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LETTER

Marine management affects the invasion success of a non-native species in a temperate reef system in California, USA

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Abstract

Despite promises that 'healthy' marine systems show increased resilience, the effects of ecosystem management strategies on invasion success in marine systems is still unclear. We show that resistance to the invasive alga, *Sargassum horneri,* in a temperate reef system occurs through alternate mechanisms in different ecosystem states. In an old marine protected area (MPA), invasion of *S. horneri* was suppressed, likely due to competitive pressure from native algae, resulting from protection of urchin predators. In a nearby fished urchin barren, invasion of *S. horneri* was also suppressed, due to herbivory by urchins whose predators are fished. Within newer MPAs with intermediate levels of interacting species, *S. horneri* was abundant. Here, neither competition from native algae nor herbivory was sufficient to prevent invasion. We confirm that invasion in marine systems is complex and show that multiple mechanisms in single systems must be considered when investigating biotic resistance hypotheses.

Keywords

algae, biotic resistance, competition, invasive species, herbivory, marine protected area, MPA, predation, *Sargassum horneri*.

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INTRODUCTION

Biological invasions are a leading threat to biodiversity in marine, freshwater and terrestrial ecosystems (Wilcove *et al*. 1998; Mack *et al*. 2000; Bax *et al*. 2003; Simberloff *et al*. 2013). Invasive alien species are defined by the Convention on Biological Diversity as species that establish outside of their native range and become 'agents of change' (CBD 2000). In addition to loss of native biodiversity, the changes these 'agents' bring to native ecosystems include alteration and degradation of habitat, disease transmission, changes in genetic diversity and shifts in trophic structure; ultimately invasive species can change the entire functioning of ecosystems (Vitousek 1990; Grosholz 2002; Roemer *et al*. 2002; Croll *et al*. 2005; Kimbro *et al*. 2009). Through these primarily negative impacts, invasive species affect humans directly and indirectly by compromising ecosystem services such as fisheries, coastal recreation and even disease regulation (Ruiz *et al*. 1997; Pejchar & Mooney 2009). In the United States alone, economic costs of damages and management of invasive species have been estimated at a staggering $120 billion USD per year (Pimentel *et al*. 2005).

Marine invasions are forecasted to increase with changes in ocean climate and rising globalisation causing increased shipping traffic, a major vector of marine invasive species (Cohen & Carlton 1998; Stachowicz *et al*. 2002; Molnar *et al*. 2008; Sorte *et al*. 2010; Seebens *et al*. 2013). Unfortunately, most marine invasions are difficult to prevent, control or reverse (Thresher & Kuris 2004; Williams & Grosholz 2008). Marine algae, in particular, have shown a remarkable ability to spread rapidly over large geographical areas after initial establishment (Chapman *et al*. 2006; Lyons & Scheibling 2009), which is problematic because eradication success for aquatic species is usually contingent on early identification and rapid response to pre-empt further dispersal (Wotton & Hewitt 2004; Anderson 2007). Currently, little is known about the ecological factors that drive invasion success or failure in marine compared with terrestrial ecosystems. Foundational work on invasion ecology suggested that invasion success was determined by the ability (or lack thereof) of native communities to suppress populations of non-indigenous species (NIS) via strong competitive interactions (Elton 1958). The concept of 'biotic resistance' has been further refined and expanded (Pimm 1991; Blossey & Notzold 1995; Keane & Crawley 2002; Callaway & Ridenour 2004; Alpert 2006; Sih *et al*. 2010) but at its core are hypotheses regarding the invasibility or resistance, via biological mechanisms, of a native community to invasion by NIS.

Biological mechanisms for resistance to an invader need not be driven by competition alone, but can also include predation, herbivory and disease. Levine *et al*. (2004) challenged conventional wisdom stemming largely from Elton's early works regarding the strength of biotic resistance via competition in terrestrial plant communities. In a meta-analysis of plant invasion experiments, they found that in addition to competition, both herbivory and diversity of resident species had negative effects on invader establishment and performance. Two recent meta-analyses have assessed the relative importance of some of the biological mechanisms promoting or preventing invasions in marine habitats (Kimbro *et al*. 2013; Papacostas *et al*. 2017). Papacostas *et al*. (2017) found that among studies describing negative interactions (comprising the majority of studies in the analysis), most showed an increase in invasion success with release from competitors and consumers (i.e. biotic resistance), but among those, predation was found to limit invasion success more often than

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competition. This contrasts with terrestrial studies where competition was at least as strongly, if not more strongly related to invasion success as other mechanisms (Levine *et al*. 2004; Kimbro *et al*. 2013).

The majority of work on biological controls on marine invasions involves experimental or observational studies that measure the direct effects of, for example, a single consumer or a single competitor on an invader (Papacostas *et al*. 2017). When multiple species are involved, it is usually in the context of diversity; testing the well-known hypothesis that diversity impedes invasion success via increased resource pre-emption (Stachowicz *et al*. 1999). However, evidence for negative effects of diversity on invasion success in marine systems is ambiguous (Dunstan & Johnson 2004; Fridley *et al*. 2007; White & Shurin 2007; Papacostas *et al*. 2017) and identity and functional traits of the native assemblage may be at least as important as diversity for resistance to invasion by marine algae (Arenas *et al*. 2006; Britton-Simmons 2006; Bulleri *et al*. 2016; South & Thomsen 2016; Stamoulis *et al*. 2017). Further evaluation of combined indirect and direct effects of competitors and consumers on populations of NIS via interactions throughout complex natural trophic webs is needed (Papacostas *et al*. 2017). Furthermore, few studies have examined the cascading effects of marine management strategies on invasions, despite promises of increased resilience in 'healthier' well-managed ecosystems (Burfeind *et al*. 2013; Giakoumi & Pey 2017).

