

Impacts of the non-native alga *Sargassum horneri* on benthic community production in a California kelp forest

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ABSTRACT: The arrival of *Sargassum horneri* throughout the Southern California Bight and the Baja Peninsula has raised concern regarding kelp forest resilience and ecosystem function following the invasion of this non-native species. To understand how *S. horneri* impacts native algal abundance and community production, we removed *S. horneri* from experimental plots over a period of 11 mo. We measured impacts on native algal communities and community productivity using SCUBA surveys and benthic chambers equipped with oxygen, temperature, and light sensors. We observed a nearly 4-fold increase in recruitment of *Macrocystis pyrifera* and a 9-fold increase in adult *M. pyrifera* stipe density in *S. horneri* removal plots, but no discernable changes in net community production among treatments. We found ephemeral increases in gross community production and community respiration in the non-removal plots that coincided with periods of peak *S. horneri* biomass. To understand the temporal dynamics of community production, we deployed benthic chambers across a rocky reef dominated by *S. horneri*. Here, temporal variation in community production was most strongly related to corresponding variation in water temperature and changes in *S. horneri* biomass related to its annual lifecycle. Overall, our study indicates that *S. horneri* presence contributed to ephemeral increases in gross community production and community respiration, but it did not affect net community production. Moreover, *S. horneri* removal can lead to increases in native algal abundances given favorable abiotic conditions. We suggest that *S. horneri* thrives in a disturbed ecosystem rather than being a driver of ecosystem change.

KEY WORDS: Kelp forest · Non-native algae · Community production · Community respiration · *Sargassum horneri*

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1. INTRODUCTION

Kelp forests support diverse and productive communities in temperate marine ecosystems, making them ecosystems of paramount importance (Schiel & Foster 2015). Primary production in these forests ranges between 400 and 1900 g C m⁻² yr⁻¹, making them comparable to terrestrial rainforests (Mann 1973, Melillo et al. 1996, Reed & Brzezinski 2009). Temporal variation in kelp forest primary production is driven by corresponding changes in environmental conditions and primary producer biomass, which

may be strongly dependent on the life-history characteristics of the dominant algae (Miller et al. 2011, Rodgers & Shears 2016, South et al. 2016). Measurements of community and primary production can be a meaningful metric of ecosystem function and instrumental in helping us understand ecosystem dynamics, especially in cases where production patterns are altered by the invasion of non-native autotrophs.

Disturbances that decrease abundance or alter the distribution of native species can aid in the establishment of non-native (i.e. invasive) species (Valentine & Johnson 2003, MacDougall & Turkington 2005, Jauni

et al. 2015, Eviner 2016). Invasive algae can proliferate, especially after native algal assemblages are experimentally reduced (Valentine & Johnson 2003, 2004) or naturally disturbed (Scheibling & Gagnon 2006, Britton Simmons & Abbott 2008, Thomsen et al. 2019), resulting in ecosystem-wide impacts including changes to native community structure (Williams & Smith 2007) and primary production (Tait et al. 2015). Understanding these changes can help elucidate the larger impacts of species invasions and inform managers on the best practices to mitigate them.

Invasive species are often documented as having long-term negative impacts on ecosystems they invade (Simberloff & Von Holle 1999). However, invasive species can also have ephemeral, and sometimes positive, impacts on an ecosystem (South et al. 2016, Flory et al. 2017, Quijón et al. 2017). *Undaria pinnatifida* has spread globally since it was first documented as invasive in Wellington Harbor, New Zealand in 1987 and has since been declared impossible to eradicate (Hay & Luckens 1987, Stuart 2002). *U. pinnatifida* is most likely to colonize in disturbed environments and have negative or neutral impacts on native algal abundance and diversity; however, these impacts are transient through time and space (Valentine & Johnson 2003, 2004, South et al. 2016). Transient impacts are likely a product of phenology. Specifically, peak *U. pinnatifida* biomass does not overlap with that of native macroalgae, decreasing the potential for competition (Hay & Villouta 2009, South et al. 2016). While community production and carbon subsidy supply may be greater during the periods when *U. pinnatifida* is abundant, total annual community production is likely lower than in areas where it has not invaded or where the native algae are able to recover (Tait et al. 2015). Similar positive ephemeral impacts on community production have been observed with other non-native annual species including *Sargassum muticum* (Pedersen et al. 2005), *Gracilaria vermiculophylla* (Thomsen & McGlathery 2007, Nejrup & Pedersen 2010), and *Codium fragile* (Thomsen & McGlathery 2007).

The fucoid alga *S. horneri* (= *S. filicinum*) (Turner) C. Agardh (Fucales, Phaeophyceae) is an invasive brown alga that originates from subtidal (2 to 20 m) rocky reefs of western Japan and South Korea (Umezaki 1984, Miller et al. 2007). *S. horneri* has high fecundity, broad dispersal capabilities, and wide-ranging temperature tolerances, which together increase its chances of establishing and proliferating in novel ecosystems (Umezaki 1984, Miller et al. 2007, Marks et al. 2018). *S. horneri* was first reported in Long Beach Harbor, California, USA, in 2003 (Miller et al. 2007) and has since spread along the California and Baja Cali-

fornia, Mexico, coasts (Riosmena-Rodríguez et al. 2012, Marks et al. 2015). *S. horneri* is now routinely observed from Isla Natividad, Baja California Sur, Mexico, to Santa Barbara, California, USA (a distance of approximately 850 km), where it has established dense populations and often overlaps in niche space with the foundational giant kelp *Macrocystis pyrifera* (Riosmena-Rodríguez et al. 2012, Marks et al. 2015, 2018). Reductions in *M. pyrifera* populations in Southern California, due to a prolonged period of warm water (e.g. Reed et al. 2016) and an El Niño-Southern Oscillation (ENSO) (e.g. Edwards 2004) that occurred during 2014 to 2016 (Edwards 2019), likely facilitated the establishment of *S. horneri* (Marks et al. 2017). In areas where *S. horneri* has replaced *M. pyrifera*, fish recruitment and distribution may be negatively impacted (Ginther & Steele 2018, Srednick & Steele 2019). However, differences in fish distributions are likely mediated by the alga's height rather than its non-native identity (Srednick & Steele 2019). Relatively little is known about the interactions between *S. horneri* and native algae or potential impacts to ecosystem function, as this is the first known spread of *S. horneri* outside of its native range (Marks et al. 2015).

