Ecology, 102(5), 2021, e03304

Variation in disturbance to a foundation species structures the dynamics of a benthic reef community

A. Raine Detmer,[1,3] Robert J. Miller,[2] Daniel C. Reed,[2] Tom W. Bell,[2] Adrian C. Stier,[1] and Holly V. Moeller[1]

[1] *Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[2] *Marine Science Institute, University of California, Santa Barbara, California 93106 USA*

Citation: Detmer A. R., R. J. Miller, D. C. Reed, T. W. Bell, A. C. Stier, and H. V. Moeller. 2021. Variation in disturbance to a foundation species structures the dynamics of a benthic reef community. Ecology 102 (5):e03304. 10.1002/ecy.3304

Abstract. Disturbance and foundation species can both have strong impacts on ecosystem structure and function, but studies of their interacting effects are hindered by the long life spans and slow growth of most foundation species. Here, we investigated the extent to which foundation species may mediate the impacts of disturbance on ecological communities, using the kelp forest ecosystem as a study system. Giant kelp (*Macrocystis pyrifera*) grows rapidly and experiences wave disturbance from winter storms. We developed and analyzed a model of the effects of variable storm regimes on giant kelp population dynamics and of the cascading effects on kelp-mediated competition between benthic community members in kelp forests. Simulations of severe storm regimes resulted in a greater abundance of understory macroalgae and a lower abundance of sessile invertebrates than did milder regimes. Both the cascading effects of periodic loss of giant kelp as well as the degree to which storms directly impacted the benthos (in the form of scouring) influenced the outcome of competition between benthic community members. The model's qualitative predictions were consistent with empirical data from a 20-yr time series of community dynamics, suggesting that interannual variability in disturbance that affects giant kelp abundance can have strong consequences for benthic community structure. Our findings point to the value of long-term studies in elucidating the interacting effects of disturbance and foundation species.

Key words: *competition; disturbance; foundation species; kelp forests; mathematical models.*

Introduction

Disturbances are major sources of environmental variability in many ecosystems and can play important roles in structuring ecological communities (Battisti et al. 2016). Disturbance can cause direct mortality, altered resource availability, and changes in ecosystem function (Battisti et al. 2016). Foundation species, habitat-forming organisms that dominate an ecosystem's biomass, are often disproportionately impacted by various forms of disturbance (Dayton 1972, Ellison et al. 2005). Usually at the base of the network of interactions that shape a given ecosystem, foundation species have strong connections to other organisms (Ellison 2019). Empirical and experimental studies have shown that shifts in foundation species abundance can cascade to affect entire communities (Dayton 1972, Peters and Yao 2012, Crotty et al. 2018, Miller et al. 2018), suggesting that the effects of disturbances on community structure may be mediated by how much disturbance impacts foundation species.

Understanding how disturbance and foundation species interact to influence community structure is of great importance to disturbance ecology. However, the role of temporally variable disturbance regimes and how they affect the dynamics of foundation species and the surrounding community remains only partially understood. To understand and predict how changes in disturbance intensity and frequency impact foundation species and, consequently, community composition and ecosystem function, studies of the effects of disturbance-driven fluctuations in foundation species abundance are needed (Castorani et al. 2018). Such studies are difficult to perform, as natural disturbance often happens at scales that require great effort to manipulate or observe, and many foundation species are slow-growing. Mechanistic models and study systems with dynamic foundation species can help with these challenges.

Here, we use giant kelp (*Macrocystis pyrifera*), a rapidly growing foundation species subject to variable disturbance regimes, to test these ideas. Often dominating subtidal reefs in southern California (Graham 2004, Miller et al. 2018), giant kelp is unique among foundation species in that it shows rapid inter- and intra-annual fluctuations in biomass (Reed et al. 2008, Reed et al. 2011, Cavanaugh et al. 2011). Large wave events can

Manuscript received 7 August 2020; accepted 12 November 2020. Corresponding Editor: Steven Morgan.
[3] E-mail: adetmer@ucsb.edu

cause extreme reductions in giant kelp biomass (Seymour et al. 1989, Reed et al. 2008, Bell et al. 2015), and kelp can rapidly recover after removal (Graham et al. 1997, Cavanaugh et al. 2011, Castorani et al. 2015).

The presence of giant kelp regulates kelp forest structure and function. The forests formed by giant kelp profoundly alter the reef habitat and are extremely productive ecosystems, supporting a diverse array of species (Schiel and Foster 2015, Miller et al. 2018). In addition to providing an energy source for kelp forest herbivores and habitat for reef-dwelling organisms (Schiel and Foster 2015), giant kelp also alters the benthic environment, where macroalgae and sessile invertebrates compete for physical space (Miller and Etter 2008, Arkema et al. 2009). The dense canopies formed by giant kelp can reduce the amount of light reaching the benthic community by up to 90% (Reed and Foster 1984, Santa Barbara Coastal LTER et al. 2020*b*). Shading by canopies of giant kelp has been shown to negatively affect understory macroalgae, which require sufficient light to grow (Pearse and Hines 1979, Clark et al. 2004, Miller et al. 2011). Some studies suggest that, by shading the benthos, giant kelp indirectly facilitates sessile invertebrates that may otherwise be outcompeted by macroalgae (Arkema et al. 2009, Miller et al. 2015). Therefore, it is possible that the frequency and intensity of major kelp-removing storms may influence whether the benthos is dominated by sessile invertebrates or understory macroalgae.

In order to synthesize these observations into a predictive framework, we developed a mechanistic model of the interactions between giant kelp, understory macroalgae, and sessile invertebrates that enabled us to quantify the cascading effects of variable disturbance frequency and intensity on benthic community composition (Fig. 1). Our model captured the dynamic response of giant kelp to disturbance by storms as well as the resulting effects on competition between benthic community members. We validated the model using a 20-yr data set on giant kelp abundance and benthic community

