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Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities

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Abstract. Disturbances often cause the disproportionate loss of foundation species but understanding how the frequency and severity of disturbance to such organisms influence biological communities remains unresolved. This gap in knowledge exists in part because of the rarity of ecologically meaningful studies capable of disentangling different elements of disturbance. Hence, we carried out a long-term (9 yr), large-scale (2,000 m^2 plots), spatially replicated (4 sites) field experiment in which we manipulated disturbance to a globally distributed marine foundation species, the giant kelp *Macrocystis pyrifera*, and tracked community responses over time. To distinguish the effects of disturbance frequency and severity on the biodiversity and composition of temperate rocky reef communities, we simulated the repeated loss of giant kelp from destructive winter waves across a background of natural variation in disturbance. By following the response of over 200 taxa from the surrounding community, we discovered that the frequency of disturbance to giant kelp changed the biomass, diversity, and composition of community guilds in a manner commensurate with their dependence on the physical (i.e., benthic light and space), trophic (i.e., living and detrital biomass), and habitat (i.e., biogenic structure) resources mediated by this foundation species. Annual winter disturbance to giant kelp reduced living and detrital giant kelp biomass by 57% and 40%, respectively, enhanced bottom light by 22%, and halved the seafloor area covered by giant kelp holdfasts. Concomitantly, the biomass of understory algae and epilithic sessile invertebrates more than doubled, while the biomass of rock-boring clams, mobile invertebrates, and fishes decreased 30–61%. Frequent loss of giant kelp boosted understory algal richness by 82% and lowered sessile invertebrate richness by 13% but did not affect the biodiversity of mobile fauna. In contrast to changes driven by disturbance frequency, interannual variation in the severity of disturbance to giant kelp had weaker, less consistent effects, causing only modest changes in assemblages of sessile invertebrates, mobile invertebrate herbivores, and fishes. Our results broaden the foundation species concept by demonstrating that repeated disturbance to a dominant habitat-forming species can outweigh the influence of less frequent but severe disturbances for the surrounding community.

Key words: biodiversity; competition; dominant species; field experiment; habitat; kelp forest; long-term ecological research; resources; species interactions; wave disturbance.

INTRODUCTION

Ecological disturbances are discrete events that change resources or the physical environment and disrupt ecosystem structure (White and Pickett 1985). Variations in disturbance frequency (number of events over time) and severity (magnitude or extent of impact) interact with species attributes (e.g., susceptibility to disturbance, dispersal ability, competitive strength) to structure ecological communities. Understanding the separate and combined roles of these disturbance elements is important and urgent because humans mediate disturbance in many ecosystems, and climate models predict global changes in disturbance frequency and severity over the coming decades (Turner et al. 2003, Ellison et al. 2005, Ummenhofer and Meehl 2017).

It is especially pressing to resolve the role of variation in the frequency and severity of disturbances that affect foundation species because these dominant habitat-forming organisms are often disproportionately impacted by disturbance (Dayton 1972, Ellison et al. 2005), and their loss can have cascading impacts on biodiversity, species interactions, and ecosystem processes (Dayton et al. 1992, Thomsen et al. 2010, Peters and Yao 2012). Such impacts occur because foundation species are often primary producers that create biogenic structure and disturbances to them change the physical environment, trophic resources, and the quality and quantity of habitat (Ellison et al. 2005, Miller et al. 2018). Ecological theory predicts that increasing disturbance to dominant species can reduce competitive exclusion and shift community structure towards inferior competitors and their associated assemblages (Amarasekare 2003). Indeed, disturbances to dominant plants have been shown to alter resource availability and restructure surrounding forest (Ellison et al. 2005, 2010) and steppe (Collins 2000, Prevéy et al. 2010, Peters and Yao 2012) communities. In coastal ecosystems, variation in marine heatwaves that bleach coral reefs (Fabina et al. 2014), ice that scours canopy-forming seaweeds in the rocky intertidal (Petraitis and Dudgeon 1999), and waves that destroy seagrass meadows (Castorani et al. 2014) changes habitat availability, competitive interactions, and community structure. However, experimentally assessing the consequences of foundation species loss are typically

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challenged by the long durations necessary to observe multiple disturbance events and capture community succession (Ellison et al. 2005, 2010).

Despite progress towards understanding how individual elements of disturbance affect communities, the relative importance of disturbance frequency, severity, and their interaction remains poorly understood (Miller 1982, Trexler et al. 2005, Miller et al. 2011, 2012). In fact, investigations of how disturbance influences biodiversity typically treat the frequency and severity of disturbance as interchangeable, contributing to disagreements or uncertainty in disturbance–diversity relationships (e.g., the intermediate disturbance hypothesis; Connell 1978, Mackey and Currie 2001, Amarasekare 2003, Fox 2013, Sheil and Burslem 2013). Moreover, disturbance frequency and severity are often conflated by natural environmental fluctuations and challenging to experimentally test with replication *in situ* over realistic scales due to feasibility and ethical constraints (Trexler et al. 2005). Thus, investigations capable of disentangling disturbance frequency and severity have been primarily limited to spatially unreplicated, small-scale (e.g., <50 m^2 sampling units), and short-term (e.g., 1–3 yr) studies that only partially capture community responses (Miller 1982, McCabe and Gotelli 2000, Turner et al. 2003, Trexler et al. 2005, Ellison et al. 2010).

In light of these gaps in knowledge, we evaluated the hypothesis that variation in the frequency and severity of disturbance to a foundation species causes predictable reorganization of the surrounding community, changing species abundances, community composition, and biodiversity. Specifically, we predicted that foundation species loss would have the greatest effects on community guilds that utilize or reply upon key physical, trophic, or habitat resources altered by the foundation species. To test our hypotheses, we carried out a uniquely long-term (up to 9 yr), large-scale (2,000 m^2 plots), spatially replicated (4 sites) field experiment in which we manipulated disturbance to the giant kelp *Macrocystis pyrifera*, a broadly distributed coastal marine foundation species (Fig. 1A). We augmented the frequency of disturbance above a natural baseline by repeatedly simulating annual disturbance to giant kelp (mimicking destructive winter waves) and quantified interannual variation in disturbance severity by measuring the amount of giant kelp lost during winter as a result of natural and experimental mortality. By following changes to important resources mediated by giant kelp and the response of the surrounding community (205 taxa across all trophic levels), we were able to disentangle the effects of disturbance frequency and severity on community structure in a highly valued temperate reef ecosystem. In doing so, our study broadens both the foundation species concept and predictions from disturbance theory by linking them in a mechanistic framework.

METHODS

Study system

The giant kelp *Macrocystis pyrifera* (Fig. 1A) is the largest and most broadly distributed kelp species, forming extensive