This study examined how *S. horneri* impacts community production on a subtidal rocky reef at Catalina Island, California, USA. We used a combination of SCUBA diver surveys and benthic chambers to quantify temporal variation in algae diversity and community production in areas invaded by *S. horneri* and in areas where *S. horneri* was removed from experimental plots. We asked: (1) How does *S. horneri* influence native algal assemblages and patterns of benthic community production? (2) What drives temporal variation in community production in ecosystems invaded by *S. horneri*? We predicted that native algal abundances and net community production (NCP), gross community production (GCP), and community respiration (CR) will be greater in *S. horneri* removal plots compared to control plots. We predicted that temporal variation in community production over the course of the study will be positively associated with the *S. horneri* annual life cycle, specifically, periods of greater *S. horneri* biomass will have greater rates of NCP, GCP, and CR.

2. MATERIALS AND METHODS

2.1. Study site

We studied how the *Sargassum horneri* invasion affected rocky reef communities on the leeward side of

Catalina Island, just outside of Big Fisherman's Cove and adjacent to the Wrigley Marine Science Center. This 9 to 18 m deep rocky reef lies within the Blue Cavern State Marine Conservation Area (SMCA) and has been historically dominated by the kelps *Macrocystis pyrifera* and *Ecklonia arborea*. Recently (ca. 2006), *S. horneri* arrived on Catalina Island and has since increased in abundance, becoming the dominant alga on this and other rocky reefs across the island (Miller et al. 2007, Marks et al. 2015, G. Sullaway pers. obs.). This expansion was likely facilitated by a period of anomalous warm water and a strong ENSO that occurred between 2014 and 2016, during which time *M. pyrifera* and *E. arborea* densities decreased (Di Lorenzo & Mantua 2016, Marks et al. 2017). The understory algal assemblage on the study reef is composed largely of the brown algae *Zonaria farlowii*, *S. palmeri*, *Dictyota flabellata* and *Dictyosporia undulata*, the fleshy red algae *Plocamium cartilagineum* and *Rhodomenia californica*, and the geniculate coralline algae *Bossiella orbigniana* and *Calliarthron cheilosporioides*. The substrate is composed largely of non-geniculate coralline algae, *Lithothamnion* spp., and rocky cobble.

2.2. Benthic chamber construction

To measure rates of community production on the rocky reefs invaded by *S. horneri*, we deployed collapsible benthic chambers modeled after those described by Haas et al. (2013) and Calhoun et al. (2017) (Fig. 1). These chambers create closed systems over the benthos where oxygen, irradiance, and temperature sensors track photosynthesis and salient ocean conditions within a known volume of water (see also Miller et al. 2009, 2011, Rodgers et al. 2015). While many past experiments examining community production in kelp forest ecosystems have relied on laboratory experiments that do not incorporate natural fluctuations in abiotic conditions, recent studies have identified techniques that measure community production *in situ*, thereby increasing ecological realism (Tait & Schiel 2011, Rodgers et al. 2015, Olivé et al. 2016). For example, *in situ* chamber designs have been developed for estimating community production by individual species (Rodgers et al. 2015, Olivé et al. 2016) and whole benthic communities (e.g. Miller et al. 2009, Haas et al. 2013). In general, estimates of NCP, GCP, and CR for the benthos can be made by measuring changes in dissolved oxygen (DO) within chambers that are placed *in situ* over macroalgae and invertebrate communities. Then, by linking temporal

changes in oxygen concentrations within the chambers to incident temperature and irradiance conditions, we can relate variation in these measures to community structure and abiotic conditions (Miller et al. 2009). Further, because these chambers encompass whole benthic communities, species interactions (e.g. shading) and invertebrate respiration are incorporated into production measurements. These interactions are often not captured in laboratory experiments but are pertinent to understanding NCP (Bracken & Williams 2013).

We constructed benthic chambers using 0.106 cm polycarbonate plastic triangle sheets glued to fiberglass-reinforced vinyl panels using Weld-On® glue. The chambers were 1.2 m tall, and frames were reinforced using aluminum rods and stainless-steel cable, which held the interior volume and benthic area of each benthic chamber constant at 192 l and 0.575 m², respectively. Flexible polycarbonate walls prevented boundary layer formation by transferring wave energy into the interior of each benthic chamber. To ensure chambers were held to the seafloor, we secured anchor chain to vinyl skirts (skirts were



Fig. 1. (a) Benthic chambers deployed with temperature, oxygen, and PAR sensors. (b) Sensor stand with PAR sensor at the top and dissolved oxygen/temperature sensor at the bottom

30.5 cm long) around the chamber perimeters. We initially verified wave energy transfer and the effectiveness of chamber-substrate seals by observing fluorescein dye movement within the chambers and ensuring it did not leak to the surrounding environment (authors' pers. obs.). We used 'clod card' dissolution rates as a proxy for relative rates of water movement inside and outside chambers (Doty 1971, for further details and methods see Appendix). Mean dissolution inside chambers was 6% lower than outside the chambers, but this difference was not significant, indicating that the chamber walls were flexible enough to allow for water movement comparable to the environment outside the chamber (paired Wilcoxon test, $p = 0.055$). We constructed PVC sensor arrays that were equipped with a photosynthetically active radiation (PAR) sensor (Odyssey Dataflow Systems) and a DO (mg l^{-1}) and temperature ($^{\circ}\text{C}$) sensor (MiniDOT logger, PME) (Fig. 1). PAR sensors were placed approximately 0.5 m above the benthos and recorded every 10 s, while oxygen and temperature sensors were placed approximately 0.2 m above the benthos and recorded every minute. Following each chamber deployment, we determined the average hourly oxygen concentration and calculated changes in DO between each consecutive hour, which provided a slope that estimated NCP within each chamber (Miller et al. 2009). We used measurements at night (i.e. in the dark) to estimate respiration by the benthic communities (CR). Finally, we added NCP and CR to estimate GCP (see also Miller et al. 2011 and Olivé et al. 2016).