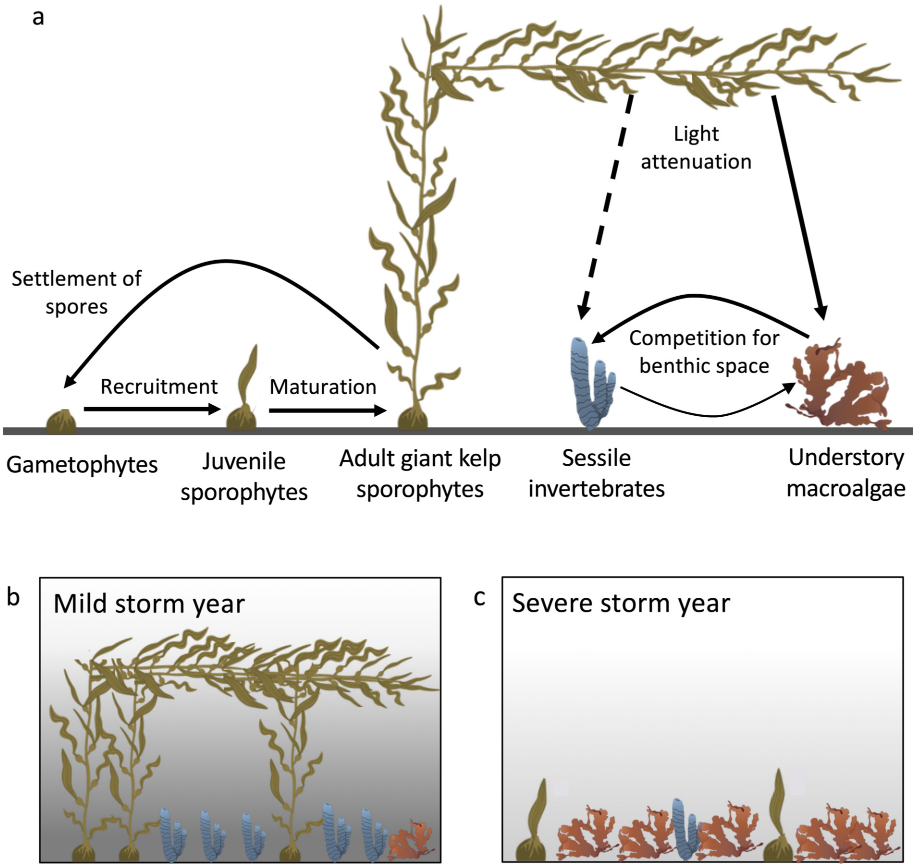

FIG. 1. Conceptual diagram of the system. (a) Life cycle of giant kelp and the main interactions between adult (mature) giant kelp, understory macroalgae, and sessile invertebrates. (b) Reef following a winter with mild storms; there is a dense canopy of mature giant kelp and the benthos is dominated by sessile invertebrates. (c) Reef following a winter with severe storms; there is some juvenile giant kelp, and the benthos is dominated by understory macroalgae. Image credit: Jane Thomas (giant kelp), Tracey Saxby (understory macroalgae), and Caroline Wicks (sponge), Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

composition collected as part of the Santa Barbara Coastal Long Term Ecological Research (SBC LTER) program. We simulated a range of storm regimes to quantify how direct disturbance (i.e., storm removal of benthic community members), foundation species-mediated disturbance (i.e., cascading effects mediated by giant kelp shading), and their combination impact benthic community composition. The model predicted shifts in benthic community composition that were largely consistent with empirical data, and it showed sensitivity to both the frequency and intensity of storms. Thus, our validated model allowed us to predict how changing disturbance regimes may impact community structure via effects on foundation species.

The Model

A stage-structured model for giant kelp

Giant kelp has a heteromorphic life cycle, with the large, canopy-forming diploid sporophyte generation alternating with small haploid gametophytes (Schiel and Foster 2015). Following other models of kelp population dynamics (Nisbet and Bence 1989, Burgman and Gerard 1990), we modeled giant kelp abundance using a three-stage model that accounts for the settlement of gametophytes, their recruitment into sporophytes, and the maturation of these sporophytes into adults (Fig. 1).

Gametophytes (G) arise from spores produced by external populations at a rate σ_{ext} as well as by local adults at a rate σ_A (see Table 1 for a list of all variables, parameters, and their meanings). Gametophytes recruit to the sporophyte stage at an intrinsic recruitment rate r_G modified by the amount of light reaching the bottom L_{benthos} (Rosenthal et al. 1974). Gametophytes that fail to recruit experience density-dependent mortality at a rate m_G:

$$\frac{dG}{dt} = \sigma_{\text{ext}} + \sigma_A A - r_G L_{\text{benthos}} G - m_G G^2 \qquad (1)$$

Juvenile sporophytes J are defined as sporophytes with fronds < 1m tall (Rassweiler et al. 2018). They arise from the recruitment of gametophytes ($r_G L_{\text{benthos}} G$). Like gametophytes, their maturation into adults depends upon an intrinsic growth rate r_J and benthic light supply, and they experience density-dependent mortality at a rate m_J

$$\frac{dJ}{dt} = r_G L_{\text{benthos}} G - r_J L_{\text{benthos}} J - m_J J^2 \qquad (2)$$

We modeled the adult giant kelp sporophytes A as frond density to account for the variable per-capita biomass observed in giant kelp (Rodriguez et al. 2013). Adult sporophyte fronds (Eq. 3) arise from the maturation of juveniles ($r_J L_{\text{benthos}} J$) and from the growth of existing adults. The maximum relative frond density is given by a carrying capacity K_A. We set $K_A = 1$, allowing us to scale our model, and its parameters, relative to a maximum frond density that may be variable across locations (Reed et al. 2008, Rodriguez et al. 2013). Individual biomass is tightly correlated with frond number (Reed et al. 2009, Rassweiler et al. 2018); thus, frond density is representative of the biomass density of giant kelp present in the ecosystem. Frond density grows logistically at a rate determined by frond growth rate g_A (a composite of frond initiation and extension rates) and the amount of light reaching the kelp canopy at the surface L_{surface}. Frond density decreases due to the senescence of fronds at a time-dependent rate $s_A(t)$

$$\frac{dA}{dt} = r_J L_{\text{benthos}} J + g_A A L_{\text{surface}} \frac{K_A - A}{K_A} - s_A(t) A. \qquad (3)$$

We modeled frond senescence using a phenomenological function that captures the ~ 100 day mean frond life span (Rodriguez et al. 2013) and synchronization of frond initiation (and subsequent growth and senescence) due to storms (Seymour et al. 1989, Cavanaugh et al. 2011, Cavanaugh et al. 2013, Rodriguez et al. 2013). Our model represents this storm-driven synchronization using a senescence function in which the degree of synchrony decays as a function of the time elapsed since the last major storm. Since the senescence of any fronds that remain after a storm will be largely asynchronous, we represented frond senescence $s_A(t)$ as a composite of two functions, one for the proportion of fronds f_{syn} that are synchronized ($a(t)$, a time-dependent sine function with a period of 110 d) and another for asynchronous fronds (a flat "baseline" senescence rate b).

$$s_A(t) = f_{\text{syn}}(t) a(t) + \left(1 - f_{\text{syn}}(t)\right) b \qquad (4)$$

For synchronized fronds, senescence follows the sinusoid senescence function $a(t)$:

$$a(t) = \begin{cases} 0 & t_{\text{sen}} < 150 \\ 0.05 \times \left(\sin\left(\frac{2\pi}{110} \times (t_{\text{sen}} - 70)\right) + 1\right) & t_{\text{sen}} \geq 150 \end{cases}$$

where the delay (150 d) accounts for the time it takes for new fronds to be initiated after complete removal of adult sporophytes, the amplitude (0.05) governs the magnitude of senescence, $2\pi/110$ rescales the period of the sine function to be consistent with a mean frond lifetime of 110 d (Rodriguez et al. 2013), t_{sen} represents the time elapsed since the last storm ($t_{\text{sen}} = t - t_{\text{storm}}$), the displacement of 70 d ensures that senescence peaks 110 d after frond initiation, and the shift of 1 ensures positive values for the senescence function.

The proportion of synchronized fronds f_{syn} decays exponentially with time since the last major storm t_{sen}. Immediately after a storm, a proportion φ_A of fronds remain (see *Periodic storm perturbations*) and continue

TABLE 1. Model variables and parameters.