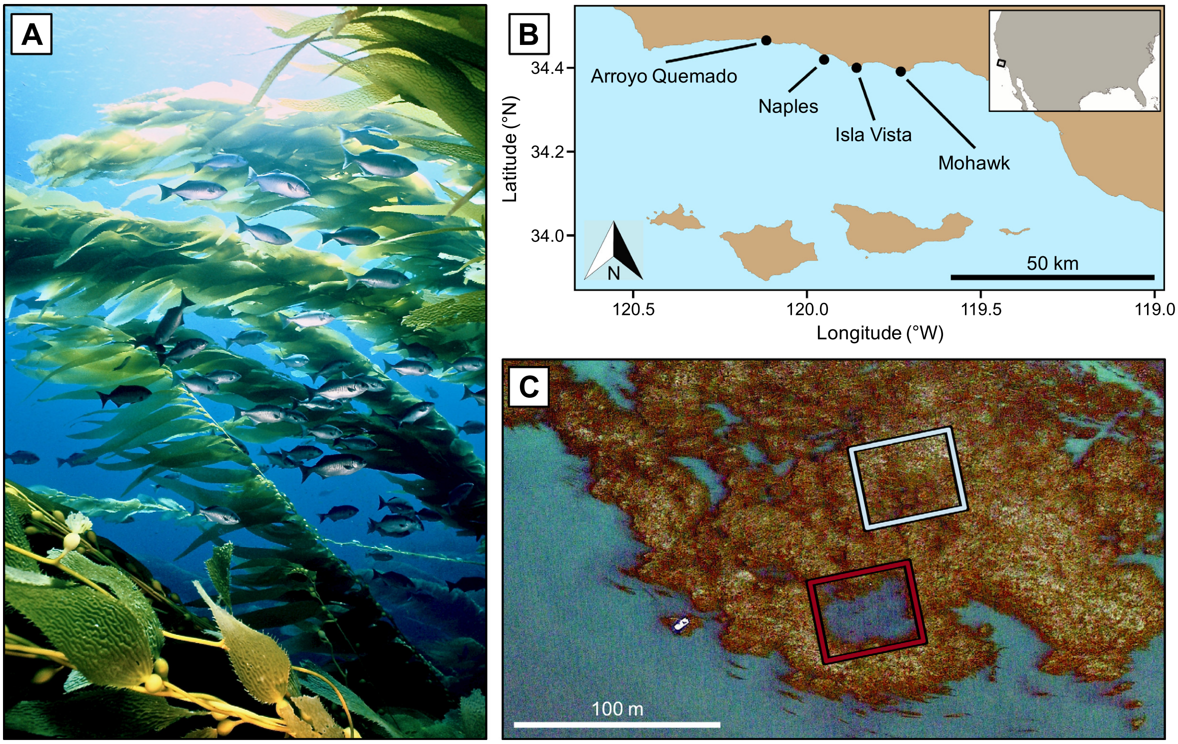

FIG. 1. Overview of the study system and experiment. (A) Giant kelp is a globally distributed foundation species that structures coastal biodiversity and ecosystem structure by forming expansive, highly productive marine forests (photo credit: Ron McPeak). (B) Disturbance to giant kelp was experimentally manipulated over 9 yr at four sites near Santa Barbara, California, USA. (C) Satellite image of Mohawk reef showing giant kelp canopy (dark brown areas) overlaid with the delineation of paired 2,000 m^2 plots, with low-frequency disturbance (i.e., control) plots in light blue and high-frequency disturbance (i.e., annual removal) plots in red (photo credit: 2013 Google, DigitalGlobe).

and highly productive forests on shallow (5–30 m depth) temperate rocky reefs. As a foundation species, giant kelp influences the structure and function of coastal ecosystems by modifying physical (e.g., light, space, hydrodynamics), trophic (i.e., living and detrital biomass), and biogenic habitat resources available to co-occurring algae, invertebrates, fishes, seabirds, and marine mammals (Schiel and Foster 2015). As such, the loss of giant kelp can change local biodiversity (Graham 2004, Miller et al. 2018) and productivity (Reed et al. 2008, 2011).

Giant kelp sporophytes (the large, habitat-forming life stage) consist of a holdfast anchored to the seafloor and a bundle of buoyant vegetative fronds extending to the ocean's surface (Fig. 1A). Because giant kelp spans the entire water column and experiences significant drag forces, it is highly susceptible to disturbance from large waves that break or dislodge adult sporophytes (Seymour et al. 1989, Bell et al. 2015*a*). Consequently, giant kelp suffers disproportionately greater loss from wave disturbance relative to other macroalgae (Dayton et al. 1992). Particularly severe disturbances can result in the local extinction of giant kelp; however, dispersal from neighboring populations and rapid growth following colonization enable most local populations to recover within 1–2 yr (Castorani et al. 2015, 2017). The frequency and intensity of destructive waves vary over space and time based on the interaction between fluctuations in regional processes that generate waves (e.g., climate, oceanography) and local differences in realized wave impacts (e.g., depth, exposure, coastal geomorphology).

We focused on giant kelp forests located off the coast of Santa Barbara, California, USA (Fig. 1B). In this region, giant kelp biomass peaks between summer and autumn, followed by declines during winter when wave disturbance is greatest (Reed et al. 2008, 2009, 2011). Beneath the giant kelp canopy lies a diverse understory of smaller kelps and other seaweeds (Fig. 1A, Harrer et al. 2013, Reed et al. 2016). This sessile community is shared with a diversity of suspension-feeding invertebrates living upon or within the reef substrate, such as sponges, anthozoans, tunicates, bryozoans, and bivalves (Arkema et al. 2009, Reed et al. 2016). Sessile benthic flora and fauna tend to rely strongly on the physical resources modified by giant kelp (e.g., light, space; Arkema et al. 2009, Miller et al. 2018). Bottom-dwelling mobile invertebrates include several herbivores that feed upon giant kelp and other algae (e.g., sea urchins, gastropods; Leighton 1966, Foster et al. 2015), as well as many carnivores that may depend on prey abundance or the quality and quantity of biogenic habitat (e.g., sea stars, lobsters, crabs, whelks; Mai and Hovel 2007, Withy-Allen and Hovel 2013). Giant kelp forests are also associated with a diversity of highly mobile and mainly carnivorous fishes (Fig. 1A; Allen et al. 2006), many of which rely on giant kelp or understory algae for habitat (Carr 1989, Holbrook et al. 1990, Schmitt and Holbrook 1990, Sievers et al. 2016).

The study was conducted at four reefs (sites), each separated by at least 10 km (Fig. 1B): Arroyo Quemado (120.12 °W, 34.47 °N), Mohawk (119.73 °W, 34.39 °N), Naples (119.95 °W, 34.42 °N), and Isla Vista (119.86 °W, 34.40 °N). Sites supported large giant kelp forests on sedimentary reefs (shale, mudstone, sandstone) at 5.1–9.3 m depth. We commenced our experiment at Arroyo Quemado, Mohawk, and Naples in January 2008 and later extended it to Isla Vista in October 2011. After establishing Naples as a study site in 2008, the kelp forest there was overgrazed by sea urchins until the end of 2010, precluding our ability to manipulate disturbance to giant kelp; hence, we excluded the first three years of data from this site. The experiment was continued at all sites until December 2016.

Experimental design

We manipulated the frequency of disturbance to giant kelp using a paired experimental design in which we designated two adjacent 40 m × 50 m plots at each of the 4 sites (8 total plots; Fig. 1C), with one plot receiving annual experimental disturbance (high frequency) and the other plot treated as an unmanipulated control (low frequency). In high-frequency disturbance plots, divers removed all giant kelp each winter (mid-February) to simulate annual mortality from wave disturbances that are most destructive during this time (Reed et al. 2011, Bell et al. 2015*a*). Low-frequency disturbance plots were subject only to natural disturbances that occurred less frequently than manipulations. In contrast to our annual experimental disturbances, giant kelp forests in the study region typically experience large wave disturbances once every 3.5 yr (Byrnes et al. 2011) and the average duration of local persistence for giant kelp patches in southern California is 4 yr (Castorani et al. 2015). However, giant kelp forests in other regions are disturbed more frequently (e.g., typically once per year in central California, USA; Reed et al. 2011, Bell et al. 2015*b*). Moreover, climate models predict changes in the frequency and severity of wave disturbances in California and other areas throughout the world that support giant kelp forests (Ummenhofer and Meehl 2017).

The severity of disturbance varied among plots and years based on the amount of giant kelp lost due to experimental removal and natural causes, mostly from large waves that are concentrated between November and March (Reed et al. 2011, Bell et al. 2015*a*). To quantify interannual variation in these losses, we defined disturbance severity as a continuous variable equal to the maximal decline in giant kelp biomass from autumn to spring (i.e., the greatest decline from mid-November to mid-February, or from mid-February to mid-May). Disturbance severity was highly variable in both low-frequency and high-frequency disturbance plots due to variation among plots and years in the amount of giant kelp available for experimental or natural removal and the intensity of winter waves. Disturbance severity did not differ significantly between low-frequency and high-frequency disturbance treatments ($t_{52} = 1.9$, $P = 0.12$), and the frequency and severity of disturbance were not conflated in statistical models (variance inflation factor, VIF = 1.6, where $\text{VIF} = 1/[1 - R^2]$; Zuur et al. 2009, 2010).

Sampling of physical, trophic, and habitat resources

We measured how disturbance altered important physical, trophic, and habitat resources that may be directly mediated by giant kelp. To estimate how disturbance to giant kelp affects herbivore food availability, we measured living and detrital biomass of giant kelp because it is the preferred food source of sea urchins (Leighton 1966, Foster et al. 2015), the most important herbivores in the system (Schiel and Foster 2015). As measures of food and habitat, we estimated living giant kelp biomass by counting fronds over 1 m tall within permanent 40 m × 2 m transects that bisected each plot (1 transect per plot) and converted to dry mass using an allometric relationship (Reed et al. 2009). We measured the wet mass of accumulated giant kelp detritus (i.e., detached blades and stipes) collected from six permanent 1 m^2 quadrats spaced uniformly along each transect.

To estimate how disturbance to giant kelp affects light available to understory algae, we measured the irradiance of photosynthetically active radiation at the seafloor within each plot every minute using light intensity loggers (MDS-MkV/L, Alec Electronics, Kobe, Japan). We summed irradiance data to obtain values for daily irradiance and averaged these for each season.

To estimate how disturbance to giant kelp affects the amount of benthic space available to other sessile organisms, we measured the percentage of the seafloor covered by giant kelp holdfasts using a uniform point contact (UPC) method at 80 paired points spaced every 1 m on either side of a 1 m wide band centered on each transect line.

