant with urchin biomass and urchin biomass is high, then slight declines in detrital production in a kelp community could cause urchins to actively graze standing kelp. Yet, if urchins increase their per-capita feeding rates through facilitation—as may occur in grazing fronts (Dean et al., 1984; Ling et al., 2019)—then

small changes in urchin biomass at a threshold might result in deforestation without a change in detrital production.

In this study, we tested how the relationship between density-dependent foraging rates and primary production alters a community's resistance to consumer-driven changes in community state using California rocky reefs dominated by *Macrocystis pyrifera* (from this point forwards, "kelp") as a model system. We first investigated how the foraging rate of urchins varied with urchin biomass using mesocosm foraging experiments. We coupled these experimental results with 21 years of spatially explicit data on kelp community dynamics to hindcast rates of detrital production and consumption. Finally, we tested the long-standing hypothesis that production of kelp detritus suppresses deforestation by quantifying how the relationship between detrital supply and predicted urchin consumption alters the dynamics of standing kelp biomass. Our results confirmed that the balance between detrital supply and urchin foraging mediates alternative states on temperate rocky reefs and builds a mechanistic understanding of how density-dependent foraging and primary production can interact to cause consumer-driven disturbances.

METHODS

Grazing experiment: How does foraging rate vary with urchin biomass?

We conducted laboratory mesocosm experiments during May–August 2019 to estimate detrital kelp grazing rates by red (*Mesocentrotus franciscanus*) and purple (*Strongylocentrotus purpuratus*) sea urchins across ranges of urchin biomass that spanned kelp- and urchin-dominated ecosystem states. To select density treatments, we characterized purple and red urchin densities in the Santa Barbara Channel, using 21 years of observational data collected by the Santa Barbara Coastal Long-Term Ecological Research program (SBC LTER, please refer to the section "*Observational data*" for details). Based on the resulting density ranges, we selected eight abundances for purple urchins (2, 3, 7, 11, 19, 22, 24, 44 individuals arena^{-1}; 1.6 m^2 arena) and six abundances for red urchins (1, 2, 3, 5, 7, 12 individuals arena^{-1}). We collected urchins of varying size using SCUBA from coastal kelp forests in the Santa Barbara Channel (California, USA), such that the collected pool of urchins approximated the 95% confidence intervals of the observed size frequency distribution of each species (Appendix S1: Figure S1). To assign urchins into density treatments, we drew from the pool of collected urchins so that urchin size varied randomly, and then measured the wet weight of each urchin (± 0.1 g) to

calculate the total biomass in a trial. Total biomass in trials ranged from 63.6–1851.9 g·m^{-2} for purple urchins and 90.7–1771.3 g·m^{-2} for red urchins. These ranges included the Ling et al. (2015) threshold associated with nonlinear reductions in macroalgae (668 $\pm$ 115 g·m^{-2}), and approached the maximum urchin biomass observed at local urchin-dominated sites (2038 g·m^{-2}).

We maintained experimental urchins in 400 L laboratory mesocosms with a continuous flow of ambient seawater at ~7 L min^{-1} (14.5 $\pm$ 0.01°C, X $\pm$ SE unless otherwise specified). We divided mesocosms into two experimental units separated by a permeable barrier, resulting in 37 arenas with 1.6 m^2 of accessible surface space (submerged vertical walls and bottom) for urchins. In preliminary trials the barrier did not lead to differences in oxygen saturation or temperature and we found no evidence for systematic differences in foraging rates by tank side (Tukey's post hoc: $p > 0.05$ for all comparisons).

Over a 9-week period, we conducted foraging trials to specifically estimate urchin foraging rates on mature kelp blades. Kelp detritus available to urchins in natural settings can consist of fronds or blades detached from the substrate in various stages of degradation. However, we collected mature kelp blades from kelp fronds attached to the substrate that were free from epiphytes, to standardize the degradation state of the blades. We replicated each urchin density treatment four times for purple urchins and three times for red urchins. Prior to initiating a trial, we fed urchins ad libitum for at least 8 days. We then randomly assigned density treatments to foraging arenas and starved the urchins for 5 days, long enough to ensure gut passage while avoiding acute effects of starvation (Guillou et al., 2000). To initiate a grazing trial, we added 250 g of kelp to each arena, an amount that in preliminary trials allowed ample forage even at the highest urchin densities. We spun kelp blades for 5 s in a salad spinner to remove water on the surface of the blades and divided kelp into 25 pieces to standardize measures and blade size. We allowed purple urchins to graze for 48 h and red urchins to forage for 96 h, because in preliminary trials red urchins exhibited comparatively slower foraging rates. At the end of each trial, we measured the amount of kelp consumed by spinning and weighing the remaining kelp following the same procedure (data available from Santa Barbara Coastal LTER; DiFiore, et al., 2021).

Per-capita consumption is well known to increase with consumer size (Rall et al., 2012). It is possible that the effect of biomass on consumption rate was confounded by the random size of urchins allocated into a trial, particularly in trials with low urchin density. To determine how body size impacted consumption rates, we conducted foraging trials in which we manipulated urchin size class at constant densities. However, analysis of the

size data suggested that the trials in which we manipulated density by sampling differently sized urchins were largely unaffected by random variation in body size (please refer to Appendix S1 for full discussion). Therefore, for simplicity we focused on the relationship between consumer biomass (g m^{-2}) and foraging rate, making the explicit assumption that foraging rate is constant per unit mass of consumer (e.g., a small urchin and a large urchin consume the same amount per unit body mass).

In control trials without urchins, we found that kelp degradation over 96 h was minimal relative to the accuracy of estimating the weight of kelp (~±2% error). There was evidence of urchin mortality in 5 of the 50 grazing trials, with an average mortality of <1% of the trial population. One trial experienced 15% mortality, but exclusion of this trial from future analyses did not qualitatively change results.

The objective of the laboratory feeding experiments was to test between three alternative hypotheses for the relationship between grazing rate and biomass. The consumption rate of a population of urchin may increase in proportion to biomass, resulting in a linear relationship between consumption and biomass (H_1). However, if urchins interfere with one another at high biomass, then increases in urchin biomass should result in total consumption rates increasing at a decelerating rate (H_2). Alternatively, if increases in urchin biomass heighten the probability that any one urchin passively encounters kelp detritus, thereby allowing its neighbors to benefit, then total consumption rate will increase at an accelerating rate (H_3).

To distinguish between these alternative hypotheses, we compared the fit of three different models to the mesocosm foraging data. A linear relationship between urchin biomass and consumption rate would support H_1. If consumption increased at a decelerating rate (H_2), then the data should follow a power-law function with an exponent <1. Alternatively, if consumption increased at an increasing rate (H_3), then the data should follow a power-law function with an exponent >1. However, urchins may not facilitate conspecific foraging across all biomasses. Therefore, we also fitted a phenomenological formulation of a sigmoid curve that allowed accelerating then decelerating grazing rates across certain ranges of density. Specifically, we fitted:

$$G_i = \frac{aB_i^2}{b^2 + B_i^2} \qquad (1)$$

where G_i is the observed consumption rate (g$_k$ m^{-2} day^{-1}), B_i is the biomass (g$_u$ m^{-2}) of urchins in trial i,

a represents the grazing rate at asymptotic biomasses (g$_u$ m^{-2} day^{-1}) and b is the urchin biomass (g$_u$ m^{-2}) at the half-maximum of the function (Bolker, 2008), where k and u refer to kelp and urchin respectively. For the linear model, we fixed the y-intercept at zero because there cannot be consumption without consumers. We compared the fit of each model (linear, power-law, and sigmoidal) using Akaike's information criterion (AIC; Aho et al., 2014; Akaike, 1973).

Observational data: How might historical foraging rates have varied across space and through time?

Our second objective was to hindcast urchin foraging rates using historical data on urchin biomass and our experimental estimate of the relationship between urchin biomass and foraging rate. The SBC LTER has conducted annual community surveys at nine sites in the Santa Barbara Channel since 2000. Specifically, researchers monitor the frond density of giant kelp along 40 × 2 m transects, which is converted to biomass based on established regression relationships (Santa Barbara Coastal LTER, Reed, et al., 2021) The SBC LTER also estimates the biomass of purple and red urchins, by averaging the number and test diameter of individuals encountered in six fixed quadrats (1 m^2) positioned along each transect. We applied our experimentally derived relationship between foraging rate and urchin biomass to this time series of red and purple urchin biomass to estimate how much kelp could have been consumed by each species. We refer to these estimates as the predicted consumptive capacity (*sensu* Stevenson et al., 2016) of urchin populations to distinguish them from actual in situ measures of kelp consumption that were not measured.

Modeling: To what extent does detritus mediate consumer-driven disturbances to kelp?

Our final objective was to test the hypothesis that declines in standing kelp biomass occur when urchin foraging exceeds detrital production (e.g., Harrold & Reed, 1985). To test this hypothesis, we combined predicted consumptive capacity with estimates of detrital supply calculated from monthly observations of kelp biomass dynamics collected by the SBC LTER at three of the nine sites (Santa Barbara Coastal LTER; Rassweiler, et al., 2021). This time series includes monthly estimates of the proportion of biomass lost as fronds and blades from attached plants growing in fixed plots. We used these

data to calculate the average proportion of the standing biomass of kelp lost as blades and fronds per day in summer from 2002–2020 at three sites. We multiplied the sum of these two loss rates by the summer standing biomass of giant kelp at each of transects where urchin biomass was measured in order to determine detrital supply at each of the transects at all nine sites. We found no evidence that the proportion of biomass lost as fronds and blades varied with standing kelp biomass or temperature (Appendix S2: Figure S1). In California, the number of blades growing at different depths is approximately the same (Clendenning, 1963) suggesting that the total fraction of biomass lost should not change with depth. In our calculation of detrital supply, we assume that all biomass lost is immediately available as detritus on the seafloor. In reality, some proportion of detrital biomass will be exported. Therefore, our estimate is likely to represent maximum detrital supply, and is conservative, as detrital supply is likely to be lower than our estimate (please refer to Appendix S2 for more details on methodology).

We used a generalized linear mixed effects model to test if the relationship between standing kelp biomass and urchin biomass was contingent on whether grazing rates exceeded detrital supply. We treated kelp biomass as the response variable and included two predictor variables as fixed effects: (1) urchin biomass, a continuous predictor, and (2) a categorical covariate encoding when consumptive capacity exceeded detrital supply (i.e., grazing > detritus). We included site and year as random intercept effects to account for the structure of the data. We assumed that sites were spatially independent, as the distance between them was greater than the scale of spatial synchrony in kelp biomass dynamics (Cavanaugh et al., 2013). In our model, a significant interaction between urchin biomass and the grazing covariate would suggest that the effects of urchins on kelp depended on whether detrital biomass exceeded consumptive capacity. A main effect of urchin biomass or the overgrazing covariate would suggest that these factors operate independently (i.e., either the biomass of urchins is what matters alone, or the amount of grazing relative to detrital biomass matters alone). Considering that biomass cannot be negative, we used a gamma distribution with log-link and added one to all kelp biomass estimates to account for zeros that could not be modeled with a gamma distribution.