Symbol	Description	Units	Simulation value
Variable			
G	giant kelp gametophytes	individuals/m^2	
J	juvenile (<1m) giant kelp sporophytes	individuals/m^2	
A	adult (≥1m) giant kelp frond density	fronds/m^2	
M	proportional cover of understory macroalgae		
I	proportional cover of sessile invertebrates		
t	time	d	
Parameter			
L_{surface}	surface irradiance	mol·m^{-2}·s^{-1}	1000
k_l	giant kelp frond extinction coefficient	m^2/fronds	2.3
σ_{ext}	supply rate of giant kelp gametophytes (via dispersal of spores) from external populations	individuals·m^{-2}·d^{-1}	0.0001
σ_A	rate of gametophyte production (via spore production) by local giant kelp sporophytes	individuals·frond^{-1}·d^{-1}	0.01
σ_M	rate of increase in benthic cover of understory macroalgae from external populations	d^{-1}	0.001
σ_I	rate of increase in benthic cover of sessile invertebrates from external populations	d^{-1}	0.0005
r_G	rate of recruitment of giant kelp gametophytes to juvenile sporophytes	m^2·s·mol^{-1}·d^{-1}	10^{-8}
r_J	rate of maturation of juvenile giant kelp sporophytes to adult sporophyte fronds	m^2·s·mol^{-1}·d^{-1}	0.00001
g_A	adult giant kelp frond growth rate	m^4·s·mol^{-1}·d^{-1}·fronds^{-1}	0.00009
g_M	understory macroalgae growth rate	m^2·s·mol^{-1}·d^{-1}	0.00006
g_I	sessile invertebrate growth rate	d^{-1}	0.008
m_G	giant kelp gametophyte mortality rate	m^2·individuals^{-1}·d^{-1}	1
m_J	juvenile giant kelp sporophyte mortality rate	m^2·individuals^{-1}·d^{-1}	1
s_M	understory macroalgae senescence rate	d^{-1}	0.009
s_I	sessile invertebrate senescence rate	d^{-1}	0.002
K_A	giant kelp frond carrying capacity	maximum proportion of fronds/m^2	1
S_T	total substrate space available for understory macroalgae and sessile invertebrate growth	proportion	1
α	competition coefficient of sessile invertebrates on understory macroalgae		0.8
β	competition coefficient of understory macroalgae on sessile invertebrates		1.25
b	baseline rate of giant kelp frond senescence	d^{-1}	0.0125
c	rate of decay in synchrony of giant kelp frond senescence		0.015
φ_A	proportion of pre-storm density of giant kelp fronds remaining after a storm		[0, 1]
φ_b	proportion of pre-storm abundance of benthic organisms remaining after a storm		[0, 1]

to experience asynchronous senescence. Newly initiated fronds $(1 - \varphi_A)A$ are synchronized; this synchrony decays because fronds senesce (and are reinitiated) stochastically (Rodriguez et al. 2013). The proportion of fronds that remain synchronized decays exponentially according to

$$f_{\text{syn}}(t) = (1 - \varphi_A)e^{-c(t_{\text{sen}} - 150)}$$

Collectively, the senescence function $s_A(t)$ captures a near-zero senescence rate following a major storm (i.e., a small value of A), a large synchronized senescence event roughly 100 d following the initiation of the first adult fronds, and the gradual decay of synchronicity as the proportion of asynchronous fronds increases (Appendix S1: Fig. S1).

Light-mediated benthic competition

We modeled the composition of the benthic community by accounting for the fractional cover of two major guilds: understory macroalgae (e.g., subcanopy kelps and small low-lying foliose and filamentous algae) and sessile invertebrates (e.g., bryozoans, sponges, anthozoans, ascidians, bivalves), which compete with macroalgae for physical space (Arkema et al. 2009). To model this, we assumed that for a given patch of reef the total space on the benthos (S_T) is composed of the space occupied by understory macroalgae (M), the space occupied by sessile invertebrates (I), and empty space that is not occupied by either of these groups (S_E). We ignored space occupied by giant kelp holdfasts, as a study on natural reefs along the Santa Barbara coast found no significant correlation between interannual variability in the percent cover of macroalgae and sessile invertebrates and interannual variability in the percent cover of kelp holdfasts (Arkema et al. 2009). Total space on the benthos (S_T) can therefore be written as

$$S_T = M + I + S_E$$

We set S_T equal to one, meaning that M and I represent the proportion of the benthos covered by understory macroalgae and sessile invertebrates, respectively.

We modeled competition for empty space following the classic Lotka-Volterra competition equations (with competition coefficients α and β). The growth rate of understory macroalgae depends upon light availability at the benthos, and both guilds experience senescence (s) and have a source of external propagules (σ)

$$\frac{dM}{dt} = g_M M L_{\text{benthos}} \frac{(S_T - M - \alpha I)}{S_T} - s_M M + \sigma_M \tag{5}$$

$$\frac{dI}{dt} = g_I I \frac{(S_T - I - \beta M)}{S_T} - s_I I + \sigma_I. \tag{6}$$

Because the growth of understory macroalgae depends upon benthic light availability, the outcome of competition is shaped by the abundance of giant kelp. We modeled light attenuation by giant kelp fronds using the Lambert-Beer law, in which light decays exponentially from surface levels according to the absorptivity of the water column

$$L_{\text{benthos}} = L_{\text{surface}} e^{-k_l A}.$$

When A is at its maximum value (i.e., $A = K_A$, the maximum density of adult sporophyte fronds), ~10% of surface irradiance reaches the bottom (Reed and Foster 1984, Santa Barbara Coastal LTER et al. 2020*b*). Thus, the attenuation coefficient k_l is ~2.3.

Periodic storm perturbations

We used a kick-flow approach to model disturbance caused by winter storms in this system. Storms are simulated by interrupting the "flows" of the differential equation simulation with a "kick" that instantaneously perturbs the state variables (here, abundances of giant kelp, understory macroalgae, and sessile invertebrates). When a storm occurs, the frond density of adult kelp sporophytes is reduced to a proportion φ_A of pre-storm abundance, and the abundance of juvenile kelp sporophytes, understory macroalgae, and sessile invertebrates is reduced to ψ_b of pre-storm abundance (Eqs. 7–10). Giant kelp gametophytes are assumed to be small enough that they suffer negligible damage (i.e., $\varphi = 1$)

$$A = \varphi_A A_{t-1} \tag{7}$$

$$J = \varphi_b J_{t-1} \tag{8}$$

$$M = \varphi_b M_{t-1} \tag{9}$$

$$I = \varphi_b I_{t-1}. \tag{10}$$

Generally, φ_A (survival of "adult" canopy-forming fronds) is assumed to be smaller than φ_b (survival of benthic organisms) because tall giant kelp fronds experience greater drag and are more strongly impacted by storm-generated swells than shorter or low-lying benthic organisms (Dayton and Tegner 1984). During mild storms, $\varphi_b = 1$ because organisms growing near the benthos suffer little damage. To simulate severe storms that rip out all of the adult kelp and scour the benthos with sediment and rocks, we set $\varphi_A = 0$ and $\varphi_b < 1$ (Appendix S1: Fig. S2). Although severe storms have been reported to damage the benthos (Ebeling et al. 1985, Seymour et al. 1989, Dayton et al. 1989), exactly how benthic damage scales with giant kelp removal is, to our knowledge, not quantified. Therefore, we performed simulations of differing levels of benthic scouring and compared these findings with LTER data. All model simulations were performed using R 3.2.3 (R Core Team 2018).