2.3. Assessing changes in algal assemblages and community production following *Sargassum horneri* removal

To assess how the removal of *S. horneri* affects native algal abundances and patterns of community production, we marked 6 circular plots (each 6 m diameter and 28.3 m^2) near the seawater intake pipes at Two Harbors on Catalina Island in May 2016. These experimental plots were allocated into 3 pairs (hereafter blocks), which were spaced approximately 15 m from each other along a 10 m isobath. One of the 2 plots per block was randomly assigned as a *S. horneri* removal plot, where all *S. horneri* were removed by hand using SCUBA every other month (i.e. in May 2016, August 2016, October 2016, February 2017, and April 2017) until April 2017. During these removals, all *S. horneri* were disposed of on land to ensure we did not further facilitate spread of the

alga. Prior to each *S. horneri* removal, all algae within each plot were quantified along 4 radially directed transects that were allocated in a 'spoke and wheel' design, where each spoke consisted of a 3 m transect originating from the center of the plot. Two 0.5 m^2 quadrats were placed at randomly selected positions along each transect while excluding the center meter of the circle, resulting in a total of 8 quadrats per plot. Within each quadrat, all algae were identified to species and enumerated. If *M. pyrifera* were present, all stipes were counted 1 m above their holdfasts and juveniles were counted by individual holdfasts.

To estimate the impact of *S. horneri* removal on benthic community production, we placed benthic chambers near the center of each experimental plot for 24 h. At the end of 24 h, all algae within the chambers were identified to lowest taxonomic level and enumerated, but otherwise left intact to allow for continued community production measurements within the plot. The abundance of all other species of macroalgae within the chamber footprints was recorded and biomass was estimated based on abundance–biomass relationships as determined at a nearby (<2 km away) 10 to 13 m deep non-SMCA rocky reef. Specifically, individuals of each species (*Z. farlowii* [$n = 35$], *D. undulata* [$n = 35$], *D. flabellata* [$n = 30$], *M. pyrifera* [$n = 15$], *E. arborea* [$n = 7$], and *S. palmeri* [$n = 30$]) were collected and weighed to determine an abundance–biomass relationship that could be used to non-destructively estimate algae weights.

2.4. Characterizing temporal patterns of community production in ecosystems invaded by *Sargassum horneri*

To understand temporal patterns of community production in ecosystems invaded by *S. horneri*, we haphazardly placed 10 to 12 chambers on the benthos along the 9–12 m isobath for 24 h periods in order to encompass full diurnal cycles. If a benthic chamber was randomly placed over an algal assemblage that included *M. pyrifera* (which was infrequent as *M. pyrifera* was initially rare at the study site), the chamber was sealed around the kelp stipes at its apex so that only the bottom ~1 m of thalli was included inside the chamber. These deployments were repeated every other month from March 2016 to April 2017, although logistic constraints and failures of the chamber-benthos seals resulted in lower sample sizes in summer and fall deployments (Table 1). During each deployment, the chambers

Table 1. Sample size for each benthic chamber deployment grouped by season

Season	Associated months	Sample size
Spring	March–May	23
Summer	June–August	12
Fall	September–November	10
Winter	November–March	17

were opened and flushed with fresh seawater every 4 h so that changes in water chemistry within them did not alter photosynthetic rates. After 24 h, all *S. horneri* within the chamber footprints was collected and weighed, and weight of native algae was estimated using previously described abundance biomass relationships due to SMCA permit restrictions.

2.5. Statistical analyses

All univariate statistical analyses were done using R-Studio (R Core Team), and all multivariate analyses were done using PRIMER-E ver. 6.0 (Clarke & Warwick 1994). All univariate data were assessed for normality and equality of variances by graphical examination of residuals and a non-significant result in Levene's tests, respectively. Multivariate data were evaluated for normality using Draftsman plots.

To evaluate the effects of *S. horneri* removal on native algal abundance through time, algal abundance data were first 4th root transformed to downweigh the influence of overly abundant species. Given the large amount of zeros in the data set, it was not possible to calculate Bray-Curtis similarities for all pairs of samples, and thus a Euclidean distance-based matrix was generated to characterize similarities among all sample pairs. Then, a 3-way blocked PERMANOVA with sample month and removal treatment considered as fixed variables and block considered as a random variable with replication was used to evaluate differences in algal abundances within quadrats among factor levels. Tests of significance between removal treatments were based on Monte Carlo tests due to the small number of unique permutations for that factor. Following this, pairwise permutation contrasts were used to evaluate differences between removal treatments during each month separately. These were accompanied by estimates of multivariate dispersions using the multivariate dispersion (MvDisp) procedure in Primer-E to evaluate how within treatment variability (i.e. among sample quadrats) compared between the removal treatments. SIMPER analyses were used

to estimate the relative importance (% contribution) of each algal species to the observed differences between the removal treatments during each sample month. Lastly, non-metric multidimensional scaling (nMDS) plots were generated to examine the relative similarities in algal assemblages between the removal treatments on each sample date. *S. horneri* abundance was removed from this analysis so we could specifically evaluate community-wide differences outside of the manipulated treatment. Separate 2-way Model I blocked ANOVAs were used to evaluate the effects of *S. horneri* removal on NCP, CR, and GCP. For each ANOVA, data were square root transformed to correct problems with homoscedasticity. Time and Treatment (Control and Removal) were considered fixed variables, and Block was considered a random variable.

To understand temporal changes in production metrics (NCP, GCP, and CR) and abiotic conditions on the reef invaded by *S. horneri*, data were log transformed to satisfy assumptions of normality and equality of variances, and separate 1-way ANOVAs were used to determine differences in each production metric, sea water temperature, *S. horneri* biomass, and mean PAR through time. For the analyses, we grouped time into 4 'seasons' based on trends in *S. horneri* biomass and in the hope of making the plots easier to interpret; however, we do not draw conclusions related to season as we were unable to replicate seasons.

3. RESULTS

3.1. Assessing changes in algal assemblages and community production following *Sargassum horneri* removal

The native algal assemblages within the *Sargassum horneri* removal and control plots varied through time (PERMANOVA: Month, pseudo- $F_{3,168} = 7.27$, $p < 0.001$) and between treatments (Treatment, Pseudo- $F_{1,168} = 3.40$, $p = 0.052$), but these factors interacted such that the relative differences between treatments varied among months (Month \times Treatment, pseudo- $F_{3,168} = 3.87$, $p = 0.024$; Table 2). When examined within each month separately, the removal and control plots did not differ during the first 2 time points (August, $t = 1.48$, $p = 0.159$; October, $t = 1.456$, $p = 0.237$) but they did differ during the latter time points (February, $t = 3.568$, $p = 0.004$; April, $t = 2.863$, $p = 0.002$; Fig. 2, Tables 2 & 3). This resulted in the assemblages being markedly different 11 mo after the clearings were established (Fig. 2). Further, the within-plot (i.e.