Invasive alien species are not the only 'change agents' in marine systems. Humans have been altering marine ecosystems for millennia through resource extraction and management. One management strategy that is widely used in marine systems globally is establishment of marine protected areas (MPAs). MPAs, by reducing local anthropogenic impacts (primarily via removal of fishing), have been widely promised to provide resilience or resistance to a variety of threats, including invasion by NIS. However, evidence for this resistance is equivocal at best. Two recent reviews of effects of MPAs on invasion by NIS have shown varied effects (positive, negative and neutral), and both acknowledge that the limited number of published studies, and lack of geographical and taxonomic coverage of NIS invasions, restricts their ability to generalise broadly about the relationships between MPAs and NIS (Burfeind *et al*. 2013; Giakoumi & Pey 2017).

Here, we seek to understand the biological mechanisms that lead to resistance of an invasive alga (*Sargassum horneri*) in a system with multiple MPAs of different ages and protection levels. In addition to biological interactions, invasion success can be affected by propagule pressure via dispersal, as well as abiotic factors (Simberloff 2009). Most marine studies do not take these factors into account (Papacostas *et al*. 2017) and those that do are often experimental manipulations at small spatial scales. Our observational study takes place across a spatial scale that effectively controls for differences in latitude, habitat, propagule supply, and abiotic oceanographic factors, yet is large enough to test the effects of entire communities on invasion within and outside of MPAs with different levels of protection.

Native to eastern Asia, *Sargassum horneri* has recently invaded and become established throughout southern California, US, and Baja California, Mexico (Marks *et al*. 2015). Using surveys from long-term monitoring programmes, we tracked the invasion on subtidal rocky reefs at Anacapa Island where a system of no-take and partial-take MPAs has been established (Fig. 1). Anacapa has displayed rapid and strong responses to the implementation of MPAs (Hamilton *et al*. 2010; Caselle *et al*. 2015). Previous work has shown large differences in the biomass of targeted fish species (Caselle *et al*. 2015) and that giant kelp forests within the older, no-take marine reserve portion of Anacapa are more resilient than fished areas to disturbance (Lafferty & Behrens 2005). Here, we describe spatial differences in abundance of invasive *S. horneri* and native species across the MPAs and fished areas, testing two mechanisms of biotic resistance: competition and herbivory. We show that the effects of management on rocky reef community structure can lead to similar outcomes in invasibility through entirely different ecological mechanisms.

MATERIALS AND METHODS

Study location

We conducted this study at Anacapa Island, one of the first locations in the Northern Channel Islands (NCI) where *Sargassum horneri* was documented in 2009 (Marks *et al*. 2015). Anacapa is the easternmost and warmest of the NCI (Caselle *et al*. 2015) and is divided into three management zones defined by two natural breaks in the island: State Marine Reserve (SMR; no-take), State Marine Conservation Area (SMCA; commercial and recreational take of CA spiny lobsters and recreational take of pelagic finfish allowed), and Reference area (open to fishing; Fig. 1). A portion of the no-take reserve, north of the eastern island, has been closed to fishing since 1978 (Old SMR) and was extended in 2003 to include the north side of the middle island (New SMR). The SMCA was also established on the north side of the western island in 2003. Thus, we considered four different protection zones: Old SMR, New SMR, SMCA and Reference area. Winds and swells generally come from the northwest and so the position of Anacapa in the more-benign eastern channel and its proximity to ports subject it to higher fishing pressure than the other NCI (Pondella *et al*. 2015).

SCUBA surveys

Fishes, invertebrates and algae are quantified annually as part of a long-term monitoring programme conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). In each protection zone, divers visually survey three sites consisting of four benthic transects for invertebrates and algae and eight transects for non-cryptic fishes (n = 12 benthic and n = 24 fish transects per protection zone). Divers quantify densities of large and mobile invertebrates, understory brown algae and giant kelp stipes on 30 × 2 m band transects. On the same transect, sessile invertebrates, small low-lying algal species and morphological groups, and *S. horneri* are quantified as percent cover using a uniform point contact (UPC) method every meter along the transect. In a separate survey,

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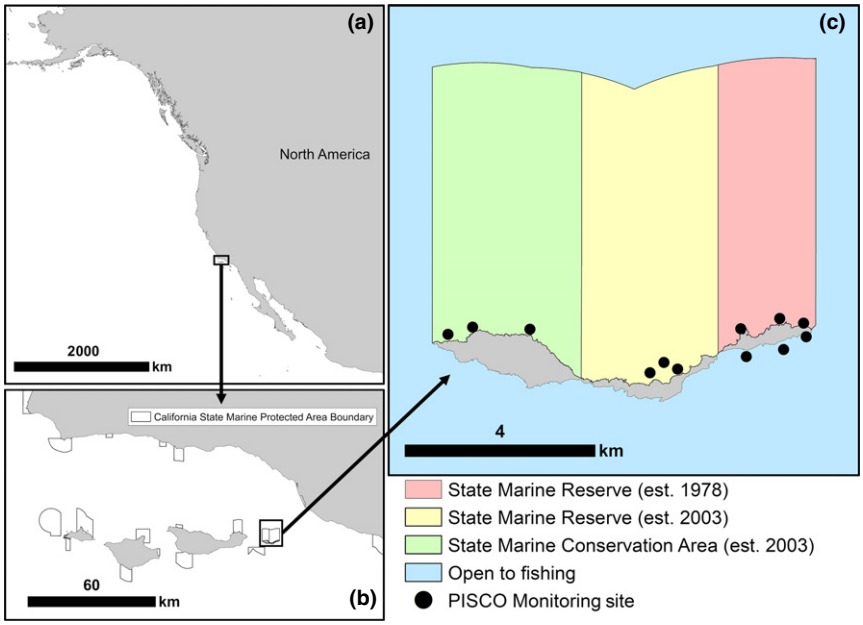

