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The Distribution, Biology and Ecology of the Invasive Seaweed *Sargassum horneri*
in its Introduced Range

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in

Ecology, Evolution and Marine Biology

by

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in its Introduced Range

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by

Lindsay Megan Marks

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ABSTRACT

The Distribution, Biology and Ecology of the Invasive Seaweed *Sargassum horneri*

in its Introduced Range

by

Lindsay Megan Marks

Sargassum horneri is a seaweed native to eastern Asia that has recently become established in the coastal waters of southern California and Baja California, Mexico. Currently, little is known about the biology and ecology of this invasive alga in its introduced range. In this dissertation and associated manuscripts, I provide a synopsis of *S. horneri* distribution, biology and ecology including: invasion chronology, local abundance, life history and dispersal, mechanisms of invasion, impact on native species, and potential for control. In Chapter 1, I present a chronology of the rapid geographic expansion of *S. horneri* in the eastern Pacific, which I generated from observations of its presence or absence from agency and university scientists in the region. Santa Catalina Island in southern California was one of the first sites of invasion, and the study site I selected for the remainder of my dissertation. In Chapter 2, I use monthly to quarterly surveys over two years to describe the life history of *S. horneri* and quantify traits capable of promoting its spread and persistence, including habitat affinity, reproductive characteristics, and seasonality in abundance and reproduction. In Chapter 3, I perform grazing assays and examine patterns of co-occurrence between *S. horneri* and resident algae to evaluate the potential influence of competition, complementarity and herbivory in controlling its invasion. In Chapter 4, I investigate whether *S. horneri* invasion is a cause or a consequence of ecological change by testing whether

disturbance facilitates its colonization and the establishment of reproductive adults, and how its removal influences the biomass and community structure of algal assemblages. In Chapter 5, I assess the feasibility of controlling the spread of *S. horneri* by investigating the effectiveness of local removal in reducing its population growth and capacity to regenerate from remnant holdfasts. I also quantify the effort required to remove established populations with and without the aid of an underwater suction device.

A general conclusion emerging from this work is that *S. horneri* is an opportunistic species, but not necessarily a strong competitor. I identified several life history characteristics that likely facilitate its invasion, including a phenology that appears to be offset from most native macroalgae that could minimize competition; the ability to use a wide range of depths and substrates that allows *S. horneri* to colonize many different environments; high fecundity and local dispersal that promote the persistence of new populations through multiple generations; occupancy of resources underutilized by native species in space and time; and increased deterrence to herbivory relative to native kelps. Colonization and establishment of *S. horneri* were unaffected by disturbance to the benthic algal community, indicating *S. horneri* was not limited by space on the reef. Resident algal assemblages likewise did not respond to *S. horneri* removal except during one year when it achieved extremely high abundance. I found no evidence that *S. horneri* regenerates from remnant holdfasts, and that removal of adults prior to reproduction can lead to a partial reduction in the subsequent generation relative to unmanipulated areas.

This research provides the first comprehensive assessment of *Sargassum horneri* distribution, biology and ecology and explains several life history characteristics and ecological interactions that have contributed to its invasion success in the eastern Pacific.

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Chapter I

Range expansion of a non-native, invasive, macroalga

Sargassum horneri (Turner) C. Agardh, 1820

in the eastern Pacific¹

Abstract

Sargassum horneri (Turner) C. Agardh, 1820 is a fast-growing brown alga native to shallow reefs of eastern Asia. It has spread aggressively throughout southern California, USA, and Baja California, México since it was discovered in the eastern Pacific in 2003 and poses a major threat to the sustainability of native marine ecosystems in this region. Here we present a chronology of the rapid geographic expansion of *S. horneri* in the eastern Pacific and discuss factors that potentially influence its spread.

Key Words: introduced species; invasion; distribution; seaweed; *Sargassum filicinum*; southern California; Baja California

Introduction

Introductions of marine non-native species continue worldwide and are expected to increase with the expansion of global trade. The spread and ecological effects of newly-established non-native species can vary; some proliferate and compete vigorously in their introduced range and are considered “invasive” (Miller et al. 2011). Introduced marine

¹ This chapter was published in *BioInvasion Records* 4(4): 243-248

macroalgae are no exception, although detailed records of the geographic expansion of introduced marine macroalgae are rare (Lyons and Scheibling 2009) despite there being at least 277 introduced seaweed species globally (Williams and Smith 2007). Documenting the spread of these species can be challenging given the logistical difficulties associated with sampling in subtidal habitats where they occur (e.g. time- and depth-limitations when using scuba and the expense of accessing remote sites). Yet such studies are valuable for not only documenting their distributions but also providing insight into the mechanisms influencing the spread of non-native species.

Here we present the chronology of the geographic expansion of the non-native macroalga *Sargassum horneri* (Turner) C. Agardh, 1820 (Fucales) along the southern region of the Pacific coast of North America, where it has spread rapidly since it was first detected in Long Beach Harbor, California, USA, in 2003 (Miller et al. 2007). We also discuss potential factors influencing the spread of this species and the implications of its invasion to native ecosystems.

Study Area

The study area encompassed the shallow coastal waters of the eastern Pacific ocean from northern California, USA, to the southern tip of Baja California, México. Much of this coast is actively monitored by government and academic researchers, and is therefore an ideal region in which to document the spatio-temporal dynamics of the spread of an invasive macroalga.

Study Species

Miller et al. (2007) initially identified the introduced population of *Sargassum* discovered in Long Beach, California as *S. filicinum* (Harvey, 1860). This annual brown alga is monoecious, with ellipsoidal pneumatocysts, and has a narrow geographic range on the coast of western Japan (Yoshida et al. 1983; Tseng et al. 1985) and southern Korea (Lee and Yoo 1992). On the basis of molecular population studies, Uwai et al. (2009) merged *S. filicinum* with *S. horneri*, a dioecious species with spherical pneumatocysts that is widespread in the warmer waters of eastern Asia (Tseng et al. 1985). Therefore, we refer to the eastern Pacific population as *S. horneri*.

The morphology of *S. horneri* changes throughout its annual, diplonic, life cycle. Embryos develop into small plants with lateral fern-like branches anchored by a common holdfast (Figure 1A). Plants give rise to a single erect frond up to several meters in length that bears numerous vegetative blades buoyed by many small gas bladders (Yoshida 1983). Eventually the frond ceases vertical growth and develops hundreds of reproductive receptacles (Figure 1B). Fertilization occurs when sperm penetrate an egg inside a conceptacle positioned on the surface of a receptacle. The resulting embryo is released and settles to the bottom. After embryos are shed the frond senesces and the entire thallus dies, completing the life cycle. Sexual reproduction is the only known means of propagation.

Miller et al. (2007) recorded the presence of *S. horneri* in the eastern Pacific in southern California shortly after it was first discovered in 2003. Rapid communication, coupled with the species' conspicuous morphology and widely distributed information on its identification, facilitated the subsequent monitoring of *S. horneri* by many researchers in California and Baja California.

Methods

We compiled records of *S. horneri* from herbaria, publications, and government and academic groups monitoring subtidal and intertidal reefs in California and Baja California (Appendix A, Table S1). Its presence or absence was recorded during ecological surveys by observers trained to identify the species. Because this region is extensively and regularly monitored by many trained observers, the spread of *S. horneri* can be described with high spatial and temporal resolution. Using these data, we present a timeline of *S. horneri* spread in southern California and Baja California.

Results

Since 2003 when *S. horneri* was first detected in Long Beach Harbor, it has spread north and south along the mainland coast and westward across several nearshore islands (Appendix A, Table S2; Figure 2). The geographic expansion of *S. horneri* is characterized by isolated introductions to new islands and locations on the mainland widely separated from existing populations, followed by the steady colonization of surrounding areas.

In 2005, just two years after *S. horneri* was first detected in Long Beach, it was found drifting on the surface 260 km south in Todos Santos Bay, Baja California, México. One year later it was confirmed to be growing on natural reefs there, and along the coast of San Diego and the leeward side of Santa Catalina Island, California. Since then it has progressively spread north in southern California and south in Baja California. By 2007, *S. horneri* had spread to Isla Natividad in Baja California, 500 km south of the nearest known population. In 2013, the northern range of *S. horneri* reached Santa Barbara, California, 186 km northwest

of Long Beach. The known northern and southern limits of the range of established populations have not changed since 2013, though additional populations were recorded within the previously established range. However, individual thalli were found floating at the surface west of the current range at Santa Rosa and San Miguel Islands in 2012 and 2015 respectively, and at multiple islands near the southern end of its range in 2015.

The abundance and persistence of the recorded populations varied. Many reports consisted of only a few individuals or groups of individuals in small patches, often at sites where *S. horneri* had not previously been recorded. Patchy distribution continued in subsequent years at many sites, and occasionally *S. horneri* was recorded at a site but not found there again. However, in some areas, such as Santa Catalina and Anacapa Islands, *S. horneri* spread profusely and was persistent, covering large portions of reefs with adult densities $> 100 \text{ m}^{-2}$ and recruit densities $> 1000 \text{ m}^{-2}$ for multiple years (e.g. Figure 1C).

Discussion

Invasive traits

Sargassum horneri has several life history characteristics that make it well adapted for colonizing distant areas and rapidly populating an area once it is established. Thalli are buoyed by gas bladders and are capable of self-fertilization, making the establishment of new populations from long-range dispersal of a single floating thallus possible. Indeed, floating *S. horneri* thalli have been observed frequently off southern California and Baja California and are estimated to remain afloat for several weeks before decomposing (Yatsuya 2008). Local population growth can occur quickly because *S. horneri* is a fast-growing ($4.46\% \text{ day}^{-1}$ adult blade weight maximum relative growth rate; Choi et al. 2008) and highly fecund alga (up to

50% of the biomass of a mature individual is composed of reproductive tissue; L. Marks unpublished data). Furthermore, the patchy distribution and reoccurrence of dense aggregations of *S. horneri* in successive years (Figure 1C) may be explained by the heavy embryos of *S. horneri* which, like other furoid algae, are thought to have limited capacity for dispersal.

Dispersal vectors

The distribution and rapid spread of *S. horneri* is likely influenced by both natural and human-mediated dispersal. Reproductive thalli can become dislodged naturally if severed from their holdfast by grazers or strong wave action and carried to new sites on ocean currents. Divers may also dislodge thalli accidentally or intentionally, inadvertently contributing to its dispersal by either freeing them to float away or transporting them elsewhere. Boaters can dislodge thalli when setting and retrieving anchors lying in *S. horneri*-populated areas. *Sargassum horneri* is also adept at growing on a variety of both natural and man-made surfaces, so vessels fouled with *S. horneri* may be an effective means of transporting it to new locations as suggested by Miller and Engle (2009). The current distribution of this seaweed includes many sites that are frequently visited by boaters and divers, such as harbors or anchorages, supporting the idea that *S. horneri* is being transported regionally by recreational and commercial vessels.

Potential for further spread

Sargassum horneri has expanded significantly further south along the eastern Pacific coast than north, spanning 6.18 and 0.76 degrees latitude from the initial detection site in

Long Beach Harbor, respectively. The thermal tolerances of *S. horneri* may play an important role in determining range limits in the eastern Pacific. Sea surface temperatures in its native range in western Japan and southern Korea average between about 18-22° C (Chu et al. 1998). Baja California water temperatures typically range between 14-22° C on the Pacific coast (Zaytsev et al. 2003), so the continued expansion of *S. horneri* southward along this peninsula is likely. Warmer average temperatures in the Gulf of California and mainland México will likely prevent expansion beyond the peninsula. Ocean temperatures north of Point Conception rarely exceed 18° C, which may prevent *S. horneri* from spreading further north under present ocean climate conditions. However, predictions for a warmer ocean in the future may serve to increase the northward expansion of *S. horneri* in the eastern Pacific.

Implications of S. horneri invasion

Sargassum horneri can be locally very abundant and highly persistent. Therefore, its continued expansion in the eastern Pacific may pose a major threat to the sustainability of native marine ecosystems. Its high growth rates and long, floating thalli may provide a competitive advantage over other macrophytes. In addition, it appears to be avoided by most herbivores (Navarro 2009; Vogt 2010), possibly due to high concentrations of phenolic compounds that have been shown to deter grazing in other furoid algae (Steinberg 1985). Mesoinvertebrates that use macroalgae as biogenic habitat and the fish that depend on these invertebrates may also be affected by the *S. horneri* invasion. Research investigating the interactions between *S. horneri* and ecologically important species is critically needed to understand how its invasion may be altering the structure and functioning of existing ecosystems of the eastern Pacific.

Conclusion

The range of *S. horneri* has expanded rapidly in the eastern Pacific since it was first detected in 2003. Its expansion to the south has been more extensive and occurred more quickly than to the north, suggesting that it may be better suited to warmer southern waters. The prevalence of *S. horneri* at popular boating and diving destinations suggests that its spread is the result of multiple introductions. The life history of this species allows distant areas to be colonized by a single individual, which facilitates its spread. The high abundance and persistence of *S. horneri* in novel areas has heightened the awareness of its invasion potential and raised concerns about its possible adverse effects on existing ecosystems. Future research aimed at determining the environmental factors affecting its spread and the ecological and economic consequences of *S. horneri* invasion will provide much needed insight into the cost and need for human intervention in controlling its invasion.

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Figures

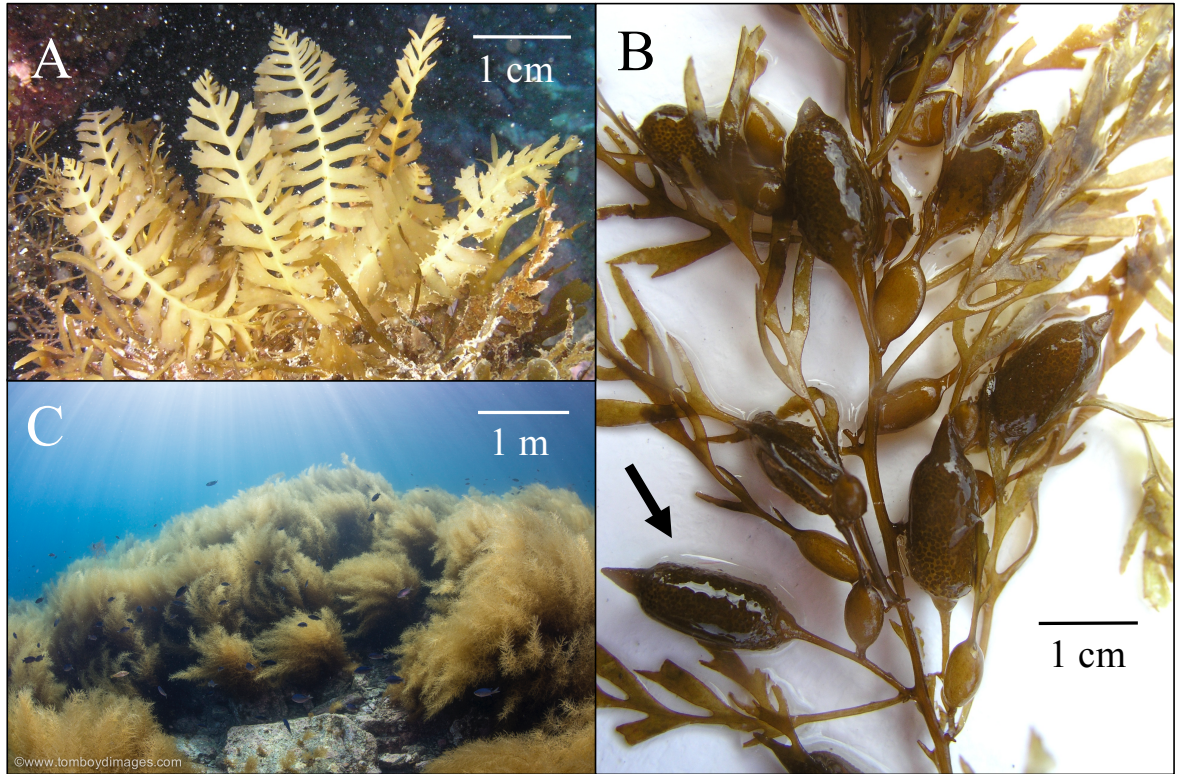


Figure 1. *Sargassum horneri* morphology and life cycle. (A) Recruit, (B) Mature thallus with reproductive receptacles indicated by arrow, (C) Thick canopy on a shallow reef. Photo credits: Jessie Alstatt (A), Dan Richards (B), Tom Boyd (C).

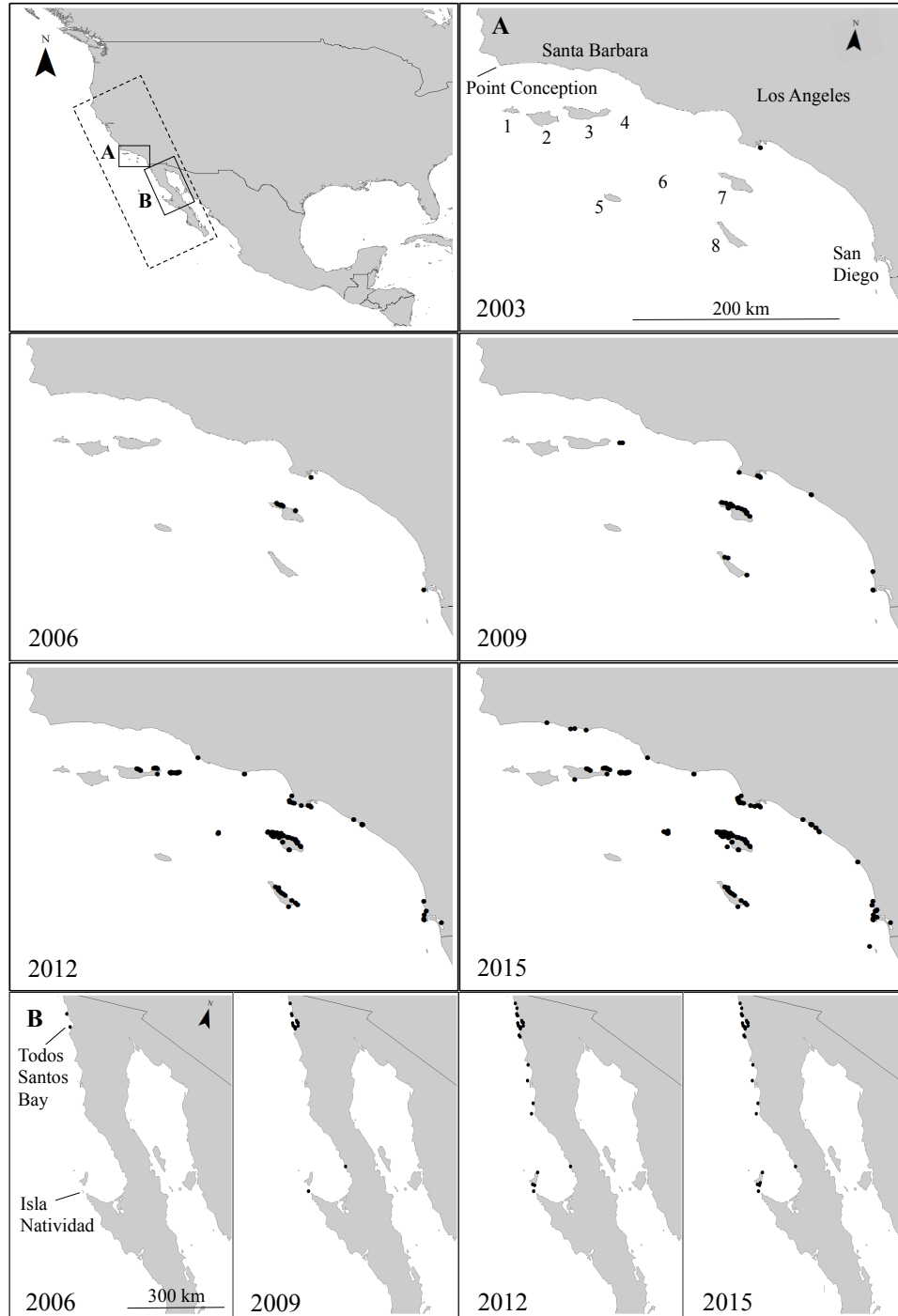


Figure 2. Chronology of geographic expansion of *S. horneri* in the southern California (A) and Baja California (B) regions. Each dot identifies a location where *S. horneri* was found attached to the substrate at least once. Each panel includes observations from all previous years to display the distribution of *S. horneri* at each interval. The California Channel Islands are identified by number as follows: 1. San Miguel, 2. Santa Rosa, 3. Santa Cruz, 4. Anacapa, 5. San Nicholas, 6. Santa Barbara, 7. Santa Catalina, 8. San Clemente. The entire study area is outlined by the dashed line. Maps created by P. Carlson.