The model described above focuses on the instantaneous relationship between urchin biomass and kelp biomass at a given site-time combination. However, community processes (e.g., detrital supply, consumption rate) are dynamic and may more accurately describe changes in kelp biomass between time points versus instantaneous measures of biomass. Therefore, we also modeled the annual change in kelp biomass at each site (s) in year (t) ($\Delta K = K_{s,t} - K_{s,t-1}$) as a function of the rate of detrital supply relative to consumptive capacity. Specifically, we estimated the proportional difference between grazing (G) and detrital supply (D), as $\frac{G_{s,t} - D_{s,t}}{G_{s,t} + D_{s,t}}$. We used a linear mixed effects model that included random effects of site and year to predict the annual change in kelp as a function of the proportional difference between grazing and detrital supply.

We conducted all analyses in R version 4.0.4 (R Core Team, 2021). We considered a parameter to be significant at $\alpha < 0.05$. For all models, we assessed if the residuals conformed to the assumed error distribution and tested for heteroscedasticity by comparing residuals and predictor variables (Harrison et al., 2018). When there was evidence for heteroscedasticity we log-transformed predictor variables. In mixed effects models, we estimated confidence intervals conditional on fixed effects and estimated p-values via the Satterthwaite's degrees of freedom method using the *lmerTest* package and confirmed significance using likelihood ratio tests (Kuznetsova et al., 2017; Zuur et al., 2009).

RESULTS

Over the last 21 years, urchin biomass in the Santa Barbara Channel has displayed considerable variation in time and space. Our experiments showed that grazing increased linearly with consumer biomass for both purple and red urchins. When applying the biomass grazing relationships developed from the mesocosm experiment to hindcast grazing rates at SBC LTER study sites, we found that—like urchin biomass—historical kelp consumption is likely to have varied considerably. Moreover, by merging our estimates of grazing with predictions of detrital kelp supply, our study offers new insights into when and where we expect urchins to deforest kelp and produce barrens.

Urchin biomass varied by species across nine kelp forest sites from 2000 to 2020 (Figure 1). At a given transect, purple urchin biomass tended to be greater on average than red urchin biomass (purple: 200.3 ± 0.4 g m^{-2}, red: 114.5 ± 0.3 g m^{-2}; ANOVA: $F_{1,1534} = 38.8$, $p < 0.001$; Figure 1a), largely due to their 10-fold higher average density (purple: 9.4 ± 0.02 ind. m^{-2}, red: 0.9 ± 0.002 ind. m^{-2}; ANOVA: $F_{1,1534} = 203.3$, $p < 0.001$). Urchin biomass has generally declined since 2000, with a peak between 2009 and 2014, although there is evidence for a recent increase at some sites (Figure 1b).

The total biomass of kelp consumed by urchins (i.e., consumptive capacity) in mesocosm experiments increased linearly with urchin biomass for both purple
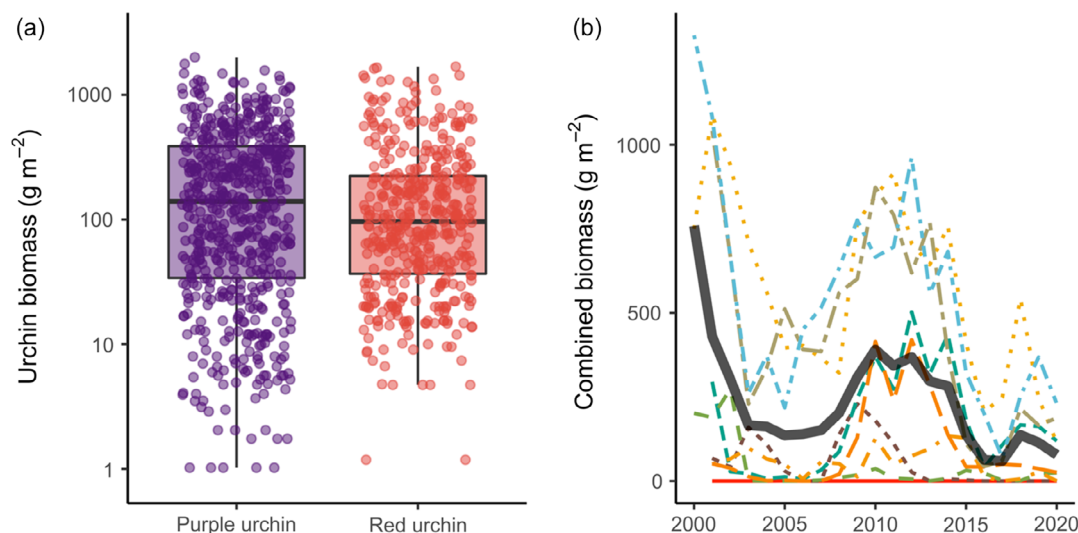
FIGURE 1 (a) Variation in biomass for purple (*Strongylocentrotus purpuratus*) and red (*Mesocentrotus franciscanus*) sea urchins across 21 years in the Santa Barbara Channel. (b) Total urchin biomass varied between sites and across years. Colored lines represent combined urchin biomass for nine sites averaged across transects. Black line represents the average biomass across all sites
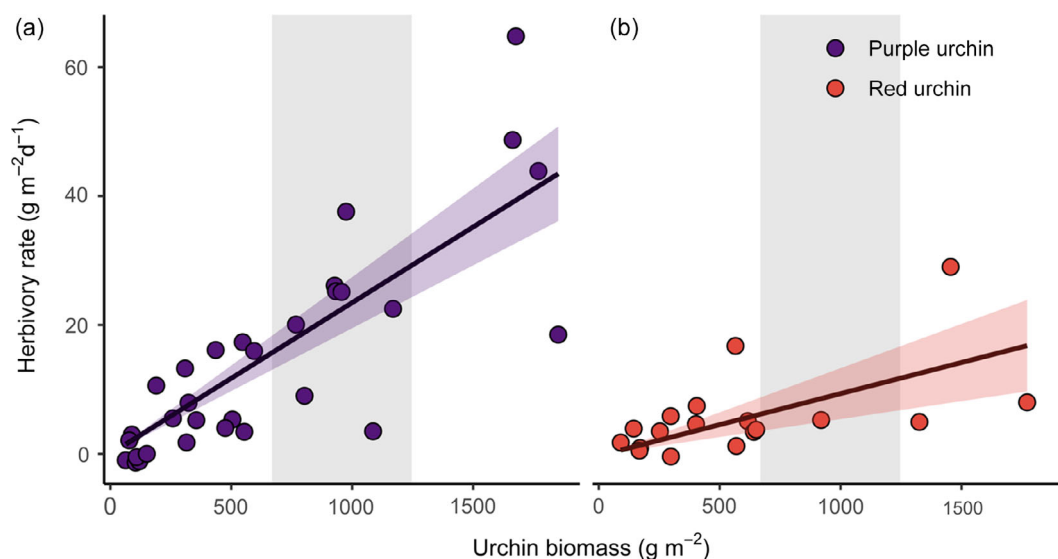

FIGURE 2 Experimental consumption rate of kelp blades by purple (a) and red (b) urchins in mesocosm foraging trials. The gray polygons represent the range of biomass that previous research has identified as possible thresholds leading to urchin-dominated community states (e.g., urchin barrens). The lower end of the range is the global average across temperate kelp forest communities (Ling et al., 2015), while the upper range is the threshold biomass for California kelp forests (Dean et al., 1984)

and red urchins (Figure 2; purple: $\beta = 0.02 \pm 0.002$, $p < 0.001$, $R^2 = 0.82$; red: $\beta = 0.0091 \pm 0.002$, $p < 0.001$, $r^2 = 0.59$). We found no evidence for a nonlinear relationship between urchin biomass and consumptive capacity. AIC comparison suggested nearly equivalent fits of linear, power-law, and sigmoid relationships for both species (ΔAIC < 2.5; Appendix S3: Tables S1, S2). However, there was no evidence of a positive or negative slope in the relationship between per-capita consumption rate and urchin biomass (Appendix S3: Figure S1; purple: $p = 0.43$, $R^2 = 0.04$; red: $p = 0.14$, $R^2 = 0.07$), suggesting that a linear relationship is the most parsimonious explanation of how population-scale foraging rates change with urchin biomass. Considering the experimental evidence that foraging rates increase linearly with urchin biomass, consumptive capacity varied in direct proportion with urchin biomass (Figure 3). There was more variation in consumptive capacity across space than through time (CV$_{time}$ = 1.29 ± 0.34, CV$_{space}$ = 1.96 ± 1.72).
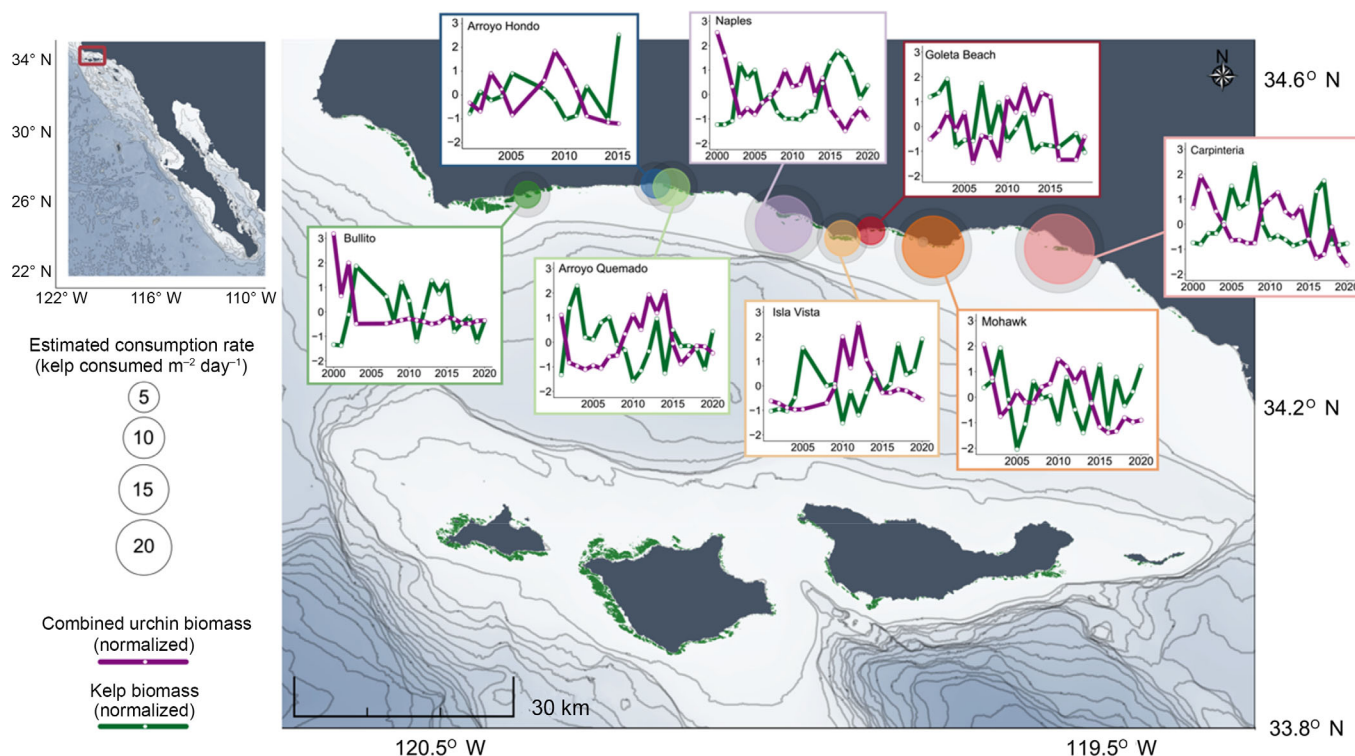
FIGURE 3 Spatial and temporal variation in the consumptive capacity of urchin populations at nine sites in the Santa Barbara Channel. The red box highlighted in the map in the upper left represents the study region. Consumptive capacity was calculated based on 21 years of urchin biomass observations and the experimental relationship between urchin biomass and foraging rate (please refer to the section "*Methods*" for details). Gray shading surrounding points represents the SE of the mean across years. Each site is accompanied by a time series of normalized kelp (*Macrocystis pyrifera*) and combined sea urchin biomass (g m^{-2}). One site was omitted for visualization purposes only. Bathymetric data from Divins and Metzger (2021)

Across 21 years of data at nine sites, urchin biomass was negatively correlated with kelp biomass, but explained only 14% of the variation in kelp dynamics (Appendix S4: Table S1). At many sites or years, kelp biomass remained high, despite urchin biomass far exceeding thresholds expected to drive transitions toward urchin-dominated deforested states either locally in Southern California (e.g., 1246 g m^{-2}; Dean et al., 1984) or elsewhere in the world (e.g., $\gg$668 g m^{-2}; Ling et al., 2015). By accounting for instances when detrital supply exceeded consumptive capacity, our best fit model explained ~70% of the variation in foraging rates (ΔAIC = 461.0; Appendix S4: Table S1), supporting the hypothesis that urchin-driven declines in kelp are mediated by the availability of detritus in the Santa Barbara Channel (Figure 4). In fact, when the rate of detrital supply was greater than consumptive capacity, kelp biomass increased with increases in urchin biomass (Figure 4a). When consumptive capacity exceeded detrital supply, kelp biomass was on average ~50× less than when consumptive capacity was less than detrital supply (Figure 4b).