Figure 1 Map of study area in the Channel Islands. (a) North America showing location of the Santa Barbara Channel and Northern Channel Islands. (b) Detail of the Santa Barbara channel and northern Channel Islands showing outlines of the Marine Protected Areas. (c) Detail of Anacapa Island showing three protection zones and sampling locations (black circles). East Island (red) is a no-take State Marine Reserve (SMR) since 1978. Middle Island (yellow) is an SMR since 2003 and West Island (green) is a partial-take State Marine Conservation Area (SMCA). The south shore (blue) is open to fishing. The south shore of the East Island is the Reference area.

all non-cryptic fishes are counted and sized within a 30 × 2 × 2 m band transect along the bottom and at midwater depths. Both benthic and fish survey transects are split between two depth strata (shallow: 5 m and deep: 12–15 m). We calculated biomass for fishes using length–weight relationships from the literature and FishBase (fishbase.org).

Sargassum horneri surveys

Three sources of data were used for *Sargassum horneri* analyses. First, to investigate the time course of invasion, we used density data (quadrat surveys) from the long-term kelp forest monitoring programme of the Channel Islands National Park (Kushner *et al*. 2013) at locations on or adjacent to the PISCO sites. In July of 2015 and 2016, we conducted additional surveys to estimate the density and biomass of *S. horneri* at all PISCO survey sites. Within six 1 × 1 m quadrats at fixed distances along the shallow transects, we recorded the abundance of *S. horneri* and maximum size (diameter for recruits, height for all other life stages) for each individual. We converted abundance to biomass using size–weight relationships for *S. horneri* (L. Marks, unpublished data). Finally, we used percent cover data from PISCO UPC surveys described above.

Statistics

Using analysis of variance (ANOVA), we tested for spatial and temporal differences in the major species or taxonomic groups comprising the community, that is, biomass of California (CA) sheephead (*Semicossyphus pulcher*); density of CA spiny lobster (*Panulirus interruptus*), red and purple urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*), giant kelp (*Macrocystis pyrifera*) and understory brown algae (including kelps of the order Laminariales and the native fucoid *Stephanocystis osmundacea*); and percent cover of crustose coralline algae, fleshy red algae and *S. horneri*. Using data from 2014 to 2016, we tested the effects of year, protection zone (four levels: Old SMR, New SMR, SMCA and Reference; fixed) and site (three sites nested in each protection zone; random). Given the strong effects of protection zone in the models, Tukey's HSD (honest significant difference) tests were used to test all possible pairwise contrasts. CA spiny lobster, urchin and *S. horneri* data were square root transformed to improve the spread of the residuals. To visualise and test for differences across protection zones for the entire fish community, and invertebrate and algal community, we used non-metric multi-dimensional scaling (nMDS) plots and PERMANOVA. Analyses were conducted using PRIMER v6.0 with PERMANOVA+ add on (Anderson *et al*. 2008) and JMP 12.

Diversity and richness

We calculated species (or taxonomic groups) diversity (Shannon Weiner index, H' [loge]) and richness (total species or taxonomic groups, S) using PRIMER. We calculated benthic diversity from band transects (large and mobile invertebrates, understory brown algae and giant kelp stipes), excluding *S. horneri*. We did not include point contact data because taxonomic resolution on these surveys is low. We used two time periods to investigate diversity and richness: prior to when *S. horneri* increased in abundance (2010–2013; 'pre-invasion') and while abundance increased markedly (2014–2016; 'post-

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invasion'; Fig. 2). We tested the effect of protection with ANOVA following the models described above, but instead of a 'year' effect, we ran models on each time group separately.

Path analysis

Path analysis and structural equation modelling (SEM) are methods commonly used to characterise relationships between biological and physical factors and assess the relative strength of direct and indirect interactions in complex kelp forest ecosystems (Britton-Simmons 2004; Arkema *et al*. 2009; Byrnes *et al*. 2011; Hamilton & Caselle 2015). SEM allows for the testing of *a priori* specified hypotheses of the direct and indirect relationships between variables (Rosseel 2011). In this study, we hypothesised that urchins affect the abundance of *S. horneri* through two distinct pathways, both directly (negatively via direct grazing) and indirectly (positively via grazing on benthic algal competitors). We used SEM to evaluate the strength of the causal relationships between species or taxonomic groups that we hypothesised to be influencing *S. horneri* abundance through these trophic linkages. We calculated the Satorra–Bentler corrected, maximum likelihood (ML) estimation of the regression coefficients using the lavaan package in R (R Core Team 2000; Rosseel 2011). In the initial model, we included the following variables: CA sheephead biomass, CA spiny lobster density, urchin density (red urchins and purple urchins combined), giant kelp stipe density, understory brown algal density, percent cover of fleshy red algae, and percent cover of *S. horneri* from site-level means for each year from 2014 to 2016. We used the same data transformations that were used in the ANOVA models and included a correlated error term between native algal groups.