Appendix A: Electronic Supplements S1-S2

Table S1. Sources for records of *Sargassum horneri* occurrence.

Table S2. Records of the occurrence of *Sargassum horneri* in California, USA, and Baja California, México, since 2003, the year it was first discovered in the eastern Pacific.

This material is available online for free download from the Long Term Ecological Research Network Data Portal at:

http://www.reabic.net/journals/bir/2015/Supplements/BIR_2015_Marks_etal_Supplement.xls

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Chapter II

Life history traits of the invasive seaweed *Sargassum horneri* in its introduced range

Abstract

Researchers have long sought to identify life history characteristics that typify invasive species. While broad generalizations have proven difficult, invasive species within some taxonomic groups tend to share certain traits. An Asian seaweed, *Sargassum horneri* (Turner) C. Agardh, 1820, that is spreading on rocky reefs along the Pacific coast of North America presents an opportunity to expand our understanding of traits of invasive macroalgae. Here we used surveys to characterize the life history of *S. horneri* and quantify traits capable of promoting its spread and persistence, including seasonality in abundance and reproduction, broad habitat affinity, and high reproductive capacity. We found that *S. horneri* occupies a wide range of suitable depths and substrates, allocates substantial biomass to reproduction, and has a phenology of biomass offset from that of most native macroalgae. A field experiment revealed *S. horneri* has a high capacity for local dispersal and recruitment that appears sufficient for maintaining populations through multiple generations. Our findings can be paired with knowledge of the life histories of co-occurring species to characterize their potential ecological interactions with *S. horneri*, which should prove useful for developing best practices for managing its spread.

Key Words: Invasive species; macroalgae; phenology; habitat affinity; fecundity; dispersal; *Sargassum filicinum*

Introduction

A fundamental yet elusive question in invasion ecology is: what makes a species invasive? Here we define invasive as a non-native species introduced by humans, either intentionally or accidentally, that exhibits rapid population growth and spread in the novel environment (Pyšek and Richardson 2006). While only a small fraction of species transported outside their native ranges proliferate and spread (Williamson and Fitter 1996a), they can become challenging or impossible to eradicate once established (Bax et al. 2003). Predicting which introduced species become invasive has clear implications for preventing their spread and has led researchers to search for intrinsic traits associated with invasiveness. Yet identifying consistent characteristics of invasive species has proven difficult; few generalities have emerged across taxonomic groups or geographic regions, likely because successful invasions are the result of both the properties of the novel environment and attributes of the introduced species (Alpert et al. 2000). Traits associated with invasiveness in plants have mostly been related to reproduction (e.g., generation time, length and season of flowering, fecundity and mode of reproduction), but dispersal, size, growth rate, resistance to herbivory, and habitat generality have also been found to be important (Hayes and Barry 2008; Kolar and Lodge 2001; Rejmánek and Richardson 1996; Pyšek and Richardson 2007; Williamson and Fitter 1996b; Hamilton et al. 2005).

Historically, the search for traits of invaders has focused on terrestrial and freshwater species (Carlton 1989), but more recent efforts have turned to marine taxa (Papacostas et al. 2017). In temperate systems, invasive macroalgae represent a small fraction of the invasive species that have been detected (Cohen and Carlton 1995; Ruiz et al. 2000; Wonham and Carlton 2005), yet invasive macroalgae can pose a major threat to native biodiversity and

ecosystem processes by modifying benthic habitat (Jones et al. 1994; Wikström and Kautsky 2004). Perhaps for this reason, a disproportionately large number of studies investigating invasive traits in marine taxa have targeted macroalgae (Papacostas et al. 2017). Invasive traits identified for macroalgae include vegetative reproduction, defenses against herbivory and tolerance to a wide range of environmental conditions, including the ability to grow on a variety of substrates and distribution across a large depth range (Maggs and Stegenga 1999; Boudouresque and Verlaque 2002; Nyberg and Wallentinus 2005).

The spread of the Asian seaweed *Sargassum horneri* (Turner) C. Agardh, 1820 along the Pacific coast of North America presents an opportunity to expand our understanding of traits of invasive macroalgae and how they interact with ecosystem processes to drive marine invasions. The presence of *S. horneri* in North America was first detected in Long Beach Harbor, California in 2003 (Miller et al. 2007). Although the introduced population was identified as *S. filicinum* (Harvey, 1859), this species has since been merged with *S. horneri* based on molecular similarities (Uwai et al. 2009). *S. horneri* has spread widely throughout southern California and Baja California, Mexico (Marks et al. 2015), and its abundance varies within the invaded range but can be extremely high (Marks et al. 2015; Kaplanis et al. 2016; Caselle et al. 2018). Although *S. filicinum* is the only variant of *S. horneri* found in North America, we refer to it as *S. horneri* as per Uwai et al. (2009) except when it is necessary to distinguish the two types.

Information about the life history of the *S. filicinum* variant of *S. horneri* is sparse. It grows to a height of several meters in rocky habitats to depths of 20 m in its native range in western Japan and southern Korea (Sawada 1955; Okuda 1977; Yoshida 1983; Tseng et al. 1985; Lee and Yoo 1992); it has been reported in the intertidal as well as the subtidal in

Mexico and the USA (Aguilar-Rosas et al. 2007; Miller and Engle 2009; Riosmena-Rodríguez et al. 2012; Cruz-Trejo et al. 2015; Marks et al. 2015). It has an annual life cycle (Yoshida 1983; Terawaki 1986), but the seasonality of growth and reproduction has been poorly described and limited to a few samples collected in Japan that suggest the maturation period spans from late spring to summer (Sawada 1955, 1956; Okuda 1977; Yoshida 1983). More detailed information on its life history in its native and invasive range is needed to understand factors that promote its spread the potential ecological impacts of its invasion on native communities, and to develop strategies for management.

In this paper, we characterize several features of the life history of the *S. filicinum* variant of *S. horneri* that may contribute to its invasion success in North America. The seasonality of growth and reproduction of an invasive species with an annual life history is integral to the nature of its interactions with native species in the invaded community, while its ability to disperse and colonize different habitats contributes the extent and speed of its spread. Here we describe the phenology of *S. horneri* within its invaded range by quantifying seasonal differences in its abundance and reproduction at Santa Catalina Island off southern California where it has become well established (Marks et al. 2015). We also evaluated its capacity for local dispersal and measured its depth range and the types of substrates occupied by different stages of its life history. Our intent is to provide a more comprehensive base of knowledge of the life history of this highly successful invader to guide informed decisions pertaining to the management of its spread.

Methods

Study Site and Species

This study was conducted in the shallow subtidal of the western portion of the leeward side of Santa Catalina Island located off the coast of southern California, USA (33.4422°N; 118.4975°W). Shallow reefs in the study area support dense stands of *Sargassum horneri*. Reefs in the study region are characterized by a mixture of bedrock, boulders, cobble and sand and extend from the intertidal to depths of 6 to 30 m where they transition to entirely sandy bottom.

Although the more widespread variant of *S. horneri* is dioecious, the invasive *S. filicinum* variant bears androgynous receptacles and is therefore capable of self-fertilization (Sawada 1958). Crossing between co-occurring populations of these two variants is thought to be rare, possibly limited by selfing in the *S. filicinum* variant or differences in peak periods of fertility (Uwai et al. 2009). Fertilization occurs within conceptacles located on the surface of reproductive structures called receptacles that are born on the lateral branches of a mature thallus (Sawada 1956). Once developed, embryos are shed from receptacles and sink to the bottom where they attach to the substratum. Lateral branches form, followed by a single stipe that grows vertically from the holdfast before reaching reproductive maturity (Sawada 1956; Yoshida 1983). Senescence follows reproduction (Terawaki 1986; Yoshida et al. 1998), completing the annual life cycle.

Study Design

Seasonality of Different Life Stages

To describe the seasonality of abundance, biomass, and reproductive phenology of *S. horneri*, we monitored populations across two annual cycles. We measured density and size of individuals within each life stage throughout the year, and developed allometric formulas to convert these measurements to units of biomass.

Sampling was done at 31 sites spanning 5 km of coastline between the Wrigley Marine Science Center (33.4469°N; 118.4851°W) and the western end of the island (33.4792°N; 118.6057°W), including many locations where *S. horneri* had previously been reported (Miller and Engle 2009). Surveys of *S. horneri* were conducted in eight 1 m² quadrats placed every 5 m along 40 m transects following a 7 m depth contour on continuous reefs. This depth is within the range of peak density, as determined by surveys described below under *Habitat Affinities*. Sites were sampled in June 2013 and every one to three months from December 2013 to June 2015. Sampling periods were assigned to seasons defined as: summer (June – August), autumn (September – November), winter (December – February), and spring (March – May).

Individual *S. horneri* were assigned to one of five different life stages based on their development (Yoshida et al. 2004). Recruits were defined as ≤ 5 cm in height (Figure 1A), while all other stages (immature, fertile, senescent) were > 5 cm tall (Figure 1B-E). Immature plants lacked reproductive structures. A thallus was considered to be fertile throughout the period from the first signs of receptacle development to the decay of spent receptacles. Fertile plants were considered “ripe” if receptacles were present and oospores were visible on the surface of receptacles, and “unripe” if oospores were not detected. Senescent thalli were

those decaying after receptacles had been spent. Because recruits grow laterally while all other life stages grow vertically, we used diameter as a measure of size for recruits and stipe length for all other stages.

We developed size to biomass relationships for each life stage (Table 1) in order to convert estimates of size and density measured non-destructively in the field into units of biomass. Representative samples of each life stage spanning the range of sizes observed from 2013-2014 were collected. Each sample was measured to the nearest cm (maximum diameter for recruits and maximum height for non-recruits) and placed in a salad spinner for 10 seconds to remove excess water before being weighed damp. The size to biomass relationship was best described by power functions for all life stages of *S. horneri* except for the senescent stage (Table 1). The biomass of senescent thalli was highly variable due to varying levels of decomposition. Therefore, we used a constant value of 5.2 g individual⁻¹, the average damp weight of 29 samples collected, to convert densities of senescent individuals into units of biomass. Density measurements and biomass estimates were standardized to the percent cover of hard-bottom habitat within each quadrat as quantified using methods described below in *Habitat Affinities*. Average density and biomass for each life stage were calculated as the mean of these values across the eight quadrats sampled at each site, and across the number of sampling periods within each season over both years.

Habitat Affinities

To characterize the habitat of *S. horneri*, we recorded the abundance of recruits and adults (i.e., all older stages) across a range of depths and substrate types. We examined both recruits and adults because patterns of habitat use or preference can change throughout a life cycle.

The depth distribution of *S. horneri* was assessed by recording its density within 1m² quadrats placed every 5 m along a transect running perpendicular to shore from the intertidal to 30 m depth or where the reef transitioned to sand, whichever came first. These depths span the range within which most native species of macroalgae occur at Santa Catalina Island. Measured depths were adjusted relative to the Mean Lower Low Water (MLLW). Recruits and adults were sampled separately on different dates to capture seasonality of their peak abundance: recruits in June and adults in April. We calculated a mean density within 5 m depth intervals at each site (1-3 quadrats averaged per interval), and averaged densities for each depth interval across all sites. Eight and four of the 31 survey sites described above were sampled in June 2012 and April 2016, respectively.

We characterized the substrate affinity of recruits and adults in the seasonal surveys described above to determine the extent to which colonization and survivorship to reproductive maturity varied in accordance with the availability of different types of bottom substrate. We recorded the type of substrate to which each recruit and adult *S. horneri* counted in the 1 m² quadrats were attached. This was done for two generations (2013 and 2014) of recruits and adults during the time of their peak abundance. The substrate categories were: bedrock, large boulder (> 100 cm diameter), medium boulder (50-100 cm diameter), small boulder (25-50 cm diameter), and cobble (< 25 cm). The occurrence of adults and recruits on the different substrate types was compared to the availability of each substrate type as measured by their percent cover in each quadrat based on a uniform grid of 25 points. Substrate types noted as being present in a quadrat, but not recorded using the uniform point sampling were assigned a value of 0.5%.

Habitat selection for the five substrate types was evaluated separately for recruits and adults using Manly's Alpha of selectivity (Chesson 1978, 1983) with the formula:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j}, i = 1, \dots, m \text{ (Chesson 1983)}$$

where α_i is Manly's Alpha for habitat i , r_i is the proportion of habitat type i used, and n_i is the proportion of habitat type i available in the study area. Where m is the highest number of habitat types (i.e., five in this study), $\alpha_i - m > 0$ indicates preference and $\alpha_i - m < 0$ indicates avoidance. Manly's Alpha was calculated using the aggregate sum of all *S. horneri* and cover of substrate types within all sampled quadrats ($n = 248$ quadrats except in April 2014 when $n = 240$ because one site was not sampled due to inclement weather).

Reproductive Characteristics

We characterized the fecundity of *S. horneri* as based on its reproductive allocation (RA) defined as the ratio of the biomass of reproductive vs. non-reproductive tissue (Mathieson and Guo 1992). When developing the size to biomass relationships described above, receptacles were separated from the thallus for all life stages possessing them: ripe and unripe fertile adults, and senescent individuals. For each thallus, RA was calculated as: damp biomass of receptacles / damp biomass of non-reproductive tissue (i.e., stipe, branches and gas bladders).

The maximum dispersal distance of embryos from attached fertile plants was estimated in a field experiment. In February 2015, prior to the onset of reproduction, we cleared *S. horneri* from seven 60 m² circular areas at two sites: Howland Landing and Lion

Head (methods in Marks et al. 2017). After clearing, cement paving blocks with a surface area of 896 cm² were placed along two intersecting perpendicular diameters at 3, 2, 1 and 0 m from the edge and within a stand of attached plants 1 m from the edge of each cleared plot. We had previously found that these blocks provided adequate substrate for *S. horneri* attachment (Marks et al. 2017). Reproduction occurred soon after blocks were deployed, and recruitment onto the blocks was sampled in September 2015 when the vast majority of individuals were large enough to be readily counted. Although most recruitment occurred on the tops and sides of blocks, occasionally blocks were found turned over and recruits were found growing on all sides. Therefore, we divided the number of recruits counted by the total surface area of the block to calculate density, which served as an indicator of settlement patterns. Average densities were calculated for each plot from the four replicate blocks per distance from the plot edge.

We used the density of recruits measured in this field experiment to estimate the maximum dispersal distance of embryos from nearby naturally-occurring reproductive plants. Several possible models (including linear and non-linear) were fit by performing a regression of recruit density on distance to reproductive plants for each plot to identify which was the most parsimonious with the data. The linear model had the lowest Akaike Information Criterion (AIC_C) score of all those we examined (Appendix B, Table S1), so we estimated maximum dispersal distances by calculating the x-intercept from individual linear models fit to each plot (Appendix B, Table S2). We then bootstrapped 2500 estimates from these 14 values to construct a distribution for the true maximum dispersal distance with 95% confidence intervals. Analyses were conducted using JMP Pro 13.

Results

Seasonality of Different Life Stages

Density and biomass of *S. horneri* showed strong but opposite seasonal patterns (Figure 2). During the summer when density was highest (125 individuals m⁻²), biomass was negligible (< 50 g m⁻² damp weight). In autumn when density was reduced by half, biomass approximately doubled. In the winter, density declined slightly but biomass peaked at ~600 g m⁻². Density continued to decline in the spring, while biomass remained high at ~500 g m⁻².

The decline in density observed from summer through spring (Figure 2A) was driven by self-thinning as a cohort matured, while the dramatic increase in biomass between autumn and winter (Figure 2B) resulted from rapid growth of the upright fronds of immature thalli. Recruit densities peaked in the summer and autumn when they accounted for virtually all individuals in the population and a majority of the biomass, respectively (Figure 3A). Densities of recruits declined > 50% by winter as individuals transitioned into the immature stage, which accounted for 52% of all individuals. The contribution of recruits to the overall biomass in winter became negligible and the immature stage accounted for 76% of the total biomass (Figure 3B). Immature stages began transitioning to adults with receptacles in winter and fertility peaked in the spring. After reproducing in late winter and spring, adults quickly senesced and died. By summer, nearly all surviving individuals that recruited the previous summer had undergone reproduction, and the few remaining senescent individuals comprised ~30% of the biomass.

Habitat Affinities

S. horneri occurred across the range of depths sampled, from the low intertidal to 30 m (Figure 4). Peak densities of recruits in June and adults in April were highest between 5 and 10 m and declined with depth. Recruits were also abundant in very shallow areas (< 5 m) whereas adults were not. All life stages were rare below 20 m depth.

S. horneri occupied all hard substrate types, but tended to be less abundant on cobble and more common on medium and small boulders than expected by chance based on substrate availability (Figure 5). Recruits were also less common on bedrock and large boulders, while adults grew on these substrate types in proportion to their availability.

Reproductive Characteristics

Reproductive allocation (RA) varied among the three life stages that possess receptacles. Fertile individuals with ripe receptacles allocated a majority of their tissue to reproduction and had a mean RA of 1.2 (Figure 6). By comparison, receptacles comprised a much smaller proportion of the biomass in fertile individuals with unripe receptacles and senescent individuals which had mean RA values of 0.4 and 0.3, respectively.

We found that the density newly settled recruits declined with distance from stands of adult *S. horneri*. On average, the recruit density on blocks placed within stands of reproductive plants 1 m outside cleared plots (-1 m) was nearly twice that of those placed in the interior of the plot (3 m position) (Figure 7A). Most of the maximum dispersal distances estimated using linear models ranged from 3 m to 9 m, but two plots had much higher estimates: 35 and 40 m (Table S2). The best estimate (median) for maximum dispersal distance was 11.2 m (95% confidence interval = 6.2 and 18.2 m; Figure 7B).

Discussion

The life history characteristics of a species introduced outside of its native range determine whether it will become invasive and its ability to rapidly colonize, reproduce and persist through multiple generations in a novel location will favor its spread. Scientists have argued that highly invasive species share key traits that affect these abilities (Williamson and Fitter 1996b; Rejmánek and Richardson 1996; Kolar and Lodge 2001; Hamilton et al. 2005, Pyšek and Richardson 2007; Hayes and Barry 2008), yet knowledge is limited for assessing whether such traits apply to invasive marine algae. We found that *S. horneri* occurred at high densities across a large habitat range, invested greatly in reproduction, and demonstrated local dispersal that resulted in dense colonization. These traits are consistent with those found for many invasive plants on land and help explain the rapid population growth observed in *S. horneri* in southern California in recent years.

Phenology is recognized as an important component of invasion success in terrestrial plants. An early, late or extended flowering period relative to native species can enhance reproductive and therefore invasion success (Crawley et al. 1996; Pyšek and Richardson 2007). The ecological significance of the seasonality of biomass and reproduction of *S. horneri*, both in terms of facilitating its spread and dictating its impacts, will depend on the phenology of native algae competing for limiting resources such as light and attachment space in this system. Most of the dominant native species of macroalgae in California are perennial, but reach a maximum biomass in the summer and autumn (Reed et al. 2009; Harrer et al. 2013). We documented strong seasonality in the annual life cycle of *S. horneri* with biomass peaks that were opposite to those reported for native species in the region. Small low-lying recruits were abundant in summer and autumn, and upright thalli developed

rapidly in the winter, attaining peak biomass in winter and spring. The vast majority of reproduction occurred in the spring, and senescence quickly followed.