Community sampling

We tracked community composition and biodiversity within each plot over time by estimating the biomass of all benthic organisms (i.e., those residing within, upon, or near the seafloor) within the 40 m × 2 m transects described previously (1 per plot). For each transect, we estimated the density or percent cover of understory macroalgae and invertebrates located either in the entire transect sampling area, in six 1 m^2 quadrats spaced every 8 m along the transect line, or at 80 paired points using the UPC method described previously, depending on species attributes (e.g., sessile vs. mobile, solitary vs. colonial; see Harrer et al. 2013, Reed et al. 2016). We counted all fishes within the transect area and up to 2 m from the seafloor, and visually estimated the length of each individual counted. For all organisms, we converted measures of abundance and size to dry biomass using taxon-specific relationships developed for the study region (Reed et al. 2016, Harrer et al. 2013, Rassweiler et al. 2018).

From 2008 to 2012, we sampled plots for all variables every 6.5 weeks (twice per season). From 2013 to 2016, we reduced sampling to every 13 weeks (once per season) during mid-February, mid-May, mid-August, and mid-November (corresponding to winter, spring, summer, and autumn, respectively). We averaged measurements made within each season during 2008–2012 to produce a single estimate per plot per season for all 9 yr. In winter, sampling was carried out prior to giant kelp removal from disturbance plots.

Statistical analyses

For each plot and season, we calculated the total biomass, species richness, and species evenness (Pielou's *J*) of understory macroalgae, sessile invertebrates, mobile invertebrates, and fishes. We further subdivided the biomass of sessile invertebrates into epilithic (i.e., living attached to and above the reef substrate) and endolithic (i.e., two species of rock-boring pholad clams that reside nearly entirely within the reef substrate). Similarly, we subdivided mobile invertebrates into those that are primarily herbivorous and primarily carnivorous according to Byrnes et al. (2011).

We specified a set of linear mixed-effect models (LMMs) to estimate the influence of disturbance frequency and severity on ecological resources (living and detrital giant kelp biomass, irradiance, holdfast cover) and aggregate community metrics of each guild (biomass, richness, evenness). Models predicted univariate responses as a function of disturbance frequency (low vs. high) and severity (a continuous measure) while controlling for covariates in the form of season and time since the experiment was initiated at that site. To control for any possible differences in the initial conditions of each plot, we used the first measurement of each response variable collected prior to experimental manipulation as a covariate (Diggle et al. 2013), except for giant kelp detritus and benthic light availability, which were not collected at all sites until after the experiment had commenced. We predicted that the effects of disturbance might amplify over time, and thus, we tested the interaction between disturbance frequency and time since the experiment was initiated. Where this interaction was significant, we tested whether slopes differed from zero using two-sided *t* tests in R 3.4.4 (R Core Team 2017) with the package *emmeans* 1.0 (Lenth 2017). We tested whether the effects of disturbance frequency or severity depended on season, but this interaction was not significant in any models and was dropped. Because we were not interested in the effects of season and time *per se*, we focused our description of the results on the effects of disturbance frequency, severity, and their interactions with covariates where significant ($P < 0.05$). We calculated estimated marginal means (i.e., adjusted means) that describe the unbiased effects of disturbance frequency and severity while controlling for fixed covariates using *emmeans* (Lenth 2017). All reported effect sizes are based on covariate-adjusted estimated marginal means. In addition to fixed factors, all models included a random intercept and slope over time for each site due to the repeated measures design and because we selected sites from a range of possible reefs and were not interested in quantifying site-specific effects (Pinheiro and Bates 2000, Zuur et al. 2009, 2010, Diggle et al. 2013).

We analyzed univariate models in R using the package *nlme* 3.1-131 (Pinheiro et al. 2017) and assessed the significance of model terms using *F* tests (Zuur et al. 2009). We checked for homogeneity of variance by plotting normalized model residuals against model predictions and individual predictors. We specified heterogeneous covariance structures where necessary to meet the assumptions of homoscedasticity (Pinheiro and Bates 2000, Zuur et al. 2009, 2010). We ensured normality of residuals using histograms and quantile-quantile plots. To meet this assumption, the percent cover of giant kelp holdfasts was arcsine transformed and living and detrital giant kelp, understory algae, sessile invertebrates, mobile invertebrate carnivores, and fishes were log transformed ($ln[x + 1]$) for models of biomass. We checked for high frequencies of zeroes in response variables using frequency plots; zero inflation was not found. We inspected data for collinearity using VIF; in all cases, collinearity was very low (VIF < 2.2; Zuur et al. 2009, 2010). All models satisfied assumptions of independent, homogeneous, and normally distributed Pearson residuals. Sample autocorrelation function analysis showed no evidence for temporal autocorrelation among residuals (Zuur et al. 2009, 2010, Diggle et al. 2013); semi-variograms and bubble plots showed no evidence of spatial autocorrelation among residuals (Zuur et al. 2009, 2010).

To estimate the influence of disturbance frequency and severity on the composition of community guilds, we analyzed Bray-Curtis dissimilarity of taxon-specific biomass using distance-based redundancy analysis (dbRDA), a multivariate multiple regression approach using constrained ordination (Legendre and Legendre 2012), in R using the package *vegan* 2.4-2 (Oksanen et al. 2017). All dbRDA models were conditional on the site to control for site-specific effects not focal to our questions (Legendre et al. 2011, Legendre and Legendre 2012). For each guild, models predicted community composition as a function of fixed factors and their interactions as described previously for LMMs. To determine the significance of dbRDA model terms, we used permutation tests (10,000 randomizations; Legendre and Legendre 2012). Prior to fitting dbRDA models, we checked data for multivariate homogeneity of group dispersions using a permutation-based test (10,000 randomizations); multivariate heterogeneity was not found for any community guilds or covariate groups. We calculated similarity percentages (SIMPER; using *vegan*) to decompose the contribution of individual taxa to overall Bray-Curtis dissimilarities between communities in low-frequency and high-frequency disturbance treatments (Legendre and Legendre 2012). For taxa identified as important in SIMPER analysis (i.e., those contributing ≥1% to the overall Bray-Curtis dissimilarity between treatments), we quantified how increased disturbance frequency affected taxon biomass using the log response ratio (i.e., the binary logarithm of the ratio of mean taxon biomass between disturbance treatments, $\log_2[\bar{x}_H/\bar{x}_L]$, where $\bar{x}_H$ is the mean taxon biomass in high-frequency disturbance plots and $\bar{x}_L$ is the mean taxon biomass in low-frequency disturbance plots; Hedges et al. 1999).

Our analyses consisted of several statistical tests, increasing the likelihood of false positives. Thus, we controlled the false discovery rate (i.e., the proportion of false positives among all significant hypotheses) using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995, García 2004). All reported P values are Benjamini-Hochberg adjusted.

RESULTS

Physical, trophic, and habitat resources

As predicted, more frequent disturbance reduced living giant kelp biomass by 57% (Fig. 2A) and accumulated giant kelp detritus by 40% (Fig. 2B, Table 1). With a reduced canopy, more frequent disturbance increased bottom irradiance by 22% (Fig. 2C, Table 1). Higher disturbance