The availability of detritus relative to consumptive capacity also predicted the variation in annual kelp dynamics. On average, the annual change in standing kelp biomass switched from positive to negative as the consumptive capacity increased relative to detrital supply (Figure 5; LMM: β = −1486.8 ± 288, p < 0.001; Appendix S4: Table S2). When consumptive capacity was greater than detrital supply (e.g., right hand side of Figure 5), kelp declined or changed little (e.g., did not increase by more than +100 g m^{-2}), 91% of the time, compared with only 42% of the time when detrital supply exceeded consumptive capacity. Generally, changes in kelp biomass were dissociated from grazing dynamics when consumption was less than detrital supply (e.g., left hand side of Figure 5), and even when urchin biomass was high, kelp biomass increased 15% of the time.

DISCUSSION

Ultimately, the productivity of a community is dynamic, driven by the complex interplay between the rates that primary producers grow and are consumed. Yet empirical determination of what controls productivity over space and time is often hampered by the availability of long-term data. Here, we combine mesocosm experiments with 21 years of spatially explicit data on rocky reef
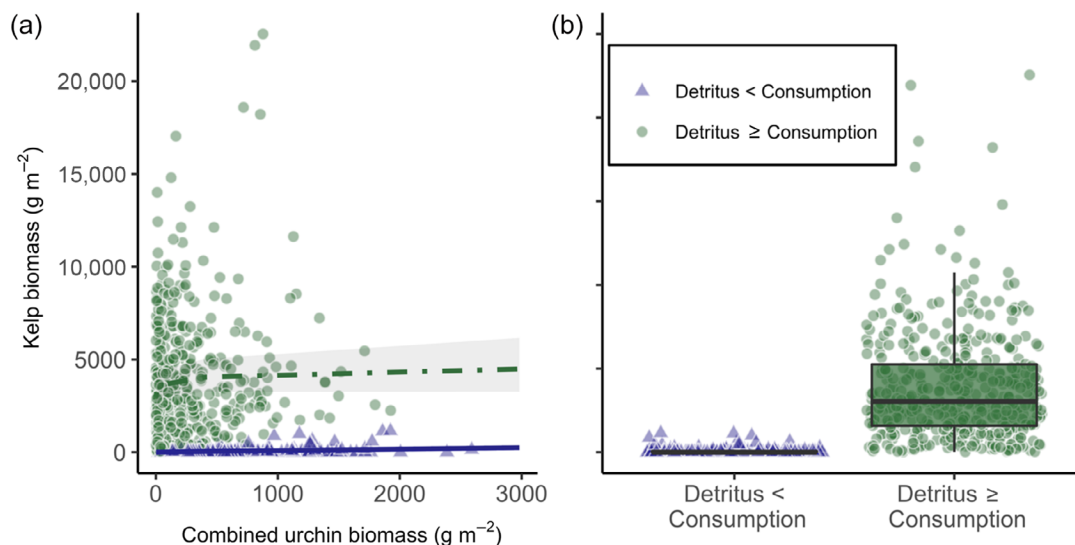
FIGURE 4   Relationship between standing kelp biomass (e.g., kelp attached to the substrate) and total urchin biomass across 21 years at sites in the Santa Barbara Channel. (a) Standing kelp biomass was best explained by an interaction between urchin biomass and whether the consumptive capacity of urchins was greater or less than the estimated detrital supply rate. Lines in (a) represent the average prediction (±95% CI) for the relationship between urchin and kelp biomass when consumption exceeded, or was less than, detrital supply from a generalized linear mixed effects model. (b) When consumptive capacity exceeded the detrital supply rate, standing kelp biomass was on average ~50× less than when detrital supply exceeded the consumption rate

community structure to demonstrate how the balance between two dynamic processes—consumption and primary production—mediated consumer-driven disturbances in the key foundation species, *Macrocystis pyrifera*, of California kelp forests.

Consumer–resource theory predicts that the rate that primary producers are consumed is dependent on resource density, consumer density, and body size (Abrams & Ginzburg, 2000; Rall et al., 2012). In our mesocosm trials we quantified how foraging rates varied as a function of consumer biomass by manipulating consumer density and sampling individuals from the size distribution observed in local populations. Previous work on various urchin species, along with evidence from our own size-based foraging trials, suggested that total biomass, rather than size-specific consumption rates, is an appropriate predictor of an urchin population's consumptive capacity (Stevenson et al., 2016; Suskiewicz & Johnson, 2017, Appendix S2). We found that, for both purple and red urchins, consumption of kelp blades increased linearly with consumer biomass, suggesting that, even at high consumer biomass, grazing rates do not decelerate due to competition or accelerate due to facilitation.

Our finding that urchins continued to eat in direct proportion to their biomass even at high densities, offers critical insight into the mechanisms triggering consumer-driven disturbances in Southern California kelp forests. By estimating the consumptive capacity of historical urchin populations as a linear function of urchin

biomass, we showed that kelp dynamics were independent of urchin biomass when the rate at which detritus was produced exceeded the consumptive capacity of urchins. However, when consumptive capacity exceeded detrital supply, the biomass of standing kelp was 50-fold less, supporting the long-standing hypothesis that the persistence of kelp forests is driven by the rate of detrital consumption relative to detrital supply (e.g., Harrold & Reed, 1985). Therefore, our work suggests that when detrital resources become limiting, kelp forests are likely to shrink or disappear, and may be transformed into urchin-dominated deforested communities with lower primary productivity. Furthermore, recent work demonstrated that urchins rapidly consume algal recruits in barren areas, leading to the bioerosion of long-lived calcareous reefs (Rasher et al., 2020), reinforcing alternative ecosystem states (Konar & Estes, 2003). Therefore, the capacity of urchins to continue to graze in proportion to their biomass suggests that, when food becomes scarce, urchins may prevent kelp regrowth and perpetuate consumer-dominated communities.

To date, efforts to predict when kelp forests will transition to urchin-dominated states have primarily focused on ecological indicators of grazing pressure such as urchin density (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015), or on factors—such as predators—that alter urchin abundance (Dunn & Hovel, 2019; Estes et al., 2010; Hamilton & Caselle, 2015). However, our study highlights the importance of focusing on the rates of
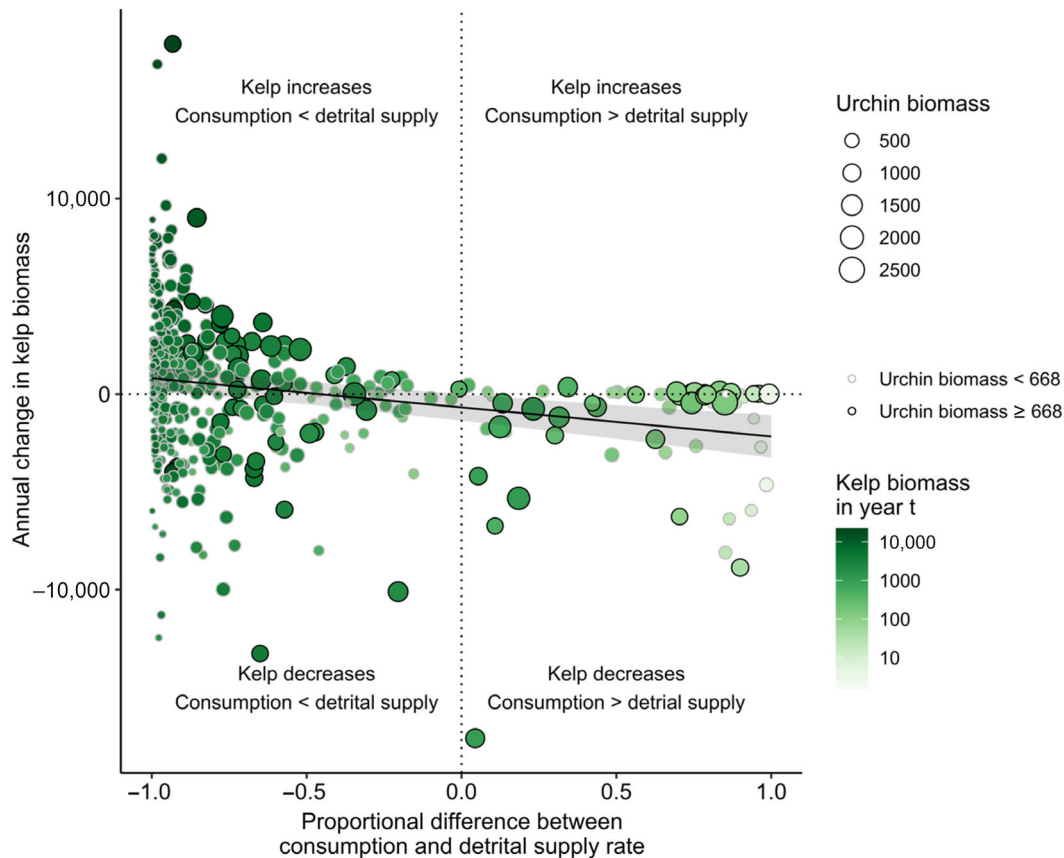
FIGURE 5 Relationship between the annual change in kelp biomass and the proportional difference between detrital supply (g m^{-2} day^{-1}) and consumptive capacity of urchin populations (g m^{-2} day^{-1}) (please refer to the section "*Methods*" for details). When the rate of detrital supply exceeds consumption (left), kelp biomass dynamics were decoupled from urchin consumption. As the consumption rate increased relative to detrital supply, the annual change in kelp biomass declined ($\beta = -1486.8 \pm 288$, $p < 0.001$). The line represents the average prediction ($\pm95\%$ CI) from a linear mixed effects model. The horizontal line at zero represents no change in kelp biomass from year to year, while the vertical line at zero represents when consumptive capacity was equal to the rate of detrital supply

community processes (detrital production and herbivory) in addition to the state variables such as the density or size of consumers and resources. In our study system, quantifying urchin biomass alone was not sufficient to accurately predict when a kelp community was at risk of deforestation. We observed numerous instances in which kelp biomass remained high, despite the presence of dense urchin populations. Instead, we found that reductions in intact kelp biomass were highest when grazing outweighed detrital supply rates. In fact, when detrital supply was higher than consumptive capacity, kelp and urchin biomass positively covaried, probably due to similar habitat requirements or because urchin population growth rates are positive when detrital resources are plentiful. The role of detrital supply in triggering a switch in urchin foraging mode (and subsequent loss in intact kelp biomass) is supported by empirical evidence that shows urchins in kelp-dominated sites consume more detritus than standing kelp, compared with urchins in urchin-dominated sites

that consume both detritus and standing kelp at similar rates (Kriegisch et al., 2019).