In Japan, dense stands of *Sargassum* are ecologically important as a source of food and as nursery habitat for sea urchins, fishes, crabs and abalone (Umezaki 1984). *S. horneri* may serve a similar role during winter and spring in the kelp forests of California where it has invaded since it reaches its peak abundance at a time when other algae that provide structural habitat and other resources are less abundant (e.g., Sánchez-Moyano et al. 2007; Jiménez et al. 2015). However, it also has the potential to outcompete native macroalgae for limited space and light, which could ultimately have negative consequences for the species that rely on recruiting into open space (e.g., Britton-Simmons 2004). Rapid growth to a large size and the suppression of natives have been identified as invasive traits in other algae (Nyberg and Wallentinus 2005), and may contribute to the success of *S. horneri*.

A wide depth range has been identified as an invasive characteristic of non-native macroalgae (Nyberg and Wallentinus 2005). Recruit and adult *S. horneri* spanned the entire range of depths that we sampled (up to 30 m). However, recruitment was highest at depths of < 10 m while densities of adults peaked in the 5-10 m range. These patterns suggest recruits take advantage of high irradiance in shallow water but as individuals grow tall, increased drag may cause them to become dislodged at shallow (< 5 m) depths where wave action is most intense while individuals are able to persist in deeper, calmer water. Decreasing irradiance could explain the general decline in density of both stages at depths greater than 10 m. Peak adult densities at moderate (5-10 m) depths may also be related to the distribution of native competitors (e.g., Bulleri et al. 2002); while most macroalgae grow within the depth range sampled here, few species span the entire range as *S. horneri* does. A wide

environmental tolerance is characteristic of many invasive species (Boudouresque and Verlaque 2002), and the presence of *S. horneri* across a broad depth range suggests a high tolerance to variation in environmental factors such as light, temperature and wave disturbance.

The ability to colonize and grow on a broad range of substrate types has also been identified as an invasive characteristic of macroalgae (Maggs and Stegenga 1999). We found *S. horneri* could colonize and survive on all hard substrate types. However, it was more likely to recruit and reach maturity on small to medium boulders, while cobble was a less favorable substrate for both recruits and adults. Recruitment was also less likely on bedrock and large boulders, but adults grew on these substrate types in proportion to their availability. The higher than predicted affinity of *S. horneri* recruits to small and medium sized boulders may be explained by differences in the stability of the various substrate types and their ability to resist being tumbled by wave disturbance. Highly stable substrates such as bedrock and large boulders are more likely to support mature assemblages of perennial native macroalgae and sessile invertebrates and thus offer little free space for new colonists (Sousa 1979), whereas highly unstable substrates such as small cobbles may be too frequently disturbed to sustain high densities of recruits. In contrast, the intermediate stability of small and medium sized boulders may be optimal for sustaining high densities of recruits. We targeted shallow (7 m) reefs in our surveys, but we also observed dense stands of *S. horneri* growing on small cobbles mixed in with sand and shell hash in protected coves and deeper (> 15 m) areas, suggesting *S. horneri* can thrive on less stable substrates under calm conditions.

The success of both invasive plants and algae is often attributed to characteristics associated with reproduction and dispersal (Pyšek and Richardson 2007; Nyberg and

Wallentinus 2005). High fecundity is a particularly important trait associated with invasiveness because rapid reproduction is required for effective colonization by an introduced species. We found that *S. horneri* allocates > 60% of its biomass to reproductive structures during the period of peak fertility. This value is within the upper range of other fucoid algae, and higher than that reported for most macroalgae (Mathieson and Guo 1992). Reproductive strategy can also contribute to invasion success and hermaphroditism is more common in invasive plants than their native counterparts (Pyšek and Richardson 2007). The *S. flicinum* variant of *S. horneri* found in California and Mexico is hermaphroditic and bears androgynous receptacles (Sawada 1958). High rates of selfing have been reported for other hermaphroditic fucoids (e.g., *Fucus spiralis*; Engel et al. 2005), and the capacity for self-fertilization in *S. horneri* may contribute to its rapid spread along the west coast of North America.

At Santa Catalina Island, *S. horneri* commonly grows in dense patches from a few m² to 100's of m² in size. High fecundity coupled with a short dispersal distance could enable *S. horneri* to persist in patches through multiple generations. Studies performed on its invasive congener *S. muticum* showed that embryos sink rapidly to the bottom when shed from receptacles (Norton and Fetter 1981) and tend not to disperse more than a few meters when released from a sessile parent plant (e.g., Deysher and Norton 1981). Our measurements of a linear decrease in colonization over distances of a few meters from sources of propagules confirm *S. horneri* dispersal is also highly localized; our model estimated a maximum dispersal distance of ~11 m. This localized dispersal coupled with high fecundity could foster the local persistence of *S. horneri* through multiple generations. However, *S. horneri* is also well-suited for long range dispersal (Miller et al. 2007); a buoyant thallus released from the

substrate through wave- or grazer-induced disturbance could float and spread propagules over long distances (Yatsuya 2008). The capacity of *S. horneri* for widespread dispersal and rapid local colonization likely contributes to its rapid spread and persistence in the invaded range.

Sargassum horneri possesses life history traits that likely contribute to its spread and persistence in North America. In our study, traits related to habitat distribution and reproduction were consistent with inherently invasive characteristics that have been identified in terrestrial plants and other marine macroalgae. The ability to use a wide range of depths and substrates allows *S. horneri* to colonize many different environments, and high fecundity and local dispersal likely facilitate persistence of new populations through multiple generations. The annual life cycle of *S. horneri* is not an inherently invasive characteristic, but may nonetheless play an important role in its invasion success when examined in the context of the invaded community. Understanding why certain species become invasive requires knowledge of life history traits of the invader in the context of the environment. Information presented here paired with knowledge of the life histories of resident species can be used to characterize potential ecological interactions with *S. horneri*. This approach will further our understanding of how invader traits and environmental factors interact to drive marine invasions which should prove useful for developing best practices for managing their spread.

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Figures



Figure 1. Life stages of *Sargassum horneri*. (A) Recruit (height ≤ 5 cm), (B) Immature (height > 5 cm without possessing receptacles), (C) Fertile unripe adult (receptacles present, indicated by arrow, but eggs not visible), (D) Fertile ripe adult (receptacles present with visible embryos), and (E) Senescent (receptacles spent, tissue degradation and loss of buoyancy evident). Photo credits: Jessie Alstatt (A), Kathy Ann Miller, University Herbarium, University of California at Berkeley (B-C), Lindsay Marks (D-E).

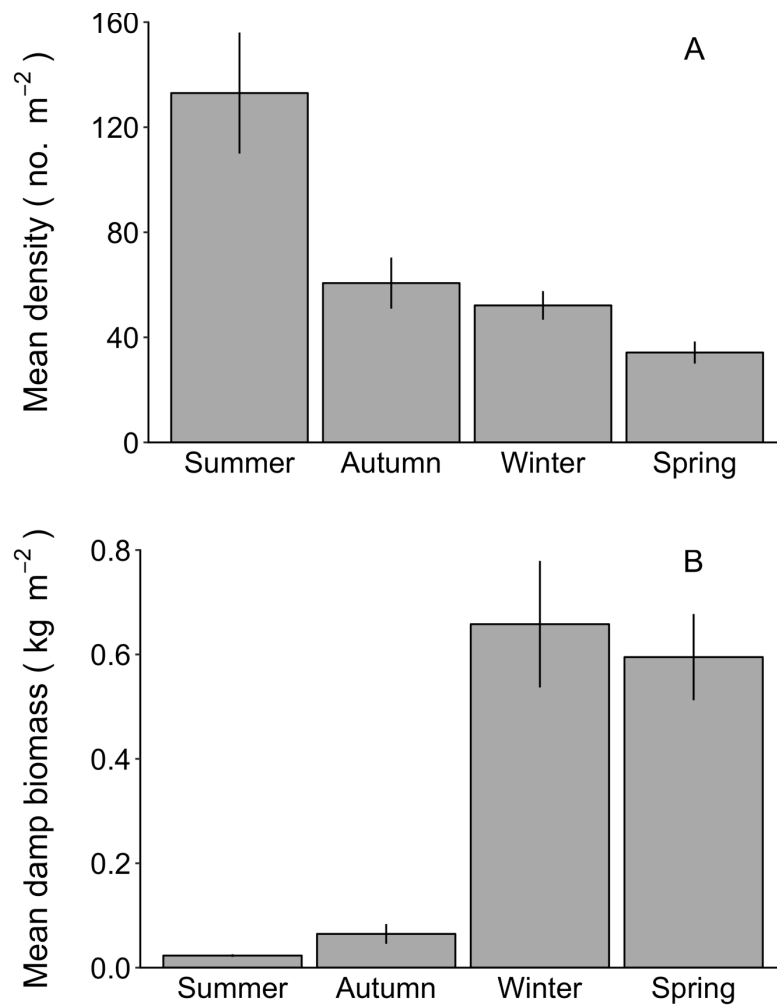


Figure 2. The mean ($\pm$ SE) density (A) and biomass (B) of *Sargassum horneri* at Santa Catalina Island. Means are averaged over all sites surveyed within each season. N = 31 sites.

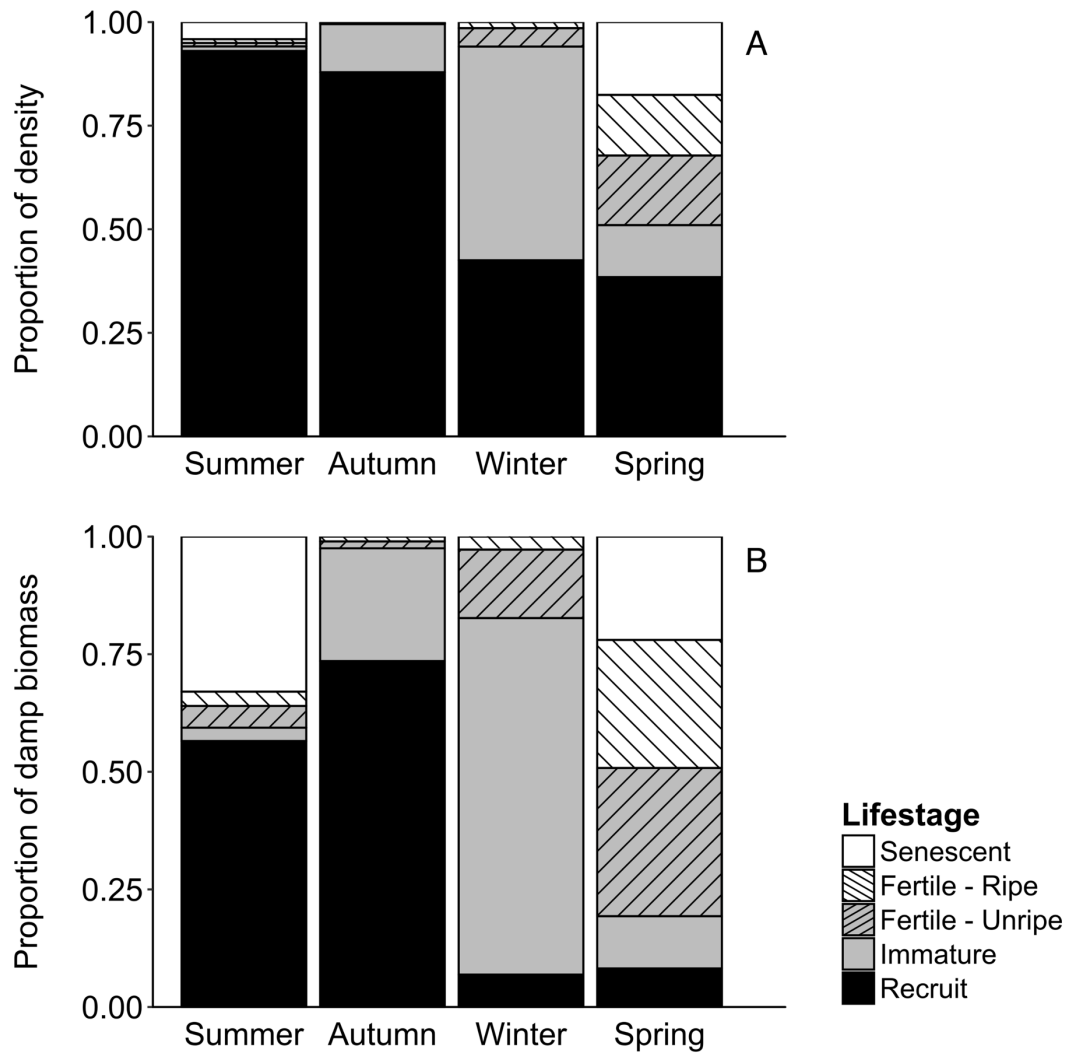


Figure 3. The mean proportion of the total density (A) and biomass (B) of *Sargassum horneri* accounted for by each life stage in each season. Means are averaged over all sites surveyed within each season. N = 31 sites.

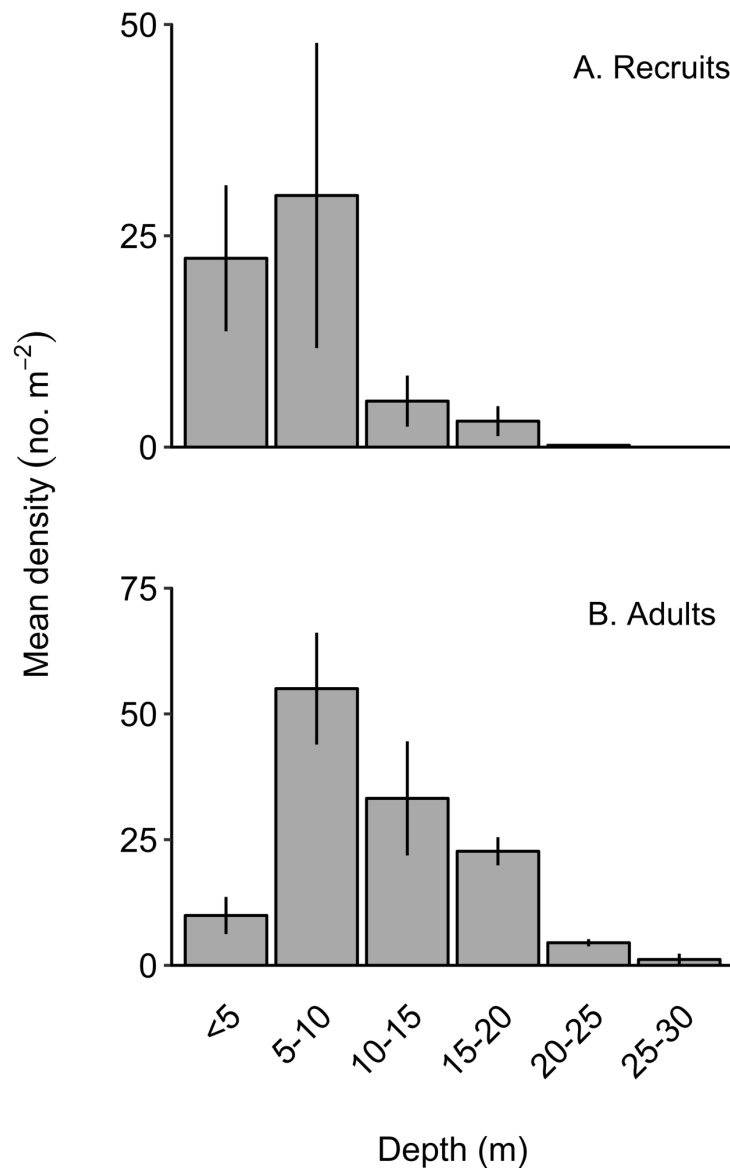


Figure 4. Depth distribution of *Sargassum horneri* (A) recruits sampled in June 2012, and (B) adults sampled in April 2016. Values are means ($\pm$ SE). N = 8 and 4 sites for recruits and adults respectively.

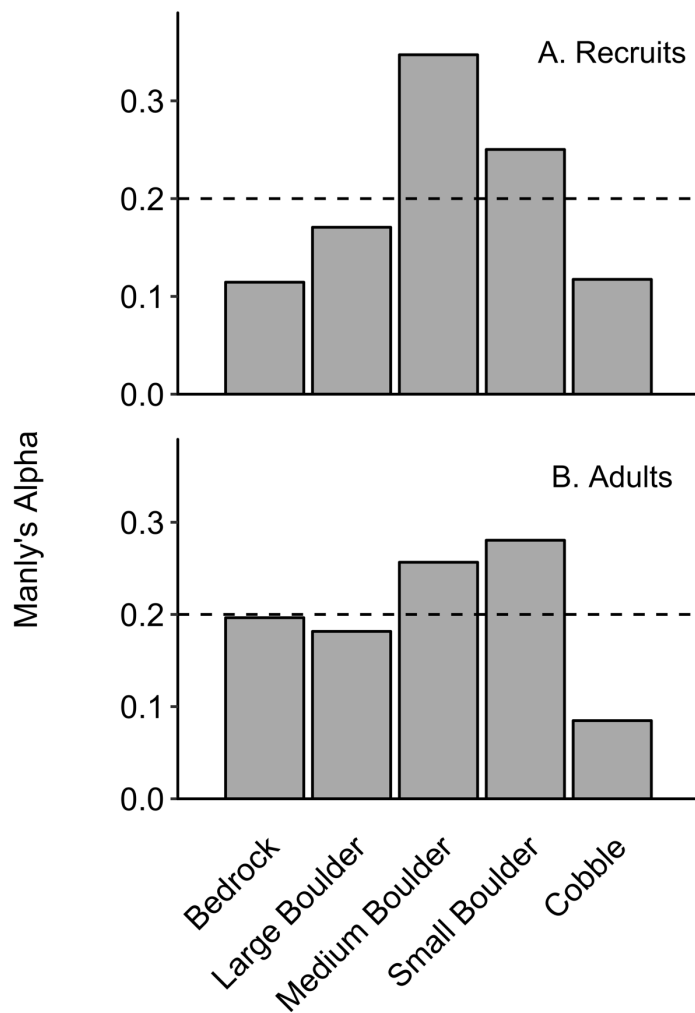


Figure 5. Substrate affinity of *Sargassum horneri* as indicated by Manly's Alpha of selectivity for (A) recruits in June 2013, 2014 and 2015 and (B) mature adults in April 2014 and 2015. The dashed line represents no preference for a habitat with values $\gg 1$ indicating a strong preference for a substrate type and values $\ll 1$ indicating a strong avoidance. See text for definitions of substrate types. $N = 248$ plots per sampling period except April 2014 when $N = 240$.

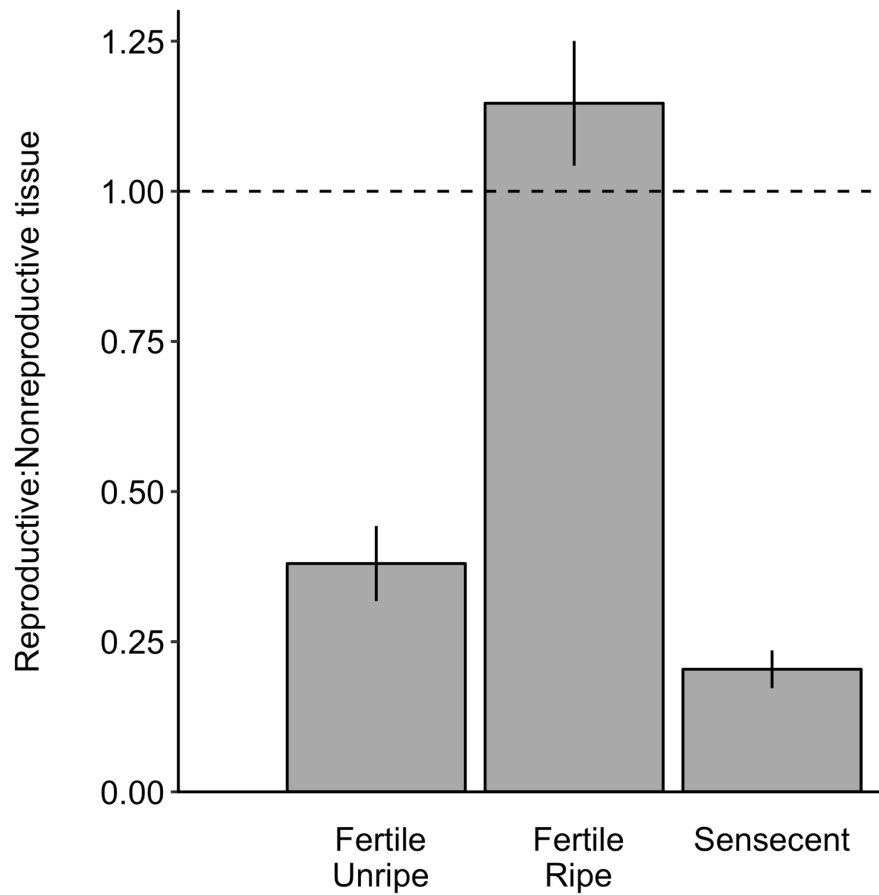


Figure 6. Reproductive allocation (ratio of reproductive to non-reproductive tissue) of all life stages of *Sargassum horneri* possessing reproductive receptacles (mean $\pm$ SE). N = 26 (fertile unripe), 31 (fertile ripe) and 28 (senescent). A ratio of 1 represents equal allocation.