Table 2. (a) Blocked-PERMANOVA results examining dissimilarities in native algal assemblages between *Sargassum horneri* removal and non-removal control plots and (b) post-hoc comparison of Month \times Treatment interaction

a) PERMANOVA						
Source	df	SS	MS	Pseudo- <i>F</i>	p(perm)	% Variation
Treatment	1	149.13	149.13	3.4	0.05	4.80 %
Block	2	55.31	27.657	3.8	0.002	1.40 %
Month	3	758.77	252.92	7.26	0.001	1.97 %
Treatment \times Block	2	87.71	43.857	6.04	0.001	5.00 %
Treatment \times Month	3	372.68	124.23	3.866	0.024	16.70 %
Block \times Month	6	208.84	34.806	4.797	0.001	7.50 %
Treatment \times Block \times Month	6	192.79	32.13	4.428	0.001	13.50 %
Res (= Quadrat)	168	1219	7.256			

b) Post-hoc comparisons: Month \times Treatment			
	<i>t</i>	p(perm)	
August	1.484	0.159	
October	1.456	0.237	
February	3.568	0.004	
April	2.863	0.002	

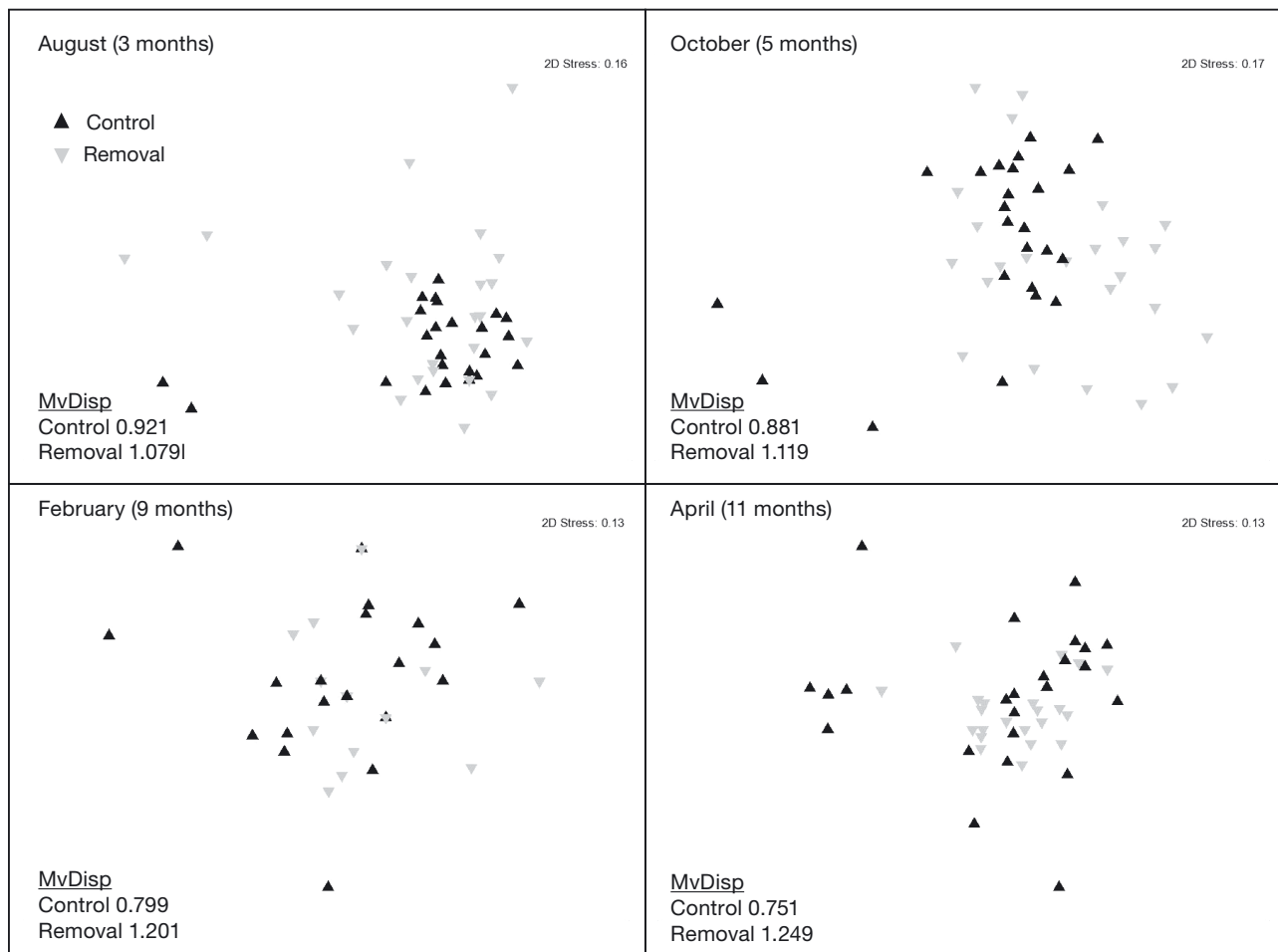


Fig. 2. Non-metric multidimensional scaling plot examining differences among algae communities in *Sargassum horneri* removal and control plots through time. Multivariate dispersion (MvDisp) indicates the variation in assemblages among sample unit, larger numbers indicate greater variability