Estimation of detrital production and consumptive capacity could offer scientists and resource managers the opportunity to identify kelp forests at risk of deforestation. Resulting "risk maps" may be particularly useful for optimizing conservation and management funds (e.g., Avila et al., 2018). For example, sites where urchin populations have a high consumptive capacity relative to detrital production are likely to be places for targeted urchin harvest before the community transitions into an urchin-dominated state. However, the factors driving deforestation by urchins may vary between different kelp ecosystems (Filbee-Dexter & Scheibling, 2014; Karatayev et al., 2021). To effectively predict the risk of deforestation in diverse kelp communities requires regionally specific research on the role of detritus and the causes of variation in detrital supply. For instance, in Southern California kelp forests, detrital dynamics exhibit a pronounced seasonal signal (Yorke et al., 2019) caused by seasonal storms

and blade senescence patterns (Rodriguez et al., 2013). Yet empirical estimates of the rates of detrital turnover, import, and export remain unclear. Furthermore, temperature is well known to alter consumption rates (Brown et al., 2004; Uiterwaal & DeLong, 2020). While we focused only on consumption rates during the boreal summer, accounting for temperature-specific grazing rates is likely to be a key component of mapping the risk of deforestation, particularly in future projections in which increasing ocean temperature will probably increase consumption rates to a thermal optimum.

The prevalence of disturbances driven by primary consumers will probably increase with global climate change and associated losses of higher predatory species (Rocca et al., 2021; Silliman et al., 2013). Therefore, it is critical to understand the mechanisms by which consumers switch from coexisting with primary producers to overgrazing the dominant producer, resulting in an alternative community state. Our study highlights the importance that detrital resources play in mediating consumer-driven disturbances on temperate rocky reefs in Southern California by demonstrating that a behavioral switch from passively feeding on kelp detritus to actively grazing on standing kelp can trigger deforestation. The importance of detrital supply in consumer–resource dynamics is not exclusive to kelp forests. For example, there is evidence that the widespread degradation of saltmarshes on the US Eastern Seaboard is linked to a change in the dominant consumer, *Littoraria irrorata*, foraging on the detritus of marsh grass to actively foraging standing biomass (Silliman et al., 2005). Recent work shows that the majority of primary consumers forage on both detrital resources and living biomass (Wolkovich et al., 2014), suggesting that declines in detrital availability, such as the switch from detritivory to herbivory by urchins in California kelp forests, could underlie consumer-driven disturbances that result in dramatic ecosystem change in other systems.

Understanding sources of variation in foraging rates is foundational to answering the long-debated question in ecology, "why is the world green?" (Hairston et al., 1960; Murdoch, 1966). The answer to this question inevitably lies in the balance between the rates at which plant matter is produced and consumed. Our research offers a case study in answering this question. We show how the consumptive capacity of urchin populations shifts in response to changes in urchin biomass and highlight how the persistence of giant kelp depends on the balance between foraging pressure and detrital production, with implications for anticipating and reversing shifts in community state.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Mae Rennick and Bartholomew P. DiFiore contributed equally to this manuscript. Bartholomew P. DiFiore and Adrian C. Stier conceived the idea. Mae Rennick, Bartholomew P. DiFiore and Joseph Curtis collected grazing data. Daniel C. Reed designed and collected the time series data. Bartholomew P. DiFiore and Mae Rennick conducted analyses. Mae Rennick, Bartholomew P. DiFiore, and Adrian C. Stier wrote the paper, and Joseph Curtis and Daniel C. Reed contributed substantial comments and revisions on drafts.

DATA AVAILABILITY STATEMENT

Long-term community data (Santa Barbara Coastal LTER, Reed, et al., 2021) are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/f1cf070648d7654ada052835afb2cfe9, and long-term productivity data (Santa Barbara Coastal LTER, Rassweiler, et al., 2021) are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/bf6049d8abc0177c72564ff014b8fe6b. Mesocosm experiments data (Santa Barbara Coastal LTER, DiFiore, et al., 2021) are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/6af4cc3b0e63b887baf1ae9201e1cd1d. Code (maerennick et al., 2021) is available in Zenodo at https://doi.org/10.5281/zenodo.5645471.

ORCID

Mae Rennick https://orcid.org/0000-0003-0414-0089
Adrian C. Stier https://orcid.org/0000-0002-4704-4145

REFERENCES

Abrams, P. A., and L. R. Ginzburg. 2000. "The Nature of Predation: Prey Dependent, Ratio Dependent or Neither?" *Trends in Ecology & Evolution* 15: 337–41.

Aho, K., D. Derryberry, and T. Peterson. 2014. "Model Selection for Ecologists: The Worldviews of AIC and BIC." *Ecology* 95: 631–6.

Akaike, H. 1973. "Information Theory and the Maximum Likelihood Principle." In *2nd International Symposium on Information Theory*, edited by B. N. Petrov and F. Csáki, 267–81. Budapest: Akademiai Ki à do.

Arditi, R., and L. R. Ginzburg. 1989. "Coupling in Predator–Prey Dynamics: Ratio-Dependence." *Journal of Theoretical Biology* 139: 311–26.

Augustine, D. J., and S. J. McNaughton. 1998. "Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance." *Journal of Wildlife Management* 62: 1165–83.

Avila, I. C., K. Kaschner, and C. F. Dormann. 2018. "Current Global Risks to Marine Mammals: Taking Stock of the Threats." *Biological Conservation* 221: 44–58.

Bell, T. W., K. C. Cavanaugh, D. C. Reed, and D. A. Siegel. 2015. "Geographical Variability in the Controls of Giant Kelp Biomass Dynamics." *Journal of Biogeography* 42: 2010–21.

Bolker, B. M. 2008. *Ecological Models and Data in R*. Princeton, NJ: Princeton University Press.

Brook, B. W., and C. J. Bradshaw. 2006. "Strength of Evidence for Density Dependence in Abundance Time Series of 1198 Species." *Ecology* 87: 1445–51.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–89.

Cavanaugh, K. C., B. E. Kendall, D. A. Siegel, D. C. Reed, F. Alberto, and J. Assis. 2013. "Synchrony in Dynamics of Giant Kelp Forests Is Driven by Both Local Recruitment and Regional Environmental Controls." *Ecology* 94: 499–509.

Clendenning, K. A. 1963. "Photosynthesis and Growth in Macrocystis pyrifera." *Proceedings of the International Seaweed Symposium* 4: 55–65

Dayton, P. K., and M. J. Tegner. 1984. "Catastrophic Storms, El Niño, and Patch Stability in a Southern California Kelp Community." *Science* 224: 283–5.

Dean, T. A., S. C. Schroeter, and J. D. Dixon. 1984. "Effects of Grazing by Two Species of Sea Urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on Recruitment and Survival of Two Species of Kelp (*Macrocystis pyrifera* and *Pterygophora californica*)." *Marine Biology* 78: 301–13.

Divins, D. L., and D. Metzger. 2021. "NGDC Coastal Relief Model." Southern California Coastal Ocean Observing System. http://www.ngdc.noaa.gov/mgg/coastal/coastal.html.

Duggins, D. O. 1981. "Sea Urchins and Kelp: The Effects of Short Term Changes in Urchin Diet." *Limnology and Oceanography* 26: 391–4.

Dunn, R. P., and K. A. Hovel. 2019. "Experiments Reveal Limited Top-Down Control of Key Herbivores in Southern California Kelp Forests." *Ecology* 100: e02625.

Estes, J. A., M. T. Tinker, and J. L. Bodkin. 2010. "Using Ecological Function to Develop Recovery Criteria for Depleted Species: Sea Otters and Kelp Forests in the Aleutian Archipelago: Ecologically Based Recovery Criteria." *Conservation Biology* 24: 852–60.

Filbee-Dexter, K., and R. E. Scheibling. 2014. "Sea Urchin Barrens as Alternative Stable States of Collapsed Kelp Ecosystems." *Marine Ecology Progress Series* 495: 1–25.

Guillou, M., L. J. Lumingas, and C. Michel. 2000. "The Effect of Feeding or Starvation on Resource Allocation to Body Components during the Reproductive Cycle of the Sea Urchin *Sphaerechinus granularis*." *Journal of Experimental Marine Biology and Ecology* 245: 183–96.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. "Community Structure, Population Control, and Competition." *The American Naturalist* 94: 421–5.

Hamilton, S. L., and J. E. Caselle. 2015. "Exploitation and Recovery of a Sea Urchin Predator Has Implications for the Resilience of Southern California Kelp Forests." *Proceedings of the Royal Society of London B: Biological Sciences* 282: 20141817.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018. "A Brief Introduction to Mixed Effects Modelling and Multi-Model Inference in Ecology." *PeerJ* 6: e4794.

Harrold, C., and D. C. Reed. 1985. "Food Availability, Sea Urchin Grazing, and Kelp Forest Community Structure." *Ecology* 66: 1160–9.

Holbrook, S. J., T. C. Adam, P. J. Edmunds, R. J. Schmitt, R. C. Carpenter, A. J. Brooks, H. S. Lenihan, and C. J. Briggs. 2018. "Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs." *Scientific Reports* 8: 7338.

Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. "Herbivores, Resources and Risks: Alternating Regulation along Primary Environmental Gradients in Savannas." *Trends in Ecology & Evolution* 25: 119–28.

Karatayev, V. A., M. L. Baskett, D. J. Kushner, N. T. Shears, J. E. Caselle, and C. Boettiger. 2021. "Grazer Behaviour Can Regulate Large-Scale Patterning of Community States." *Ecology Letters* 24: 1917–29.

Kautz, M., A. J. Meddens, R. J. Hall, and A. Arneth. 2016. "Biotic Disturbances in Northern Hemisphere Forests–A Synthesis of Recent Data, Uncertainties and Implications for Forest Monitoring and Modelling." *Global Ecology and Biogeography* 26: 533–52.

Klemmer, A. J., S. A. Wissinger, H. S. Greig, and M. L. Ostrofsky. 2012. "Nonlinear Effects of Consumer Density on Multiple Ecosystem Processes." *Journal of Animal Ecology* 81: 770–80.

Konar, B., and J. A. Estes. 2003. "The Stability of Boundary Regions between Kelp Beds and Deforested Areas." *Ecology* 84: 174–85.

Kriegisch, N., S. E. Reeves, E. B. Flukes, C. R. Johnson, and S. D. Ling. 2019. "Drift-Kelp Suppresses Foraging Movement of Overgrazing Sea Urchins." *Oecologia* 190: 665–77.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26.

Lawrence, J. M. 1975. "On the Relationships between Marine Plants and Sea Urchins." *Oceanography and Marine Biology: An Annual Review* 13: 213–86.