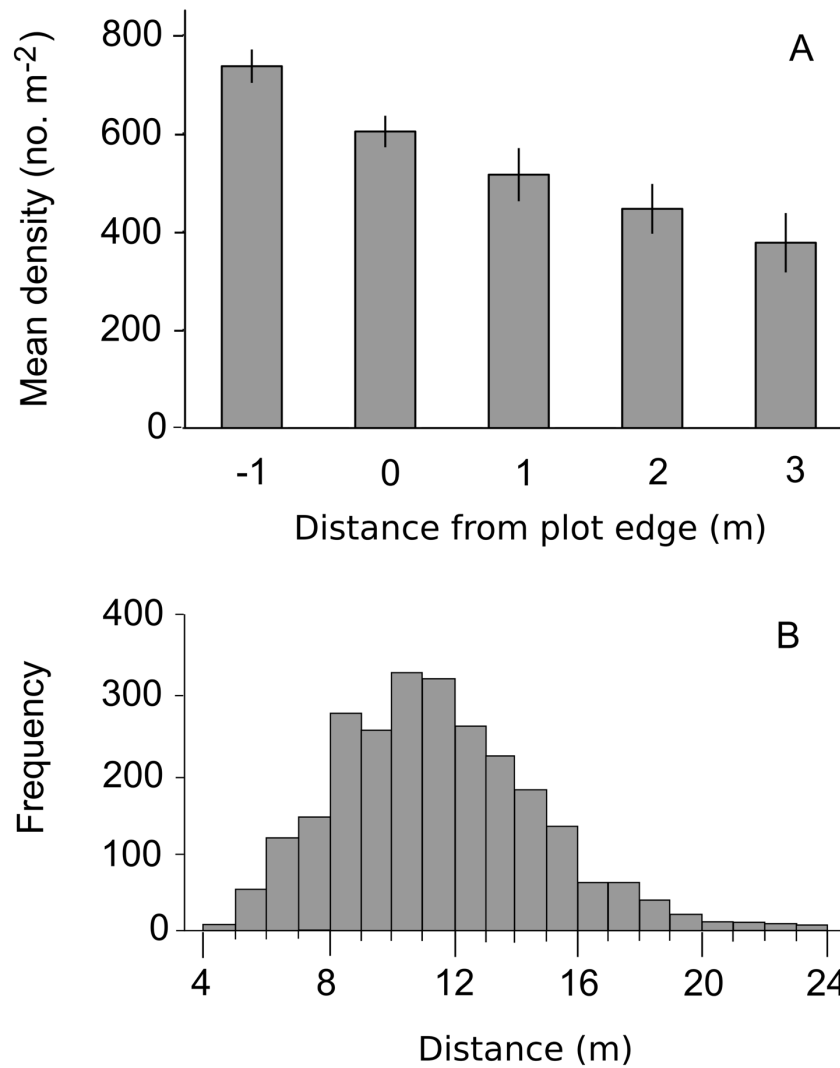


Figure 7. Dispersal of *Sargassum horneri* propagules into experimentally cleared circular plots (N = 14 plots). (A) Mean ($\pm$ SE) density of *S. horneri* recruits on blocks within cleared plots at distances of 0 – 3 from the plot edge and with a stand of reproductive adults 1 m outside the plot (-1 m). (B) Distribution of bootstrapped sample means of maximum dispersal distance of *S. horneri* propagules using data from the experimentally cleared plots.

Tables

Table 1. Regression coefficients (a = intercept, b = slope) and r^2 values for the relationship between size and biomass for different life stages of *Sargassum horneri*. Regression equations are of the form $y = ax^b$, where y = biomass (damp g) and x = size (cm). Biomass for the senescent life stage was calculated as the mean and SE (5.2 ± 0.9 damp g) of 29 individuals with minimum and maximum sizes measured as 15 cm and 190 cm, respectively.

Life stage	Size metric (cm)	a	b	r^2	p	n	Min size measured	Max size measured
Recruit	max diameter	0.0179	1.7633	0.94	<0.0001	35	3	18
Immature	max height	0.0992	1.2711	0.81	<0.0001	85	20	286
Fertile - Unripe	max height	0.0496	1.4817	0.62	<0.0001	104	8	293
Fertile - Ripe	max height	0.0147	1.7641	0.54	<0.0001	65	32	307

Appendix B: Supplemental Tables S1-S2

Table S1. Akaike Information Criterion (AIC_c) values for each model fit to a regression of recruit density on distance for each plot to identify the most parsimonious model.

Model	AIC_c	ΔAIC_c	AIC_c Weight
linear	4084.19	-	0.59
exponential - 2 parameters	4084.92	0.72	0.41
exponential - 3 parameters	4107.52	23.33	0
quadratic	4107.33	23.13	0

Table S2. Parameters for linear models of recruit density on distance fit for each plot as $y = \beta x + \alpha$ where β = slope and α = y-intercept, and maximum embryo dispersal distance is estimated as $x = -\beta / \alpha$.

Site	Plot	β	α	x
Howlands	1	-58.59	534.04	9.11
	2	-157.09	589.56	3.75
	3	-19.25	771.48	40.07
	4	-136.16	695.87	5.11
	5	-100.45	590.96	5.88
	6	-78.96	514.23	6.51
	7	-99.05	753.63	7.61
Lion Head	1	-18.69	672.71	35.99
	2	-78.96	610.77	7.73
	3	-91.80	668.81	7.29
	4	-119.14	559.43	4.70
	5	-42.13	775.95	18.42
	6	-121.93	633.65	5.20
	7	-104.35	358.26	3.43

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Chapter III

Roles of competition, complementarity and herbivory on the invasion success of *Sargassum horneri*

Abstract

Invasive species are a growing threat to conservation in marine ecosystems, yet we lack a predictive understanding of ecological factors that influence the success of marine invasive species. I used surveys and manipulative experiments to investigate whether the invasion of an exotic seaweed, *Sargassum horneri*, may be influenced by three mechanisms of invasion recognized in terrestrial plants: competition, complementarity or herbivory. Surveys across a depth range of 0 – 30 m revealed that the biomass of *S. horneri* and other subcanopy-forming macroalgae were inversely related, where *S. horneri* peaked at intermediate depths (5-20 m) while the aggregated biomass of various resident (i.e., native and naturalized) species peaked at either very shallow (< 5 m) or deeper (> 20 m) depths. The seasonal biomass of *S. horneri* and resident algae also displayed opposite seasonal trends, and removal of *S. horneri* from experimental plots indicated the seasonality of native algae was not driven by fluctuation in *S. horneri*. The complementary life histories of *S. horneri* and resident algae suggest competition between them may be weak. The greatest potential for competitive interactions exists at intermediate depths and during the spring and summer when *S. horneri* and resident algae achieve their peak biomass, respectively. Results from grazing assays and surveys suggest that native herbivores favor native kelp over *Sargassum* as a food source, indicating that reduced palatability may also promote the invasion of *S. horneri*.

Introduction

Marine ecosystems are increasingly threatened by invasive species as global trade expands and human-mediated introductions via commercial shipping occur at escalating rates (Cohen & Carlton 1998; Stachowicz et al. 2002; Molnar et al. 2008; Sorte et al. 2010; Seebens et al. 2013). Developing a predictive understanding of factors influencing the success of marine invasive species has clear implications for managing their spread and impacts. Yet relative to terrestrial systems, little is known about the ecological processes that influence marine invasions (Papacostas et al. 2017; Caselle et al. 2018). In terrestrial ecosystems, once an introduced species becomes established, biotic interactions with resident species can play a major role in limiting population growth, spread and ecological impacts (Elton 1958; Levine et al. 2004; Maron and Vilà 2001; Parker and Hay 2005). These interactions can either promote or inhibit “invasion”, here defined as the process by which an exotic species exhibits rapid population growth and spread in the novel environment (Valery et al. 2008).

Much of our understanding about how biotic interactions influence invasions comes from experiments with terrestrial plants which have shown that competition with natives and herbivory can affect invasion success (Levine et al. 2004). Competition for limited resources among native and invasive species is expected to be most intense when they have with similar life histories and resource requirements (MacArthur and Levins 1967); invasion is promoted when exotic plants employ resource acquisition strategies superior to native competitors. Invasion success can also be promoted when exotic species have functional traits or resource requirements that differ from the native biota, which allows them to take advantage of underutilized resources in space and time (Crawley et al. 1996; Lloret et al.

2005; Mack 2003). Such complementarity of life history characteristics and resource requirements can facilitate invasions by allowing exotics to avoid interacting with natives with superior competitive abilities. Like native plants, native consumers can promote or hinder invasion depending on their dietary preference. For example, herbivores that prefer exotic plants to natives can inhibit invasion, while those that prefer native plants can facilitate invasion by reducing the strength of competition between exotic and native plants (Maron and Vilà 2001; Grosholz 2010). Studies investigating whether the same mechanisms of terrestrial plant invasions affect the success of exotic marine macrophyte invaders will help to evaluate the generality of biotic interactions influencing invasions across ecosystems.

The invasion of seaweed in California allows us to explore the potential roles of competition, complementarity and herbivory in the spread of a marine macrophyte. Native to eastern Asia, *Sargassum horneri* was detected in California in 2003 (Miller et al. 2007) and has since spread throughout southern California and Baja California, Mexico (Marks et al. 2015). Several life history characteristics of *S. horneri* make it a classic “weedy” invader with r-selected traits (Baker 1965). This annual, monocious species is highly fecund with >60% of its biomass dedicated to reproductive tissue at its peak of fertility, it has highly localized propagule dispersal but also has the ability to disperse long distances via the dislodgement and drifting of fertile adults, and it has broad habitat requirements (Chapter 2). Throughout the invaded range, *S. horneri* has become highly abundant on some reefs but remains rare on others (Marks et al. 2015; Caselle et al. 2018). The purpose of this study was to investigate whether the abundance of *S. horneri* where it has colonized may be influenced by competition, complementarity or herbivory.

Knowledge of the life history traits of exotic seaweeds relative to natives, such as the phenology of their growth or preferred habitats, can help generate predictive explanations for where certain invaders should be most abundant across an environment (Valentine et al. 2007). It has been hypothesized that *S. horneri* does not thrive where native understory algae are dense or in low light areas shaded by a dense overstory canopy (Caselle et al. 2018). However, areas dominated by *S. horneri* may result from its ability to take advantage of underutilized resources which allow it to coexist with native algae (i.e., complementarity) rather than superior competitive abilities that allow it to displace native algae. Spatial variation in resources can affect where invaders succeed, and resource availability and biotic interactions will vary across the environment. The depths at which macroalgae can grow are limited by sunlight, and various morphologies and pigmentation that influence photosynthesis allow species to specialize at certain depths (Kirk 1983). The strength of competition between *S. horneri* and resident algae may therefore change with depth depending upon the species composition and biomass of macroalgae across depth zones. Detailed information on patterns of distribution of *S. horneri* and native algae can provide valuable insight into the relative importance of competition versus complementarity in accounting for the invasion success of *S. horneri*.

The effects of herbivores like sea urchins in structuring temperate marine communities are well documented (Mann 1977; Shears and Babcock 2002; Lafferty 2004), but less is known about their potential role in influencing invasions. Exotic seaweeds with traits that deter herbivory (i.e., structural or chemical defenses) can gain an advantage over native competitors in areas with high grazing pressure. Species in the order Fucales are known to have high levels of phenolic compounds that deter grazing (Geiselman and

McConnell 1981; Alstyne 1988; Estes and Steinberg 1988). As a fucoid, *S. horneri* therefore may be less palatable than native kelps which by comparison are less well defended against herbivory (Estes and Steinberg 1988, Van Alstyne et al. 1999). Preferential consumption of native algae could facilitate the spread of *S. horneri* by weakening the strength of competition from other, more palatable algae.

The goal of this study was to address the question: what are the potential roles of competition, complementarity and herbivory in controlling the invasion of *S. horneri*? I documented patterns of co-occurrence between *S. horneri* and other algae to evaluate the potential for interactions between them (i.e., competition versus complementarity) and performed field experiments involving the major herbivores to examine their grazing preferences for *S. horneri* versus other algae. Given the uneven distribution of *S. horneri* across its depth range and throughout the year (Chapter 2), I predicted that *S. horneri* and resident algae interact differently during various seasons and at different depths. To test this prediction, I assessed the distribution of *S. horneri* and other algae across depths and seasons and experimentally manipulated *S. horneri*. The direct or indirect influence of herbivory on *S. horneri* is likely to vary spatially with the distribution of herbivores. Using a combination of feeding experiments and distributional surveys I examined whether herbivores facilitate *S. horneri* by preferentially consuming other resident algae.

Methods

Study species and sites

Field experiments and descriptive investigations were conducted on rocky reefs at Santa Catalina Island, located 35 km offshore of Long Angeles, California, USA. The study sites were located near the Wrigley Marine Science Center (WMSC) (33.44222°N, 118.49750°W) on the leeward side of the island. Reefs were characterized by moderate slopes and habitat consisted of bedrock, boulders, cobble and sand. These rocky reefs transition to entirely sandy bottom at depths of about 30 m.

The primary grazers here include sea urchins and herbivorous snails. *Centrostephanus coronatus*, the most common species of urchin, takes refuge in crevices and forages within < 1 m from its shelter during the night before returning to the same location before sunrise (Nelson and Vance 1979). This behavior leads to the formation of urchin “halos” where they commonly graze down algae within small territories.

Reefs at Santa Catalina Island are typically dominated by macroalgal assemblages including the canopy-forming kelp *Macrocystis pyrifera*, subcanopy-forming species of kelp (e.g., *Eisenia arborea*, *Agarum fimbriatum*) and furoid algae (e.g., *Sargassum palmeri*, *Sargassum muticum*, *Stephanocystis neglecta* and *Halidrys diocia*), and understory-forming species including a variety of low-lying brown, green and red algae. These species occur in differing abundances across depths, throughout the year and across years depending on winter storm activity and El Nino/La Nina cycles. *Sargassum horneri* was first detected at Santa Catalina Island in 2006 (Miller et al. 2007) and has since become one of the most common macrophytes. Although *S. horneri* has been documented across a wide depth range, it is most abundant at intermediate depths. The biomass of *S. horneri* is strongly seasonal:

rapid growth to several meters tall occurs in the winter, reproduction peaks in the spring (Chapter 2). If the depth distribution or seasonality of its biomass differ from that of native algae, *S. horneri* may experience minimal competition for light or space in places or during the time of year where or when its populations need these resources.

Potential roles of competition vs. complementarity on invasion

Depth distribution of *S. horneri* and other algal taxa

Sargassum horneri spans the depth range within which most species of brown algae at Santa Catalina Island occur (0 – 30 m), but peaks in abundance at intermediate depths between 5 – 10 m (Chapter 2). To determine whether this distribution is related to the distribution of other large brown algae that may compete with *S. horneri*, I documented the depth distribution of these taxa using visual surveys. I measured the number of *S. horneri* and other species of subcanopy-forming macroalgae by recording their abundance within 1 m² quadrats placed every 5 m along four transects running perpendicular to shore from the intertidal to 30 m depth or where the reef transitioned to sand, whichever came first. Although understory algae also may compete with *S. horneri*, I was limited by time during these deep dives and was only able to sample densities of subcanopy algae. Size increases dramatically as subcanopy-forming algae mature, so I distinguished recruits (defined as ≤ 5 cm tall) from adults (defined as > 5 cm tall) and estimates of density were converted to units of damp biomass using existing species- and stage-specific density-to-biomass relationships (Harrer et al. 2013) or those I developed (Supplemental Table 1; Unpublished data, SBC LTER). Because these algae grow only on hard bottom substrate, I visually estimated the percent cover of rock within each quadrat and standardized density estimates to m⁻² hard

bottom. I performed these surveys in April of 2016, the time of year when the biomass of *S. horneri* reaches its peak (Chapter 2).

Measured depths were adjusted relative to the Mean Lower Low Water (MLLW) and quadrats were binned into depth intervals of 5 m. Between one and three quadrats were sampled within each depth interval at each site, depending on the grade of the reef. The total biomass of each species within a quadrat was calculated as the sum of the biomass of its juvenile and adult stages. A two-way ANOVA was used to test whether the biomass of *S. horneri* and the cumulative biomass of all other furoid algae and kelps that form the subcanopy varied by depth interval. The mean and standard error of biomass for these taxa were also calculated for each depth interval from the four sites. The average biomass of each species within each depth interval was estimated as the mean of all quadrats sampled within that range for each site. The biomass of *S. horneri* and the cumulative biomass of all other furoid algae and kelps that form the subcanopy were calculated in the same manner.

Seasonal patterns of algal dominance

Comparison of the phenology of *S. horneri* and co-occurring native algae will indicate when species may interact throughout the year and may help explain its invasion success. Because algae compete for space and light, the seasonality of both biomass and cover on the reef must be considered. To document the seasonal patterns of space occupancy and biomass of *S. horneri* and native algae, I conducted seasonal observations in the field. At Isthmus Reef (33.44757 N; 118.48980 W), I established permanent 1 m² plots at ~ 6 m depth, within the range where *S. horneri* is most abundant. Plots were established on areas of reef comprised of > 90% rock and with a high density (i.e., at least 30 individuals) of *S. horneri*,

and were separated by a distance of at least 2 m. To document whether seasonal patterns of growth of native algae were influenced by *S. horneri*, I added an experimental component to my seasonal abundance measurements. Twenty-four plots in total were established and half were randomly assigned as *S. horneri*-removal-treatment while the other half were unmanipulated controls. Comparison of removal- and unmanipulated plots allowed us to determine whether the seasonality of native algae I observed was independent of *S. horneri* abundance. Plots were established in February 2014, and *S. horneri* was removed from removal-treatment plots every 6 to 12 weeks thereafter. Following the initial removal treatment, the community was sampled once per season (i.e., Summer in June, Autumn in September, Winter in December and Spring in March) for three years through June 2017.

The benthic algal community assemblages were characterized using the surveys described below. Biomass was estimated from data collected in these surveys using previously published allometric relationships (Harrer et al. 2013) or those I developed (Supplementary Table 1; Unpublished data, SBC LTER) and standardized to kg m⁻² hard bottom based on my characterization of the substrate within each plot.

We measured the number and estimated the average size of all *S. horneri* and all other subcanopy-forming macroalgae. Size metrics varied depending on the species but matched those used in the past to develop allometric relationships. I distinguished juvenile (i.e., ≤ 5 cm tall) from adult (i.e., > 5 cm tall) life stages and used stage- and size-specific formulas to convert these measurements to damp biomass.