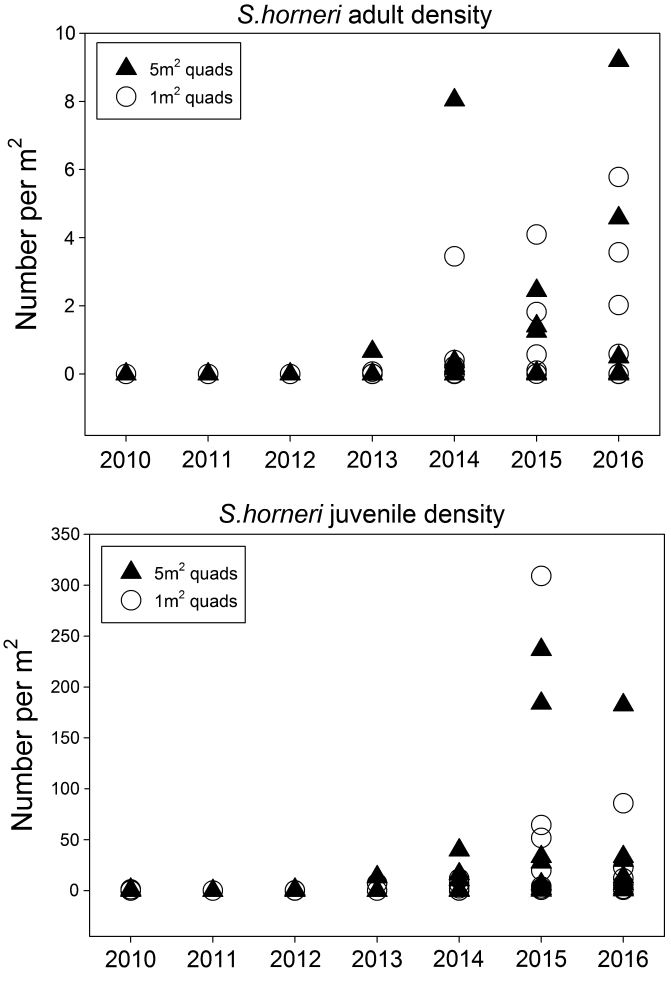

Figure 2 Time course of invasion of *Sargassum horneri* to sites at Anacapa Island. Data are mean density (number per m^2) per site per year for (top) adult and (bottom) juvenile *S. horneri*. Density data come from the Channel Islands National Park Service Kelp Forest Monitoring programme using two methods (1 and 5 m^2 quadrats) from 2010 to 2016.

RESULTS

Time course of *S. horneri* invasion

Though *S. horneri* was first documented at Anacapa Island in 2009, densities did not start to increase rapidly until 2013–2014 (Fig. 2), coinciding with a warm water event and El Nino conditions in the region. By 2015, some sites had densities of 200–300 individuals m^{-2}, but variation among sites was high.

Native kelp forest community

We present the mean density or biomass of the key components of the kelp forest community that are trophically related and are likely drivers of *S. horneri* biomass, either directly or indirectly (Table 1, Fig. 3a–g, Appendix S1: Table S1). Two predators of urchins, CA sheephead and CA spiny lobster, were more abundant in MPAs than the reference sites. Biomass of CA sheephead was higher at the Old SMR, SMCA and New SMR, all locations where fishing is banned for this species, and lowest in the Reference area, although significant variation occurred among sites within protection zones (Table 1, Fig. 3a). CA spiny lobster had the highest density, where it is protected (Old and New SMRs), and very low density, where it is fished (SMCA and Reference area, Fig. 3b). Urchin density was greatest in the Reference area, moderate in the SMCA and very low in the Old and New SMRs (Fig. 3c). We also detected a significant temporal effect for urchins, likely due to consistently decreasing urchin density in the New SMR (Table 1). Native fleshy algae were generally most abundant in the protected areas and much less abundant out of protected areas (Fig. 3d–f) although two sites in the New SMR had low densities of understory brown algae. Crustose coralline algae (CCA) showed an opposite pattern to the fleshy native algae, with high percent cover in the Reference area and lowest percent cover in the Old SMR (Fig. 3g). An MPA at neighbouring Santa Cruz Island showed similar community patterns between a new (established in 2003) SMR and adjacent fished Reference areas (see Appendix S2: Fig. S1 and Fig. S2).

We used nMDS to visualise and PERMANOVA to test for differences across protection zones in the entire assemblages of fishes (biomass) and invertebrates and algae (density). PERMANOVA models showed significant differences among protection zones for both assemblage types (Appendix S1: Table S2

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and S3). However, fish assemblages did not separate with protection zone as clearly as invertebrate/algal assemblages, where all four levels of protection were different and the MPA sites were particularly distinct from the reference sites (Appendix S1: Fig. S1).

Spatial patterns of *S. horneri* biomass

We observed strong spatial variation in *S. horneri* biomass across Anacapa (Fig. 3h). Unlike native algal species, which tended to increase or decrease consistently with levels of protection, the highest biomass of *S. horneri* occurred in the New SMR and SMCA. Low biomass was observed in both the Old SMR and Reference area. Spatial patterns in percent cover from PISCO surveys showed very similar results (Appendix S3: Fig. S1). Using percent cover data for ANOVA, we found strong effects of protection zone, but no effect of year or site nested within protection zone (Table 1). Similarly, at Santa Cruz Island, *S. horneri* was established in the New SMR but not in the fished Reference area (Appendix S2: Fig. S2H).