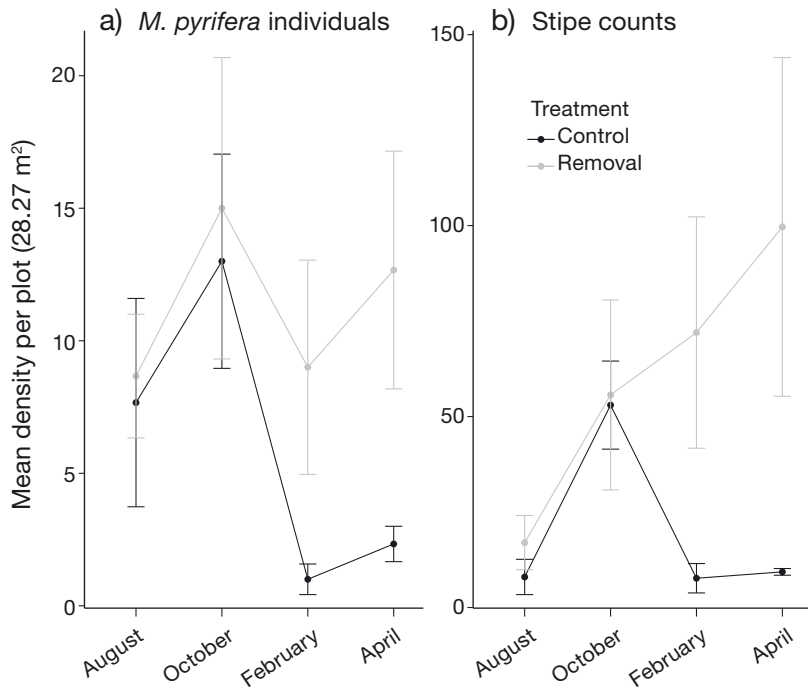


Fig. 3. Number of *Macrocystis pyrifera* individuals and stipes (mean \pm SE) per plot through time

quadrat to quadrat) variation in these assemblages was greater in the removal plots and appeared to increase slightly over the experiment, while at the same time it was lower and appeared to decrease slightly in the control plots (quantified using MvDisp, Fig. 2). Specifically, juvenile kelps were 3.7 times more abundant in the *S. horneri* removal plots than the control plots (2.92 ± 0.47 ind. vs. 0.79 ± 0.29 ind. per 28.3 m², respectively; mean \pm SE) after 11 mo. Additionally, mean densities of *M. pyrifera* individuals and stipes were greater in removal plots than control by the conclusion of the experiment (Fig. 3). Likewise, geniculate coralline algae, understory brown algae such as *Zonaria farlowii* and *Dictyopteris undulata*, and fleshy red algae such as *Plocamium cartilagineum* were more abundant in *S. horneri* removal plots upon conclusion of the experiment (Table 3).

Interestingly, observed differences in algal community composition did not translate to strong differences in community production between *S. horneri* removal and control

Table 3. Average abundance and % contribution from SIMPER analysis of algae between control and removal plots through time. Diss: dissimilarity

Survey month	Species	Average abundance				
		Removal	Control	Diss/SD	% Contribution	% Cumulative
August (3 mo)	<i>Corallina</i> spp.	0.294	0.577	0.45	27.51	27.51
	<i>Dictyopteris undulata</i>	2.22	2.13	0.69	15.38	42.89
	<i>Sargassum palmeri</i>	0.899	1.11	0.91	13.96	56.86
	<i>Zonaria farlowii</i>	0.827	0.929	0.93	12.78	69.64
	<i>Rhodomenia californica</i>	0	0.477	0.39	9.76	79.39
	Juvenile kelp	0.267	0.25	0.74	4.15	83.55
	<i>Eisenia arborea</i>	0.197	0.142	0.5	3.67	87.22
	<i>Cystosiera osmundaceae</i>	0	0.184	0.33	2.97	90.19
October (5 mo)	<i>Zonaria farlowii</i>	1.66	1.18	0.82	19.7	19.7
	<i>Dictyopteris undulata</i>	1.22	1.8	0.91	19.66	39.36
	<i>Sargassum palmeri</i>	0.792	1.13	0.81	19.22	58.57
	<i>Corallina</i> spp.	0.072	0.431	0.39	15.31	73.89
	<i>Macrocystis pyrifera</i>	0.309	0.042	0.45	5.06	78.94
	<i>Rhodomenia californica</i>	0.101	0.185	0.36	4.94	83.88
	<i>Sargassum muticum</i>	0.317	0	0.48	4.9	88.78
	<i>Colpomenia peregrina</i>	0.244	0	0.33	4.08	92.87
February (9 mo)	<i>Zonaria farlowii</i>	0.786	0.285	0.88	31.73	31.73
	<i>Dictyopteris undulata</i>	0.498	0.339	0.62	26.09	57.82
	<i>Sargassum palmeri</i>	0.55	0.451	0.78	22.09	79.91
	<i>Eisenia arborea</i>	0.208	0.083	0.59	6.46	86.37
	<i>Corallina</i> spp.	0	0.142	0.28	6.29	92.66
April (11 mo)	<i>Corallina</i> spp.	0.922	0.215	3.85	28.61	28.61
	Juvenile kelp	1.22	0.392	2.75	20.04	49
	<i>Dictyopteris undulata</i>	1.42	1.11	2.47	18.33	67.34
	<i>Zonaria farlowii</i>	1.08	0.618	1.87	13.88	81.22
	<i>Plocamium cartilagineum</i>	0.203	0	0.667	4.95	86.17
	<i>Sargassum palmeri</i>	0.269	0.368	0.594	4.41	90.58

plots over the course of the experiment (Fig. 4, Table 4). We did not find statistically significant differences among treatments for any production metric (2-way blocked ANOVAs: NCP–Treatment $F_{1,15} = 2.739$ $p = 0.119$; GCP–Treatment $F_{1,15} = 1.30$ $p = 0.272$; CR–Treatment $F_{1,15} = 3.73$ $p = 0.071$). However, patterns emerged indicating that *S. horneri* may have an additive impact on overall metabolism at times when it is rapidly growing and has high biomass. For instance, in fall, GCP and CR were 1.6 and 1.9 times greater, respectively, and *S. horneri* was 7.7 times denser in the control plots than the removal plots (control: 147 ± 30 ind. m^{-2} ; removal: 19 ± 2.8 ind. m^{-2}) (Fig. 4). This increase in metabolism range occurred when *S. horneri* was growing and likely created an additive rather than substantive contribution to GCP and CR. This change in magnitude was not reflected in the overall

NCP (Fig. 4), indicating that all 3 measurements of production are valuable when evaluating ecosystem function through community production.