The percent cover of the understory benthic community was estimated using a uniform point contact (UPC) method. At 49 uniformly distributed points within each 1 m² plot, the identity of all sessile organisms (i.e., invertebrates or algae) within 5 cm of the

bottom was recorded. This 5 cm height cut-off allowed us to estimate the cover of all organisms directly occupying space on the reef. Subcanopy-forming species of macroalgae (i.e., > 5 cm tall) were only recorded using UPC if their holdfasts or juvenile (i.e., $\leq$ 5 cm tall) stages intersected the sampling grid. The substrate type (e.g., reef or sand) intersecting each point was also noted, and unoccupied reef was recorded as “bare rock”. Percent cover was determined as the fraction of points a taxon or unoccupied reef intercepted $\times$ 100. Multiple organisms may intersect a single point if they overlay one another, but a species or morphological group was only recorded once at a given point even if it intersected that point multiple times. Using this technique, the percent cover of all taxa combined in a plot can exceed 100% but the percent cover of any individual species or morphological group cannot. Percent cover estimates of all low-lying species of algae were converted to damp biomass.

Because overlapping organisms sometimes resulted in > 100% cover within a plot, I adjusted percent cover estimates prior to summarizing and analyzing these values with respect to space occupancy. The availability of unoccupied reef was adjusted by standardizing my measurements of percent cover of bare rock to percent cover of bare rock per m² hard bottom. The percent cover of each taxon was likewise standardized to percent cover per m² hard bottom but also to the plot area occupied by at least one organism. These adjusted values reflect the composition of the total area of hard reef occupied by an organism or left vacant.

Algae were later classified into the following groups: *S. horneri*, other subcanopy-forming algae, and understory algae. Prior to analysis, the biomass of taxa in these groups were aggregated within each plot. Because the percent cover of subcanopy-forming species within 5 cm of the bottom (i.e., holdfasts and juveniles) was extremely low, I aggregated the

adjusted percent cover estimates for all understory and subcanopy-forming algae within each plot. These groupings allowed us to describe how the abundance of *S. horneri*, other resident algae, and unoccupied reef vary by season, and to ask whether the abundance of algae and unoccupied reef is influenced by the presence of *S. horneri*. Although crustose coralline algae and turf algae were also included in estimates of total algal cover within a plot, I do not present these data because they were not germane to my questions about interactions between *S. horneri* and other foliose algae.

The seasonality of *S. horneri*, other algae and unoccupied reef were tested using linear mixed effects models by fitting regressions for each response variable of interest. The biomass and percent cover of *S. horneri* were modeled as a function of season with random effects of year and quadrat (random intercept model) using data from non-removal plots where *S. horneri* was not manipulated. All other response variables of interest (biomass of understory or subcanopy algae; percent cover of understory + subcanopy algae or bare rock) were modeled using data from all experimental plots and included removal-treatment as a fixed effect and the interaction between removal-treatment and season. Analyses were performed using the lmer function in the lme4 statistical software package (Bates et al. 2015) in R (R Core Team, 2017). Models were compared using likelihood ratio tests (LRT) with chi-square test statistics to select the best fit based on Akaike Information Criterion (AIC). Single-parameter models were compared against a null model with only the random effects included, and full models with season, removal-treatment and their interaction were compared against one with the interaction excluded. Visual inspection of all model residuals did not reveal any obvious deviations from homoscedasticity or normality, except in the case of the biomass of *S. horneri*. I used the boxcoxmix package in R (Almohaimed and Einbeck

2017) to identify the optimal transformation of these data to achieve normality of residuals and ran this model on data transformed by the formula: $(x+1)^{-1.9}$. However, using transformed data did not change the qualitative results. Post hoc contrasts between seasons and removal-treatment were tested for significance with a Tukey HSD test using the using the lsmeans package (Lenth 2016).

Influence of grazers on invasion

A field experiment was used to assess the palatability of *S. horneri* compared to native species of kelp and of *Sargassum*. For comparison, I selected two species of kelp *Macrocystis pyrifera* and *Eisenia arborea*, two of the prominent known palatable species of algae in the area, and two other *Sargassum* species, *S. muticum* and *S. palmeri*. Because *Sargassum* species are furoid algae which typically have chemical defenses, I anticipated a preference for the native kelps over all three *Sargassum* species. I also explored whether *S. horneri* is more prevalent than native foliose algae in heavily grazed areas.

In September 2016, I performed grazing assays and surveys of benthic algae at Isthmus Reef. Replicate arrays of different species of algae were deployed on the reef for periods of 48 hours. Arrays were either exposed to grazing by urchins and snails or placed inside cages nearby that were designed to exclude these grazers. Cages were constructed from 1 cm-gauge plastic mesh and were cylindrical in shape (1 m in height and 0.5 m in diameter) with mesh covering the top. The volume was sufficient to prevent abrasion of the algal arrays placed inside. Cages were open at the bottom and a 1 m-wide skirt made of shade cloth was attached to the base. Prior to the experiment, each cage was placed over a flat section of reef and all

organisms underneath were removed to ensure no snails or urchins were present inside. Skirts were secured such that cages remained stationary and grazers > 1 cm were unable to enter.

During each of four deployments, 15 arrays were placed adjacent to urchin halos while another 15 were placed inside cages. Urchin halos were defined as sections of the reef adjacent to a small ledge where ≥ 10 urchins were found and grazing activity was apparent from a lack of algae growing within a ~ 30 cm radius. Some herbivorous snails were also present in the halos, including *Tegula eiseni*, *Tegula aureotincta*, *Megastrea undosa* and *Norrisia norrisii*. Cages were left in the same location throughout the experiment, but I selected unique halos for each deployment so that herbivores would be naïve to the arrays. In the days preceding each deployment, I collected similarly sized blades or stipes of the five target species: *S. horneri*, *S. muticum*, *S. palmeri*, *M. pyrifera* and *E. arborea*. Each array contained one sample of each species. Damp weights were quantified prior to deployment and immediately after collection by spin-drying samples for 10 s before weighing them. Three repeat measurements of each sample were taken by re-hydrating the sample and repeating the drying and weighing process. The average of three replicate measurements for each sample was used to ensure I could detect small changes in tissue loss.

Herbivore preference was assessed by comparing algal weights measured before and after deployment in the exposed versus caged arrays. I calculated the percent of biomass lost as:

$$\% \Delta = \left[\frac{g_{\text{final}} - g_{\text{initial}}}{g_{\text{initial}}} \right] * 100$$

where G_{initial} and G_{final} represent the mean of the three replicate weights measured for each sample before and after deployment, respectively. I fit a linear mixed effects model using the lmr4 package in R with percent change in biomass as the response variable, and treatment

(caged/exposed) and algal species as fixed effects. I also included deployment, array, and the initial weight of a sample as random effects. Full models with the main effects in question (i.e., treatment, algal species, and their interaction) were compared against additive or null models without the effects in question using likelihood ratio tests (LRT) with chi-square test statistics to select the best fit based on Akaike Information Criterion (AIC). A subsequent model was run using only data from exposed treatments and post hoc contrasts between species were tested for significance with a Tukey HSD test to determine which species were preferentially consumed. Model assumptions of normality and homoscedasticity were validated through visual inspection of the residuals.

To provide a more time-integrated assessment of the feeding preferences of grazers, I tested whether *S. horneri* had a higher relative abundance and resident foliose algae had a lower relative abundance in heavily grazed areas. During the final deployment, I characterized the benthic algal community adjacent to the urchin halos compared to nearby reference areas on the reef. Using a point contact sampling method, I estimated the percent cover of all algae and unoccupied space at 49 uniformly distributed points within 1m² quadrats. I placed the quadrats adjacent to the 15 halos used in the fourth deployment of assays and randomly selected 15 other nearby locations with high algal cover. To compare the algal composition near urchin halos and in reference areas, I standardized estimates of cover for individual algal taxa to the total cover of algae within each quadrat. I ignored unoccupied space, which was common at urchin halos ($X = 49.8 \%$, $SD = 16.3\%$) but rare in reference areas ($X = 5.8\%$, $SD = 4.1\%$). Algae were identified to the lowest taxonomic level possible, and were later classified into the following groups: *S. horneri*, subcanopy algae, understory algae, and crustose coralline algae. I used one-tailed two-sample t-tests to test the

predictions that the cover of native foliose algae (i.e., understory or subcanopy algae) is lower and *S. horneri* is higher near urchin halos. Because crustose coralline algae factored into my calculations of total percent cover of algae but I had no a priori predictions about its differing abundance, I analyzed this group using a two-tailed t-test.

Results

Potential roles of competition vs. complementarity on invasion

The depth distribution of *S. horneri* was inversely related to the aggregated biomass of other subcanopy-forming algae (Figure 1A). Two-way ANOVA revealed a significant main effect of both taxonomic group (i.e., *S. horneri* vs. other subcanopy-forming alga) ($F(1) = 4.26$, $p = 0.04$) and depth bin ($F(5) = 10.6$, $p < 0.0001$) on biomass, with a significant interaction between the two factors ($F(5) = 11.84$, $p < 0.0001$). *Sargassum horneri* was present from the intertidal (0 m) to the deepest depths sampled (30 m), but its biomass peaked between 5 and 10 m with $1.8 \pm 0.4 \text{ kg m}^{-2}$ (mean $\pm$ SE) and decreased with depth (Figure 1B). Subcanopy algae were also present across the range of depths sampled, but the aggregated biomass of these species and their identity varied (Supplemental Table 2). Biomass of furoid species (such as *Stephanocystis neglecta*, *Halidrys dioicia* and *Sargassum palmeri*) as well as the native kelp *Eisenia arborea* peaked at shallow depths, with a combined biomass of $0.9 \pm 0.3 \text{ kg m}^{-2}$ (mean $\pm$ SE) above 5 m depth. *E. arborea* also occurred at deeper depths, and with the other native kelp *Agarum fimbriatum* had a combined biomass of $0.9 \pm 0.4 \text{ kg m}^{-2}$ (mean $\pm$ SE) in the deepest zone sample (25-30 m).

The biomass of *S. horneri* and the aggregated biomass of other resident algae showed opposite seasonal trends. *Sargassum horneri* biomass displayed a strong seasonality in

unmanipulated plots, remaining low during summer and autumn ($< 0.05 \text{ kg m}^{-2}$), but increasing slightly in winter (0.14 kg m^{-2} ; Tukey's post hoc, $p < 0.001$) and dramatically in the spring (1.84 kg m^{-2} ; $p < 0.0001$) (Figure 2A; Table 1A). The biomass of other subcanopy-forming algae displayed little seasonality, reaching a minimum of $\sim 0.3 \text{ kg m}^{-2}$ during summer but remaining relatively constant throughout the year (Figure 2B; Table 1B). Conversely, the aggregated biomass of resident understory algae peaked during summer at $\sim 0.9 \text{ kg m}^{-2}$, declined by winter to $\sim 0.5 \text{ kg m}^{-2}$ ($p < 0.001$) and remained similarly low into the spring (Figure 2C). The seasonality of both understory and subcanopy-forming algae was not significantly different between plots containing *S. horneri* and those where it was consistently removed (Table 1C) indicating the patterns observed were not driven by the fluctuation in biomass of *S. horneri*.

The percent cover of *S. horneri* changed seasonally in unmanipulated plots (Figure 3; Table 2A) and was inversely related to its biomass. During the summer, autumn and winter it maintained $\sim 10\%$ cover, but in the spring this decreased to $\sim 4\%$ (Tukey's post hoc, $p < 0.0001$) (Figure 3A). The cover of understory and subcanopy algae also changed seasonally, and this seasonality was apparent in the presence and absence of *S. horneri* (Table 2B). Peak cover of this group occurred in summer ($\sim 50\%$) and remained high through autumn. It then decreased to $\sim 30\%$ by winter ($p < 0.0001$) and stayed low through spring (Figure 3B). The availability of unoccupied reef likewise changed seasonally (Figure 3C; Table 2C). It was lowest during the summer when bare rock cover was 15% in unmanipulated plots but steadily increased through the autumn, winter and spring when it reached a maximum of 32% ($p < 0.0001$) (Figure 3C). Removal of *S. horneri* significantly increased the cover of bare rock by $\sim 10\%$ in summer ($p = 0.01$) but not during other seasons ($p > 0.05$).

Influence of grazers on invasion

The amount of algae consumed during the grazing assays varied significantly among the five species of algae tested (Figure 4A; Table 3). Although exposure to herbivores resulted in slightly greater losses of biomass for the three *Sargassum* species compared to caged specimens, the difference in the change in biomass between caged and uncaged treatments was not significant. By contrast, significantly more biomass of *M. pyrifera* and *E. arborea* was lost in uncaged urchin halos compared to inside cages. The effect of grazing was strongest on *M. pyrifera*, which lost on average 76% of its biomass during the 48 hour assays compared to 38% for *E. arborea* and 12 to 18% for the three species of *Sargassum*.

Surveys revealed that the taxonomic composition of algae varied between urchin halos and nearby reference areas (Figure 4B). One-tailed t-tests confirmed my predictions that the cover of *S. horneri* was higher within urchin halos compared to nearby areas away from urchin halos ($t = 1.84$, $df = 28$, $p = 0.04$), while that of understory algae was lower ($t = -5.17$, $df = 28$, $p < 0.0001$). The subcanopy algae was composed primarily of the native *Sargassum palmeri*, which showed little loss of tissue in the grazing assays, and the cover of this group did not differ within and outside of urchin halos ($t = -0.24$, $df = 28$, $p = 0.81$). The cover of crustose coralline algae was significantly greater in urchin halos when compared to nearby areas according to Welsh's two-tailed t-test ($t = 4.56$, $df = 15.51$, $p < 0.001$).

Discussion

Resident communities can either promote or inhibit biological invasion through multiple mechanisms depending on the traits of both the introduced and native species. While there appears to be general consensus that competition, complementarity and consumption

are important mechanisms controlling invasion in terrestrial plant communities, their influence on invasive marine macrophytes has rarely been studied, particularly on a single species. I compared herbivore preference and spatial and temporal patterns of abundance for the invasive seaweed *Sargassum horneri* compared to resident macroalgae to evaluate the potential for competition, complementarity and consumption to influence its invasion on temperate reefs.

Potential roles of competition vs. complementarity on invasion

The vertical distribution of *S. horneri* compared to functionally similar algae could reflect the strength of their competitive interactions or physiological preferences for different parts of the environment. I found that the biomass of *S. horneri* displays spatial complementarity with other subcanopy algae. Although *S. horneri* had a wide depth range, it was most abundant at intermediate depths (5-20 m). Other furoid algae were most abundant shallower than 5 m, whereas kelps became more abundant at deeper depths below *S. horneri*'s peak abundance. One possible explanation for this inverse relationship is that *S. horneri* grows optimally under the physical conditions characteristic of the intermediate depths between the distribution of these two other groups. Alternatively, perhaps robust subcanopy-forming macroalgal communities deter *S. horneri* at very deep (>20) and very shallow depths (<5), while increased space and light available in between allow *S. horneri* to thrive there without competition. In its native Japan, *S. horneri* grows from the intertidal to 20 m (Yoshida 1983), but is most common on shallow reefs from the low intertidal to 4 m (Tkaba and Mizokami 1982). However, it is unclear whether this reported distribution is driven by reef topography, a lack of sampling effort at deeper depths, or other factors. In

Baja California, Mexico, another part of the invaded range, *S. horneri* has been reported to occur from the intertidal (Aguilar-Rosas et al. 2007; Cruz-Trejo et al. 2015) to at least 8 m depth (Riosmena-Rodríguez et al. 2012). The distribution of other macroalgae I observed may also have been a consequence of *S. horneri* peak abundance at intermediate depths.

Performing similar surveys on reefs without *S. horneri* would have allowed us to test this, but all reefs in the region were heavily invaded, prohibiting such a comparison. However, the shallow distribution of *S. horneri* in other regions indicates versatility in light requirements, and opportunistic growth in places where competition is minimal.

The seasonal phenology of the macroalgal community suggests that, as with space, *S. horneri*'s peak growth is complementary to that of native macroalgae. The biomass of *S. horneri* is low from June through December and peaks in March. Other subcanopy-forming algae follow a similar trend, but the magnitude of their variation in biomass is low. This was unsurprising since the primary species in this group was the native *Sargassum* species, *S. palmeri*, which has a similar phenology as *S. horneri*. Conversely, the aggregated biomass of understory algae was highest in June and decreased through September, December and March. This pattern was consistent in the presence and absence of *S. horneri* (i.e., in removal- and non-removal plots), indicating it was not a consequence of *S. horneri* but rather a natural cycle. This conclusion is substantiated by similar estimates of seasonal biomass of understory algae in other places in southern California prior to invasion by *S. horneri* (Harrer et al. 2013). Because the giant kelp, *M. pyrifera*, was absent from my survey and experimental sites throughout nearly the entire course of this study, I did not include it in my results. However, the biomass of *M. pyrifera* is known elsewhere in southern California to peak in the summer and autumn and is lowest during winter and spring (Reed et al. 2009).

The patterns I observed in biomass of native algae were similar to those for percent cover of reef they occupied, which fluctuated and was minimized in March when unoccupied reef was at a maximum. This coincides with the reproductive peak of *S. horneri* (Chapter 2) when bare substrate is required for recruitment.

These results show that *S. horneri* has the greatest biomass at depths where and during the season when the abundance of native macroalgae is lowest. The consistent phenology of *S. horneri* in its native and invaded range (Chapter 2) and of native algae in the presence and absence of *S. horneri* suggest complementarity between this non-native seaweed and other non-fucoid competitors through the year. While the increased abundance of *S. horneri* at depths where native algae were less abundant may also indicate complementarity, it suggests *S. horneri* may not be able to compete with longer-lived algae where they collectively grow in greater abundance. In a recent study, Caselle et al. (2018) hypothesized two mechanisms of biotic resistance were controlling the invasion of *S. horneri*. They found that the abundance of *S. horneri* was low in an historic marine protected area (MPA) relative to newer MPAs. This pattern was attributed to competitive pressure from abundant native algae in the old reserve resulting from protection of urchin predators and thus low urchin abundances. In a nearby fished urchin barren, the abundance of *S. horneri* was also suppressed, presumably due to herbivory by urchins which were at very high density due to the fishing of their predators. With little other food, urchins would then eat the less preferred *S. horneri*. Within newer MPAs with intermediate levels of interacting species, however, neither competition from native algae nor herbivory was thought to be sufficient to prevent invasion. The negative correlation between *S. horneri* and native algae observed by Caselle et al. (2018) at Anacapa Island, where the biomass and diversity of macroalgae is

generally higher than at Catalina Island where my study took place, suggest that this complementarity may allow *S. horneri* to achieve high abundances only in places where competition from native algae is not strong.

Influence of grazers on invasion

The high fecundity, heavy colonization and rapid growth of *S. horneri* may allow it to respond strongly to facilitation by grazers. Herbivores can mediate interspecific competition among algae through preferential consumption of certain species (Estes and Steinberg 1988; Vance and Schmitt 1979), and these preferences may arise from morphological differences or chemical defenses of the algae. I assessed the preference of native grazers for *S. horneri* versus other common species of kelp and *Sargassum* to evaluate whether consumption is a mechanisms of resistance to or facilitation of invasion by *S. horneri*. I predicted that because *S. horneri* is a furoid alga, which typically have high levels of phenolic compounds that deter grazing, *S. horneri* and the other *Sargassum* species may therefore be less palatable than co-occurring kelps (Van Alstyne et al. 1999). My results support this hypothesis, demonstrating that grazers consume the native kelps *M. pyrifera* and *E. arborea* while avoiding *S. horneri* as well as the two other *Sargassum* species presented in the assay. These results also confirm the suggestion from Caselle et al. (2018) that urchins (albeit different species) preferentially consume native algae when it is available and avoid *S. horneri*, reducing the strength of competition from the native species of macroalgae.

The composition of the benthic algal community reflected the grazer preferences I observed. The species of urchin common in this study, *Centrostephanus centrotus*, is known to consume only preferred species of algae, decreasing their abundance dramatically before

switching to less-preferred species (Vance and Schmitt 1979). I found that native foliose algae are reduced and *S. horneri* is more dominant adjacent to urchin halos where I placed these arrays compared to nearby reference areas, and *S. palmeri*, the other common *Sargassum* species, was no different. It appears that, while grazers avoid both species of *Sargassum* in favor of native foliose algae, only *S. horneri* responds to this lack of herbivory with increased abundance. It may be that *S. horneri* is able to colonize space created on the reef more readily due to its high fecundity; a smaller-bodied and longer-lived, perennial species, with lower reproductive capacity, *S. palmeri* may be slower to colonize available space. Traits related to rapid growth and high fecundity, as well as deterrence to herbivory, are often associated with invasive plants (Pyšek and Richardson 2007). However, defenses often come at a fitness cost (Koricheva 2002) and shorter lived, r-selected plants are not typically heavily defended (Strauss et al. 2002). Yet *S. horneri* is a species with r-selected traits that allow it to rapidly colonize available space, and it is also a member of a family with high levels of chemical defenses. These traits are likely what allow *S. horneri* to proliferate in places with weak biotic resistance.