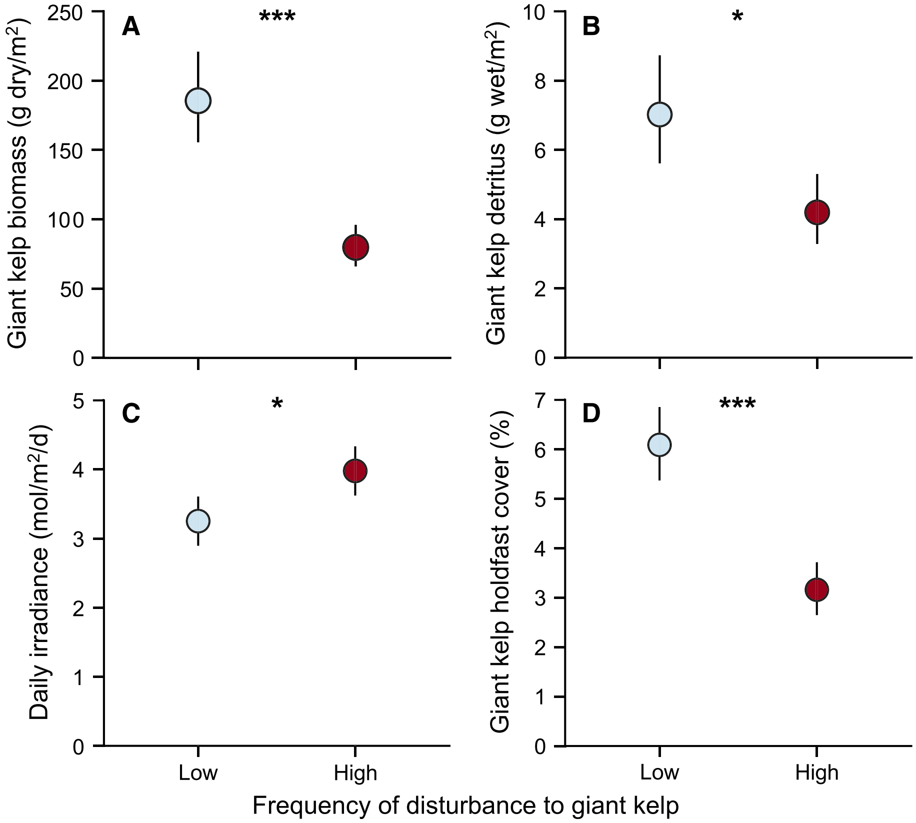

FIG. 2. Experimental increases in the frequency of disturbance to giant kelp altered ecological resources by reducing (A) living and (B) detrital giant kelp biomass, (C) enhancing daily irradiance at the seafloor, and (D) decreasing the percentage of the seafloor area covered by giant kelp holdfasts. Points indicate estimated marginal means (adjusted for fixed covariates) and error bars show 95% confidence intervals. Asterisks indicate the level of significance in the difference (*P < 0.05; **P < 0.01; ***P < 0.001).

frequency also enhanced space availability through a relative decrease of 48% in the seafloor area occupied by giant kelp holdfasts (6.1% vs. 3.2%; Fig. 2D, Table 1). In contrast to disturbance frequency, interannual variation in disturbance severity had no detectable effects on detrital giant kelp biomass, bottom light availability, or benthic space occupied by giant kelp holdfasts (Table 1). As expected, disturbance severity had a moderate negative association with giant kelp biomass (Appendix S1: Fig. S1).

Table 1. Results of analysis of ecological resources.

Response variable and source of variation	df	*F*	*P*
A. Giant kelp biomass*			
Disturbance frequency	1	37.3	**<0.001**
Disturbance frequency × Time since start	1	1.5	0.31
Disturbance severity	1	15.2	**<0.001**
Initial giant kelp biomass	1	24.4	*<0.001*
Season	3	10.9	*<0.001*
Time since start	1	2.1	0.22
Residual	204		
B. Giant kelp detritus*			
Disturbance frequency	1	5.4	**0.046**
Disturbance frequency × Time since start	1	0.6	0.51
Disturbance severity	1	1.1	0.39
Season	3	10.0	*<0.001*
Time since start	1	21.4	*<0.001*
Residual	205		
C. Bottom irradiance			
Disturbance frequency	1	8.4	**0.012**
Disturbance frequency × Time since start	1	0.5	0.57
Disturbance severity	1	1.0	0.42
Season	3	18.9	*<0.001*
Time since start	1	0.7	0.48
Residual	93		
D. Percent cover of giant kelp holdfasts†			
Disturbance frequency	1	27.4	**<0.001**
Disturbance frequency × Time since start	1	4.7	0.11
Disturbance severity	1	0.1	0.14
Initial percent cover of giant kelp holdfasts	1	2.3	0.094
Season	3	7.4	*0.002*
Time since start	1	1.4	0.45
Residual	196		

Notes: Bold face indicates $P < 0.05$ for disturbance frequency, severity, and their interactions. Italics indicate $P < 0.05$ for covariates.

*Log transformed ($ln[x + 1]$).

†Arcsine transformed.

Understory algae and sessile invertebrates

Consistent with our hypotheses, the strongest response to frequent disturbance to giant kelp was by sessile benthic flora and fauna. However, these guilds responded divergently based on whether they live above or below the reef substrate. More frequent disturbance to giant kelp was associated with an average of 123% greater biomass of understory algae (Fig. 3A), a difference that steadily widened over the duration of the study from 43% to 234% (Table 2A, *disturbance frequency × time since start*; Appendix S2: Fig. S1). Similarly, increased disturbance frequency resulted in an average of 100% greater biomass of epilithic sessile invertebrates (Fig. 3B, Table 2A), a difference that widened slightly over the course of the experiment as biomass declined more rapidly in low-frequency disturbance plots than in high-frequency disturbance plots (Table 2A, *disturbance frequency × time since start*; Appendix S2: Fig. S1). On the other hand, the biomass of endolithic sessile invertebrates declined by 56% with more frequent disturbance (Fig. 3C, Table 2A).

Disturbance frequency also changed the biodiversity of sessile guilds. More frequent disturbance to giant kelp resulted in 82% more species of understory algae (7.4 vs. 13.5 species; Fig. 4A, Table 2B; 51 observed taxa) but a 9% drop in understory algal evenness (Fig. 4F, Table 2C) as some species flourished more than others (Fig. 5A). Increased disturbance frequency was associated with 13% fewer species of sessile invertebrates (12.8 vs. 11.1 species; Fig. 4B, Table 2B; 64 observed taxa) but no change in the evenness of this guild (Fig. 4G, Table 2C). Along with these aggregate changes, increased disturbance frequency significantly altered the composition of understory algae and sessile invertebrate guilds, mainly due to 48–75% decreases in the biomass of rock-boring clams and 47–450% increases in the biomass of common understory kelps, red algae,

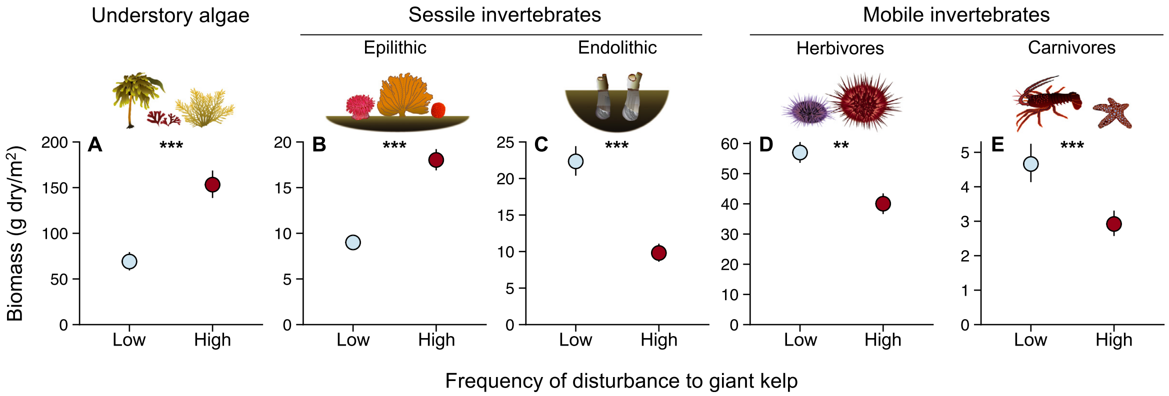

Fig. 3. Experimental increases in the frequency of disturbance to giant kelp altered algal and invertebrate community guilds by enhancing the biomass of (A) understory macroalgae and (B) epilithic sessile invertebrates, and reducing the biomass of (C) endolithic sessile invertebrates and (D) herbivorous and (E) carnivorous mobile invertebrates. Points, error bars, and asterisks as in Fig. 2. The effect of disturbance frequency on fish biomass is shown in Fig. 6.

TABLE 2. Results of univariate analysis of aggregate community metrics.