Ling, S. D., and C. R. Johnson. 2009. "Population Dynamics of an Ecologically Important Range-Extender: Kelp Beds Versus Sea Urchin Barrens." *Marine Ecology Progress Series* 374: 113–25.

Ling, S. D., R. E. Scheibling, A. Rassweiler, C. R. Johnson, N. Shears, S. D. Connell, and A. K. Salomon. 2015. "Global Regime Shift Dynamics of Catastrophic Sea Urchin Overgrazing." *Philosophical Transactions of the Royal Society B: Biological Sciences* 370: 20130269.

Ling, S. D., N. Kriegisch, B. Woolley, and S. E. Reeves. 2019. "Density-Dependent Feedbacks, Hysteresis, and Demography of Overgrazing Sea Urchins." *Ecology* 100: e02577.

Little, C. J., E. A. Fronhofer, and F. Altermatt. 2020. "Nonlinear Effects of Intraspecific Competition Alter Landscape-Wide Scaling Up of Ecosystem Function." *The American Naturalist* 195: 432–44.

maerennick, B. DiFiore, and jlscurtis512. 2021. "Rennick, et al. Ecology: Code (v1.0.1)." Zenodo. https://doi.org/10.5281/zenodo.5645471.

McKie, B. G., M. Schindler, M. O. Gessner, and B. Malmqvist. 2009. "Placing Biodiversity and Ecosystem Functioning in Context: Environmental Perturbations and the Effects of Species Richness in a Stream Field Experiment." *Oecologia* 160: 757–70.

Murdoch, W. W. 1966. "Community Structure, Population Control, and Competition." *The American Naturalist* 100: 219–26.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. "Universal Temperature and Body-Mass Scaling of Feeding Rates." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 2923–34.

Rasher, D. B., R. S. Steneck, J. Halfar, K. J. Kroeker, J. B. Ries, M. T. Tinker, P. T. W. Chan, et al. 2020. "Keystone Predators Govern the Pathway and Pace of Climate Impacts in a Subarctic Marine Ecosystem." *Science* 369: 1351–4.

Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone, and D. A. Siegel. 2011. "Wave Disturbance Overwhelms Top-Down and Bottom-Up Control of Primary Production in California Kelp Forests." *Ecology* 92: 2108–16.

Reice, S. R. 1991. "Effects of Detritus Loading and Fish Predation on Leafpack Breakdown and Benthic Macroinvertebrates in a Woodland Stream." *Journal of the North American Benthological Society* 10: 42–56.

Rocca, C., P. Daleo, J. Nuñez, B. R. Silliman, O. Iribarne, C. Angelini, and J. Alberti. 2021. "Flood-Stimulated Herbivory Drives Range Retraction of a Plant Ecosystem." *Journal of Ecology* 109: 3541–54.

Rodriguez, G. E., A. Rassweiler, D. C. Reed, and S. J. Holbrook. 2013. "The Importance of Progressive Senescence in the Biomass Dynamics of Giant Kelp (*Macrocystis pyrifera*)." *Ecology* 94: 1848–58.

Sala, E., C. F. Boudouresque, and M. Harmelin-Vivien. 1998. "Fishing, Trophic Cascades, and the Structure of Algal Assemblages: Evaluation of an Old but Untested Paradigm." *Oikos* 82: 425.

Santa Barbara Coastal LTER, B. DiFiore, M. Rennick, J. Curtis, D. Reed, and A. Stier. 2021. SBC LTER: Sea Urchin Foraging Rates on Giant Kelp ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/6af4cc3b0e63b887baf1ae9201e1cd1d.

Santa Barbara Coastal LTER, D. Reed, and R. Miller. 2021. "SBC LTER: Reef: Annual Time Series of Biomass for Kelp Forest Species, Ongoing since 2000 ver 10." Environmental Data Initiative. https://doi.org/10.6073/pasta/f1cf070648d7654ada052835afb2cfe9.

Santa Barbara Coastal LTER, A. Rassweiler, S. Harrer, D. Reed, C. Nelson, and R. Miller. 2021. "SBC LTER: REEF: Net Primary Production, Growth and Standing Crop of *Macrocystis pyrifera* in Southern California ver 4." Environmental Data Initiative. https://doi.org/10.6073/pasta/bf6049d8abc0177c72564ff014b8fe6b.

Schröder, A., L. Persson, A. M. de Roos, and P. Lundbery. 2005. "Direct Experimental Evidence for Alternative Stable States: A Review." *Oikos* 110: 3–19.

Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. "Drought, Snails, and Large-Scale Die-Off of Southern U.S. Salt Marshes." *Science* 310: 1803–6.

Silliman, B. R., M. W. McCoy, C. Angelini, R. D. Holt, J. N. Griffin, and J. van de Koppel. 2013. "Consumer Fronts, Global Change, and Runaway Collapse in Ecosystems." *Annual Review of Ecology, Evolution, and Systematics* 44: 503–38.

Sommer, U. 1992. "Phosphorus-Limited *Daphnia*: Intraspecific Facilitation Instead of Competition." *Limnology and Oceanography* 37: 966–73.

Spindel, N. B., L. C. Lee, and D. K. Okamoto. 2021. "Metabolic Depression in Sea Urchin Barrens Associated with Food Deprivation." *Ecology* 102: e03463.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. "Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future." *Environmental Conservation* 29: 436–59.

Stevenson, C. F., K. W. Demes, and A. K. Salomon. 2016. "Accounting for Size-Specific Predation Improves our Ability to Predict the Strength of a Trophic Cascade." *Ecology and Evolution* 6: 1041–53.

Suskiewicz, T. S., and L. E. Johnson. 2017. "Consumption Rates of a Key Marine Herbivore: A Review of the Extrinsic and Intrinsic Control of Feeding in the Green Sea Urchin." *Marine Biology* 164: 131.

Uiterwaal, S. F., and J. P. DeLong. 2020. "Functional Responses Are Maximized at Intermediate Temperatures." *Ecology* 101: e02975.

Wernberg, T., S. Bennett, R. C. Babcock, T. de Bettignies, K. Cure, M. Depczynski, F. Dufois, et al. 2016. "Climate Driven Regime Shift of a Temperate Marine Ecosystem." *Science* 353: 169–72.

Wolkovich, E. M., S. Allesina, K. L. Cottingham, J. C. Moore, S. A. Sandin, and C. de Mazancourt. 2014. "Linking the Green and Brown Worlds: The Prevalence and Effect of Multichannel Feeding in Food Webs." *Ecology* 95: 3376–86.

Yorke, C. E., H. M. Page, and R. J. Miller. 2019. "Sea Urchins Mediate the Availability of Kelp Detritus to Benthic Consumers." *Proceedings of the Royal Society B: Biological Sciences* 286: 20190846.

Zuur, A. F., E. N. Leno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer-Verlag.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Rennick, Mae, Bartholomew P. DiFiore, Joseph Curtis, Daniel C. Reed, and Adrian C. Stier. 2022. "Detrital Supply Suppresses Deforestation to Maintain Healthy Kelp Forest Ecosystems." *Ecology* e3673. https://doi.org/10.1002/ecy.3673

Ecology

Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems

Mae Rennick[1*], Bartholomew P. DiFiore[1*], Joseph Curtis[1], Daniel C. Reed[2], Adrian C. Stier[1,2]

[1]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93116, USA
[2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93116, USA

Appendix S1: Effect of consumer body size on foraging rates

It is widely known that consumption rates vary with consumer body size as individuals grow through ontogeny (Uiterwaal and DeLong 2020). The theoretical basis for increases in consumption with body size is that across species and individuals of all taxa, larger organisms have higher total metabolic rates but lower mass-specific metabolic rates (Brown et al. 2004). Therefore, larger organisms tend to consume more on average than smaller organisms but less per unit mass (Rall et al. 2012). The size-scaling of consumption rates means that the relationship between biomass (g m^{-2}) and consumption rate can change with the specific size-distribution of consumers.

Our primary interest was the effect of consumer (sea urchin) biomass (g m^{-2}) on foraging rates of *Macrocystis pyrifera*. In the biomass treatments described in the main text, we manipulated the density (ind. m^{-2}) of urchins assigned to a treatment. We then summed the weight of each individual urchin in each trial to estimate biomass (g m^{-2}) and used biomass as our main predictor variable in experimental models. To ensure that individual body size did not confound our estimate of the relationship between biomass and consumption we randomly selected urchins of different sizes from the collected pool of urchins. However, despite randomly sampling from the pool of urchins it is possible that two treatments with equivalent biomass could be composed of many small individuals or a few large individuals.
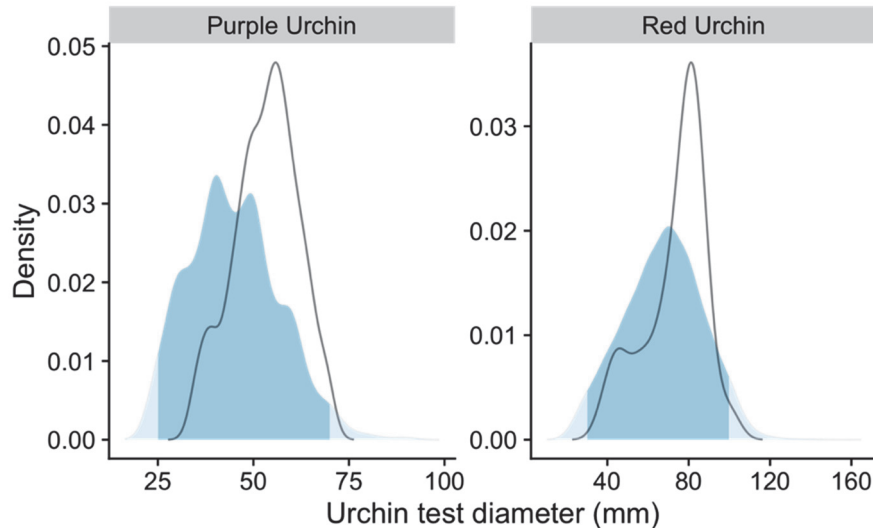
Figure S1. Comparison of observed (blue filled polygons) and experimental (black lines) size frequency distributions for both purple and red urchins. Observational data was taken from five sites monitored annually (2008-2020). Experimental size-frequency distributions represent the pool of urchins used in biomass foraging trials. Dark blue filled regions of observed size-frequency distributions represent the 95% percentiles.

To ensure that the collected pool of urchins emulated the size distribution of urchins locally, we compared the sizes of urchins used in the biomass trials to observational data available through the Santa Barbara Coastal Long-term ecological research program. The observational urchin biomass data described in the main text is estimated from the density (ind. m^{-2}) and *average* size of urchins encountered along a transect. Therefore, to compare we used a separate data set that monitors urchins size structure along a single transect at five of the sites in the broader data set (Reed and Miller 2021). Across all trials the pool of collected urchins approximated the 95% CI of the observed size-frequency distribution of each species of urchin sampled between 2008 and 2020 (Fig. S1). On average, the urchins we used in experimental trials in 2018 tended to be larger than the observed mean test diameter across all years and sites.