I found that the success of *S. horneri* on southern California reefs results largely from its ability to occupy resources underutilized by native species in space and time, and to resist grazing relative to native kelps. The complementary life histories *S. horneri* and resident algae suggests competition may be weak, but the greatest potential for competitive interactions exists at intermediate depths and during the seasons when *S. horneri* and native taxa are at their peak biomass (spring and summer, respectively). Future work testing the impact of *S. horneri* on native algae should focus on these habitats and seasons. *S. horneri* has a classic, r-selected “weedy” life history – it colonizes new areas quickly, but does not

appear to be a strong competitor. The ability of *S. horneri* to capitalize on available resources while displaying a higher tolerance to herbivory likely accounts for its successful invasion in southern California. These results highlight the importance of considering invasive species in the context of native assemblages when addressing questions about why invasions occur.

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Figures

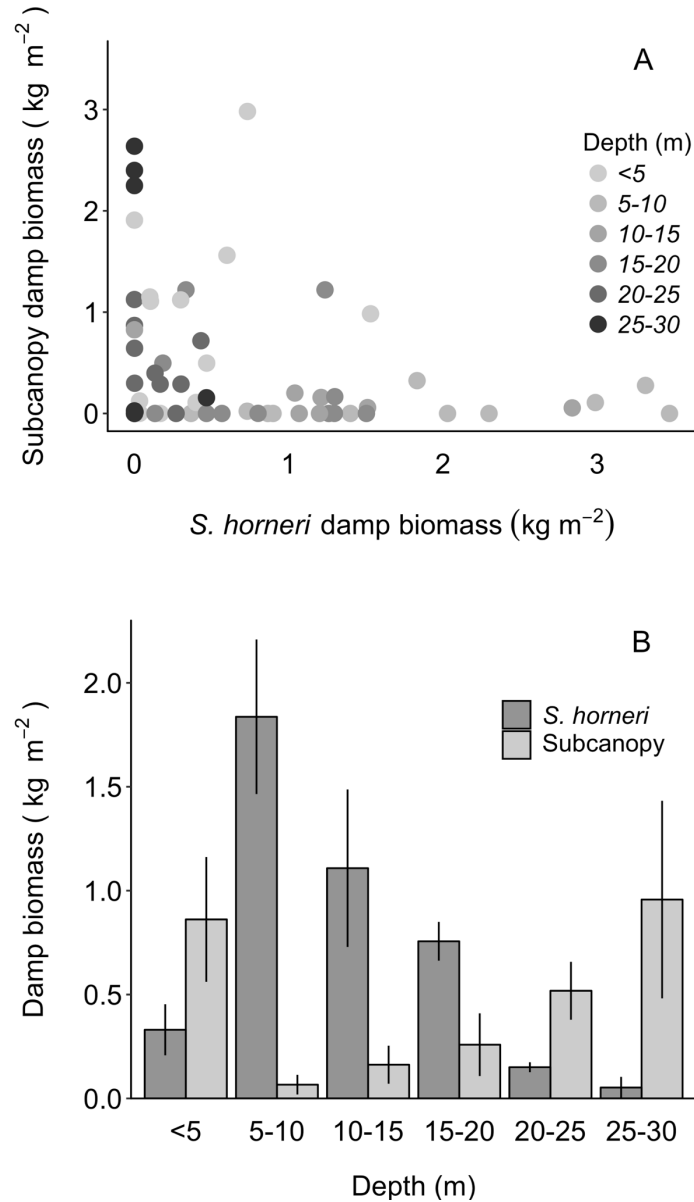


Figure 1. Biomass of *Sargassum horneri* and cumulative biomass of all other subcanopy algae within 1m^2 quadrats sampled along a transect running perpendicular to shore. (A) Points are shaded by depth bin of the quadrat sampled, $N = 64$ quadrats sampled across 4 sites. (B) Data are damp biomass (mean $\pm$ SE) of *S. horneri* and the cumulative damp biomass of all other subcanopy algae. The mean and SE of individual species is provided in Supplement Table 2. $N = 4$ sites per depth bin except 25-30 m where $N = 3$ sites.

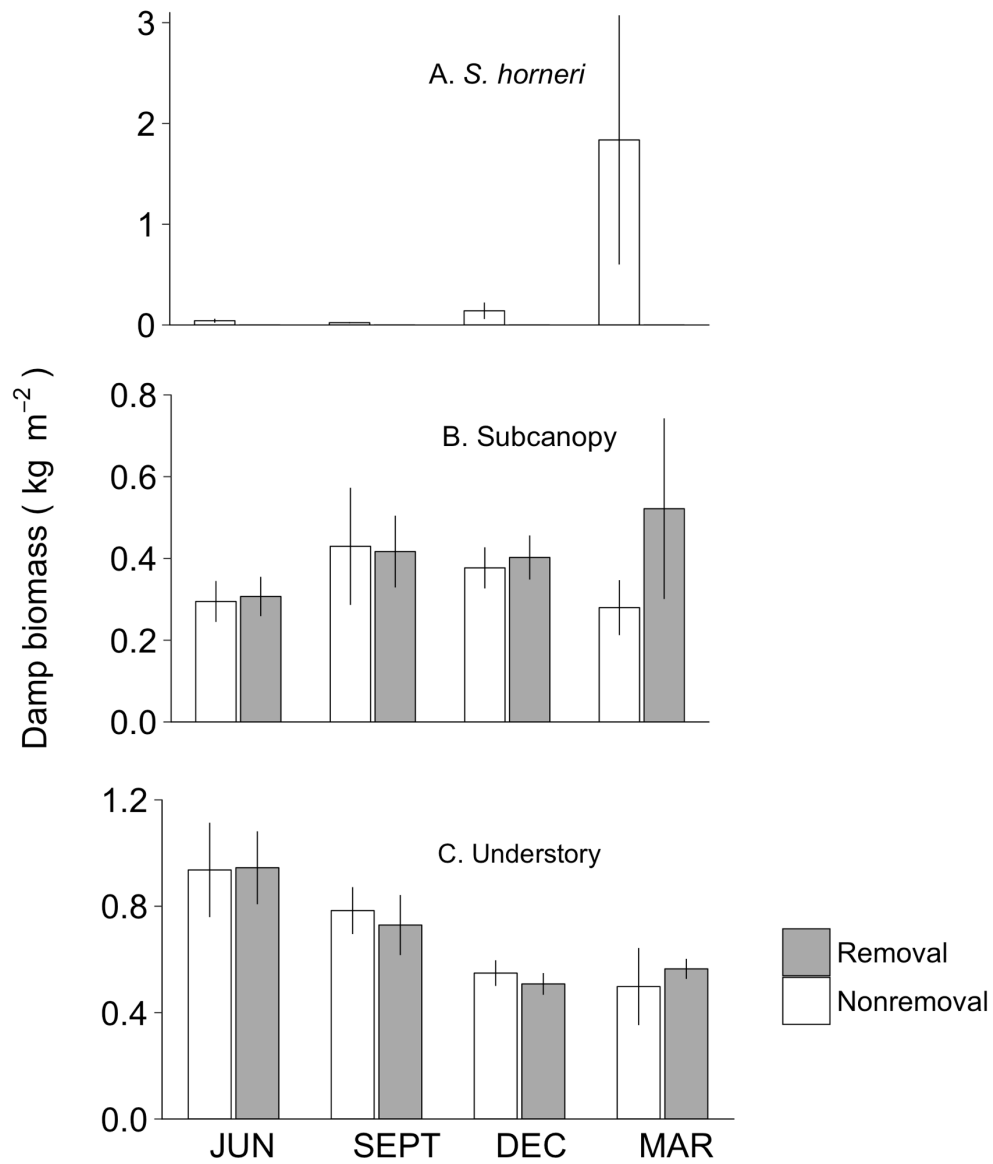


Figure 2. Mean ($\pm$ SE) seasonal biomass of (A) *Sargassum horneri*, (B) subcanopy-forming algae, and (C) understory algae in *S. horneri*-removal and non-removal plots. N = 4 years for spring (March) and summer (June), and 3 years for autumn (September) and winter (December).

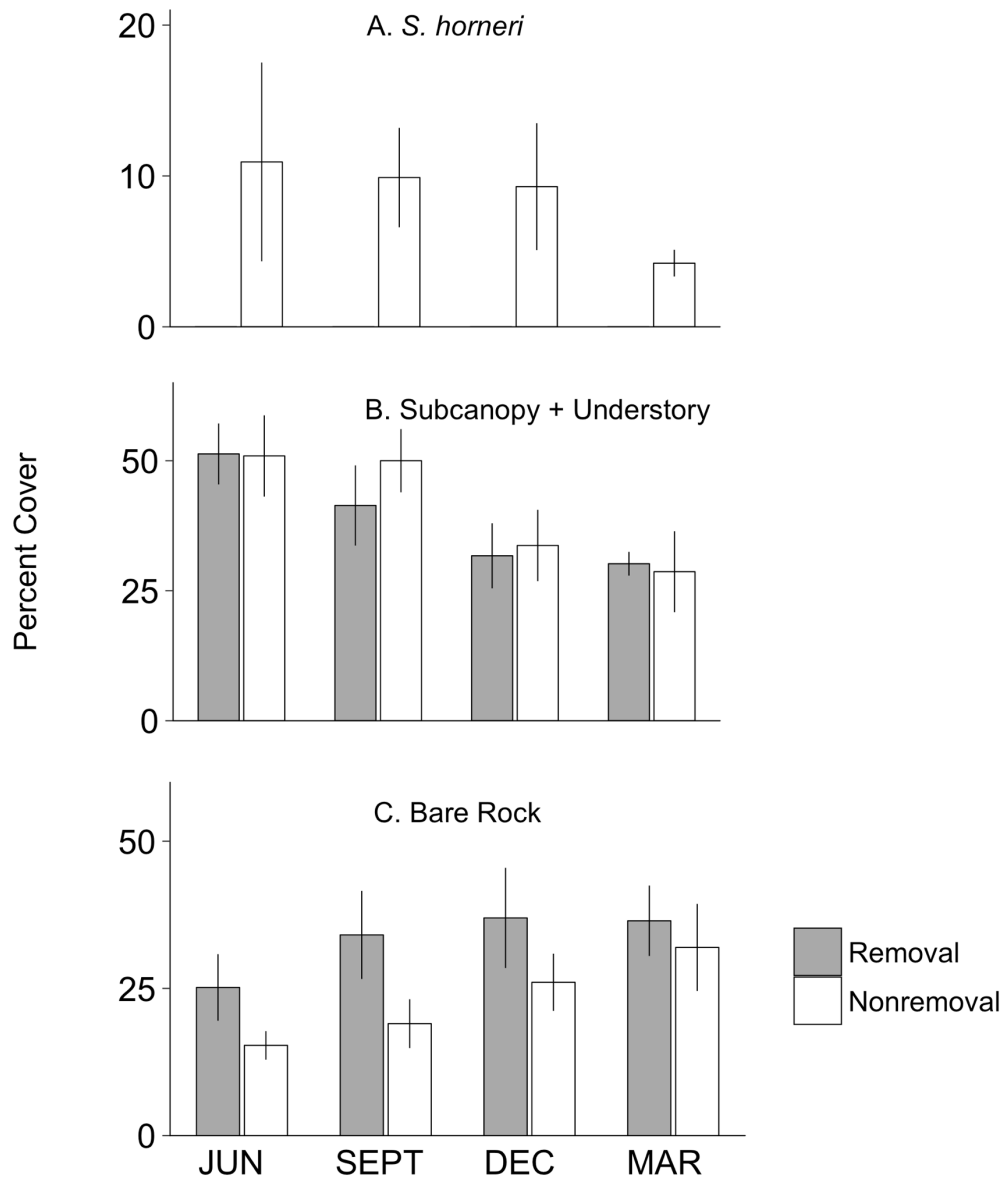


Figure 3. Space occupancy in *Sargassum horneri*-removal and non-removal plots by season. Data are percent cover (mean $\pm$ SE) standardized to percent per m² hard substrate within 5 cm of the reef. Groups presented are cover of (A) *S. horneri*, (B) subcanopy and understory algae, and (C) bare rock. N = 4 sampling periods per season for spring (March) and summer (June), and 3 for autumn (September) and winter (December).

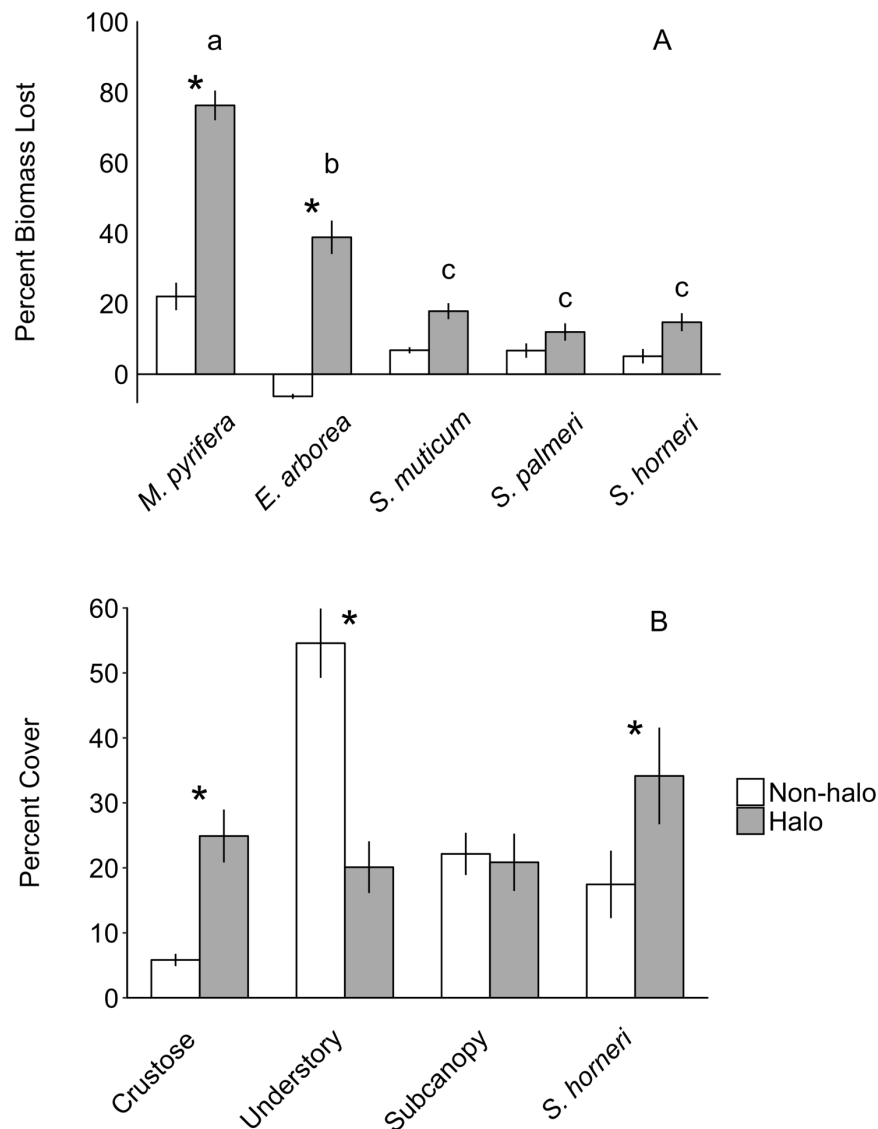


Figure 4. Evidence for consumer avoidance of *Sargassum horneri*. (A) The percent change in biomass (mean $\pm$ SE) of algae deployed adjacent to urchin halos (grey bars) and inside mesh cages (white bars) over 48-hour deployments. Asterisks indicate statistical differences between treatments. Lower-case letters differentiate statistically significant difference between species in arrays adjacent to halos (Tukey pairwise comparison, $p < 0.05$). $N = 57$ exposed and 60 caged arrays from 4 deployments. (B) Composition of benthic algae adjacent to urchin halos and in nearby reference areas. Data are mean proportion of the total percent cover of benthic algae measured in 1m^2 quadrats. $N = 15$ quadrats sampled per treatment. Asterisks indicate significant differences ($p < 0.05$) between treatments.

Tables

Table 1. Results from likelihood ratio tests (LRT) and model selection for determining the influence of experimental factors and their interactions on the percent cover of (A) *Sargassum horneri*, (B) understory and subcanopy-forming algae, and (C) unoccupied reef. Individual parameters were tested against the null model and interactions were tested against a full model with all parameters. Models were ranked according to Akaike Information Criterion (AIC) selection with lower AIC values indicating a better fit of the data. Significance was based on chi-square test statistics.

	Model	df	AIC	χ^2	Chi df	p ($> \chi^2$)
A. Percent Cover of <i>S. horneri</i>						
Individual parameters	Null	4	2595			
	Season	7	2553.5	47.594	3	< 0.0001
B. Percent Cover of Understory and Subcanopy Algae						
Individual parameters	Null	4	2666.4			
	Season	7	2550.5	121.87	3	< 0.0001
	Removal	5	2668.1	0.2769	1	0.599
Interactions	Season + Removal	8	2552.3			
	Season * Removal	11	2550.8	7.4897	3	0.058
C. Percent Cover of Bare Rock						
Individual parameters	Null	4	2595			
	Season	7	2553.5	47.594	3	< 0.0001
	Removal	5	2592.3	4.7013	1	0.0301
Interactions	Season + Removal	8	2550.8			
	Season * Removal	11	2550.3	6.4117	3	0.093

Table 2. Results from likelihood ratio tests (LRT) and model selection for determining the influence of experimental factors and their interactions on the damp biomass of (A) *Sargassum horneri*, (B) understory algae, and (C) subcanopy-forming algae. Individual parameters were tested against the null model and interactions were tested against a full model with all parameters. Models were ranked according to Akaike Information Criterion (AIC) selection with lower AIC values indicating a better fit of the data. Significance was based on chi-square test statistics.

	Model	df	AIC	X ²	Chi df	p (> X ²)
A. Biomass of <i>S. horneri</i> †						
Individual parameters	Null	4	43.1			
	Season	7	-82	131.09	3	< 0.0001
B. Biomass of Understory Algae						
Individual parameters	Null	4	220.1			
	Season	7	96.1	129.91	3	< 0.0001
	Removal	5	222.1	0.0183	1	0.994
Interactions	Season + Removal	8	98.1			
	Season * Removal	11	102	2.1521	3	0.541
C. Biomass of Subcanopy Algae						
Individual parameters	Null	4	251.3			
	Season	7	246.3	10.966	3	0.012
	Removal	5	253	0.348	1	0.555
Interactions	Season + Removal	8	248			
	Season * Removal	11	246.4	7.6175	3	0.055

† data transformed by: $(x + 1)^{-1.9}$

Table 3. Results from likelihood ratio tests (LRT) and model selection for determining the probability of percent change in biomass of algae across experimental factors and their interactions. Individual parameters were tested against the null model and interactions were tested against a full model with all parameters. Models were ranked according to Akaike Information Criterion (AIC) selection with lower AIC values indicating a better fit of the data. Significance was based on chi-square test statistics.