Table 1 Nested analysis of variance (ANOVA) testing the effects of year, protection zone and sites nested in protection zone on patterns of fish, invertebrate and algal biomass, density and percent cover at Anacapa Island

Model r^2	Factors	d.f.	*F*-ratio	*P*-value
A. CA Sheephead biomass				
0.76	Year	1, 35	0.84	0.37
	ProtectionZone	3, 35	11.36	**0.0015**
	Site [ProtZone]	8, 35	4.75	< **0.0001**
B. CA spiny lobster density				
0.74	Year	1, 35	3.70	0.07
	ProtectionZone	3, 35	16.01	< **0.0001**
	Site [ProtZone]	8, 35	1.73	0.14
C. Urchin density				
0.85	Year	1, 35	22.40	< **0.0001**
	ProtectionZone	3, 35	33.02	< **0.0001**
	Site [ProtZone]	8, 35	1.59	0.14
D. Giant kelp stipe density				
0.54	Year	1, 35	2.92	0.10
	ProtectionZone	3, 35	5.69	**0.0046**
	Site [ProtZone]	8, 35	0.99	0.47
E. Understory brown algae density				
0.83	Year	1, 35	3.90	0.06
	ProtectionZone	3, 35	29.30	< **0.0001**
	Site [ProtZone]	8, 35	3.05	0.02
F. Fleshy red algae percent cover				
0.84	Year	1, 35	0.02	0.90
	ProtectionZone	3, 35	33.14	< **0.0001**
	Site [ProtZone]	8, 35	2.39	**0.048**
G. CCA percent cover				
0.74	Year	1, 35	0.59	0.45
	ProtectionZone	3, 35	14.92	< **0.0001**
	Site [ProtZone]	8, 35	2.47	0.042
H. *Sargassum horneri* percent cover				
0.66	Year	1, 35	2.38	0.13
	ProtectionZone	3, 35	11.44	< **0.0001**
	Site [ProtZone]	8, 35	0.87	0.55

Years included in analysis are 2014–2016. Statistically significant *P*-values are in bold text.
CCA, crustose coralline algae.

Diversity and richness

To test the effects of benthic diversity (H') and species (or taxonomic group) richness (S) on invasion success, we assessed variation of these metrics with protection level prior to invasion (2010–2013) and during invasion (2014–2016). Diversity varied significantly among protection zones in both time periods (Table S1), but the spatial patterns differed (Fig. 4). Prior to invasion, diversity was greatest in the Old SMR and lower and not different across the other zones. During the invasion, diversity remained low in the Reference area and was high and not different among the three protected zones (Fig. 4). Species richness showed no significant variation among zones during either time period (Fig. 4, Appendix S4: Table S1).

Direct and indirect interactions

We constructed a simple path analysis to evaluate the direct and indirect interactions between the main ecologically connected groups in our system (Fig. 5). In the initial model, all parameters had a significant effect except for giant kelp, so we removed it from the model and calculated the chi-square test statistic and Akaike information criterion (AIC) for each model to compare the two nested models (Britton-Simmons 2004). Both chi-square and AIC values for the model without giant kelp were lower (ML chi-square estimate = 6.98, AIC = 1120.6 for model without giant kelp; ML chi-square estimate = 7.42, AIC = 1559.6 for model including giant kelp), and the reduced model had a non-significant ML chi-square estimate ($P = 0.32$, d.f. = 6), so we present the results of that model here (Appendix S5: Table S1). The model indicates that urchins have a strong direct negative effect on the invasive alga as well as positive indirect effects, likely mediated by grazing on native algae. Urchin predators have strong direct effects on urchins, with CA spiny lobster showing stronger negative effects than CA sheephead. The model illustrates the importance of both consumption (i.e. grazing on *S. horneri* by urchins) and competition (i.e. via space occupation, shading, or abrasion between native understory brown and red algae and *S. horneri*).

DISCUSSION

Here, we show that biotic resistance to an invasive alga can be achieved within a temperate reef system but surprisingly that resistance can be realised through alternative mechanisms arising from dramatically different ecosystem states (Appendix S6: Fig. S1). In one case – in a mature kelp forest within an old MPA – invasion of *Sargassum horneri* was suppressed. Here, urchin predators were abundant, urchins were very rare, and native algae was abundant, and the likely mechanism for invasion resistance was strong competitive pressure from an established native algal assemblage for light and space (Airoldi 2000; Clark *et al.* 2004). In the other case – in a fished urchin barren – invasion by *S. horneri* was also suppressed. Urchin predators were rare, urchins were abundant, and native algae was rare; the likely mechanism for resistance was herbivory by urchins (Bulleri *et al.* 2009).