Response variable and source of variation	df	Understory algae		Sessile invertebrates: Epilithic		Sessile invertebrates: Endolithic		Mobile invertebrates: Herbivores		Mobile invertebrates: Carnivores		Fishes	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
A. Biomass													
Disturbance frequency	1	45.3	**<0.001**	101.4	**<0.001**	62.0	**<0.001**	12.2	**0.002**	22.9	**<0.001**	2.4	0.20
Disturbance frequency × Time since start	1	9.5	**<0.001**	5.8	**0.036**	0.6	0.51	17.8	**<0.001**	<0.1	0.85	7.0	**0.021**
Disturbance severity	1	1.8	0.26	7.2	**0.019**	7.6	**0.016**	0.3	0.66	0.1	0.79	7.2	**0.019**
Initial biomass	1	21.1	*<0.001*	1.0	0.42	12.3	*0.002*	15.8	*<0.001*	49.0	*<0.001*	35.3	*<0.001*
Season	3	9.7	*<0.001*	0.5	0.75	3.2	0.05	0.7	0.62	2.2	0.1	7.2	*0.001*
Time since start	1	0.4	0.62	17.9	*<0.001*	3.9	0.10	59.1	*<0.001*	16.9	*<0.001*	1.0	0.44
Residual	204												
B. Species richness	df	*F*	*P*		*F*	*P*		*F*	*P*	*F*	*P*	*F*	*P*
Disturbance frequency	1	35.3	**<0.001**		10.9	**0.004**		3.1	0.14	0.8	0.46	4.0	0.10
Disturbance frequency × Time since start	1	2.9	0.16		0.4	0.62		<0.1	0.87	2.4	0.20	2.5	0.19
Disturbance severity	1	3.8	0.10		0.8	0.45		10.5	**0.004**	0.8	0.45	0.9	0.44
Initial species richness	1	<0.1	0.71		9.0	*0.009*		8.0	*0.013*	0.8	0.46	4.4	0.08
Season	3	12.6	*<0.001*		1.5	0.31		1.8	0.22	2.0	0.20	9.6	*<0.001*
Time since start	1	<0.1	0.85		9.0	*0.009*		65.5	*<0.001*	27.2	*<0.001*	40.9	*<0.001*
Residual	204												
C. Species evenness	df	*F*	*P*		*F*	*P*		*F*	*P*	*F*	*P*	*F*	*P*
Disturbance frequency	1	26.2	**<0.001**		2.4	0.20		<0.1	0.85	1.8	0.26	4.5	0.072
Disturbance frequency × Time since start	1	2.2	0.22		3.7	0.11		0.2	0.73	0.3	0.63	3.3	0.132
Disturbance severity	1	2.0	0.25		1.1	0.39		1.5	0.32	0.1	0.78	0.2	0.73
Initial species evenness	1	8.3	*0.012*		33.6	*<0.001*		1.4	0.33	<0.1	0.62	1.2	0.37
Season	3	1.9	0.21		0.2	0.87		3.8	*0.027*	0.7	0.62	1.5	0.30
Time since start	1	1.4	0.32		0.6	0.53		2.4	0.20	7.4	*0.018*	10.5	*0.004*
Residual	204												

Notes: Sessile invertebrate richness and evenness were pooled between epilithic and endolithic taxa because the latter group comprised of only two species but over half of the total guild biomass. Degrees of freedom were equal for models across all guilds. Bold face indicates $P < 0.05$ for disturbance frequency, severity, and their interactions. Italics indicate $P < 0.05$ for covariates. Data for biomass models of understory algae, sessile invertebrates, mobile invertebrate carnivores, and fishes were log transformed ($ln[x + 1]$) to meet model assumptions.

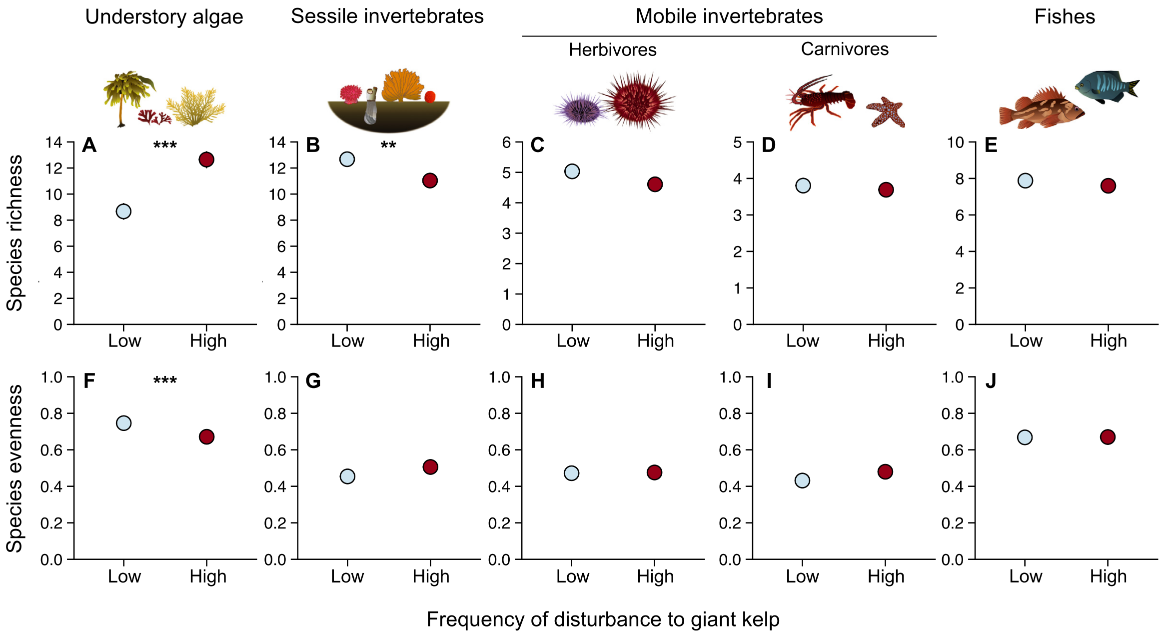

FIG. 4. Experimental increases in the frequency of disturbance to giant kelp altered biodiversity by (A) enhancing the richness of understory macroalgae, (B) reducing the richness of sessile invertebrates, and (F) reducing the evenness of understory macroalgae. Changes in disturbance frequency had no effect on the richness or evenness of all other community guilds (C–E, G–J). Points, error bars, and asterisks as in Fig. 2.