MODEL ANALYSIS AND COMPARISON WITH LTER DATA

Effect of storms on giant kelp dynamics

We first focused on how disturbance intensity affects this system over the course of a single year. We simulated years with either severe or mild winter storms and then validated our model by comparing our results with monthly LTER data on frond density from "mild" and "severe" years (Santa Barbara Coastal LTER et al. 2020*a*). We differentiated between mild and severe years using data on kelp frond density in March (an indication of removal due to winter storms, Cavanaugh et al. 2011, Reed et al. 2011), month of peak kelp frond density (indicative of recovery time, Cavanaugh et al. 2011), and significant wave heights from a spectral refraction wave hindcast model (to identify years with wave events large enough to remove kelp holdfasts, Coastal Data Information Program; Bell et al. 2015, O'Reilly et al. 2016; model *available online*).[4] A more detailed description of these analyses is given in Appendix S1: *Giant kelp dynamics.* For each year, we converted frond density to

---

[4] http://cdip.ucsd.edu/MOP_v1.1/

normalized frond density such that the maximum density in a given year had a value of 1, with all other densities in the year scaled accordingly. We then computed the average monthly normalized frond densities of all the years in each class. In years with relatively mild storms, kelp recovered quickly, and fronds reached their peak density early in the year (Fig. 2a). In years with severe winter storms, recovery was slow and kelp fronds did not reach their maximum density until late in the year (Fig. 2b and c). For severe years, we performed an ensemble run with our model in which we varied the timing of severe storms over the winter season over the range of dates of large wave events in the wave model hindcasts (5 December–1 March, see Appendix S1: Fig. S4). We computed the average frond density throughout the following year and compared this to the observed averages from severe years (Fig. 2b). We also selected an individual severe year (2010) and compared its monthly frond densities to a simulation in which the timing of severe storms aligned with the wave model hindcasts for that year (Fig. 2c).

Cascading effects of storm regimes on benthic cover

We then investigated whether there were differences in the composition of the benthic community in “mild” and “severe” years. Using the same storm regimes described above, we ran three simulations representing potential levels of storm damage to the benthos: one in which severe storms left the benthos intact (no scouring), one in

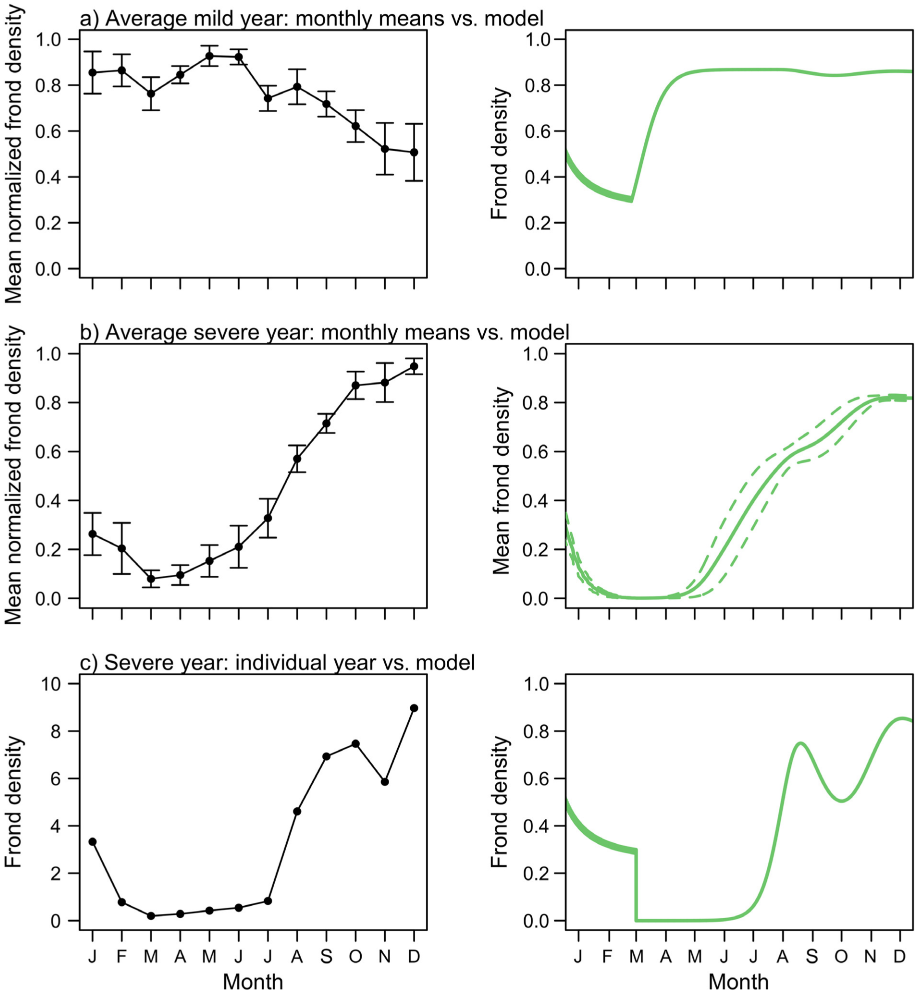

FIG. 2. Time series of mild and severe storm years. (a) Average normalized frond density in each month of the mild years (2007, 2009, 2011, and 2015) compared to a model simulation of a mild year, in which mild storms ($\varphi_A = 0.95$) occurred every day between December and March. (b) Average normalized frond density in each month of the severe years (2006, 2008, 2010, and 2014) compared to the average frond density resulting from an ensemble run of severe ($\varphi_A = 0$) winter storms in which severe storms occurred between 5 December and 1 March (dashed lines are 95% confidence intervals). The error bars represent the standard error. (c) Monthly density of fronds at Mohawk in a representative severe year (2010) compared to the model output when a severe storm was simulated on the same date as the one that occurred that year.

which severe storms scoured the benthos but did less damage than to adult giant kelp (intermediate scouring), and one in which storms did equal damage to the benthos and adult giant kelp (proportional scouring); see Appendix S1: Fig. S2 for visualization of these scenarios. Regardless of scour type, severe storms drove reductions in sessile invertebrate cover and increases in understory macroalgal cover in severe storm years compared to mild storm years. The differences in cover between mild and severe years increased with the severity of scouring (Fig. 3a).

Using data on benthic cover from the SBC LTER (Santa Barbara Coastal LTER and Reed 2020*a*), we then calculated the mean cover of sessile invertebrates and understory macroalgae on Mohawk Reef in mild and severe years (Fig. 3b; see Appendix S1: *Analyses of benthic cover* for details on our analyses). We found that the percent cover of understory macroalgae was significantly higher in severe years than mild years ($t = -12.95$, $P << 0.001$), while the percent cover of sessile invertebrates was significantly lower in severe years ($t = 5.26$, $P << 0.001$).