3.2. Characterizing temporal patterns of community production in ecosystems invaded by *Sargassum horneri*

Overall, community production on a subtidal reef invaded by *S. horneri* followed a temporal pattern

Table 4. Results from a 2-way randomized blocked-ANOVA test for differences in production metrics between removal and control plots. NCP: net community production; GCP: gross community production; CR: community respiration. Statistically significant values ($p < 0.05$) in **bold**

Production metric	p:Season	p:Treatment	p:Replicate	p:Season × Treatment
NCP	0.130	0.119	0.480	0.805
GCP	0.048	0.272	0.500	0.552
CR	0.022	0.071	0.749	0.636

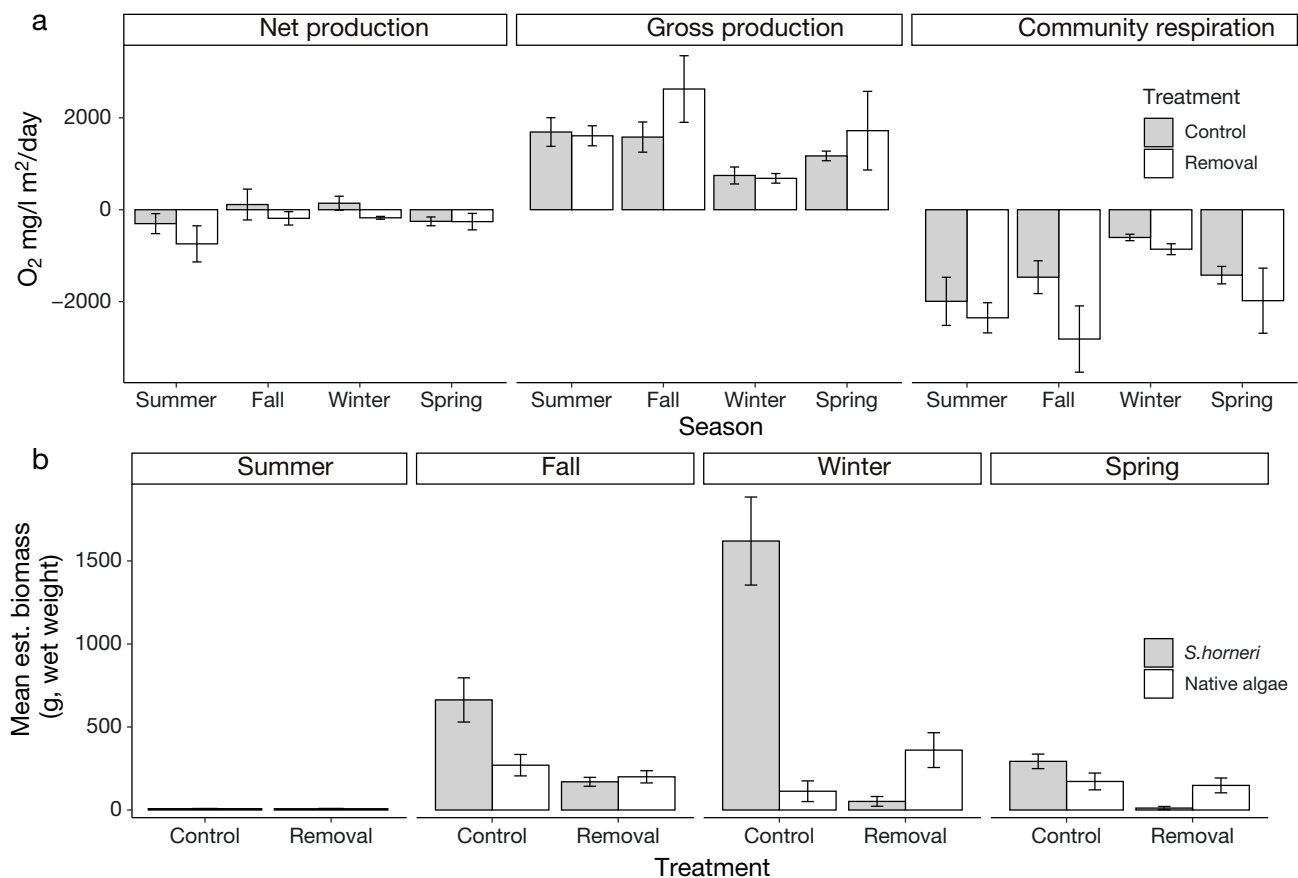


Fig. 4. (a) Seasonal mean net community production, gross community production, and community respiration, and (b) algae biomass between control and *Sargassum horneri* removal plots by season (± 1 SE)