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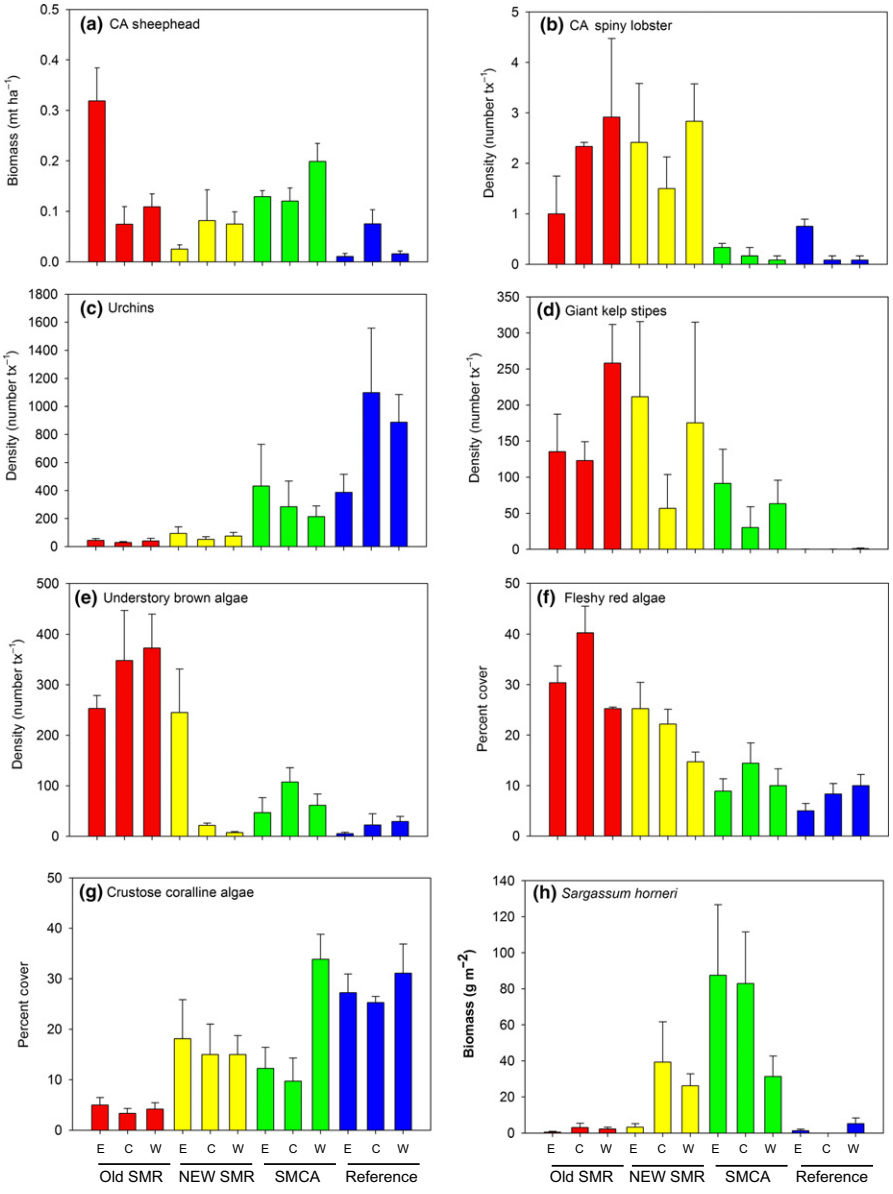

Figure 3 Means and standard errors of biomass, density or percent cover of major, ecologically interacting species or taxa across sites within different protection zones at Anacapa Island. See methods for levels and timing of protection in the different zones. E(ast), C(entral) and W(est) refer to sites within protection zones. All data are from PISCO annual surveys from 2014 to 2016 except *S. horneri* biomass which are from quadrat surveys in 2015 and 2016.

Alternatively, *S. horneri* was highly abundant within MPAs that were more recently established and had intermediate levels of urchin predators, urchins and native algae. In this case, neither the competitive pressures from native algae nor grazing pressure from herbivorous urchins was sufficient to prevent the establishment and rapid proliferation of the invasive alga. This indicates a potentially bi-modal, density-dependent effect of grazers on the invasive alga. Grazers exert both direct (by consumption) and indirect (by altering the abundance and assemblage of native competitors) effects on invasive algal performance (Bulleri *et al.* 2009). We hypothesise that at very high densities, grazers indiscriminately consume any available algae, while at very low densities, they may prefer native species but grazing pressure is too weak to reduce the competitive advantage of native algae. However, at intermediate grazer densities, preferential herbivory on native algae may be substantial enough to facilitate *S. horneri*. Urchins have been shown to graze a non-native alga only in the absence of preferred native kelp (Sumi & Scheibling 2005), and grazer preference studies have also shown that native macroalgae are preferred over *Sargassum* species in their invasive ranges, which could have major implications for the trajectory of the macroalgal community (Monteiro *et al.* 2009; Schwartz *et al.* 2016). These findings are consistent with the spatial patterns of *S. horneri* abundance observed here.

In addition to the direct and indirect effects of key species in our rocky reef system, we also investigated the effects of benthic community diversity on patterns of invasion. Highly

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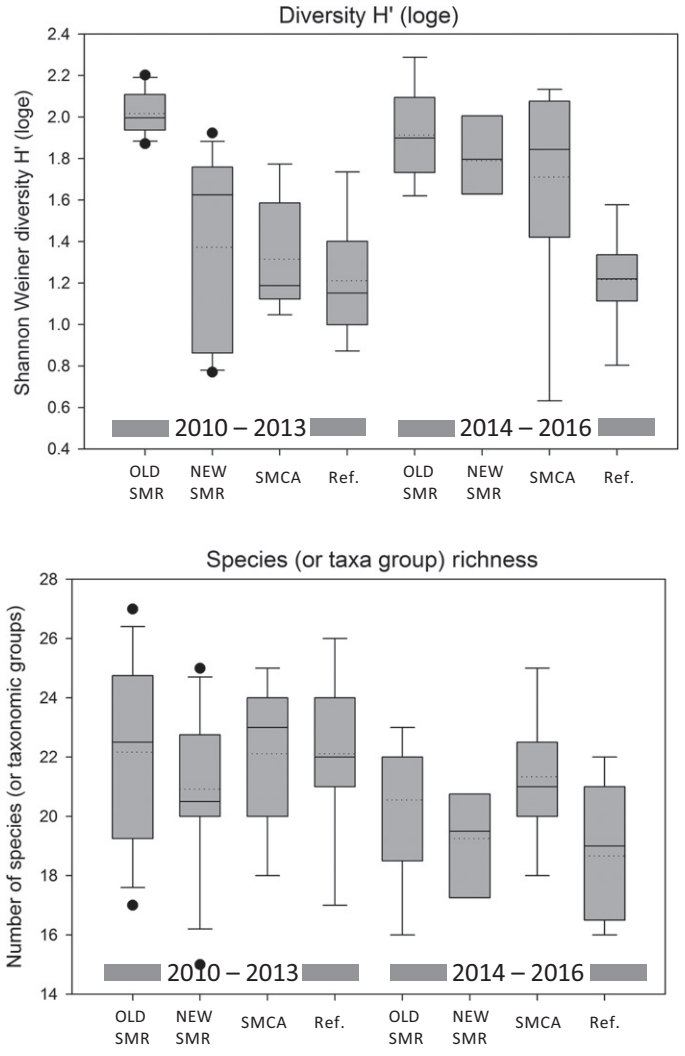