Shifts in benthic community composition over interannual timescales

Having compared our model's predictions to the dynamics at Mohawk Reef over intra-annual timescales, we next used higher temporal resolution LTER data to investigate whether our model could produce interannual benthic community dynamics similar to those observed at Mohawk. These data are collected seasonally as part of the SBC LTER's long-term kelp removal experiment (Santa Barbara Coastal LTER and Reed 2020*b*); only data from the control plot (no kelp removal) were included in our analyses. For each sampling date, we calculated the average percent cover of sessile invertebrates and understory macroalgae (excluding giant kelp holdfasts) across all sampling locations, as well as the density of giant kelp fronds (Fig. 4a). We determined the years in which major storms occurred (Appendix S1: Fig. S4; vertical black lines, Fig. 4), and ran a model simulation in which severe storms (with intermediate benthic scouring; $\varphi_A = 0$ and $\varphi_b = 0.1$) occurred at the same time points as in the wave model hindcast data set. Our model predicted community shifts over similar time scales (Fig. 4). In particular, both the data and model show rapid increases in understory macroalgae following storms, and, in 2008 and 2010, increases in sessile invertebrates over longer timescales. However, natural benthic communities are much more dynamic than our model predicts, with all three groups showing additional changes in abundance unrelated to our identified storms (Fig. 4a).

Effects of varying storm frequency and severity on giant kelp and benthic cover

To investigate how future changes in storm regimes may affect this system, we evaluated the model's

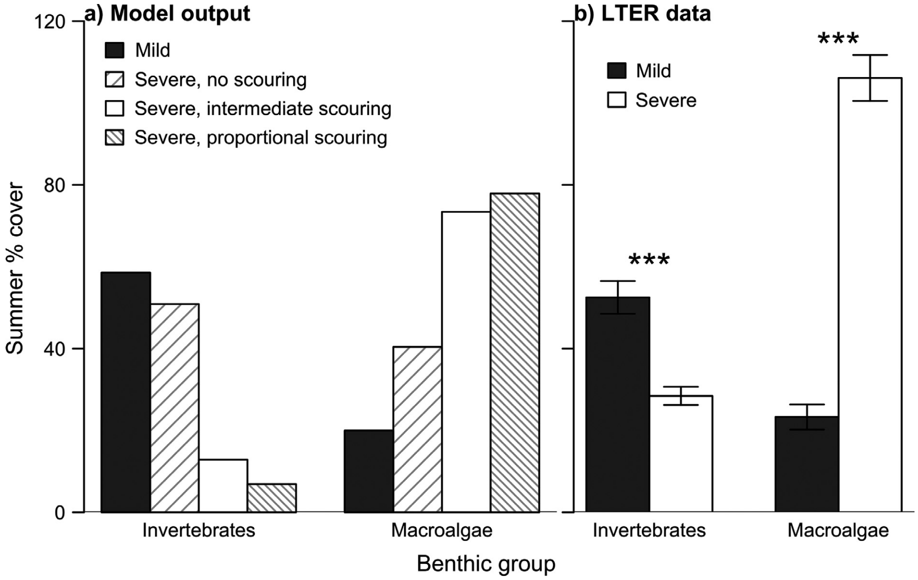

FIG. 3. Percent cover of sessile invertebrates and understory macroalgae in mild vs. severe years. (a) Percent cover of sessile invertebrates and understory macroalgae as given by model simulations of mild and severe years. Values were taken from the summer (15 July) of each simulated year in order to correspond to when annual LTER data are collected. In the "severe, no scouring" scenario, severe winter storms did not damage the benthos ($\varphi_b = 1$). In the "severe, intermediate scouring" and "severe, proportional scouring" scenarios, severe storms scraped the benthos to varying degrees ($\varphi_b = 0.1$ and $\varphi_b = 0$, respectively). Mild storms did not scour the benthos in any simulations. (b) Average percent cover of sessile invertebrates and understory macroalgae in the summer at Mohawk reef in mild ($n = 4$) and severe ($n = 4$) years. Error bars represent standard error. *** $P < 0.001$.

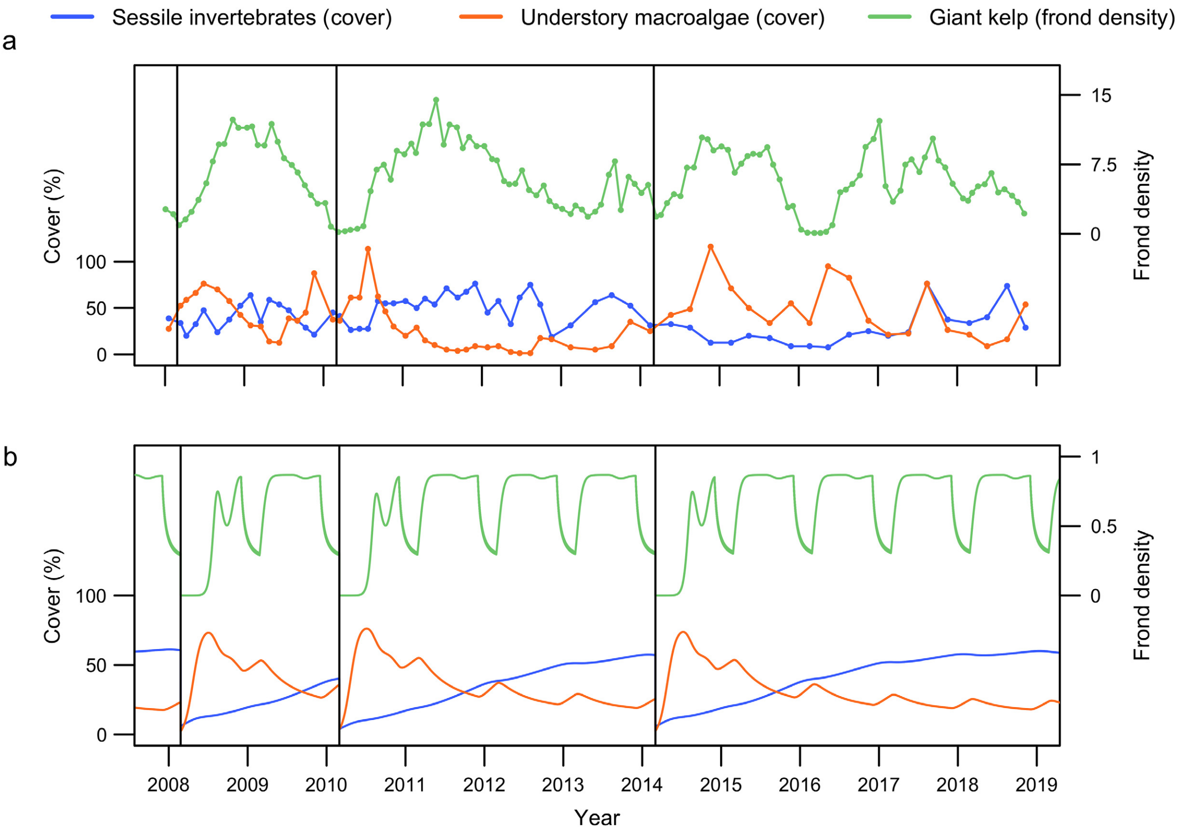

FIG. 4. Storm regimes and benthic community dynamics. (a) Giant kelp frond density (green) and mean percent cover of sessile invertebrates (blue) and understory macroalgae (orange) on Mohawk Reef from January 2008 to November 2019. Major wave events (see Appendix S1: Fig. S4) are marked with black vertical lines. (b) Model simulation of a similar storm regime.

sensitivity to both the frequency and intensity of major kelp-removing storms. We simulated severe storm frequencies ranging from one every five years to one every year (with mild storms occurring each winter). At each frequency, we also varied storm intensity: the proportion of adult giant kelp sporophytes remaining (φ_A) ranged from 0.3 (least severe) to 0 (most severe). The proportion of benthic community members remaining (φ_b) was varied according to each of the three levels of scouring: no scouring (least severe), intermediate scouring, and proportional scouring (most severe; Appendix S1: Fig. S2). Finally, we ran simulations in which only juvenile giant kelp sporophytes, but not understory macroalgae or sessile invertebrates, were scoured. This allowed us to separate direct (clearing of benthic space) and indirect (increases in benthic light availability due to removal of kelp sporophytes) effects of scouring.