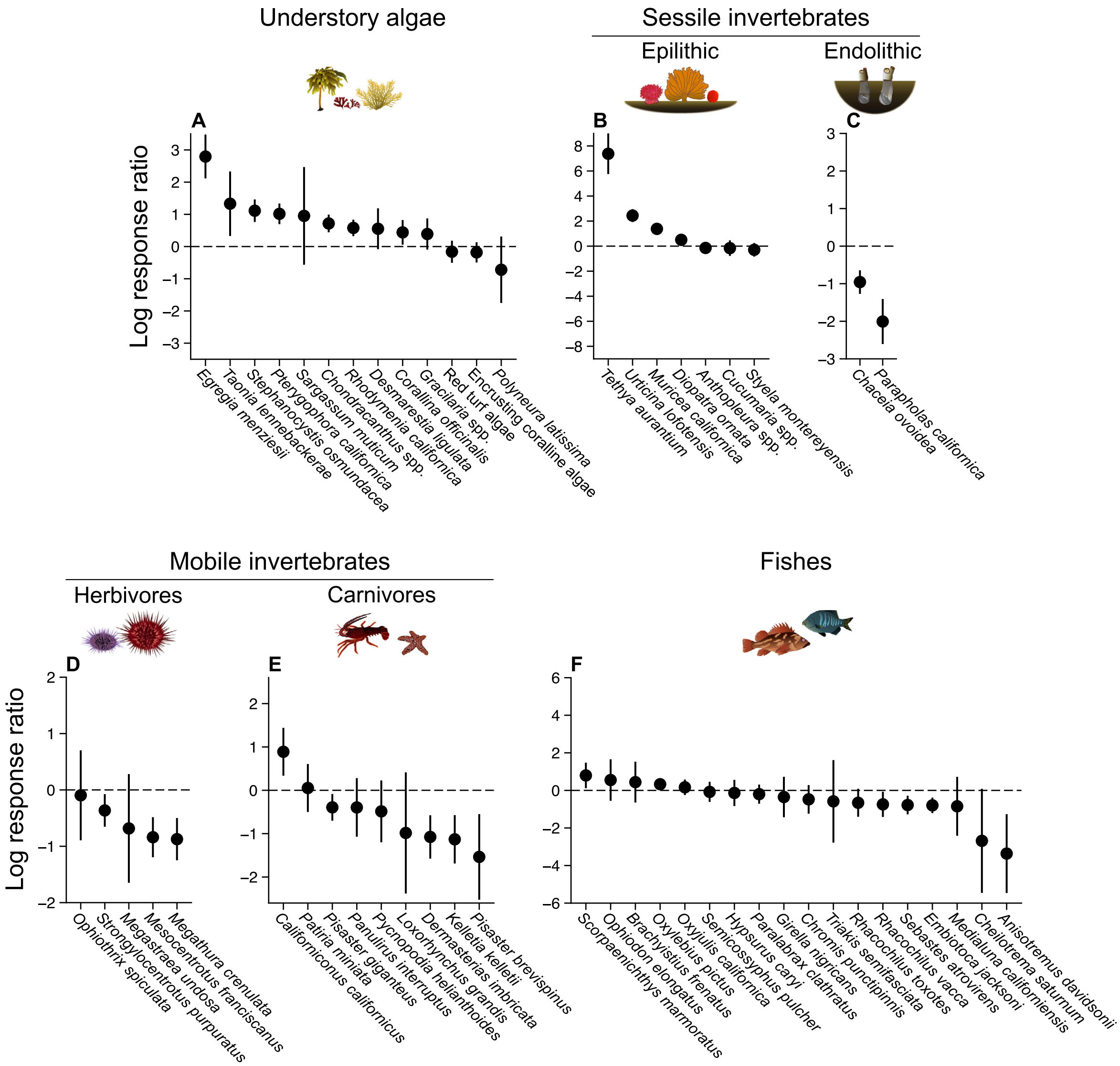

FIG. 5. Experimental increases in the frequency of disturbance to giant kelp altered the composition of community guilds, as illustrated by changes in the log response ratio of individual taxa identified as important in SIMPER analysis (i.e., those contributing ≥ 1% to the overall Bray-Curtis dissimilarity between treatments). Points represent the binary logarithm of the ratio of mean taxon biomass between disturbance treatments ($\log_2[\bar{x}_H/\bar{x}_L]$, where $\bar{x}_H$ is the mean taxon biomass in high-frequency disturbance plots and $\bar{x}_L$ is the mean taxon biomass in low-frequency disturbance plots; ±95% confidence interval). A one-unit increase in the log response ratio represents a doubling of taxon biomass in high-frequency disturbance plots relative to low-frequency disturbance plots (hence, a log response ratio of 0 indicates that biomass did not change with more frequent disturbance, 1 indicates that biomass doubled, 2 indicates that biomass quadrupled, and so forth).

sponges, anemones, and sea fans (Fig. 5A–C, Table 3; Appendix S3: Table S1; overall dissimilarity = 73% and 79%, respectively). These compositional shifts increased over the duration of the study (Table 3).

In contrast to disturbance frequency, increasing severity of disturbance to giant kelp had relatively few effects on the biomass, richness, evenness (Table 2), or composition (Table 3) of understory algae and sessile invertebrate guilds, resulting only in very slight increases in the biomass of epilithic and endolithic sessile invertebrates (Appendix S4: Fig. S1).

Mobile invertebrate herbivores

Mobile invertebrate herbivores were strongly influenced by variation in the frequency of disturbance to giant kelp. Consistent with our predictions, more frequent disturbance was associated with 30% lower biomass of benthic mobile invertebrate herbivores (Fig. 3D), a difference that narrowed over the course of the experiment as biomass in both treatments declined (Table 2A, *disturbance frequency × time since start*; Appendix S2: Fig. S1). The frequency of disturbance to giant kelp had no effect on the richness or evenness of benthic mobile invertebrate herbivores (Fig. 4C, H, Table 2B, C; 18 observed taxa). The composition of mobile invertebrate herbivores shifted with more frequent disturbance (Table 3; Appendix S3: Table S1; overall dissimilarity = 65%), primarily due to declines of 22–44% in the biomass of red and purple sea urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*; Fig. 5D).

TABLE 3. Results of multivariate analysis of community composition using distance-based redundancy analysis (dbRDA).

		Understory algae		Sessile invertebrates		Mobile invertebrates				Fishes	
						Herbivores		Carnivores			
Source of variation	df	Pseudo-*F*	*P*	Pseudo-*F*	*P*	Pseudo-*F*	*P*	Pseudo-*F*	*P*	Pseudo-*F*	*P*
Disturbance frequency	1	10.5	**<0.001**	20.3	**<0.001**	3.2	**0.026**	3.6	**0.005**	2.7	**0.002**
Disturbance frequency × Time since start	1	3.0	**0.006**	2.2	**0.036**	0.8	0.62	1.5	0.22	1.9	**0.029**
Disturbance severity	1	1.4	0.26	1.4	0.28	3.0	**0.028**	1.9	0.10	2.5	**0.004**
Season	3	3.7	*<0.001*	0.9	0.62	0.6	0.85	1.4	0.17	2.8	*<0.001*
Time since start	1	27.0	*<0.001*	6.4	*<0.001*	37.1	*<0.001*	47.5	*<0.001*	9.8	*<0.001*
Residual	205										

Notes: Sessile invertebrates were pooled between epilithic and endolithic taxa because endolithic taxa consisted of only two species but over half of the total guild biomass. Degrees of freedom were equal for models across all guilds. Bold face indicates $P < 0.05$ for disturbance frequency, severity, and their interactions. Italics indicate $P < 0.05$ for covariates.

Disturbance severity had no detectable influence on the biomass or evenness of herbivorous benthic mobile invertebrates (Table 2; Appendix S4: Fig. S1) but was associated with a shift in species composition (Table 3) and had a weak positive effect on richness (i.e., an increase of less than one species across the observed range of disturbance severity, Table 2B; Appendix S4: Fig. S1).

Mobile invertebrate carnivores and fishes

The frequency of disturbance to giant kelp altered guilds of carnivorous mobile invertebrates and fishes in a manner consistent with changes in biogenic habitat and declines of secondary trophic resources (i.e., prey). Increased disturbance frequency was associated with a 37% decrease in the biomass of benthic mobile invertebrate carnivores (Fig. 3E, Table 2A). Disturbance frequency did not significantly affect the richness or evenness of mobile invertebrate carnivores (Fig. 4D, I, Table 2B, C; 16 observed taxa) but did alter species composition (Table 3; Appendix S3: Table S1; overall dissimilarity = 81%) due to a 4% increase in the biomass of a common omnivorous sea star (the bat star *Patiria miniata*) and 24–67% decreases in the biomass of seven secondary and tertiary consumers that include predatory sea stars (four species), lobsters, crabs, and whelks (Fig. 5E).

During the course of the study, the biomass of reef-associated fishes decreased 61% (~1.0 g dry$\cdot$m$^{-2}\cdot$yr^{-1}) under high disturbance frequency but did not change under low disturbance frequency (Fig. 6, Table 2A, *disturbance frequency × time since start*). Disturbance frequency did not significantly affect reef fish richness or evenness (Fig. 4E, J, Table 2B, C; 56 observed taxa), but did lead to compositional shifts (Table 3; Appendix S3: Table S1; overall dissimilarity = 84%). As anticipated, frequent disturbance altered the local biomass of several common fish species in ways consistent with their dependence on biogenic habitat formed by giant kelp or understory algae (Fig. 5F). For example, the biomass of several species positively associated with giant kelp for foraging or refugia (Holbrook et al. 1990, Schmitt and Holbrook 1990), such as pile perch (*Rhacochilus vacca*), black surfperch (*Embiotoca jacksoni*), and kelp rockfish (*Sebastes atrovirens*), declined 38–45% with frequent disturbance. On the other hand, the biomass of striped surfperch (*E. lateralis*), which forage in understory macroalgae (Holbrook et al. 1990, Schmitt and Holbrook 1990), increased 60%. As with total fish biomass, fish community composition diverged over the duration of the study as a function of disturbance frequency (Table 3, *disturbance frequency × time since start*).

Disturbance severity negatively affected fish biomass and altered fish composition but had no detectable influence on the biomass or composition of mobile invertebrate carnivores, or the richness or evenness of either guild (Tables 2, 3; Appendix S4: Fig. S1).

DISCUSSION

Across a broad array of ecosystems, disturbances can impact communities by destroying one or a few dominant species (Dayton 1972, Dayton et al. 1992, Ellison et al. 2005, 2010). Despite accelerating changes to disturbance regimes worldwide (Ummenhofer and Meehl 2017), disentangling effects of the frequency and severity of such disturbances at meaningful spatiotemporal scales and aligning them with theoretical predictions have remained persistent challenges in community ecology (Miller 1982, Mackey and Currie 2001, Trexler et al. 2005, Hughes et al. 2007). Our study makes a conceptual advance in resolving how these

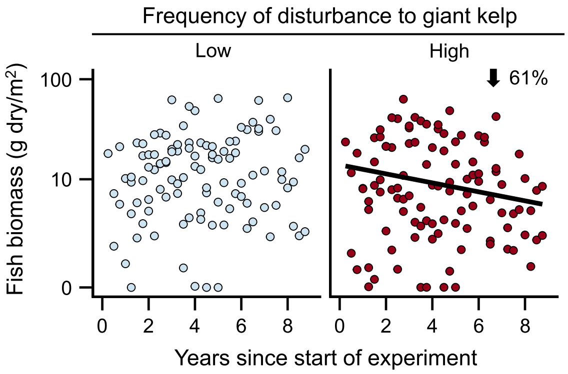

FIG. 6. Over the course of the experiment, reef fish biomass did not change in low-frequency disturbance plots (left) but decreased by 61% in high-frequency disturbance plots (right; note log scale). Points show fish biomass and the line indicates the significant estimated marginal mean trend (adjusted for fixed covariates; $P < 0.05$).

disturbance attributes influence communities by applying the mechanistic framework of the foundation species concept to general predictions from disturbance theory. Results from our nine-year experiment show that the frequency of disturbance to a resilient marine foundation species can change ecological resources, alter community structure, and outweigh the effects of temporal variation in disturbance severity. By tracking the response of 205 reef taxa across all trophic levels, we discovered that repeated annual winter loss of giant kelp led to changes in community biomass and composition that were commensurate with the degree to which species utilize or rely upon physical (light and space), trophic (living and detrital kelp biomass), and habitat (biogenic structure) resources mediated by giant kelp. In contrast to disturbance frequency and despite broad variation in the amount of giant kelp lost in a given year, we found that disturbance severity had relatively minor and inconsistent community impacts, leading only to modest changes in the biomass of sessile invertebrates and fishes, and shifts in the composition of mobile invertebrate herbivores and fishes. Although contrary to some theoretical expectations (Miller et al. 2011, 2012), the consistent lack of interaction between disturbance frequency and severity that we found for a giant kelp forest community is consistent with that observed by McCabe and Gotelli (2000) for stream macroinvertebrates.