	Model	df	AIC	X²	Chi df	p (> X²)
Individual parameters	Null	5	5596			
	Species	9	5450.2	153.79	4	< 0.0001
	Treatment	6	5494.5	103.53	1	< 0.0001
Interactions	Species + Treatment	10	5311.1			
	Species * Treatment	14	5202.4	116.71	4	< 0.0001

Appendix C: Supplemental Tables S1-S3

Table S1. Coefficients (a = intercept, b = slope), r^2 , and P values or se for formulas to convert count, density, size or percent cover to damp biomass (g) for species of macroalgae at Santa Catalina Island without existing relationships for a morphologically similar species (Harrer et al. 2013; Unpublished data, SBC LTER). The independent variable (either a size measurement, density or percent cover), N (the number of individuals, fronds or quadrats that were analyzed), and the range of values of the independent variable sampled are provided. Methods for developing formulas followed those in Harrer et al. 2013. For relationships best fit by a power function $y = ax^b$ where y is biomass and x is size, regression coefficients a (intercept) and b (slope) are given. For those best fit by a linear function $y = bX$, the parameter is b (slope) provided. For linear equations used to estimate biomass from density data when a size-to-biomass formula was known, the size s used in the formula to generate the slope b is provided.

Taxon	Lifestage	Independent Variable	Range	s	a	b	r^2	N	p	se
<i>Sargassum horneri</i>	Adult	Max height cm	8 - 307	-	0.0285	1.5544	0.64	283	<0.0001	-
<i>Sargassum horneri</i>	Juvenile	Max diameter cm	3 - 18	-	0.0179	1.7633	0.94	35	<0.0001	-
<i>Sargassum muticum</i>	Adult	Max height cm	6 - 204	-	0.0300	1.7054	0.85	55	<0.0001	-
<i>Sargassum horneri</i>	Adult	Density	-	94 cm	-	33.26	-	-	-	-
<i>Sargassum horneri</i>	Juvenile	Density	-	5 cm	-	0.31	-	-	-	-
<i>Sargassum muticum</i>	Adult	Density	-	38.6 cm	-	23.16	-	-	-	-
<i>Sargassum muticum</i>	Juvenile	Count	-	-	-	0.38	-	10	-	0.08
<i>Sargassum palmeri</i>	Adult	Frond length cm	5 - 48	-	0.0444	1.9404	0.72	53	<0.0001	-
<i>Sargassum palmeri</i>	Adult	Number fronds	-	19.3 cm	-	13.8	-	-	-	-
<i>Sargassum palmeri</i>	Adult	Density	-	4 fronds	-	55.2	-	24	-	-
<i>Stephanocystis neglecta</i>	Adult	Number fronds	-	18 cm	-	7.4	-	7	-	-
<i>Stephanocystis neglecta</i>	Adult	Frond length cm	13 - 60	-	0.2229	1.2125	0.66	31	<0.0001	-
<i>Codium setchelli</i>	-	Percent cover 10 cm ²	5 - 80	-	-	0.32	0.27	13	0.0107	-
<i>Halimnion gracile</i>	-	Percent cover 10 cm ²	5 - 100	-	-	0.0925	0.32	26	0.0018	-
<i>Zonaria farlowii</i>	-	Percent cover 10 cm ²	5 - 95	-	-	0.191	0.72	17	<0.0001	-

Table S2. Depth distribution of *Sargassum horneri* and other subcanopy algae. Data are g damp biomass (mean $\pm$ SE).
N = 4 sites sampled per depth bin except 25-30 m where N = 3.

Depth (m)	N	<i>Sargassum horneri</i>	<i>Sargassum palmeri</i>	<i>Sargassum muticum</i>	<i>Halidrys dioica</i>	<i>Stephanocystis neglecta</i>	<i>Eisenia arborea</i>	<i>Agarum fimbriatum</i>
< 5	4	330.4 $\pm$ 122.9	285.5 $\pm$ 119	4.6 $\pm$ 1.6	281.3 $\pm$ 85	27 $\pm$ 27	263.2 $\pm$ 127.1	0 $\pm$ 0
5-10	4	1836.7 $\pm$ 372	30.3 $\pm$ 21.7	9 $\pm$ 9	0 $\pm$ 0	27 $\pm$ 27	0 $\pm$ 0	0 $\pm$ 0
10-15	4	1108 $\pm$ 379	54.5 $\pm$ 38	4.6 $\pm$ 4.6	0 $\pm$ 0	27 $\pm$ 27	76.3 $\pm$ 76.3	0 $\pm$ 0
15-20	4	756.3 $\pm$ 93.3	55.2 $\pm$ 39	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	203.4 $\pm$ 117.4	0 $\pm$ 0
20-25	4	150.3 $\pm$ 23.9	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	13.5 $\pm$ 13.5	185 $\pm$ 185	319 $\pm$ 63
25-30	3	52.5 $\pm$ 51.5	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	12 $\pm$ 12	507 $\pm$ 247.1	438.1 $\pm$ 268.4

Table S3. Proportional percent cover of algae adjacent to urchin halos and in reference areas.

Taxonomic Group	Taxon	Halo				Non-halo			
		Mean	SD	SE	N	Mean	SD	SE	N
Encrusting Algae	Encrusting brown spp.	0	0	0	15	0.1	0.4	0.1	15
	Encrusting coralline spp.	21.6	15.2	3.9	15	5.4	3.6	0.9	15
	Encrusting red spp.	3.3	3.9	1	15	0.3	0.7	0.2	15
Understory Algae	<i>Asparagopsis taxiformis</i>	0.3	1	0.3	15	1.1	2.2	0.6	15
	<i>Corallina chilensis</i>	0.5	1.3	0.3	15	3.3	3.4	0.9	15
	<i>Codium fragile</i>	0.9	2	0.5	15	0.5	1.8	0.5	15
	<i>Colpomenia sinuosa</i>	0	0	0	15	0.4	0.8	0.2	15
	<i>Dictyota</i> spp.	0.1	0.4	0.1	15	0.2	0.6	0.2	15
	<i>Dictyopteris undulata</i>	1.3	2.4	0.6	15	1.3	2.6	0.7	15
	Filamentous red spp.	0.1	0.4	0.1	15	0.5	0.9	0.2	15
	<i>Halimnion gracile</i>	1.4	3.1	0.8	15	21.7	18.5	4.8	15
	<i>Lithothrix aspergillum</i>	0	0	0	15	2	2.4	0.6	15
	<i>Laurencia pacifica</i>	0	0	0	15	0.4	0.7	0.2	15
Subcanopy Algae	<i>Plocamium cartilagineum</i>	0	0	0	15	2.3	5.8	1.5	15
	<i>Pterocladia capillacea</i>	0	0	0	15	0.4	1.4	0.4	15
	<i>Rhodomenia californica</i>	0	0	0	15	0.1	0.4	0.1	15
	Red algal turf spp.	2.1	4.9	1.3	15	0.5	1.7	0.4	15
	<i>Zonaria farlowii</i>	13.4	13.1	3.4	15	20	14.8	3.8	15
	<i>Stephanocystis neglecta</i>	0	0	0	15	1.1	2	0.5	15
	<i>Eisenia arborea</i>	0	0	0	15	0.5	2	0.5	15
<i>Sargassum horneri</i>	<i>Sargassum palmeri</i>	20.9	17.1	4.4	15	20.6	12	3.1	15
	<i>Sargassum horneri</i>	34.1	28.8	7.4	15	17.5	20.1	5.2	15

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Chapter IV

Ecological causes and consequences of invasion by *Sargassum horneri*

Abstract

Introduced algae comprise a large portion of marine invasive species, yet their ecological causes and consequences are poorly known. I experimentally evaluated the effects of the introduced seaweed, *Sargassum horneri*, on the native algal community at Santa Catalina Island in southern California, USA by manipulating its abundance on shallow reefs where it had become established. *Sargassum horneri* was removed from 1 m⁻² plots and the response of resident algae was measured every three months over three consecutive years and compared to assemblages in unmanipulated plots. I detected no effect of removal on algal diversity, and minimal effects on algal biomass and community structure. Differences between removal treatments were apparent only in March 2017 when *S. horneri* biomass in unmanipulated plots was substantially higher than in previous sampling periods, and these differences were driven primarily by a native congener, *S. palmeri*. I also tested whether disturbance facilitated *S. horneri* invasion. In 1 m⁻² plots, I simulated a disturbance mimicking scour during storms that removed much of the resident algae, and measured the colonization (i.e., density of recruits) and establishment (i.e., density of adults) of *S. horneri* in the subsequent year. Disturbance did not increase colonization nor establishment of *S. horneri*, indicating these populations are not limited by primary space. These results suggest that *S. horneri* is not a strong competitor but instead appears to attain high abundance by

occupying underutilized niches. This work contributes to the limited body of knowledge about marine invasive algae, including why invasions occur and under what circumstances they impact recipient communities.

Introduction

Introduced algae comprise a large portion of marine invasive species (Schaffelke et al. 2006; Williams and Smith 2007; Thomsen et al. 2009), but predicting their impacts on native communities has been hindered by a paucity of empirical data and the logistical challenges of studying them (Schaffelke and Hewitt 2007; Davidson et al. 2015). Exotic seaweeds have the potential to affect communities where they invade by out competing native algae and by altering the provision of food and habitat for consumers (Schaffelke and Hewitt 2007). Such effects, however, have been assessed experimentally for only ~2% of species (Thomsen et al. 2009). Strong competition for light and substrate can lead to the decline or exclusion of native seaweeds (DeWreede 1996; Casas et al. 2004; Britton-Simmons 2004) while disturbance can increase the susceptibility of marine communities to invasion by reducing the intensity of competition (Byers 2002; Ruiz et al. 1999; Britton-Simmons and Abbott 2008; Dunstan and Johnson 2007; Valentine et al. 2007). Hence, studies that assess the ecological effects of exotic species by comparing invaded and non-invaded areas may confound invasion impact with invasion success (Gurevitch and Padilla 2004; Didham et al. 2005; Sol et al. 2008; Thomsen et al. 2014). Field experiments where invaders and native assemblages are manipulated are needed to determine the strength and direction of their interactions and distinguish ecological causes from consequences of invasion (MacDougall and Turkington 2005; Guido and Pillar 2014). In the present study, I

experimentally evaluated the effects of the introduced seaweed *Sargassum horneri* (Turner) C. Agardh on the native algal community at Santa Catalina Island in southern California, USA by manipulating its abundance on shallow reefs where it had become established. I also tested whether disturbance facilitated *S. horneri* invasion.

Sargassum horneri is a large brown macroalga native to eastern Asia. First detected in southern California in 2003, *S. horneri* has spread across hundreds of km of coastline in California and Baja California, Mexico (Marks et al. 2015). Within the invaded range, *S. horneri* grows in varying abundance on rocky reefs from the intertidal to >30 m (Chapter 2) becoming a dominant macroalga (in terms of percent cover or biomass) in some areas. It is unclear whether this dominance results from competitive displacement of resident species, opportunistic colonization in disturbed habitats, or occupation of an underutilized niche (Chapter 3). It has been hypothesized that *S. horneri* is deterred by strong competition from native algae (Caselle et al. 2018) and disturbance may facilitate its spread by reducing the strength of competition. However, during its reproductive phase, *S. horneri* can form dense canopies (Figure 1A-B), which have the potential to alter benthic communities by limiting how much light reaches the understory (Reed and Foster 1984; Santelices and Ojeda 1984; Benes and Carpenter 2015). As an annual species with a strong seasonality (Chapter 2), it is important to evaluate the potential impacts of *S. horneri* during various phases of its life cycle throughout the year.

The aims of this work were to explore whether disturbance influences the susceptibility of native algal assemblages to invasion by *Sargassum horneri* and whether the ecological effects of *S. horneri* on the invaded algal community vary at different times during its annual growth cycle. I used a factorial field experiment to answer two questions: (1) what

is the effect of physical disturbance on the colonization (i.e., density of recruits) and establishment (i.e., density of adults) of *S. horneri*?, and (2) what is the impact of *S. horneri* on the diversity, biomass and composition of resident algae? If disturbance facilitates *S. horneri* invasion, then I anticipated increased colonization and establishment of *S. horneri* in experimentally disturbed plots relative to unmanipulated control plots. If invasion by *S. horneri* results from its ability to outcompete resident algae, then I expected the biomass and diversity of resident algae to increase in areas where I experimentally removed *S. horneri*. Alternatively, if the invasion success of *S. horneri* relies on its ability to occupy underutilized niches, then I expected to see no change in the resident algal assemblage in response to *S. horneri* removal.

Methods

Study System

Experiments were conducted at 6 m depth on Isthmus Reef, located 0.5 km offshore of the leeward side of Santa Catalina Island (33.4476° N, 118.4898° W) from March 2014 through July 2017. This moderately sloping reef consists primarily of bedrock with some scattered boulders, cobble and sand. *Sargassum horneri* was moderately abundant (i.e., ~30 adults m⁻²) in the study area and covered 4-10% of the bottom depending on the time of year (Chapter 3). Resident algae (defined here as all non-encrusting macroalgae other than *Sargassum horneri*) occupied ~40-60% of primary space and consisted of low-lying (< 5 cm tall) understory species of brown, red and green algae, and larger subcanopy-forming brown algae such as *Sargassum palmeri* and *Eisenia arborea*. All but two species of resident algae were native to the region; the non-native *Sargassum muticum* and *Codium fragile* occurred in

low abundance. The surface canopy-forming giant kelp, *Macrocystis pyrifera*, was present at the beginning of the experiment (8.4 ± 0.6 fronds m^{-2}), but it declined quickly during a warming trend and disappeared by December 2014 for the duration of the study. Consequently, its presence did not factor into my analyses.

Effects of disturbance on S. horneri

To test the hypothesis that disturbance facilitates the invasion of *Sargassum horneri* by increasing available resources (i.e., space and light), I compared the densities of *S. horneri* recruits (i.e., ≤ 5 cm tall) and subsequent adults (i.e., > 5 cm tall) in experimentally disturbed and undisturbed plots. The corners of twenty-four 1 m^2 plots were marked with eyebolts fastened with marine epoxy into the rock to allow repeated sampling. In March 2015 half of these plots ($n=12$) were assigned with randomly generated numbers as disturbed (D+) and scraped using a wide bladed knife to remove non-encrusting algae to mimic a severe storm that scours the bottom (Figure 1C). The other 12 plots were not disturbed (D–) and served as controls. Dispersal from mature *S. horneri* thalli is highly localized (Chapter 2) such that stands of adults surrounding the cleared 1 m^2 area were sufficient to seed the plots. Scraping resulted in disturbed plots (+D) having an average percent cover of 48% bare rock, 42% encrusting coralline algae and 7% remnant holdfasts of *S. horneri* and resident algae and 3% sessile invertebrates. By comparison, the average percent cover in control plots was 17% bare rock, 22% encrusting coralline algae, 54% resident algae, 4% *S. horneri* and 3% sessile invertebrates. At this site, *S. horneri* recruitment peaks during summer, and maximum adult density is attained during spring when plants reach maturity (Chapter 4). Therefore, after simulating the disturbance in March, I sampled densities of *S. horneri* recruits in June 2015

to evaluate the effects of disturbance on its colonization and densities of *S. horneri* adults the following March (2016) to evaluate the effects of disturbance on its establishment. Estimates of density were later standardized to density m^{-2} hard bottom based on my characterization of the substrate within each plot to account for variation in the proportional cover of rock and sand among the plots. After observing a marked increase in the density of adult *S. horneri* in March 2017 I re-scraped the disturbance plots to remove non-encrusting algae and repeated the experiment to examine whether the effects of disturbance on the colonization and establishment of *S. horneri* varied between years that differed in the abundance of *S. horneri* in the surrounding area.

Linear regressions were used to describe the relationship between the density of *S. horneri* recruits in June when they are most abundant and the density of adults during the peak reproductive season in March (Chapter 3). Recruit densities were log-transformed to meet the model assumptions of normality and homoscedasticity of residuals.

The effect of physical disturbance in March on the density of *S. horneri* recruits the following June was tested using 2-way ANOVA with year (i.e., 2015 and 2017) and disturbance treatment as factors. A two-sided t-test was used to determine the effect of disturbance on *S. horneri* adults in March 2016.

Effects of S. horneri on the native algal assemblage

To test the hypothesis that *Sargassum horneri* decreases the diversity and abundance of other algae, I continually removed *S. horneri* and compared the resident algal assemblages in *S. horneri* removal and unmanipulated control plots over three years. *S. horneri* was removed from 12 randomly assigned 1 m^2 plots (S–) beginning in March 2014 and every 6 to

12 weeks thereafter until June 2017 (Figure 1D). S⁻ plots had a 30 cm buffer zone around the perimeter where *S. horneri* was weeded to minimize edge effects such as shading by individuals outside of the plot. Removal entailed divers using knives to pry holdfasts off the substrate, minimizing disturbance to the other biota within the plot as much as possible. This resulted in the near absence of *S. horneri* in S⁻ plots for the remainder of the study, while the amount of *S. horneri* varied naturally among years and seasons in 12 control (S⁺) plots. Because competitive interactions may also vary with time and among seasons, I sampled the algal communities in all S⁺ and S⁻ plots just prior to the initial removal of *S. horneri* in March 2014 and quarterly thereafter (i.e., June, September, December, March) over three consecutive growing seasons (2014-15, 2015-16, 2016-17).

Algae were identified to the lowest taxonomic level possible, which in most cases was species (Supplemental Table 1). In each plot, I measured the number and estimated the average size of all subcanopy-forming algae. The abundance of understory algae was measured as percent cover using a uniform point contact (UPC) method. At 49 uniformly distributed points within each 1 m² plot, the identity of all understory algae within 5 cm of the bottom was recorded. The substrate type (e.g., reef or sand) intersecting each point was also noted. Percent cover was determined as the fraction of points a taxon intercepted x 100. Although multiple organisms may intersect a single point if they overlay one another, a taxon was only recorded once at a given point even if it intersected that point multiple times. Using this technique, the percent cover of all taxa combined in a plot can exceed 100%, but the percent cover of any individual species or morphological group cannot. If a taxon was present in the plot but not recorded at one of the 49 points, then it was assigned a percent cover value of 0.5%.

Density and size data of subcanopy algae and percent cover data of understory algae were converted to taxon-specific estimates of damp biomass using previously published relationships (Reed et al. 2009; Harrer et al. 2013) or relationships that I developed (Chapter 4; Unpublished data, SBC LTER). Values of damp biomass were standardized to kg m^{-2} hard bottom to account for slight variation in the percent cover of hard substrate within each plot.

The effects of *S. horneri* removal on the biomass of resident algae were analyzed using univariate and multivariate methods on data collected between June 2014 and June 2017. The biomass of *S. horneri* was excluded from these analyses to test specifically for its effects on the resident algal assemblages (Thomsen et al. 2016).

The impact of *S. horneri* manipulation on the taxonomic diversity (Shannon Diversity Index H) and aggregate biomass of resident algae was explored using linear mixed effects models (LMM; Gelman and Hill 2006). Aggregate biomass of resident algae was calculated as the summed biomass of all resident algae within each plot. Because I predicted that treatment effects may differ by season and could develop over time, I included season, treatment (S+ or S-), and days since the initial removal treatment as main effects. To account for variation associated with resampling individual plots, I included plot as a random effect and the summed biomass of resident algae within each plot at the start of the experiment prior to the first removal of *Sargassum horneri* as a covariate. Full models with the main effects in question (i.e., season, treatment, time, and the time-treatment interaction) were compared against null or full models without the effects in question using likelihood ratio tests (LRT) with chi-square test statistics to select the best fit based on Akaike Information Criterion (AIC). Model assumptions of normality and homoscedasticity were validated through visual inspection of the residuals. To identify which time periods contributed to the

time x removal interaction, I used Tukey's honest significant difference post hoc analysis to compare the means of S+ and S- treatments for each sampling period.

To visualize and test for differences in the composition of the algal community between S+ and S- plots, I used non-metric multi-dimensional scaling (nMDS) and analysis of similarities (ANOSIM). Based on the outcome of the LMMs, I pooled the biomass of individual taxa by season for all March and June sampling periods before 2017. I then compared the mean biomass of each taxon in March and June 2017 to the means for March and June averaged over 2014-2016. The manipulation of *S. horneri* was considered a categorical, fixed factor with two levels: removal (S-) and non-removal (S+). I used an unrestricted permutation of raw data (999 permutations) on Bray-Curtis similarity matrices with square root transformation applied. A similarity percentage (SIMPER) analysis was used to determine the taxa that contributed most to dissimilarity between S- and S+ plots when significant differences were observed.