Our model predicted that understory macroalgae dominate the benthos in summer only under high frequencies of intense winter storms (Fig. 5). However, when storms removed understory macroalgae and sessile invertebrates, the level of disturbance required for understory macroalgae to dominate decreased relative to the scenarios without benthic scouring and with scouring of juvenile giant kelp sporophytes only (Fig. 5, Appendix S1: Fig. S5). Increasing the frequency of high-intensity ($\varphi_A = 0$) winter storms resulted in a decrease in the summer abundances of adult giant kelp and sessile invertebrates and an increase in the summer abundance of understory macroalgae, but the magnitude of these changes in abundance varied depending on the scouring scenario (Fig. 5). When the entire benthos was scoured, the storm frequency at which benthic dominance “flipped” between sessile invertebrates and understory macroalgae (vertical lines in Fig. 5) decreased with increasing degrees of benthic scouring (Fig. 5). When only juvenile giant kelp sporophytes were scoured, the effects of increasing storm frequency on benthic composition varied slightly with the degree of scouring but were overall very similar in each scenario (Fig. 5). When storm frequency was kept fixed, we found that the system was generally resilient to changes in storm intensity until very high intensities were reached (Appendix S1: Fig. S6).

DISCUSSION

Foundation species support entire communities, and shifts in their abundance can have cascading

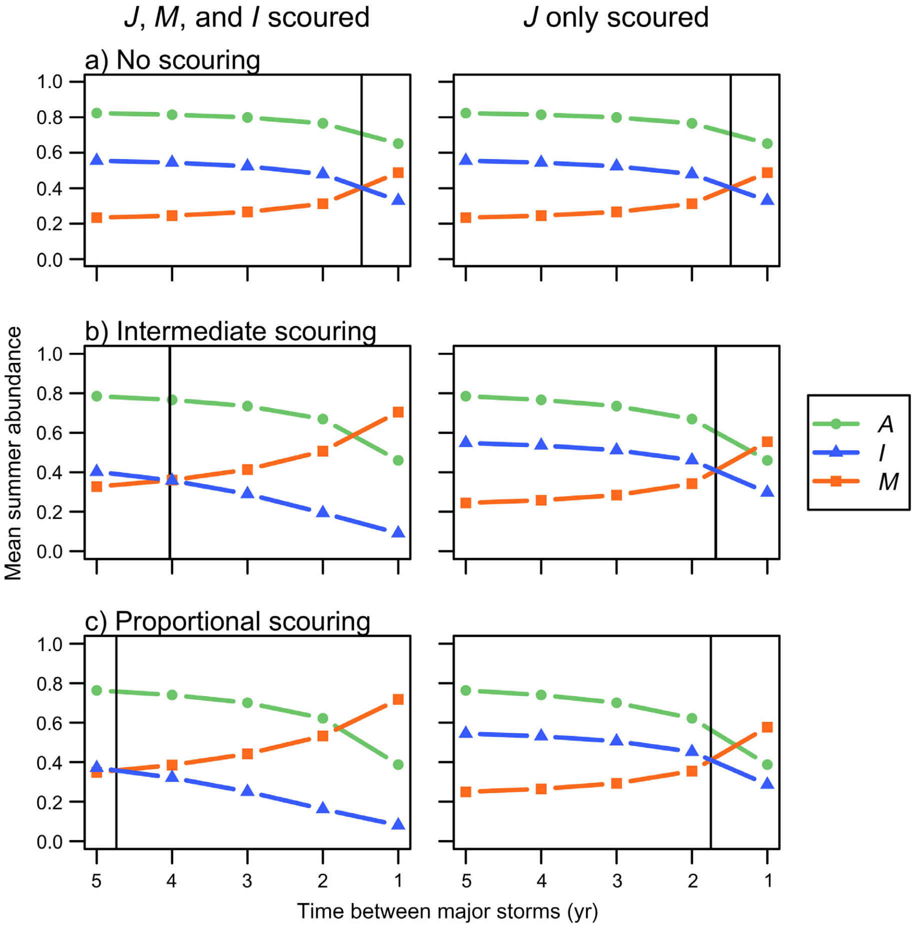

FIG. 5. Effects of storm frequency on giant kelp and the benthic community. The average frond density of adult giant kelp *A* (green), fractional cover of understory macroalgae *M* (orange), and fractional cover of sessile invertebrates *I* (blue) are shown from model simulations with different frequencies of high-intensity ($\varphi_A = 0$) storms. Averages were computed using summer (July–-September) abundances across all years in a single storm cycle. Simulations were run with (a) no scouring, (b) intermediate scouring, and (c) proportional scouring. In the left column, all benthic organisms (except giant kelp gametophytes) were scoured, while in the right column, only juvenile giant kelp sporophytes *J* were scoured. The storm frequencies at which dominance flips between sessile invertebrates and understory macroalgae are denoted with vertical black lines.

consequences for community structure. Here, we combined a novel mathematical model and a 20-year data set on the fast-growing foundation species giant kelp (*Macrocystis pyrifera*), the storms that remove its biomass, and the benthic community modulated by its presence. Our study provides an example of how disturbances and foundation species can jointly promote the coexistence of competitors. Our Lotka-Volterra model of benthic competition predicts competitive exclusion, but whether understory macroalgae or sessile invertebrates are competitively dominant depends on the level of light reaching the benthos. By causing fluctuations in giant kelp abundance (and thus benthic irradiance), periodic storms can prevent one benthic group from being competitively dominant for long enough to exclude the other. Previous studies have demonstrated that variation in the spatial distribution (patch size) of foundation species can influence biodiversity; this is seen when, for example, the habitats formed at the edges and interiors of patches support different species (Crotty et al. 2018). Our results suggest that temporal variability in the abundance of a foundation species may influence diversity in a similar way: when foundation species are volatile, the resulting environmental heterogeneity can promote the coexistence of species with different resource requirements. In the case of giant kelp, periodic disturbance can be an important driver of such volatility. In this way, our findings support the Intermediate Disturbance Hypothesis (Sousa 1979), as coexistence between benthic community guilds is driven by periodic disturbance.