Figure 4 Means and standard errors of (top) fish and benthic invertebrate and algal diversity (H') and (bottom) fish and benthic invertebrate and algal species richness.

diverse communities are thought to resist invasion through ecological niche pre-emption and by increasing the potential for strong competitive interactions (Clark & Johnston 2011). However, evidence for this relationship is equivocal: experiments at small spatial scales show negative relationships between diversity and invisibility, while larger-scale observational studies show positive relationships between native and non-native diversity (reviewed in Levine & D'Antonio 1999; Levine *et al*. 2002; Fridley *et al*. 2007). Unlike many studies, we tracked the native communities both before widespread establishment of the invasive species and during a period of increasing abundance. The two areas that resisted invasion (Old SMR and Reference) had the highest and lowest diversity prior to and during the invasion. Interestingly, the invaded locations (i.e. new SMR and SMCA) had low native diversity prior to the invasion, but at both sites, diversity increased over the course of the invasion, indicating that the effects of marine protection on diversity might not be hampered by the invasion. We used standard diversity indices, here but these may not best reflect properties of communities responsible for invasion resistance (Dukes 2001); better measures might include functional properties of communities (Villéger *et al*. 2008). However, this study provides more evidence for complex and nonlinear diversity–invasibility relationships (Byers & Noonburg 2003), especially in the context of marine management.

The relatively small geographical scale of this study makes it unlikely that the spatial variation in community structure, and relative prevalence of *S. horneri*, arose due to large-scale environmental factors or habitat characteristics. The strong differences in community assemblages between sites that are separated by such short distances (< 10 km) suggest that management designation is the primary factor driving the ecological dissimilarities reported here. Temperate MPAs have been shown to increase kelp abundance and overall kelp forest resilience through the restoration of urchin predator populations (Babcock *et al*. 1999; Shears & Babcock 2002; Lafferty & Behrens 2005; Ling *et al*. 2009; Hamilton & Caselle 2015). The results of this study indicate that some MPAs can facilitate resilience to invasive species through the indirect relationships between urchin predators and native algae. However, in this study, only the old (*c*. 40 year) established MPA resisted invasion, while the newer (*c*. 13 year) MPAs were heavily invaded. These newer MPAs appear to be in a transitional state between urchin barren and kelp forest (increasing urchin predators, declining urchins and increasing native algae), resulting in abundant uncolonised space with only a moderate number of grazers, which potentially created conditions that facilitated the invasion. This suggests that the timing of protection (and native community change) relative to the timing of invasion is an important factor to consider when assessing the effectiveness of MPAs at resisting invasions or when designing MPAs with specific goals related to buffering from invasive species. Studies have shown that recovery of top predators within temperate MPAs and subsequent trophic cascades and restoration of native algal communities occur at decadal or multi-decadal time scales (Guidetti & Sala 2007; Babcock *et al*. 2010; Leleu *et al*. 2012). Our results indicate that similar time scales may be necessary for the development of stable benthic communities that are resistant to invasion.

The pattern of invasion resistance in the fished urchin barren sites is difficult to valuate. Though reduced prevalence of the invasive species may be considered a positive outcome, the situation was generated due to trophic dynamics in an ecosystem state that is ostensibly undesirable (Filbee-Dexter & Scheibling 2014). We found lower benthic biodiversity in the unprotected, urchin-dominated Reference area, and many studies have documented the importance of kelp forests to maintenance of biodiversity relative to unproductive urchin barrens (Edgar *et al*. 2004; Graham 2004; Ling 2008). Invasion resistance due to urchin herbivory may be precarious because urchins in dense barrens are prone to disease epidemics (Lafferty 2004), and this could lead to a reduction in grazing pressure that ultimately facilitates invasion. This also has implications for kelp forest restoration, because urchin removal programmes have been proposed as an effective restoration tool (Baskett & Salomon 2010) and have already been implemented in California waters with some success (Ford & Meux 2010; Claisse *et al*. 2013). Invasion potential