Immobile organisms (e.g., plants, sessile animals) should respond strongly to the disturbance of a foundation species that alters the physical environment and the availability of resources. Indeed, we found that frequent loss of giant kelp increased the availability of light and space on the seafloor, causing a proliferation of space-holding flora and fauna (e.g., foliose algae, sponges, anemones, sea fans) that are consistent with earlier observations of community change following giant kelp loss (Dayton et al. 1992, Byrnes et al. 2011). This result agrees with experiments in other coastal ecosystems (Sousa 1979, Petraitis and Dudgeon 1999, Toohey et al. 2007, Castorani et al. 2014) as well as general theory (Amarasekare 2003), indicating that disturbance to foundation species can facilitate the coexistence of inferior competitors. This conclusion is also consistent with experiments in semiarid sagebrush steppe showing that the loss of a dominant native deep-rooted shrub facilitates invasive forbs that exploit deep soil water (Prevéy et al. 2010). Similarly, long-term experiments reveal that annual removal of dominant desert grasses and shrubs shift assemblages to functionally similar co-dominant or sub-dominant plants (Peters and Yao 2012). Interestingly, however, while frequent disturbance to giant kelp enhanced the abundance and richness of understory algae, it also reduced evenness within this guild, as some species of smaller kelps and macroalgae flourished more than others.

In contrast to the frequency of disturbance to giant kelp and despite the fact that more severe winter disturbances were associated with less giant kelp biomass throughout the subsequent year, disturbance severity had minimal effects on community structure, causing slight changes among assemblages of sessile invertebrates, mobile invertebrate herbivores, and fishes. This result was not due to low variation in disturbance severity over the course of our experiment, as we observed broad values of annual giant kelp loss (winter loss of 0 to 1.1 kg dry/m^2) that encompassed over 90% of the range of giant kelp standing biomass observed in 15 yr of monitoring within our study region (Rassweiler et al. 2018). Instead, we suspect that most flora and fauna integrated the effects of disturbance to giant kelp over super-annual time periods and thus were fairly insensitive to year-to-year variation in disturbance severity. More broadly, disturbance severity probably had limited effects across community guilds because of the high resilience of giant kelp to disturbance. Giant kelp has extremely high fecundity, a short generation time (approximately one or more generation per year), unparalleled vegetative growth, and undergoes rapid population expansion during suitable conditions (Castorani et al. 2015, 2017, Schiel and Foster 2015). Therefore, during our experiment, giant kelp generally recovered from winter disturbances within 1 yr. Only when giant kelp was lost year after year (i.e., in high-frequency disturbance plots) did strong, consistent effects manifest in the surrounding community.

Our results also support the idea that repeated loss of foundation species alters communities through indirect species interactions (Ellison et al. 2005). By facilitating subdominant understory algae and epilithic sessile invertebrates, frequent disturbance caused declines in weak spatial competitors (two species of rock-boring clams), likely due to overgrowth competition. Likewise, decreases in understory algal evenness with frequent disturbance may have changed competition for light or space within this guild. The importance of giant kelp as a foundation species mediating negative interactions agrees with recent studies of giant kelp forest interaction networks (Byrnes et al. 2011, Miller et al. 2018). However, giant kelp also structures reef communities through positive interactions by facilitating a diversity of epiphytes (Yoshioka 1982), epifauna (Coyer 1979), and other organisms living above the seafloor that were not measured in our study (e.g., fishes and invertebrates within the giant kelp canopy).

Because foundation species are often dominant primary producers, the frequency and severity of disturbance to them may indirectly affect primary consumers by mediating the abundance and reliability of trophic resources (Ellison et al. 2005, 2010). We found that frequent disturbance caused large, consistent decreases in living and detrital giant kelp biomass, which likely contributed to the decline of herbivorous invertebrates. Particularly strong declines of sea urchins reinforce the importance of accumulated detrital kelp for these ubiquitous marine grazers (Krumhansl and Scheibling 2012). Nevertheless, dense sea urchin barrens can also persist despite low primary productivity (Filbee-Dexter and Scheibling 2014). Our findings for marine grazers align with the results of long-term experiments in tallgrass prairies showing that increased fire frequency changes the composition of dominant plants and their invertebrate herbivores (grasshoppers; Collins 2000). Frequent loss of giant kelp may have had even stronger effects on the abundance of herbivorous invertebrates if not for a marine heatwave that reduced sea urchin abundances in all plots during the final years of our experiment (Reed et al. 2016).

Disturbance altered the assemblage of mobile consumers that rely on giant kelp forests for prey and biogenic habitat. The frequency of disturbance to giant kelp was negatively related to the biomass of mobile invertebrate carnivores and associated with compositional shifts that included local declines in several important secondary and tertiary predators (e.g., sea stars, lobsters). These changes may have been catalyzed by local decreases in preferred prey or biogenic habitat that offers shelter from predation (Mai and Hovel 2007, Withy-Allen and Hovel 2013). Because many mobile invertebrates and fishes move across the landscape at spatial scales larger than our experimental plots, it is plausible that changes in their local abundance and composition were the result of movement to neighboring habitats with more favorable ecological resources or environmental conditions. The effects of frequent giant kelp loss on carnivorous invertebrates may have been partially masked by the regional decline of sea stars due to pandemic wasting disease that occurred in the final years of our study (Reed et al. 2016).

Many reef fishes also utilize giant kelp forests as habitat for foraging or sheltering (Sievers et al. 2016, Miller et al. 2018), and over the course of our study, fish biomass declined with annual disturbance to giant kelp but did not change under natural baseline disturbance frequencies. Disturbance frequency altered local abundances of several common fish species in a manner consistent with their associations with biogenic habitat used for foraging or refugia. As anticipated, the severity of giant kelp disturbance in a given year slightly lowered fish biomass and altered fish composition, likely due to emigration of some species following giant kelp loss (Stouder 1987). Hence, disturbance may generally modify assemblages of mobile consumers by changing habitat directly through the repeated loss of the foundation species and indirectly by altering the abundance of other habitat-forming species. Disturbance may have caused additional changes to communities of species inhabiting the upper water column that was not sampled in our experiment, such as the many fishes, epifaunal invertebrates, and epiphytic organisms associated with the giant kelp canopy (Coyer 1979, Yoshioka 1982).

In contrast to sweeping changes in the biomass and composition of all community guilds, more frequent disturbance to giant kelp altered the richness and evenness of sessile taxa only. On average, increased disturbance frequency resulted in about 6 additional species of understory algae (an 82% rise) and about 2 fewer species of sessile invertebrates (a 13% drop). These significant changes in biodiversity challenge recent theoretical models that predict weak diversity-disturbance relationships at relatively small spatial scales (Miller et al. 2012, Fox 2013). Moreover, our experiment reinforces the value of long-term ecological research for understanding the multifaceted effects of disturbance on biodiversity (Collins 2000, Turner et al. 2003, Ellison et al. 2010, Peters and Yao 2012), as a prior study using data from the first two years of our experiment found stronger effects of disturbance severity on richness and predicted that annual disturbance would reduce the diversity of mobile secondary and tertiary consumers (Byrnes et al. 2011). Contrary to these forecasts, we found that repeated disturbance reduced the biomass and shifted the composition of mobile consumers but did not affect their richness or evenness. Our new findings are important to informing the conservation and management of biodiversity under climate change because models predict shifts in the frequency and severity of wave disturbances to kelp forests in California and elsewhere globally (Ummenhofer and Meehl 2017).