However, our model showed that benthic scouring (which “reset” benthic cover by scouring the benthos) was also necessary for maintenance of benthic diversity. Because kelp grows rapidly, when it is removed understory macroalgae have a limited window of time in which to become established before the kelp canopy shades them out (Foster 1975*a*). If storms leave the benthos undisturbed (our modeled no scouring scenario), understory macroalgal growth following kelp removal is limited because most substrate is still occupied by invertebrates. When storms damage the benthos and remove existing organisms (our intermediate and proportional scouring scenarios), understory macroalgae can quickly colonize the emptied substrate and inhibit invertebrate recovery. These results are consistent with those of other studies that found that the effects of kelp removal on the benthic community differed depending on whether or not the benthos was disturbed (Arkema et al. 2009), and they reinforce the importance of available substrate to understory macroalgal and sessile invertebrate abundance (Witman 1987, Miller et al. 2018, Castorani et al. 2018).

The role of variable storm regimes in driving giant kelp biomass and subtidal reef community structure is of both scientific and conservation interest. Climate models predict that global climate change may cause increases in storm severity and frequency along much of giant kelp's range (Ummenhofer and Meehl 2017). In southern California, severe storms currently occur at a frequency of approximately once every 3.5 yr (Byrnes et al. 2011). Giant kelp populations are generally capable of recovering between these events (Bell et al. 2015), and our results and those of previous studies suggest that this periodic disturbance may promote coexistence in kelp forests (Byrnes et al. 2011, Castorani et al. 2018). However, our model predicts that if storms intensify and increase in frequency, the annual removal of giant kelp may enable understory macroalgae to remain dominant throughout each year (Fig. 5). This shift to a continuously macroalgae-dominated benthos could potentially lead to reductions in the diversity of mobile predators that feed on sessile invertebrates, thus having cascading impacts on the kelp forest community (Miller et al. 2018).

Under contemporary conditions, our model predicts that giant kelp forests are resilient: even after severe storms, the kelp canopy recovers (though the timing of this recovery varies with storm frequency and intensity, Fig. 5). However, our model likely overestimates the resilience of giant kelp, as kelp abundance is only reduced by storms and senescence. Other major impacts on kelp growth and abundance, such as temperature stress, nutrient limitation, and herbivory by sea urchins, were not included (Jackson 1977, Harrold and Reed 1985, Cavanaugh et al. 2019). These missing factors may explain why our model does not capture several large declines in frond density observed at Mohawk Reef (Fig. 4). We also did not consider variable population connectivity (external supply was kept constant), but external propagule supply may also impact kelp patch resilience (Castorani et al. 2015). Thus, severe storms that extirpate multiple, connected kelp patches could impact the persistence of giant kelp (and consequently sessile invertebrates) more severely than our model predicts.

Our model groups benthic community members into coarse categories of understory macroalgae and sessile invertebrates, ignoring potentially important functional distinctions between species. For instance, understory macroalgae have diverse life histories, resource requirements, and growth forms (Foster 1975*a*). The macroalgae we modeled most closely resemble shade-intolerant ephemeral species, which recruit in the spring when canopy cover is low, rapidly increase in biomass, and then die later in the year (Foster 1975*a*). The traits of shade-tolerant perennial species, which tend to persist during high kelp years, were not accounted for. These species include mid-canopy kelps, which may have less of a negative effect on sessile invertebrate abundance than do understory algae (Arkema et al. 2009). Mid-canopy kelps dominate macroalgal biomass on local reefs (Lamy et al. 2020) but are poorly represented in the LTER percent cover data we analyzed (Santa Barbara Coastal LTER and Reed 2020*a*, *b*). Consequently, percent cover is not an accurate indicator of the abundance of these species, and our analyses may have underestimated their effects on sessile invertebrates.

Sessile invertebrates are also more diverse than modeled here. In our model, the growth and senescence rates of sessile invertebrates are such that this group can fluctuate greatly in abundance within the span of a year. Thus, our model likely best represents fast-growing, ephemeral species like some bryozoans (Foster 1975*b*) and our results may be inaccurate for long-lived, slow-growing species (e.g., gorgonians) whose populations respond to environmental changes over longer time scales (Grigg 1977). Another potentially important distinction is between epilithic (living on the substrate) and endolithic (living within the substrate) species. A recent study found that these groups responded differently to annual removal of giant kelp, with kelp removal sites having lower endolithic but higher epilithic invertebrate biomass than control sites (Castorani et al. 2018).

Although stylized, our mathematical representation of kelp forest dynamics allows us to formalize data-driven hypotheses not easily tested with existing data or manipulative experiments. For example, the model enhances our ability to understand the extent to which changes in different parameters alter the outcome of competition between understory macroalgae and sessile invertebrates. This allows for causal inferences that are not easy to get at by simply analyzing time series data. Further, the model enables us to examine how changes in kelp demographic rates, disturbance regimes (e.g., storm frequency and severity), and interaction strengths under varying environmental conditions influence community structure. Such syntheses allow us to better leverage long-term ecological data sets.

CONCLUSION

Our work highlights the value of mathematical models as tools to synthesize long-term data sets, formalize hypotheses about the key processes occurring in complex systems, and predict changes in these processes over time. The results of this study support the idea that disturbance-driven fluctuations in the abundance of foundation species can have cascading effects on associated communities. In the case of dynamic foundation species such as giant kelp, periodic turnovers in biomass due to disturbance and rapid recovery can result in variable resource availability. Here, we found that one consequence of this environmental heterogeneity is that it can promote the temporal coexistence of competitors. Future work could investigate the extent to which this may be true in other systems, as well as additional ways in which the impacts of disturbance on ecological communities may be mediated by foundation species.

Acknowledgements

We thank Max Castorani for providing the results of his light attenuation analyses, Andrew Rassweiler and Alexandra Brown for helpful discussions on kelp senescence functions, and Bart DiFiore and members of the Moeller Lab at the University of California, Santa Barbara for comments and feedback on manuscript drafts. We also thank Clint Nelson and the many staff and students of the Santa Barbara Coastal Long Term Ecological Research program for their assistance in collecting the data. This research was supported by an NSF REU stipend and NSF Graduate Research Fellowship (to A. R. Detmer) and by the U.S. National Science Foundation's Long-Term Ecological Research program under the Division of Ocean Sciences grants 9982105, 0620276, 1232779 and 1831937. A. R. Detmer, A. C. Stier, and H. V. Moeller designed the research, and A. R. Detmer and H.V. Moeller developed the mathematical model. A. R. Detmer analyzed the model, incorporated empirical data, and drafted the manuscript. T. W. Bell, R. J. Miller, and D. C. Reed contributed data and modifications to the model. All authors contributed to writing the paper.

Literature Cited

Arkema, K. K., D. C. Reed, and S. C. Schroeter. 2009. Direct and indirect effects of giant kelp determine benthic community structure and dynamics. Ecology 90:3126–3137.

Battisti, C., G. Poeta, and G. Fanelli. 2016. An introduction to disturbance ecology: a road map for wildlife management and conservation. Springer International Publishing, Cham, Switzerland.

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 42:2010–2021.

Burgman, M. A., and V. A. Gerard. 1990. A stage-structured, stochastic population model for the giant kelp Macrocystis pyrifera. *Marine Biology 105:15–23.*

Byrnes, J. E., D. C. Reed, B. J. Cardinale, K. C. Cavanaugh, S. J. Holbrook, and R. J. Schmitt. 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. Global Change Biology 17:2513–2524.