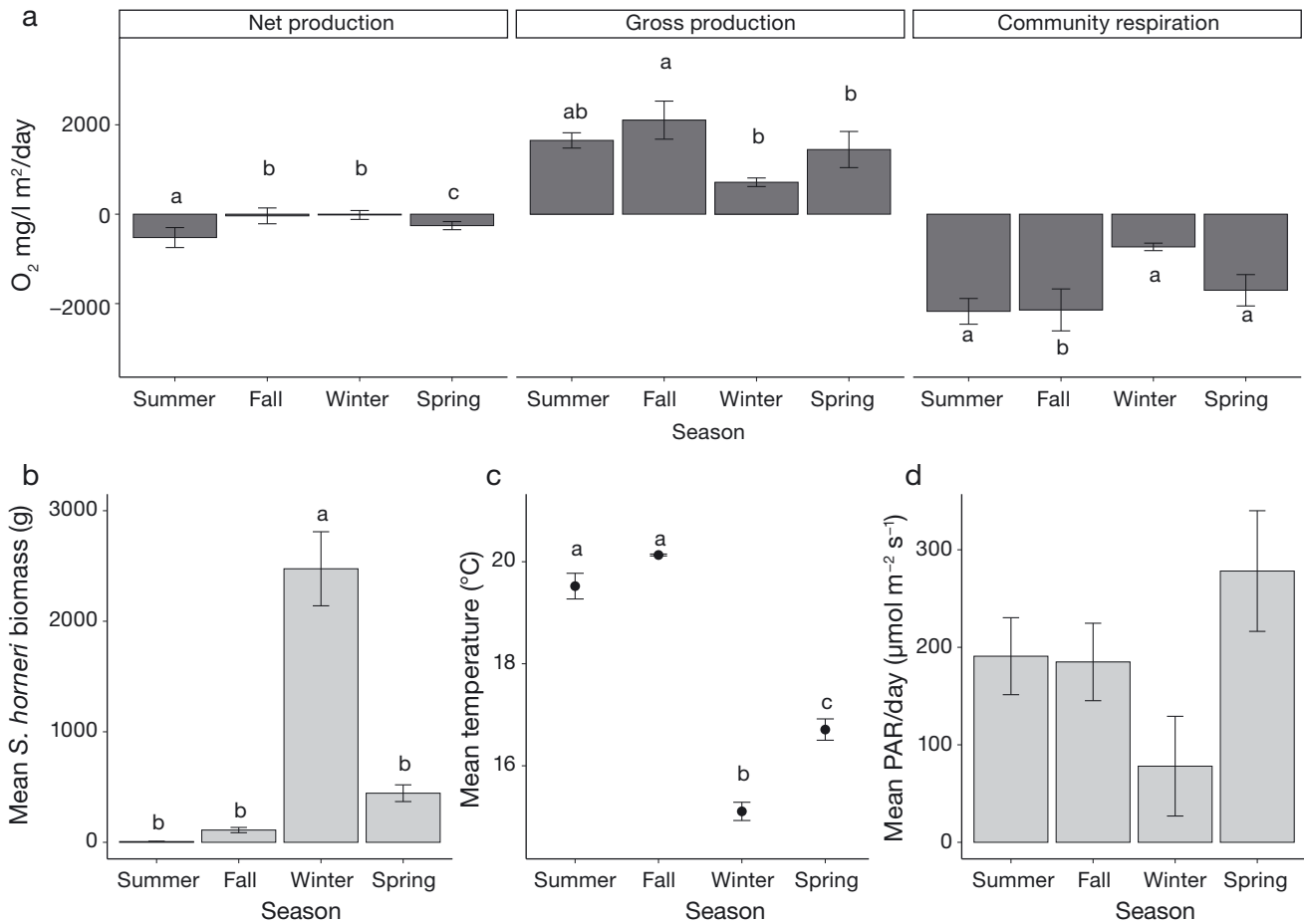


Fig. 5. Means of (a) community production (net and gross) and respiration, (b) *Sargassum horneri* biomass, (c) ocean temperature, and (d) photosynthetically active radiation (PAR) on a reef invaded by *S. horneri* (± 1 SE). Different letters denote significant differences according to Tukey's post-hoc test

Table 5. Results from univariate ANOVA testing for differences in production metrics (NCP, GCP, CR) and environmental variables (biomass, temperature, and PAR) on a reef invaded by *Sargassum horneri*. Statistically significant values ($p < 0.05$) in **bold**. See Table 4 for definitions of production metric abbreviations

Dependent variable	p:season
NCP	<0.001
GCP	<0.001
CR	<0.001
<i>S. horneri</i> biomass (g)	<0.001
Temperature ($^{\circ}\text{C}$)	<0.001
PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.107

that was coincident with the annual life cycle of the alga. Specifically, GCP and CR were both greatest during fall (GCP: $2709.5 \pm 320.06 \text{ mg O}_2 \text{ l}^{-1} \text{ m}^{-2} \text{ d}^{-1}$; CR: $-2368.8 \pm 272.2 \text{ mg O}_2 \text{ l}^{-1} \text{ m}^{-2} \text{ d}^{-1}$), and lowest during winter (GCP: $1038.6 \pm 538.8 \text{ mg O}_2 \text{ l}^{-1} \text{ m}^{-2} \text{ d}^{-1}$; CR: $-748.15 \pm 138.1 \text{ mg O}_2 \text{ l}^{-1} \text{ m}^{-2} \text{ d}^{-1}$; mean \pm SE)

(Fig. 5a, Table 5). Additionally, the greatest difference between GCP and CR, which may be the best estimate of the impact of the alga on ecosystem function (M. S. Edwards et al. unpubl.), occurred during the fall when the *S. horneri* population was rapidly growing and the alga presumably had heightened metabolic activity and increasing biomass (Gómez & Wiencke 1996). Mean benthic PAR varied temporally but these differences were not significant through time (Fig. 5d). Temperature was greatest in summer and fall (Fig. 5c, Table 5), coinciding with higher rates of GCP (Fig. 5) on the reef.

4. DISCUSSION

We found that *Sargassum horneri* presence contributed to ephemeral increases in GCP and CR that were not reflected in NCP, indicating that all 3 measurements of production are valuable when evaluat-

ing ecosystem function through community production (Edwards et al. 2020). Additionally, *S. horneri* removal led to increases in native algal abundances during a period of favorable abiotic conditions, while cooler nutrient-rich waters, in concert with *S. horneri* removal, likely facilitated observed increases in native algal abundances in our *S. horneri* removal plots. Compared to our removal plots, control plots exhibited minimal *Macrocystis pyrifera* recruitment or native algal growth, indicating that once *S. horneri* is established, it can impede native algal abundance. While *M. pyrifera* proliferates in water temperatures ranging from 8 to 17°C, (North et al. 1986, Schiel & Foster 2015), *S. horneri* has been documented in temperatures ranging from 18 to 22°C and has established in the Eastern Pacific in temperatures ranging from 14 to 22°C (Chu et al. 1998, Marks et al. 2015). Our study began on the tail end of an anomalously warm water period (Reed et al. 2016), when *M. pyrifera* was nearly absent from the subtidal community at Catalina Island. At this time, mean water temperatures at our study site in summer 2016 were $19.5 \pm 0.25^\circ\text{C}$ (Fig. 5c) and we did not observe *M. pyrifera* in our study site. When water temperatures cooled down to $15.1 \pm 0.17^\circ\text{C}$ in winter 2016, we began to see *M. pyrifera* growth (Fig. 3). During this time, we observed a 9-fold increase in *M. pyrifera* stipe density and a 3-fold increase in juvenile kelp abundance in areas where *S. horneri* had been removed. *M. pyrifera* densities at our study site (Removal: 3.68 ± 1.64 ind. m^{-2} ; Control: 0.34 ± 0.03 ind. m^{-2} , Fig. 3a) were overall much lower than what McAlary et al. (1998) observed on Catalina Island in the mid-1990s (10 to 12 ind. m^{-2}) or what Edwards (2004) observed for several kelp forests throughout the southern California mainland (i.e. 6 to 12 ind. m^{-2}). Moreover, the dominant understory brown algae observed during this study, *Zonaria farlowii* and *Dictyopteris undulata*, both have an affinity for warm water conditions (Marks et al. 2017). We suggest that suitable abiotic conditions in concert with *S. horneri* removal are related to the increase in native algae and especially *M. pyrifera* abundance at our site. It appears that *S. horneri* may be taking advantage of an environmental shift and acting as a 'passenger' to abiotic change rather than driving an ecosystem shift (MacDougall & Turkington 2005).