While we randomly selected urchins from the collected pool of urchins, it is possible that the effect of biomass on consumption rate was confounded by the random size of urchins allocated into a trial, particularly in trials with low urchin density. The results of these trials and our estimate of consumptive capacity is therefore contingent on the assumption that foraging rates were invariant with body size (e.g. a small urchin and large urchin consume the same amount per unit of body mass). To test this assumption, we conducted body size foraging trials (*hereafter*, "size trials") in a similar manner to the biomass foraging trials described in depth in *Methods*. Specifically, we estimated the foraging rates of 6 and 5 size classes of purple (10-19, 20-29, 30-39, 40-49, 50-59, 60-70 mm test diameter) and red urchins (10-29, 30-49, 50-69, 70-89, 90-110 mm test diameter), respectively, in randomized trials replicated six times per size class for purple urchins and three times per size class for red urchins. In the size trials, we held the density of urchin constant (7 and 5 ind. arena^{-1} for purple and red urchins, respectively), but allowed urchin size class to vary. We measured the individual mass of each urchin in a size class and estimated the average mass of urchins in a size class treatment. We did not reused urchins between trials and we conducted trials according to the same schedule described in the main text for the

biomass trials. We calculated the total amount of kelp consumed by the population of urchins in a trial and divided by the abundance, to estimate the per-capita herbivory rate.

The results of the size trials demonstrate that kelp consumption by purple urchins increased at a decelerating rate with body mass (Fig. S2a; log-log regression where $\beta = 0.32 +- 0.05$). The power-law function fit the foraging rate data more parsimoniously than a simple linear model ($\Delta AIC = 6.2$) suggesting that larger purple urchins consume disproportionately less than smaller purple urchins per unit body mass. However, as can be seen in Fig. S2a, the confidence intervals for the power-law relationship were broad and fully cover the confidence intervals
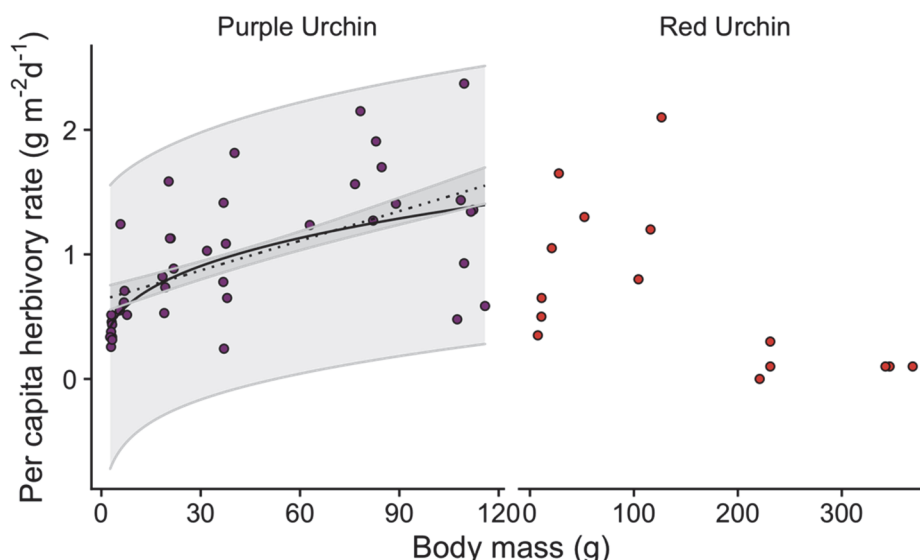

Figure S2. Consumption of kelp detritus in experimental mesocosms by purple (left) and red (right) urchins as a function of biomass. Biomass was manipulated by holding density constant (7 and 5 ind. arena[-1]) and manipulated the size class of individuals. Purple urchins were divided into 6 size classes, while red urchins were divided into 5. The solid black line represents the predictions of a power-law function, which described the consumption of purple urchins better than a simple linear model (). The dotted line represents the predictions for a simple linear regression. Shaded regions represent +- SE of the model predictions.

Red urchin consumption rates appeared to be highest at intermediate size classes, with a pronounced decline in consumption by the largest urchin size class (Fig. S2b). However, for red urchins we found no statistical evidence for power-law, or exponential relationship between body size and consumption rate ($p > 0.05$). We found a marginally significant linear decline in consumption with body size. However, decreases in total consumption with body size are biologically unlikely and were likely the result of low replication. Therefore, we assume that consumption rates were invariant per unit body mass for red urchins.

To ensure that our main conclusions were resistant to size-specific differences in purple urchin consumption rates, we predicted the experimental herbivory rates based on the individual size of urchins used in the trials where we manipulated density. Specifically, we used the best fit model for the relationship between body size (g) and consumption rate to predict how much the population of urchins in each density trial consumed. We found that the predicted herbivory rate from the size trials, was similar to the experimentally observed foraging rates of purple urchins (Fig. S3).
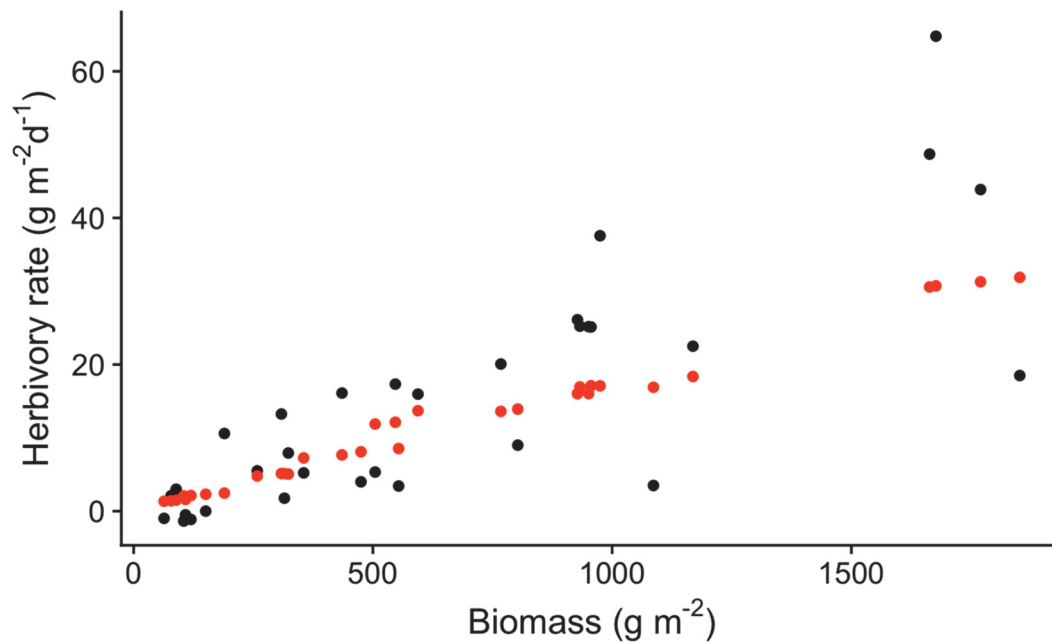
Figure S3. Observed herbivory rate of purple urchins as a function of urchin biomass, where biomass represents a manipulation of density (ind. m^{-2}). Black points are the observed data. Red points are predictions of the herbivory rate based on the individual sizes of each urchin used in the trial and the relationship between individual size and consumption rate depicted in Fig. S2.

We acknowledge that estimating consumptive capacity based on the relationship between biomass, where biomass represents a random draw of individuals from the size distribution, may lead to misestimation of consumption capacity, particularly for site-years when size-distributions are highly skewed. For instance, our estimate of consumptive capacity will likely overestimate actual consumption per unit mass when sizes are skewed towards larger individuals, and underestimate consumption per unit mass when sizes are skewed towards smaller individuals. We did not correct for size-specific effects in our estimation of consumptive capacity, largely because we only had data on individual size-frequency distributions from a limited number of sites (1 transect each at 5 sites vs. 3-8 transects each at 9 sites) and years (2008-2020 vs. 2001-2020). Furthermore, it is likely that considering the extent of the observational data, site-years when size distributions were strongly skewed larger or smaller likely averaged out across the data set. Finally, previous work has shown that urchin biomass, rather than body size-based estimates of consumption, is the best predictor of kelp dynamics (Stevenson et al. 2016).

References

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. TOWARD A METABOLIC THEORY OF ECOLOGY. Ecology 85:1771–1789.

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. Philosophical Transactions of the Royal Society B: Biological Sciences 367:2923–2934.

Reed, D, R. Miller. 2021. SBC LTER: Reef: Long-term experiment: Kelp removal: Urchin size frequency distribution ver 21. Environmental Data Initiative. https://doi.org/10.6073/pasta/fd564dddfe7b77fe9e4bd8417f166057. Accessed 2021-08-17.

Uiterwaal, S. F., and J. P. DeLong. 2020. Functional responses are maximized at intermediate temperatures. Ecology 101:e02975.

Stevenson, C. F., K. W. Demes, and A. K. Salomon. 2016. Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. Ecology and Evolution 6:1041–1053.

Ecology

Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems

Mae Rennick[1*], Bartholomew P. DiFiore[1*], Joseph Curtis[1], Daniel C. Reed[2], Adrian C. Stier[1,2]

[1]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93116, USA
[2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93116, USA

Appendix S2: Estimating net primary productivity and biomass losses in *Macrocystis pyrifera*

A central calculation in our manuscript is the estimate of detrital production in giant kelp, *Macrosystis pyrifera* (hereafter, "kelp"). Previous work conducted through the Santa Barbara Coastal Long-term Ecological Research program (SBC LTER) developed the methodology and published a dataset for net primary productivity that includes estimates of detrital production. We summarize the pertinent information here and discuss our assumptions in estimating detrital productions rates. We refer the reader to Rassweiler et al. (2018) for a more complete treatment of the methods and calculations.

Field methods and length-weight conversions to measure standing kelp biomass

At permanent plots at three sites, SBC LTER researchers have conducted monthly measures of kelp biomass growth and losses since 2002. In each plot ($200\ m^2 - 480\ m^2$ depending on site), divers count the number of fronds at 1-m for each kelp plant. Divers then measure the length of fronds in the water column, the length of the longest fronds in the canopy, and the length of any subsurface fronds (e.g. fronds not reaching the water surface). The length of fronds in each section (canopy, water column, and subsurface) is then used to estimate the total frond length of the plant. To assess the accuracy of the methodology, researchers removed whole plants and carefully measured the total frond length of each section out of the water which was strongly correlated with field estimates of frond length ($N = 55$ plants, $r^2 = 0.99$, slope = 1.02; Rassweiler et al. 2018). The total standing kelp biomass ($kg\ m^{-2}$) is estimated by converting the frond length of each section to mass based on laboratory length-weight conversions specific to each section. The SBC LTER published estimates of standing kelp biomass in units of dry mass by converting wet to dry mass based on a ratio that is consistent across space and time (0.094, $n = 1022$). We utilize this ratio to back convert published dry mass estimates to wet mass in our manuscript as our experimental estimate of kelp consumption by urchins were in units of wet mass.

The SBC LTER estimates frond loss rates at 10-15 focal plants per site per sampling interval. At each sampling, a diver counts and bands all existing fronds with a loose zip tie. At the next sampling, the diver then counts the remaining fronds inside the zip tie and any new fronds.