The degree to which local-scale variation in disturbance frequency or severity altered beta diversity (i.e., spatial dissimilarity in species composition) at scales not captured in our experiment is unknown, and further studies are needed to determine how the spatial attributes of disturbance interact with disturbance frequency and severity to structure biodiversity at local to regional scales (Lamy et al. 2018). Careful consideration of how foundation species mediate ecological resources and alter species interactions will progress community ecology towards improved predictability of how multiple disturbance attributes influence biodiversity. Long-term experimental efforts in this direction offer the promise of new insights into theory on foundation species and disturbance in a broader spatial and temporal context.

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LITERATURE CITED

Allen, L. G., D. J. Pondella II, and M. H. Horn, editors. 2006. The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, California, USA.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109–1122.

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.

Bell, T. W., K. C. Cavanaugh, D. C. Reed, and D. A. Siegel. 2015*a*. Geographical variability in the controls of giant kelp biomass dynamics. Journal of Biogeography 42:2010–2021.

Bell, T. W., K. C. Cavanaugh, and D. A. Siegel. 2015*b*. Remote monitoring of giant kelp biomass and physiological condition: an evaluation of the potential for the Hyperspectral Infrared Imager (HyspIRI) mission. Remote Sensing of Environment 167:218–228.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B 57:289–300.

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

Carr, M. H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 126:59–76.

Castorani, M. C. N., K. A. Hovel, S. L. Williams, and M. L. Baskett. 2014. Disturbance facilitates the coexistence of antagonistic ecosystem engineers in California estuaries. Ecology 95:2277–2288.

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, P. T. Raimondi, F. Alberto, T. W. Bell, K. C. Cavanaugh, D. A. Siegel, and R. D. Simons. 2017. Fluctuations in population fecundity drive variation in demographic connectivity and metapopulation dynamics. Proceedings of the Royal Society B: Biological Sciences 284:20162086.

Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. The American Naturalist 155:311–325.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Coyer, J. A. 1979. Ph.D. dissertation. The invertebrate assemblage associated with *Macrocystis pyrifera* and its utilization as a food resource by kelp forest fishes. University of Southern California, Los Angeles, California, USA.

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. Allen Press, Lawrence, Kansas, USA.

Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs 62:421–445.

Diggle, P. J., P. Heagerty, K.-Y. Liang, and S. L. Zeger. 2013. Analysis of longitudinal data, 2nd edition. Oxford University Press, New York, New York, USA.

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., A. A. Barker-Plotkin, D. R. Foster, and D. A. Orwig. 2010. Experimentally testing the role of foundation species in forests: the Harvard Forest Hemlock Removal Experiment. Methods in Ecology and Evolution 1:168–179.

Fabina, N. S., M. L. Baskett, and K. Gross. 2014. The differential effects of increasing frequency and magnitude of extreme events on coral populations. Ecological Applications 25:1534–1545.

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.

Foster, M. C., J. E. K. Byrnes, and D. C. Reed. 2015. Effects of five southern California macroalgal diets on consumption, growth, and gonad weight, in the purple sea urchin *Strongylocentrotus purpuratus*. PeerJ 3:e719.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology & Evolution 28:86–92.

García, L. V. 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos 105:657–663.

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.

Harrer, S. L., D. C. Reed, S. J. Holbrook, and R. J. Miller. 2013. Patterns and controls of the dynamics of net primary production by understory macroalgal assemblages in giant kelp forests. Journal of Phycology 49:248–257.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Holbrook, S. J., M. H. Carr, R. J. Schmitt, and J. A. Coyer. 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bulletin of Marine Science 47:104–114.

Hughes, A. R., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecology Letters 10:849–864.

Krumhansl, K. A., and R. E. Scheibling. 2012. Production and fate of kelp detritus. Marine Ecology Progress Series 467:281–302.

Lamy, T., D. C. Reed, A. Rassweiler, D. A. Siegel, L. Kui, T. W. Bell, R. D. Simons, and R. J. Miller. 2018. Scale-specific drivers of kelp forest communities. Oecologia 186:217–233.

Legendre, P., and L. Legendre. 2012. Numerical ecology, 3rd edition. Elsevier, Amsterdam, The Netherlands.

Legendre, P., J. Oksanen, and C. J. F. ter Braak. 2011. Testing the significance of canonical axes in redundancy analysis. Methods in Ecology and Evolution 2:269–277.

Leighton, D. L. 1966. Studies of food preferences in algivorous invertebrates of southern California kelp beds. Pacific Science 20:104–113.

Lenth, R. 2017. emmeans: Estimated marginal means, aka least-squares means. R package version 1.0. https://CRAN.R-project.org/package=emmeans

Mackey, R. L., and D. J. Currie. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492.

Mai, T. T., and K. A. Hovel. 2007. Influence of local-scale and landscape-scale habitat characteristics on California spiny lobster (*Panulirus interruptus*) abundance and survival. Marine and Freshwater Research 58:419–428.

McCabe, D. J., and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia 124:270–279.

Miller, T. E. 1982. Community diversity and the interactions between the size and frequency of disturbance. American Naturalist 120:533–536.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. How frequency and intensity shape diversity-disturbance relationships. Proceedings of the National Academy of Sciences of the United States of America 108:5643–5648.

Miller, A., D. Reilly, S. Bauman, and K. Shea. 2012. Interactions between frequency and size of disturbance affect competitive outcomes. Ecological Research 27:783–791.

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

Oksanen, J., et al. 2017. vegan: Community ecology package. R package version 2.4-2. https://CRAN.R-project.org/package=vegan

Peters, D. P. C., and J. Yao. 2012. Long-term experimental loss of foundation species: consequences for dynamics at ecotones across heterogeneous landscapes. Ecosphere 3:1–23.

Petraitis, P. S., and S. R. Dudgeon. 1999. Experimental evidence for the origin of alternative communities on rocky intertidal shores. Oikos 84:239–245.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York, New York, USA.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R. C. Team. 2017. nlme: Linear and nonlinear mixed effects models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme

Prevéy, J. S., M. J. Germino, and N. J. Huntly. 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. Ecological Applications 20:1890–1902.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://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., A. Rassweiler, and K. 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.

Reed, D., L. Washburn, A. Rassweiler, R. Miller, T. Bell, and S. Harrer. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. Nature Communications 7:13757.

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

Schmitt, R. J., and S. J. Holbrook. 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. Oecologia 84:419–429.

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.

Sheil, D., and D. F. R. P. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. Trends in Ecology & Evolution 28:571–572.

Sievers, K. T., R. J. Barr, J. M. Maloney, N. W. Driscoll, and T. W. Anderson. 2016. Impact of habitat structure on fish populations in kelp forests at a seascape scale. Marine Ecology Progress Series 557:51–63.

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

Stouder, D. J. 1987. Effects of a severe-weather disturbance on foraging patterns within a California surfperch guild. Journal of Experimental Marine Biology and Ecology 114:73–84.

Thomsen, M. S., T. Wernberg, A. Altieri, F. Tuya, D. Gulbransen, K. J. McGlathery, M. Holmer, and B. R. Silliman. 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology 50:158–175.

Toohey, B. D., G. A. Kendrick, and E. S. Harvey. 2007. Disturbance and reef topography maintain high local diversity in *Ecklonia radiata* kelp forests. Oikos 116:1618–1630.

Trexler, J. C., W. F. Loftus, and S. Perry. 2005. Disturbance frequency and community structure in a twenty-five year intervention study. Oecologia 145:140–152.

Turner, M. G., S. L. Collins, A. L. Lugo, J. J. Magnuson, T. S. Rupp, and F. J. Swanson. 2003. Disturbance dynamics and ecological responses: the contribution of long-term ecological research. BioScience 53:46–56.

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.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Withy-Allen, K. R., and K. A. Hovel. 2013. California spiny lobster (*Panulirus interruptus*) movement behaviour and habitat use: Implications for the effectiveness of marine protected areas. Marine and Freshwater Research 64:359–371.

Yoshioka, P. 1982. Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. Ecology 63:457–468.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2485/suppinfo

Data Availability

Datasets supporting this article were developed through the Santa Barbara Coastal Long Term Ecological Research (LTER) project and are publicly available through the US LTER Network: bottom irradiance (https://doi.org/10.6073/pasta/ca886073ad26a1df6d6b9b0d1750e49b); giant kelp biomass (https://doi.org/10.6073/pasta/4a0c29c3cd85d2e446df6e3f78339b42); percent cover of giant kelp holdfasts (https://doi.org/10.6073/pasta/ecefb6d9eaf25662e74702bb1b380f2b); giant kelp detritus (https://doi.org/10.6073/pasta/d586ebe59056d752a3b7cac3ccde063b); biomass of algae, invertebrates, and fishes (https://doi.org/10.6073/pasta/6c44395ee7d2f70ddc2c19ea969fff3f).