In this study, we estimated community production, which means we cannot explicitly identify the extent to which production is related to changes in algal abundance associated with *S. horneri* removal versus changes to the heterotrophic communities as they are associated with certain algal species. We hypothesize

that differences in production between removal and control plots are strongly related to changes in algae production rather than changes to the meso-consumer community. *S. horneri* is a structurally complex species that likely supports higher invertebrate abundances than *M. pyrifera* per unit area. Studies on the morphologically similar *S. muticum* suggest that it supports high abundances of invertebrates compared to less structurally complex native species (Gestoso et al. 2010). However, it should be noted that *S. horneri* has a chemical anti-fouling component that discourages invertebrate settlement. This may limit invertebrate abundances on the algae (Cho 2013), which could lead to lower than expected invertebrate abundances. There are likely differences in invertebrate communities between *S. horneri*-dominated assemblages and native assemblages, but this is not expected to significantly shift the results of this study; if anything, it may result in our underestimating rates of production from algae. This is a clear area for future research and would contribute to a greater understanding of *S. horneri* impacts on ecosystem function.

We hypothesize that the lack of differences in NCP between experimental treatments is due, in part, to compensatory production by understory algae. Similarly, Miller et al. (2011) did not observe differences in production between *M. pyrifera* removal plots compared to control plots. They hypothesized that compensatory production by understory algae and phytoplankton occurs with canopy removal and may dampen expected variability in production (Miller et al. 2011). Sub-canopy algae, such as *S. horneri*, do not form an extensive surface canopy comparable to that of *M. pyrifera* and this may limit the ability for compensatory production (Pfister et al. 2019). While an ecosystem's ability to compensate for these types of shifts requires further research, it indicates an impressive capacity to buffer short-term disturbances (Miller et al. 2011, Lamy et al. 2019). Differences in community production between *S. horneri* removal and control plots were ephemeral. Compared to *S. horneri* removal plots, control plots had greater GCP and CR (Fig. 4) in fall when *S. horneri* had the greatest growth rates and was increasing in biomass (Fig. 4, Marks et al. 2018). While NCP is often used to measure changes in community production and ecosystem function, we found support for the idea that GCP and CR may better reflect changes to ecosystem function (Edwards et al. 2020).

Community production metrics (NCP, GCP, and CR) were temporally variable in an ecosystem fully inundated with *S. horneri*, and this variability is likely related to changes in *S. horneri* biomass and

water temperature. The annual life history of *S. horneri* means that biomass varies significantly over the course of a year. This annual lifecycle is notably different from that of the perennial *M. pyrifera* and other native understory algal species found in southern California subtidal rocky reefs (excluding *Desmarestia ligulata*). Research in other subtidal macroalgae ecosystems have found that the biomass of the dominant species drives relative rates of community production (Miller et al. 2011, Rodgers & Shears 2016). In our study, *S. horneri* was the dominant species for the majority of the year throughout the ecosystem, except when senescent in summer. We found that the highest CR rates occurred during periods with warmer water and greater *S. horneri* growth and biomass (Fig. 5a,c). Similarly, Tait & Schiel (2013) found that natural fluctuations in temperature led to increased community respiration and decreased NCP. In our study, increased respiration was balanced by increased GCP, so we did not see decreased rates of NCP. However, this compensation may not occur over longer time scales and has the potential to alter ecosystem NCP (Tait & Schiel 2013).

When considering management action that focuses on non-native alga removal, it is important to note that our removal plots were relatively small (28.3 m²). Marks et al. (2017) recommends plots larger than 60 m² for effective *S. horneri* management. This requires a large amount of time, effort, and funding. Native algae responses to non-native species removal may have varied results depending on oceanographic conditions. Removal of a non-native species in ocean conditions not amenable to native species growth may result in an ecosystem lacking structure and community production, and in fact may further facilitate non-native species establishment. Instead, we recommend removal occurs in conditions favorable to native algae growth.

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Appendix. Relative water motion measured with clod cards
— methods and results

We constructed clod cards using plaster of Paris (mixed sensu Doty 1971) in tapered cylindrical molds and dried them for 48 h at 25°C. Next, we glued plaster to tiles and took initial weight. We deployed the cards inside and outside chambers for 24 h ($n = 27$) over the course of 3 consecutive days at the onset of this project. After 24 h, we removed the tiles and dried them for 48 h at 25°C.

We subtracted the pre- and post-deployment weights to get the dissolution rate in 24 h and compared this based on card location (inside or outside chamber) using a paired Wilcoxon test. We used a non-parametric test because both a Shapiro-Wilk test and quantile plot indicated that data were slightly heteroskedastic. We found that mean dissolution inside the chambers was 6% lower than outside the chambers, but this difference was not significant, indicating that the chamber walls were flexible enough to allow for substantial water movement (paired Wilcoxon test, $p = 0.055$; Fig. A1).

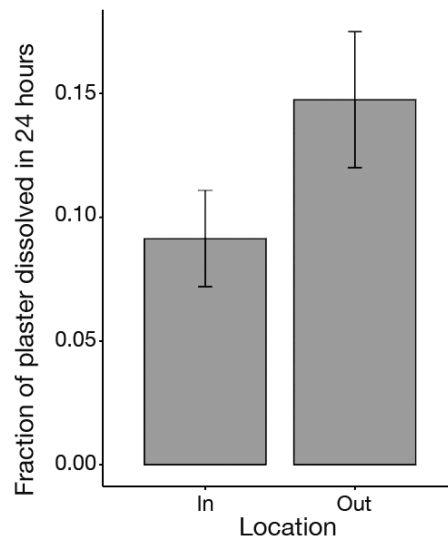


Fig. A1. Clod card dissolution rates inside and outside of chamber (paired Wilcoxon test, $p = 0.055$)