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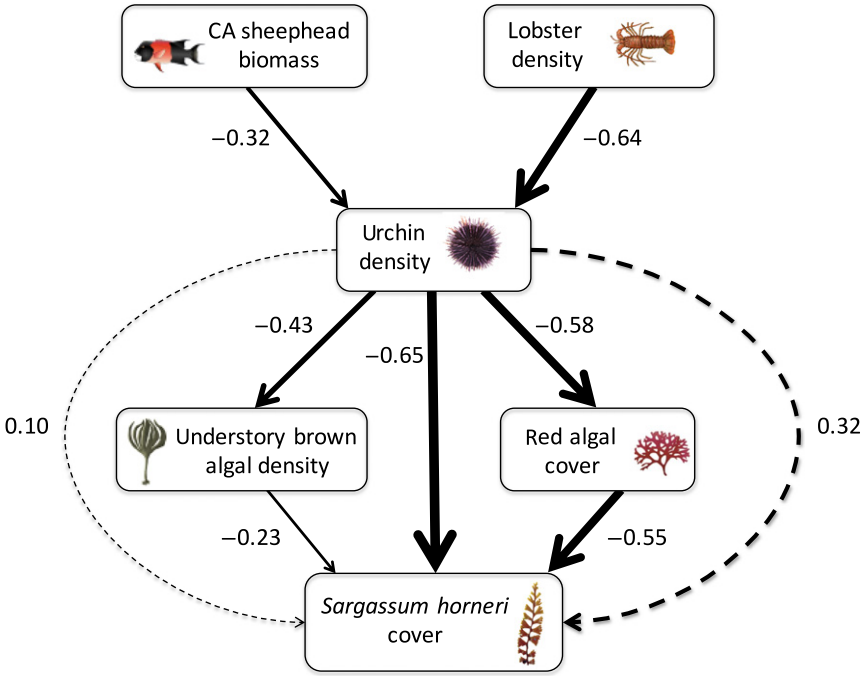

Figure 5 Path diagram showing standardised correlation coefficients of the direct (solid arrows) and indirect (dashed arrows) effects of predators (CA sheephead and CA spiny lobster), urchins and native algae (understory brown and benthic red algae) on the invasive alga, *Sargassum horneri*. Arrow thickness represents the strength of the correlation.

should be carefully considered when restoration efforts utilise consumer population manipulation to restore native communities.

Marine protected areas are essentially large-scale experiments that permit investigation of the effects of human activities on reef communities and, in this case, the resulting potential for invasion. While we have documented similar patterns across a network of MPAs spanning two islands, expanding the geographical scope of these surveys would provide much needed insight into the generality of the patterns we observed. Correlative studies such as this one are critical for identifying potential mechanisms of resistance which can then be experimentally tested. The density-dependent effect of urchin preference for native algae over *S. horneri* and the competitive interactions between *S. horneri* and native macroalgae should be evaluated in an experimental framework to test the hypotheses that we present here regarding biotic resistance to its invasion.

Presently, it is unclear whether the community within the new MPAs will develop into a healthy state. The macroalgal community currently consists of a mix of native understory species, giant kelp and abundant *S. horneri*, but experimental manipulations would reveal whether *S. horneri* is hindering the recovery of giant kelp and other native algae. Observational evidence suggests *Sargassum* species have the ability to exclude native macroalgae in their invasive ranges (Stæhr *et al.* 2000). Experimental removal of *S. muticum* on an invaded reef resulted in increased abundance and growth rates of native understory and canopy-forming species, due to a release from shading by the invasive alga, further demonstrating the potential for suppression of native populations by non-native *Sargassum* (Britton-Simmons 2004). Experimental evidence also indicates that invasive algae can opportunistically colonise where native algae have been reduced by disturbance, and subsequently inhibit the recovery of native species (Scheibling & Gagnon 2006). This is especially troubling considering that some of the projected effects of climate change (e.g. increased storm frequency and severity, warm water events, ocean acidification) could intensify disturbances to temperate marine ecosystems (Dayton & Tegner 1984; Connell & Russell 2010; Wernberg *et al.* 2013). If invasions (rates of which are also predicted to increase with climate change; Stachowicz *et al.* 2002) coincide with these disturbances, they may slow or prevent kelp forest recovery, which in turn could have significant ecological and economic consequences. Many kelp forest inhabitants, including commercially harvested species, rely on giant kelp for food or habitat (Graham 2004). For example, a variety of important California kelp forest fish use giant kelp canopy for recruitment substrate (Carr 1994; Love *et al.* 2002; White & Caselle 2008). Though *Sargassum* species provide important habitat within their native ranges (Terawaki *et al.* 2003), *S. horneri* is an annual species and the timing of its peak canopy-forming phase is out-of-sync with the settlement period of most of the important kelp forest fish species in California (Love *et al.* 2002; Wilson *et al.* 2008; Caselle *et al.* 2010). Additionally, large-scale inhibition of giant kelp populations may have implications for carbon sequestration (Wilmers *et al.* 2012) and physical protection from coastal erosion (Dubi & Tørum 1997).

Currently, the relative importance of biological mechanisms of resistance to invasion in marine ecosystems is not well understood, and the influence of indirect effects via trophic

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interactions and marine management even less so. Here, we demonstrate, at spatial scales relevant to entire kelp forest communities, that invasion success is highly context dependent and that similar invasional outcomes can be achieved via different ecological processes. Where Burfeind *et al*. (2013) found only neutral or positive effects of protection on invasion success, we found both positive and negative effects, dependent on the age of the MPA and the condition of the native community. It has been suggested that degradation of the environment by humans might enhance invasion success, but the magnitude of this effect and more importantly, the functional relationship between degradation and invasion is currently unknown for most marine communities (Ruiz *et al*. 1997). Clearly, much like in terrestrial systems, invasion in marine systems is complex and unlikely to result from single mechanisms. However, this is the first demonstration, albeit correlative, of multiple mechanisms of biotic resistance at relevant whole community scales for marine systems. This work has both theoretical and management implications; understanding the mechanisms of invasion resistance may allow managers to design strategies for future invasion resistance. Large-scale experimentation on kelp forests and rocky reefs, paying close attention to management effects and indirect interactions in the communities, may provide added context to competing hypotheses within the realm of biotic resistance, but this study clearly demonstrates that multiple mechanisms in single systems must be considered.

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AUTHOR CONTRIBUTIONS

JEC and KD conceived the study. All authors designed the research and collected field data. JEC and KD performed the statistical analyses. All authors wrote the manuscript.

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