Castorani, M. C. N., D. C. Reed, F. Alberto, T. W. Bell, R. D. Simons, K. C. Cavanaugh, D. A. Siegel, and P. T. Raimondi. 2015. Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system. Ecology 96:3141–3152.

Castorani, M. C. N., D. C. Reed, and R. J. Miller. 2018. Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. Ecology 99:2442–2454.

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.

Cavanaugh, K. C., D. C. Reed, T. W. Bell, M. C. N. Castorani, and R. Beas-Luna. 2019. Spatial variability in the resistance and resilience of giant kelp in southern and Baja California to a multiyear heatwave. Frontiers in Marine Science 6:413.

Cavanaugh, K., D. Siegel, D. Reed, and P. Dennison. 2011. Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. Marine Ecology Progress Series 429:1–17.

Clark, R. P., M. S. Edwards, and M. S. Foster. 2004. Effects of shade from multiple kelp canopies on an understory algal assemblage. Marine Ecology Progress Series 267:107–119.

Crotty, S. M., S. J. Sharp, A. C. Bersoza, K. D. Prince, K. Cronk, E. E. Johnson, and C. Angelini. 2018. Foundation species patch configuration mediates salt marsh biodiversity, stability and multifunctionality. Ecology Letters 21: 1681–1692.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81–96 in *Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas, USA.*

Dayton, P., R. Seymour, P. Parnell, and M. Tegner. 1989. Unusual marine erosion in San Diego County from a single storm. Estuarine, Coastal, and Shelf Science 29:151–160.

Dayton, P., and M. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science 224:283–285.

Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. Marine Biology 84:287–294.

Ellison, A. M. et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Ellison, A. M. 2019. Foundation species, non-trophic interactions, and the value of being common. IScience 13:254–268.

Foster, M. 1975*a*. Algal succession in a Macrocystis pyrifera *forest. Marine Biology 32:313–329.*

Foster, M. 1975*b*. Regulation of algal community development in a Macrocystis pyrifera *forest. Marine Biology 32:331–342.*

Graham, M. H. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems 7:341–357.

Graham, M., C. Harrold, S. Lisin, K. Light, J. Watanabe, and M. Foster. 1997. Population dynamics of giant kelp Macrocystis pyrifera *along a wave exposure gradient. Marine Ecology Progress Series 148:269–279.*

Grigg, R. W. 1977. Population dynamics of two gorgonian corals. Ecology 58:278–290.

Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169.

Jackson, G. A. 1977. Nutrients and production of giant kelp, Macrocystis pyrifera*, off southern California. Limnology and Oceanography 22:979–995.*

Lamy, T., C. Koenigs, S. J. Holbrook, R. J. Miller, A. C. Stier, and D. C. Reed. 2020. Foundation species promote community stability by increasing diversity in a giant kelp forest. Ecology 101:e02987.

Miller, R. J., and R. J. Etter. 2008. Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. Ecology 89:452–462.

Miller, R. J., K. D. Lafferty, T. Lamy, L. Kui, A. Rassweiler, and D. C. Reed. 2018. Giant kelp, Macrocystis pyrifera*, increases faunal diversity through physical engineering. Proceedings of the Royal Society B 285:20172571.*

Miller, R. J., H. M. Page, and D. C. Reed. 2015. Trophic versus structural effects of a marine foundation species, giant kelp (Macrocystis pyrifera*). Oecologia 179:1199–1209.*

Miller, R. J., D. C. Reed, and M. A. Brzezinski. 2011. Partitioning of primary production among giant kelp (Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. Limnology and Oceanography 56: 119–132.*

Nisbet, R. M., and J. R. Bence. 1989. Alternative dynamic regimes for canopy-forming kelp: a variant on density-vague population regulation. American Naturalist 134:377–408.

O'Reilly, W., C. Olfe, J. Thomas, R. Seymour, and R. Guza. 2016. The California coastal wave monitoring and prediction system. Coastal Engineering 116:118–132.

Pearse, J. S., and A. H. Hines. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. Marine Biology 51:83–91.

Peters, D. P. C., and J. Yao. 2012. Long-term experimental loss of foundation species: consequences for dynamics at ecotones across heterogeneous landscapes. Ecosphere 3:27.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rassweiler, A., D. C. Reed, S. L. Harrer, and J. C. Nelson. 2018. Improved estimates of net primary production, growth, and standing crop of Macrocystis pyrifera *in Southern California. Ecology 99:2132.*

Reed, D. C., and M. S. Foster. 1984. The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. Ecology 65:937–948.

Reed, D. C., A. Rassweiler, and K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89:2493–2505.

Reed, D., A. Rassweiler, and K. Arkema. 2009. Density derived estimates of standing crop and net primary production in the giant kelp Macrocystis pyrifera*. Marine Biology 156:2077–2083.*

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 92:2108–2116.

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 94:1848–1858.*

Rosenthal, R. J., W. D. Clarke, and P. K. Dayton. 1974. Ecology and natural history of a stand of giant kelp, Macrocystis pyrifera, off Del Mar, California. Fishery Bulletin 72:670–684.

Santa Barbara Coastal LTER, A. Rassweiler, S. Harrer, D. Reed, and J. Nelson. 2020*a*. SBC LTER: Reef: Net primary production, growth and standing crop of Macrocystis pyrifera *in Southern California ver 3. Environmental Data Initiative. https://doi.org/10.6073/pasta/e2a696a11bd57eddc25e5eb4657fe59a*

Santa Barbara Coastal LTER & Reed, D. 2020*a*. SBC LTER: Reef: Kelp Forest Community Dynamics: Cover of sessile organisms, Uniform Point Contact ver 28. Environmental Data Initiative. https://doi.org/10.6073/pasta/dc0668f21c9c8d73d28727d4c5371fe9

Santa Barbara Coastal LTER & Reed, D. 2020*b*. SBC LTER: Reef: Long-term experiment: Kelp removal: Cover of sessile organisms, Uniform Point Contact ver 27. Environmental Data Initiative. https://doi.org/10.6073/pasta/9ef0a3d317f6553e1600a0e5af016e43

Santa Barbara Coastal LTER, D. Reed, and S. Harrer. 2020*b*. SBC LTER: Kelp removal experiment: hourly photon irradiance at the surface and seafloor ver 17. Environmental Data Initiative. https://doi.org/10.6073/pasta/19a018572f8e42624151497f7da3706f

Schiel, D. R., and M. S. Foster. 2015. The biology and ecology of giant kelp forests. University of California Press, Berkeley, California, USA.

Seymour, R. J., M. J. Tegner, P. K. Dayton, and P. E. Parnell. 1989. Storm wave induced mortality of giant kelp, Macrocystis pyrifera*, in Southern California. Estuarine, Coastal, and Shelf Science 28:277–292.*

Sousa, W. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Ummenhofer, C. C., and G. A. Meehl. 2017. Extreme weather and climate events with ecological relevance: a review. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160135.

Witman, J. D. 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecological Monographs 57:167–187.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3304/suppinfo

DATA AVAILABILITY STATEMENT

All data and code used in this study are available at http://doi.org/10.5281/zenodo.4284015. The full data sets used are available on the Santa Barbara Coastal Long Term Ecological Research Program's website: https://sbclter.msi.ucsb.edu/data/index.html.