Calculating net primary productivity and detrital production

The SBC LTER estimates net primary production based on a simple, exponential model of kelp growth, which assumes that standing kelp (*S*) grows over the monthly sampling interval at a

constant mass-specific rate (g) and declines with losses in biomass at a constant mass-specific rate (l). The instantaneous rate of change in standing kelp biomass is thus described by

$$\frac{dS}{dt} = S(g - l) \qquad eq.1$$

To estimate changes in biomass over the sampling interval, the SBC LTER assumes that biomass at the end of the sampling interval (S_t) is dependent on biomass at the start (S_0), such that $S_t = S_0 e^{(g-l)t}$. Mean NPP is then estimated by integrating instantaneous NPP over the time interval and dividing by the number of days in the sampling period

$$\overline{NPP} = \frac{gS_0}{g - l}\left(e^{(g-l)T} - 1\right) \qquad eq.2$$

To estimate l, the SBC LTER quantifies losses of whole plants, whole fronds, fronds lost due to propeller damage, blades lost to senescence, and dissolved exudates. For our manuscript we needed to estimate the rate of detrital production that is available as forage for urchins, which we assume to be the fraction of biomass lost from standing kelp biomass as fronds (f) and blades (b). Whole plants are most often lost in winter during large storm events and our focus is on urchin consumption rates at summer time water temperatures. Therefore, we exclude whole plant loss rates. We also exclude losses due to propeller damage, as these losses are seasonally associated with the start of the commercial lobster season and account for a small fraction of losses. We also exclude dissolved exudates as we assume that these are not resources available to urchins.

To estimate the fraction of biomass lost as whole fronds, the SBC LTER utilized the field counts of the change in the number of fronds at 1-m between samplings to estimate the daily loss rate of fronds from each plant (k), such that

$$f_k = -\frac{1}{T}\ln\left(1 - \frac{F_T}{F_0}\right) \qquad eq.3$$

The fraction lost as fronds is then averaged across plants (n = ~15) at each site in each sampling period. We assume that fronds lost over a sampling interval are of an average size so that fractional frond loss can be used to estimate the fraction of biomass lost.

The calculation of the biomass lost as blades is based on previously developed models of blade life span and the proportion of remaining biomass (e.g. not already lost as fronds) that is composed of blades. In 2012, Rodriguez et al. (2016) tracked individual kelp blades to estimate blade biomass loss rates. Subsequently, Rassweiler et al. (2017) developed an individual-based model to predict the fraction of biomass lost per unit blade mass for subsurface, water-column, and canopy blades. Using these relationships, the SBC LTER publishes monthly estimates for the fraction of standing kelp biomass lost as blades senesce (b) as

$$b = b_{sub} fracBld_{sub} + b_{wc} fracBld_{wc} + b_{can} fracBld_{can} \qquad eq.4$$

where *fracBld* represents the fraction of standing biomass contained in blades in each respective section during the sampling interval.

Extrapolation to non-NPP survey sites and assumptions

In our manuscript, we utilized the relationship between production (both gains and losses) and kelp biomass developed for the three sites where the SBC LTER conducts NPP surveys to extrapolate estimates for all sites where annual surveys monitor kelp and urchin biomass ($N = 9$). The three NPP survey sites are also present in the broader set of sites where the SBC LTER monitors urchin biomass. However, urchin and kelp biomass are monitored annually at different sampling scales than those used for the NPP surveys (e.g. annual surveys are based on 80 m^2 transects, while NPP surveys are based on 200-480 m^2 transects). Therefore, even at NPP survey sites we estimate production following the methods outlined here on the individual transects where kelp and urchins are simultaneously measured in the annual surveys.

To estimate NPP at annual survey transects, we used published regression relationships between NPP and kelp frond density (Rassweiler et al. 2021; *see* Castorani et al. 2021 *for a similar approach*). To estimate detrital production, we calculated the sum of the fraction of blades and fronds lost in summer in each year between 2002-2019, and took the average across sites and years. Based on this average, we then estimated the detrital production at each of the nine sites by multiplying $\overline{d}$ by the standing kelp biomass at a transect in a year.

In calculating an estimate of detrital production, we assume that *all* the biomass lost as blades and fronds is immediately available to urchins on the seafloor. In all likelihood, some fraction of the biomass lost is transported out of the transect area by currents. Therefore, we consider our estimate of *M. pyrifera* detrital production to be conservative: urchins likely have less detrital biomass available than our estimate predicts. Thus, even with a conservative estimate of detrital production (e.g. a higher estimate of detrital production than urchins actually experience), our analysis demonstrates that standing kelp biomass declines as the predicted consumption rate of urchins increases relative to detrital production.

Our protocol also assumes that the relationship between kelp production (e.g. both NPP and losses) and standing kelp biomass is constant in time and space. Previous work demonstrates that production-biomass relationship differs seasonally but we assume that the relationship has not changed across the time series (Rassweiler et al. 2018). To account for seasonal variation, we used estimates of the production-biomass relationship developed for the summer season. In terms of detrital production, we found little evidence for temporal or spatial patterns at the NPP survey sites, and the fraction of biomass lost as blades and fronds varied randomly between sites and years (Fig. S1a). If kelp populations tend to grow logistically, then biomass losses would likely increase with standing biomass per unit area. While total detrital production increased with kelp biomass (Fig. S1b, we found no evidence that the fraction of biomass lost increased with standing biomass (Fig. S1c), consistent with previous work demonstrating that exponential growth models describe kelp biomass dynamics as well as logistic population models (Rassweiler et al. 2018). We also found no evidence that the fraction of biomass lost changed with variation in average monthly temperature (Fig. S1d).
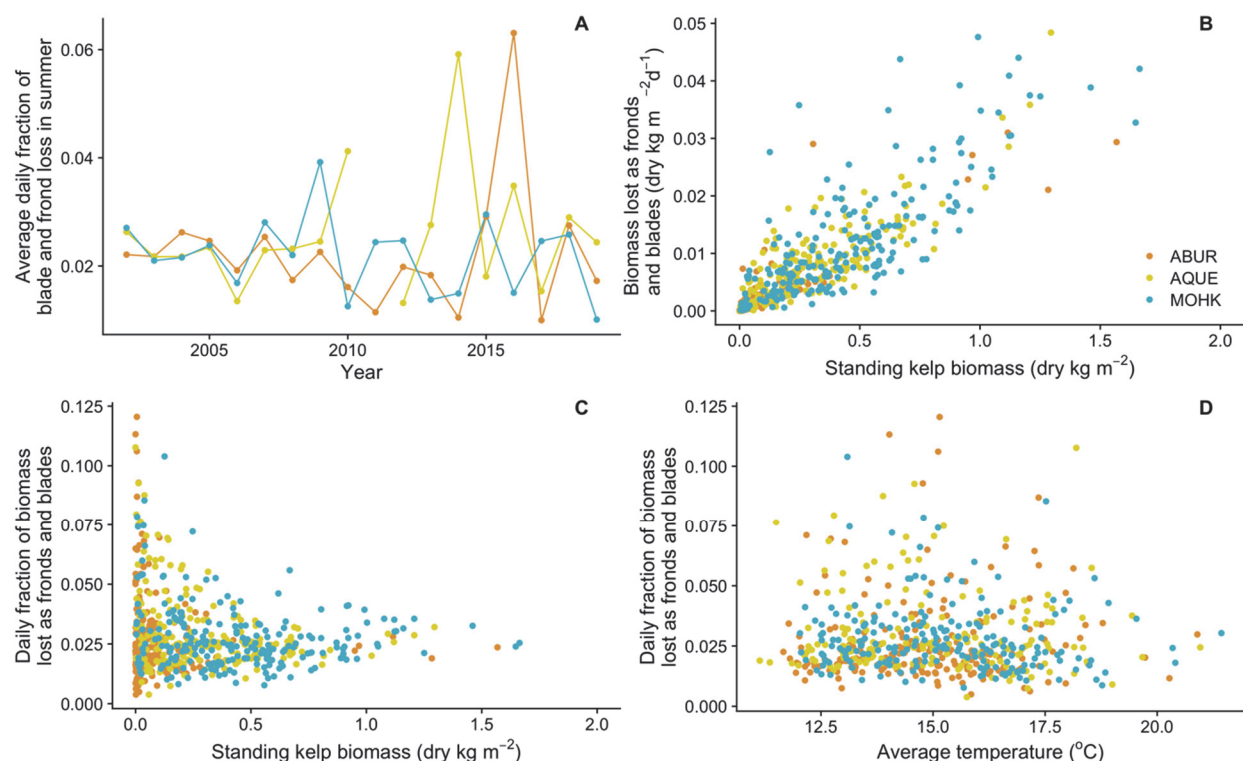
Figure S1. Trends in the fraction of kelp biomass lost as blades and fronds in the summer season at three sites where the SBC LTER conducts NPP surveys (A). Total production of blade and frond detritus increased with standing kelp biomass (B), but there is no evidence that the fraction of biomass contributing to detritus varied with standing kelp biomass (C). The fraction of biomass lost and blades and fronds did not vary with monthly average water temperature.

Assessing the accuracy of estimated detrital production

Unfortunately, there are no *in situ* measures of the rate that detritus reaches the seafloor and is exported from kelp forests. Therefore, we are left to provide the best estimate possible with the available data. However, the SBC LTER quantified detrital biomass at one transect at five of the nine sites examined in this manuscript monthly from 2008-2012 and quarterly thereafter (Reed and Miller 2021). To assess the accuracy of our protocol to estimate detrital production, we compared our estimated detrital production to the observed biomass of *M. pyrifera* detritus during the summer. We limited this analysis only to the period in which detritus was collected monthly, as it is unlikely that the collected detritus on a particular day in a quarter has any relationship with the estimated rate of detrital production per day. We found that the observed biomass of detritus was consistently lower than our estimated detrital supply rate (Fig. S2), which makes sense considering that detritus experiences degradation, consumption, and export on time scales less than a month.
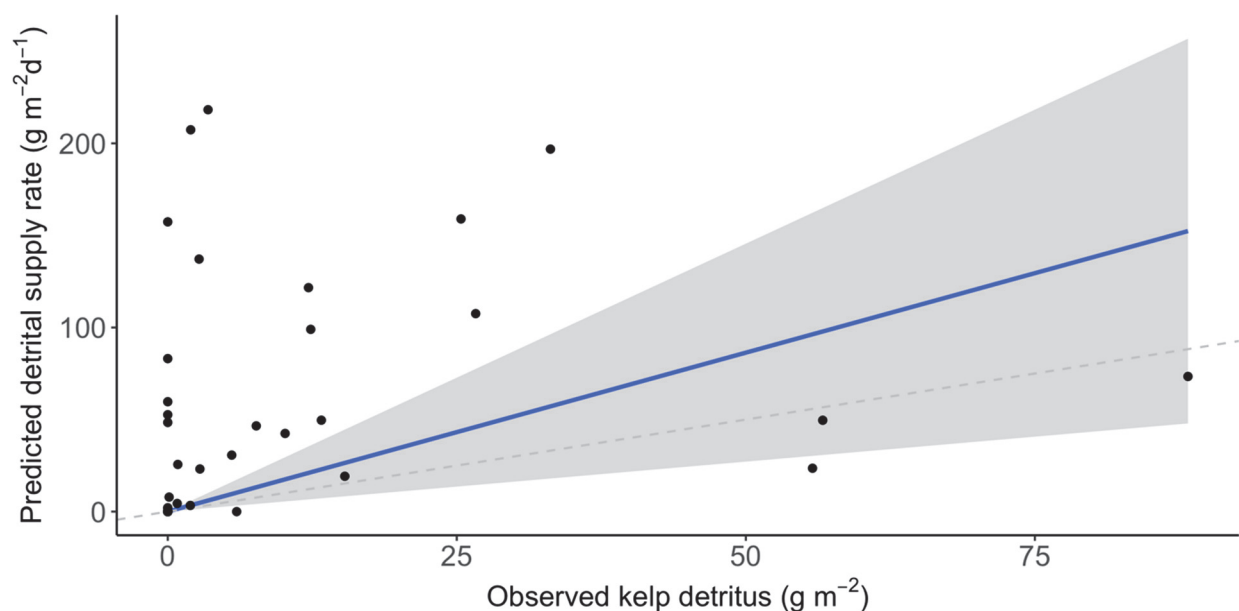
Figure S2. The relationship between predicted detrital supply estimating according to the methods described in this appendix and monthly measured of kelp detritus biomass at five sites between 2008-2012. The dashed line is the 1:1 relationship, while the blue line and gray polygon represents a simple least squares regression with the intercept fixed at 0 ($\beta = 1.7 \pm 0.6$, $p < 0.01$). The predicted detrital supply rate tended to be greater than observed kelp detritus.

References

Castorani, M. C. N., S. L. Harrer, R. J. Miller, and D. C. Reed. (2021). Disturbance structures canopy and understory productivity along an environmental gradient. Ecology Letters. doi.org/10.1111/ele.13849.

Rassweiler A., G. Rodriguez, S. Harrer, D. Reed. (2017). SBC LTER: REEF: *Macrocystis pyrifera* blade area and loss in Southern California. Environmental Data Initiative. http://doi.org/10.6073/pasta/2d78cd888e92b4cef8615e60a9aab83d.

Rassweiler, A., Reed, D. C., Harrer, S. L., Nelson, J. C. (2018). Improved Estimates of Net Primary Production, Growth, and Standing Crop of *Macrocystis* pyrifera. Ecology. 99:2132--2132. DOI: 10.1002/ecy.2440

Rassweiler, A, S. Harrer, D. Reed, C. Nelson, R. Miller. 2021. SBC LTER: REEF: Net primary production, growth and standing crop of Macrocystis pyrifera in Southern California ver 4. Environmental Data Initiative. https://doi.org/10.6073/pasta/bf6049d8abc0177c72564ff014b8fe6b. Accessed 2021-08-04.

Reed, D, R. Miller. (2021). SBC LTER: Reef: Long-term experiment: Kelp removal: Detritus biomass ver 23. Environmental Data Initiative. https://doi.org/10.6073/pasta/83b28bf44cb24efd52188c9e12998ddb. Accessed 2021-08-04.

Rodriguez, G. E., Reed, D. C., Holbrook, S. J. (2016). Blade Life Span, Structural Investment, and Nutrient Allocation in Giant Kelp. Oecologia. 182:397--404. DOI: 10.1007/s00442-016-3674-6driguez 2016

Ecology

Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems

Mae Rennick[1*], Bartholomew P. DiFiore[1*], Joseph Curtis[1], Daniel C. Reed[2], Adrian C. Stier[1,2]

[1]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93116, USA
[2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93116, USA

Appendix S3: *Experimental grazing rates of sea urchins*

We used an AIC-model selection approach to distinguish between competing hypotheses for the functional form of the relationship between consumer density and grazing rates. Specifically, we sought to determine if urchin grazing rates accelerated, decelerated, or increased in direct portion (i.e. linearly) to urchin density in mesocosm trials. Therefore, we fit linear, power-law, and sigmoid functions, and compared model fits using AIC.

Table S1. Coefficient estimates and AIC-comparison for competing models describing the relationship between purple urchin (*Strongylocentrotus purpuratus*) grazing rate (g m^{-2} d^{-1}) and urchin biomass density (g m^{-2}). Urchins foraged on giant kelp (*Macrocystis pyrifera*) blades in laboratory mesocosms.

Purple Urchins	Linear $G = \beta B + 0$			Power-law $G = \alpha B^{\beta}$			Sigmoid $G = \dfrac{\alpha B^2}{\beta^2 + B^2}$		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
β	0.02	0.02 – 0.03	**<0.001**	1.07	0.7 – 1.5	**<0.001**	1164.7	590.8 – 1738.6	**<0.001**
α				0.01	-0.02 – 0.05	0.472	59.23	31.2 – 87.3	**<0.001**
Observations	32			32			32		
R^2	0.824			-			-		
AIC	236.2			238.1			238.1		
ΔAIC	0.0			1.9			1.9		
LLV	-116.120			-116.043			-116.070		

Table S2. Coefficient estimates and AIC-comparison for competing models describing the relationship between purple urchin (*Strongylocentrotus purpuratus*) grazing rate (g m^{-2} d^{-1}) and urchin biomass density (g m^{-2}). Urchins foraged on giant kelp (*Macrocystis pyrifera*) blades in laboratory mesocosms.

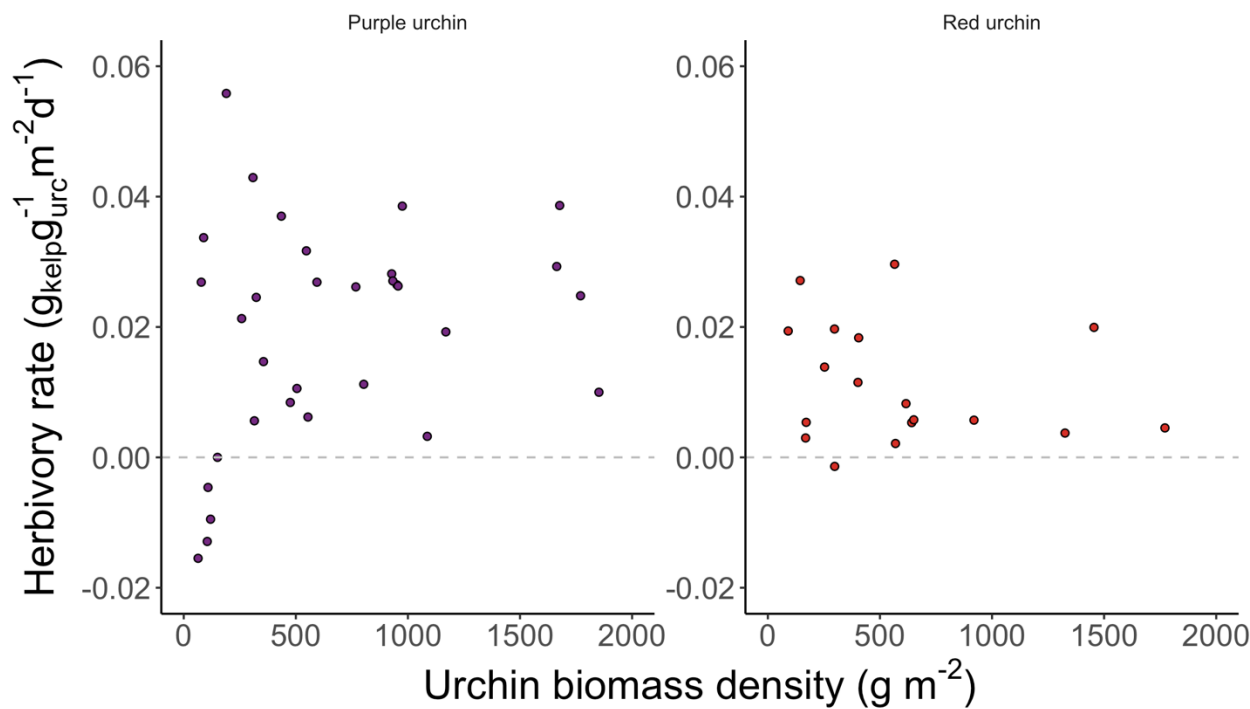| Red Urchins	Linear $G = \beta B + 0$			Power-law $G = \alpha B^\beta$			Sigmoid $G = \dfrac{\alpha B^2}{\beta^2 + B^2}$		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
β	0.01	0.01 – 0.01	**<0.001**	0.79	0.1 – 1.5	**0.036**	698.1	-6.6 – 1402.8	0.070
α				0.04	-0.1 – 0.2	0.683	15.5	3.3 – 27.6	**0.024**
Observations	18			18			18		
R^2	0.595			-			-		
AIC	117.6			119.3			119.8		
ΔAIC	0.0			1.7			2.2		
LLV	-56.815			-56.639			-56.886		

Figure S1. Herbivory rate of purple (left; *Strongylocentrotus purpuratus*) and red (right; *Mesocentrotus franciscanus*) sea urchins foraging on giant kelp blades (*Macrocystis pyrifera*) per unit of urchin biomass as a function of urchin biomass density. There was no evidence for trends in per unit biomass grazing rates for either species (*see results for model details*).

Ecology

Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems

Mae Rennick[1*], Bartholomew P. DiFiore[1*], Joseph Curtis[1], Daniel C. Reed[2], Adrian C. Stier[1,2]

[1]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93116, USA
[2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93116, USA

Appendix S4:

Table S1. Coefficients and model comparison for models describing the effect of urchin biomass density (g m^{-2}) and a binary dummy variable describing if predicted urchin consumption rates exceeded detrital supply on living kelp biomass density (g m^{-2}). Models were fit assuming gamma distributed errors with a log-link function in the glmmTBM package (Brooks et al. 2017). Marginal R^2 values consider only the variance explained by the fixed effects, while conditional R^2 values account for variance accounted for by both fixed and random effects (Nakagawa et al. 2017, Lüdecke 2021).

	Final Model			Model A			Model B			Model C		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	22.58	15.61 – 32.67	**<0.001**	61.97	45.77 – 83.91	**<0.001**	71.09	52.71 – 95.89	**<0.001**	2729.46	1888.56 – 3952.32	**<0.001**
Urchin biomass	3.89	2.75 – 5.51	**<0.001**	1.20	1.07 – 1.35	**0.002**				0.87	0.74 – 1.03	0.102
Detritus >= Consumption	171.61	120.01 – 245.40	**<0.001**	64.09	47.58 – 86.32	**<0.001**	52.84	40.59 – 68.79	**<0.001**			
Urchin biomass × Detritus >= Consumption	0.23	0.19 – 0.40	**<0.001**									
Random Effects												
σ^2		1.47			1.54			1.55			2.48	
τ$_{00}$		0.02 $_{site}$			0.01 $_{site}$			0.03 $_{site}$			0.12 $_{site}$	
		0.07 $_{year}$			0.11 $_{year}$			0.11 $_{year}$			0.27 $_{year}$	
Observations		595			595			595			595	
Marginal R^2 / Conditional R^2		0.695 / 0.712			0.658 / 0.683			0.652 / 0.680			0.014 / 0.143	
AIC		9564.7			9602.0			9608.7			10027.9	
ΔAIC		0.00			37.3			43.9			463.1	
LLV		-4775.3			-4795.0			-4799.4			-5008.9	

Table S2. Coefficient table for a linear mixed effects model describing the effect of the proportional difference between urchin grazing rate and detrital supply on the annual change in living kelp biomass. We estimated the proportional difference between grazing (G) and detrital supply (D), as $\frac{G_{s,t}-D_{s,t}}{G_{s,t}+D_{s,t}}$ for each site (s) and year (t).

Predictors	Estimates	CI	p
Intercept	-680.65	-1358.14 – -3.17	**0.049**
Proportional difference between consumption and detrital supply	-1486.79	-2051.12 – -922.46	**<0.001**

Random Effects

σ^2	11332652.54
$\tau_{00\ year}$	1049877.20
$\tau_{00\ site}$	58926.11
Observations	481
Marginal R^2 / Conditional R^2	0.055 / 0.139
Deviance	9200.892
AIC	9184.512
LLV	-4587.256

References

Brooks, M.E., K. Kristensen, K.J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Maechler, and B.M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378-400.

Lüdecke D (2021). _sjPlot: Data Visualization for Statistics in Social Science_. R package version 2.8.7, <URL:https://CRAN.R-project.org/package=sjPlot>.

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of The Royal Society Interface 14: 0213.