All univariate statistical models and tests were completed using RStudio (version 1.1.414) for R Statistical Computing Package (R Team 2016). Linear mixed models were fit using the lme4 package (Bates et al. 2015) and posthoc comparisons were performed using the multcomp library (Hothorn et al. 2008). All multivariate analyses were conducted using PRIMER v7.0.

Results

Effects of disturbance on S. horneri

Despite a dramatic increase in the abundance of *S. horneri* observed in 2017 compared to 2015 (Figure 2), disturbance had no effect on the colonization (i.e., density of recruits in June) in either year as revealed by a 2-way ANOVA ($F_{1,44} = 0.016$, $p = 0.901$) (Figure 3A). Establishment (i.e., density of adults in March 2016) was also unaffected by disturbance one year prior ($t_{46} = 0.1132$, $p = 0.9104$) (Figure 3B). Colonization significantly predicted establishment in a cohort ($r^2 = 0.33$, $p = 0.0001$), where lower densities of recruits in 2014-2015 ($\sim 40\text{-}100\text{ m}^{-2}$) generated lower densities of adults ($\sim 20\text{-}40\text{ m}^{-2}$) compared to 2016 when higher (315 m^{-2}) densities of recruits generated adult densities averaging about 80 m^{-2} (Figure 2).

Effects of S. horneri on the native algal assemblage

The diversity of resident algae decreased over the course of the study, independent of the removal of *Sargassum horneri* (Figure 4A; Table 1A). The total biomass of resident algae fluctuated seasonally in both S– and S+ plots and was unaffected by *S. horneri* manipulation until March 2017 when biomass in S– plots was double that of S+ plots (Figure 4B; Table 1B; Tukey's HSD, $p = 0.0006$; all other periods $p > 0.05$). This difference was driven by a bloom in resident algae in removal plots and coincided with a dramatic inflation in the biomass of *S. horneri* in S+ plots (Figure 4C). The biomass of resident algae in removal and control plots began to converge again by June 2017 when *S. horneri* biomass declined.

Because *S. horneri* manipulation had no influence on the total biomass of resident algae until March 2017, we examined community structure in two distinct timeframes: before and after the inflation of *S. horneri*. ANOSIM models revealed a high degree of overlap in community structure with significant differences between treatments in both seasons of 2017 (March: global $R = 0.116$, $p = 0.002$; June: global $R = 0.101$, $p = 0.002$). In contrast, the composition of the resident algal assemblage in March and June was similar in S- and S+ plots from 2014-2016. (March: global $R = 0.011$, $p = 0.285$; June: global $R = -0.02$, $p = 0.915$) (Figure 5). SIMPER analysis revealed that differences in algal communities were explained by a few taxa. In March 2017, nearly fifty percent of the dissimilarity between removal and non-removal treatments were driven by just two species (Table 2). *Sargassum palmeri* accounted for approximately one third of the dissimilarity, while the understory brown algae *Zonaria farlowii* accounted for 15% (Figure 6A). In June 2017, three taxa accounted for almost half of the dissimilarity: *Zonaria farlowii* (18%), *Sargassum palmeri* (14%), and *Colpomenia sinuosa* (12%) (Figure 6B).

Discussion

Sargassum horneri is a highly successful invasive species with the potential to alter coastal communities as a result of the high biomass it achieves (Marks et al. 2015; Chapter 2). Observational studies have shown that the prevalence of *S. horneri* is variable, but highest in places or during times when native algae are less abundant (Cruz-Trejo et al. 2015; Caselle et al. 2018; Chapter 3). It is unclear, however, whether this pattern is a consequence of *S. horneri*, or whether it achieves higher invasion success in disturbed habitats where competition from native algae may be reduced.

Physical disturbance mimicking scour during storms did not affect the colonization or establishment of *S. horneri* in the subsequent year. I found no effect of scouring the bottom on the density of recruits in disturbed plots relative to undisturbed ones, either in 2015 when ambient densities of reproductive adults were low, or in 2017 when they were high. The number of recruits was not tightly coupled to the number of adults in the 2015 cohort, which were similarly abundant between treatments, indicating that high recruitment is not necessary to achieve a high density of adults, nor is disturbance needed to create bare space for *S. horneri* to reach high densities. These results suggest that factors other than physical disturbance seem to play a more important role in controlling the colonization and establishment of *S. horneri*. For instance, the ability of *S. horneri* to occupy a variety of substrates, including highly fragmented ones (i.e., cobble, Chapter 2) less suitable for other large algae with high buoyancy and drag (e.g., Deysher et al. 2002), may contribute to its ability to colonize in high abundances, even in areas densely populated with other algae.

Contrary to my prediction that *S. horneri* removal would yield an increase in the biomass and composition of resident algae, I detected few effects over a three-year period. Taxonomic diversity declined over the course of this study, but was unresponsive to *S. horneri* removal. The total biomass of resident algae was also unaffected by *S. horneri* manipulation until 2017 when some native species flourished in response to *S. horneri* removal. Although the biomass of *S. horneri* was moderate relative to other reefs in the region from 2014-2016 (Chapter 2) and comparable to the aggregate biomass of other algae during its peak biomass season (Chapter 3), its removal had no impact on the resident algae during this period. I did observe changes in the algal community towards the end of the study, but rather than gradually developing over time as predicted, these coincided with a

large increase in the ambient biomass of *S. horneri* in March 2017. Studies of aquatic plants and animals, marsh grasses and marine macroalgae have shown that impacts scale with the abundance of an invader (e.g., Thomsen et al. 2009; Theuerkauf et al. 2017; White and Shurin 2011). In this case, *S. horneri* had no detectable effects until it reached extremely high abundance, at which point only modest impacts to the resident algal community occurred.

When removal experiments evaluating the effects of invaders on the native community fail to detect a response, the lack of source propagules available to recolonize cleared space is a potential explanation (Kettenring and Adams 2011). The impacts of invasive species are often assessed once they have already become abundant when resident assemblages may have already been considerably altered by the invader (e.g., Scheibling and Gagnon 2006; South et al. 2016; Valentine and Johnson 2005; Corbin and D'Antonio 2012; South and Thomsen 2016) or environmental stressors that compromised assemblages and led to the invasion in the first place (MacDougall and Turkington 2005; Eastwood et al. 2007). My experiment took place during an anomalously warm period (Bond et al. 2015; Kintisch 2015) when the dominant macroalga, the giant kelp *M. pyrifera*, was suppressed and algal diversity was declining. These conditions may have modulated the response of the system to *S. horneri* removal, and repeating this experiment during more typical climate and when *M. pyrifera* is present may yield different results. Another reason removal experiments fail to detect effects is that they are run for an insufficient amount of time. For example, after 18 months of removing the invasive alga *Caulerpa racemosa* from experimental plots, only a partial recovery of the native macrophyte assemblage was observed relative to uninvaded reefs (Klein and Verlaque 2011). The lack of complete recovery was attributed to an insufficient duration of the experiment. At Santa Catalina Island where *S. horneri* has been

present since 2006, there were no uninvaded reefs to use for such a comparison. However, I ran this experiment over multiple years to allow for the gradual recovery of resident algae. Although I detected the first significant response three years after the removal treatment began, recovery was not gradual or linear, suggesting more time would not have yielded substantially different results.

The success of invasive macroalgae has often been attributed to opportunistic, r-selected traits (Bulleri et al. 2010; Scheibling and Gagnon 2006; South and Thomsen 2016), but their rapid colonization and spread are not always correlated with negative ecological impacts (Ricciardi and Cohen 2007; Davidson et al 2015). *S. horneri* has several r-selected life history traits that likely facilitate its invasion (Chapter 2), yet it may not be a strong competitor against resident algae. The biomass of mature individuals relative to the size of their holdfasts is high; a small ($\sim 1 \text{ cm}^2$) holdfast supports adults that grow several meters tall. Even though a few individuals can produce a large amount of biomass (Chapter 2), they are unlikely to displace natives via competition for primary space on the bottom. The canopy formed by adults does have the potential to limit the amount of light that reaches the understory during the time of year when it is present (January – early June at Santa Catalina Island, Chapter 2). However, even if light limitation by *S. horneri* canopy caused the changes in the algal community that I observed in 2017, it is unlikely to play a major role in the dynamics of algal assemblages over the long term due to the ephemeral and highly variable nature of the canopy.

Impacts of invasive species are often context-dependent, differing between regions, habitats and response variables (e.g., D'Antonio et al. 2000), and invasive macroalgae are no exception (Thomsen et al. 2009; Thomsen et al. 2011; Schaffelke and Hewitt 2007; Williams

and Smith 2007; Petrocelli and Cecere 2015). The minor impact of *S. horneri* on resident algae that I detected contrasts with other invasive canopy-forming seaweeds that have been shown to inhibit native species (e.g., Britton-Simmons 2004; Bulleri et al. 2010; De Wreede 1983; Scheibling and Gagnon 2006). In particular, a congener *Sargassum muticum*, which is also invasive on the northeast Pacific coast but now uncommon at Santa Catalina Island, negatively affected resident macroalgae in subtidal habitats (Britton-Simmons 2004). While the two species have similar morphologies and life histories, a perhaps important distinction is that *S. muticum* is a deciduous perennial that sheds its reproductive and vegetative foliage each year, but regenerates fronds from perennating holdfasts. This regeneration allows the persistence of individuals through multiple years, whereas *S. horneri* must recolonize each year and may therefore be more vulnerable to the inter-annual variability of other algae. However, my results are consistent with other experimental tests of invasibility and impact with canopy-forming algae with an annual life cycle. The invasive, annual kelp, *Undaria pinnatifida*, has been shown to have weak or transient effects on native algae, displacing only other ephemeral algae with phenology that is synchronized with its own (South and Thomsen 2016) and interacting weakly with other species (South et al. 2016).

Despite its dominance at Santa Catalina Island and elsewhere, *Sargassum horneri* does not appear to be a strong competitor. I found that it did not displace resident algae except during times when it was extremely abundant, and this effect was temporary. Disturbance to the resident algal community did not increase colonization nor establishment of *S. horneri*, suggesting these populations are not limited by primary space. Taken together, these results suggest that *S. horneri* appears to attain high abundance by occupying underutilized niches. Because giant kelp *M. pyrifera* is such an ecologically important species that was absent

during this study, further research should examine the competitive interactions between it and *S. horneri*. Nevertheless, this work contributes to the limited body of knowledge about marine invasive algae, including why invasions occur and under what circumstances they impact recipient communities.

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Figures

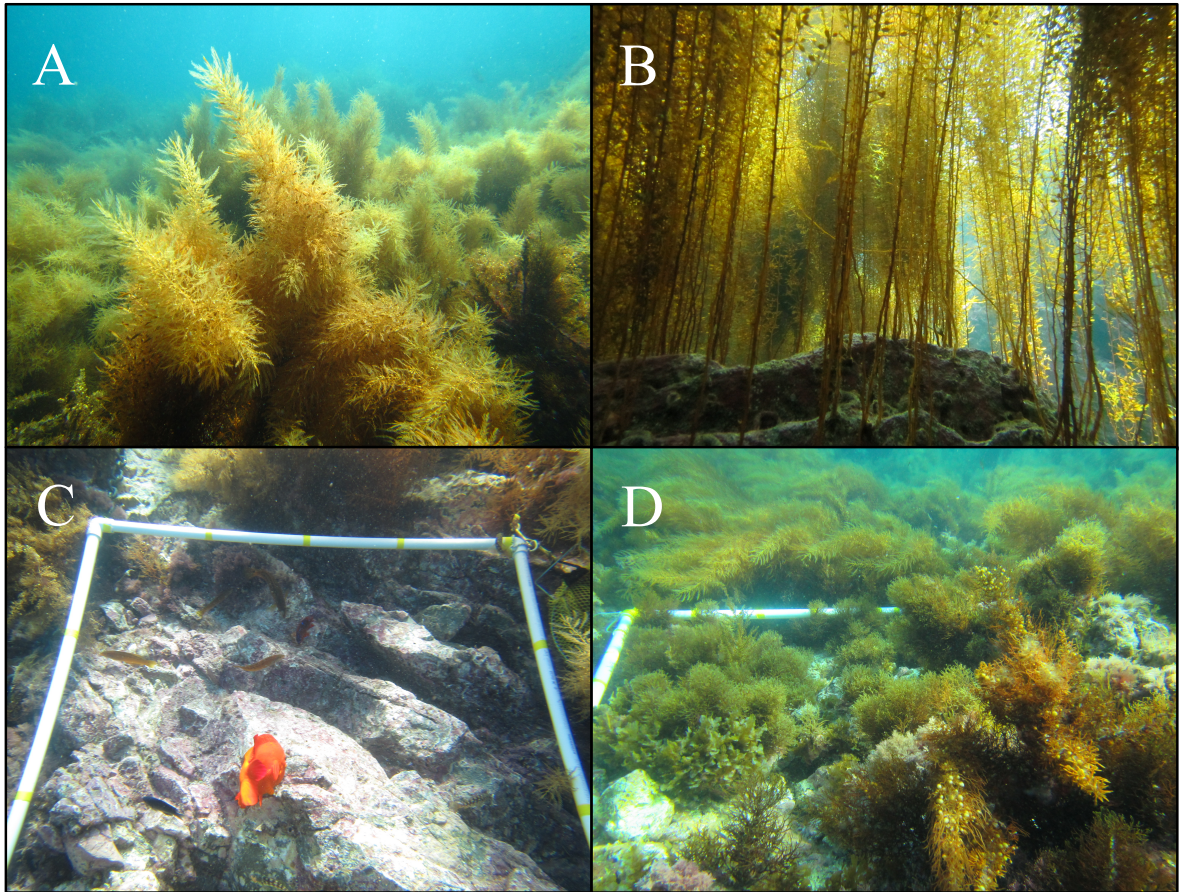


Figure 1. Photographs from Isthmus Reef showing differences in experimental treatments. In unmanipulated plots (S+ D–), *Sargassum horneri* was left intact and formed a canopy during Spring, shown here from above (A) and below (B). (C) Disturbance (D+) plots were left devoid of nearly all erect algae following the simulation of a storm that scours the bottom. (D) In *S. horneri*-removal treatment (S –) plots, resident algae were left intact. (Photo credits: Lindsay Marks).

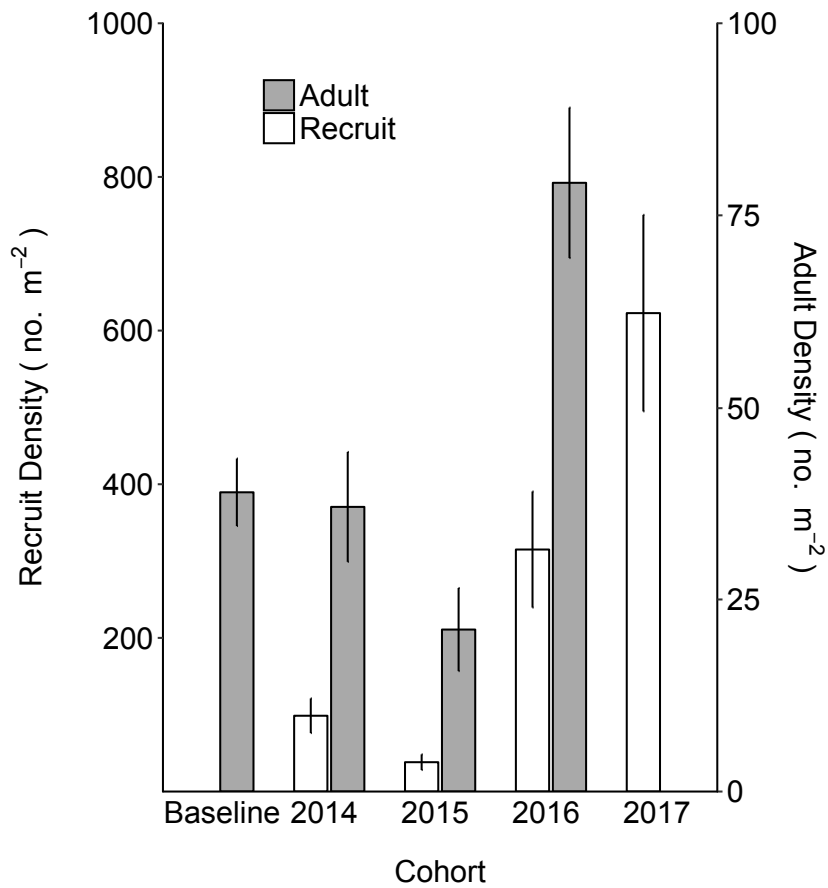


Figure 2. Density (mean $\pm$ SE) of *Sargassum horneri* in control plots. Adults (grey bars) were sampled in March and recruits (white bars) were sampled in June. Data are shown as recruits followed by adults of the same cohort the following March. Baseline adult density data is from the pre-removal census.

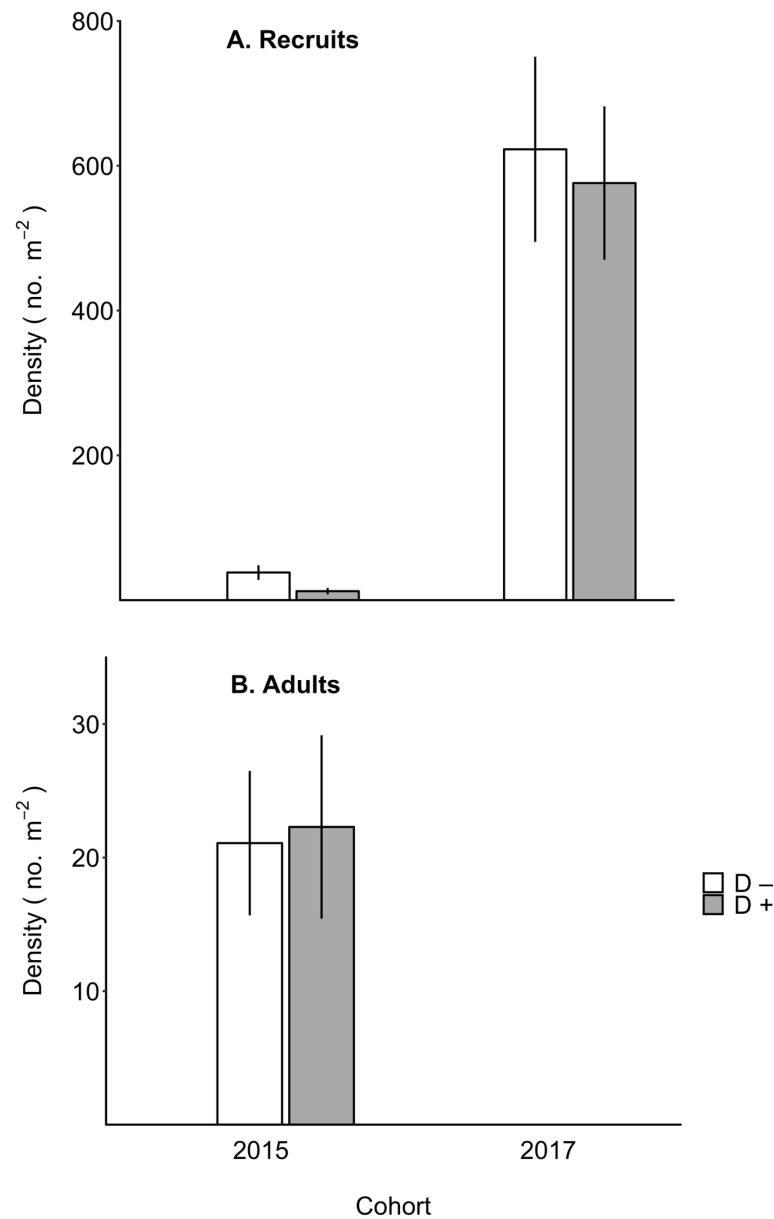


Figure 3. Results from disturbance experiment. Data are density (mean $\pm$ SE) of *Sargassum horneri* recruits (A) and subsequent adults (B) measured in June and March, respectively, following simulated disturbances in 2015 and 2017. Adults from the 2017 cohort have not yet been sampled. N = 12 plots treatment⁻¹.

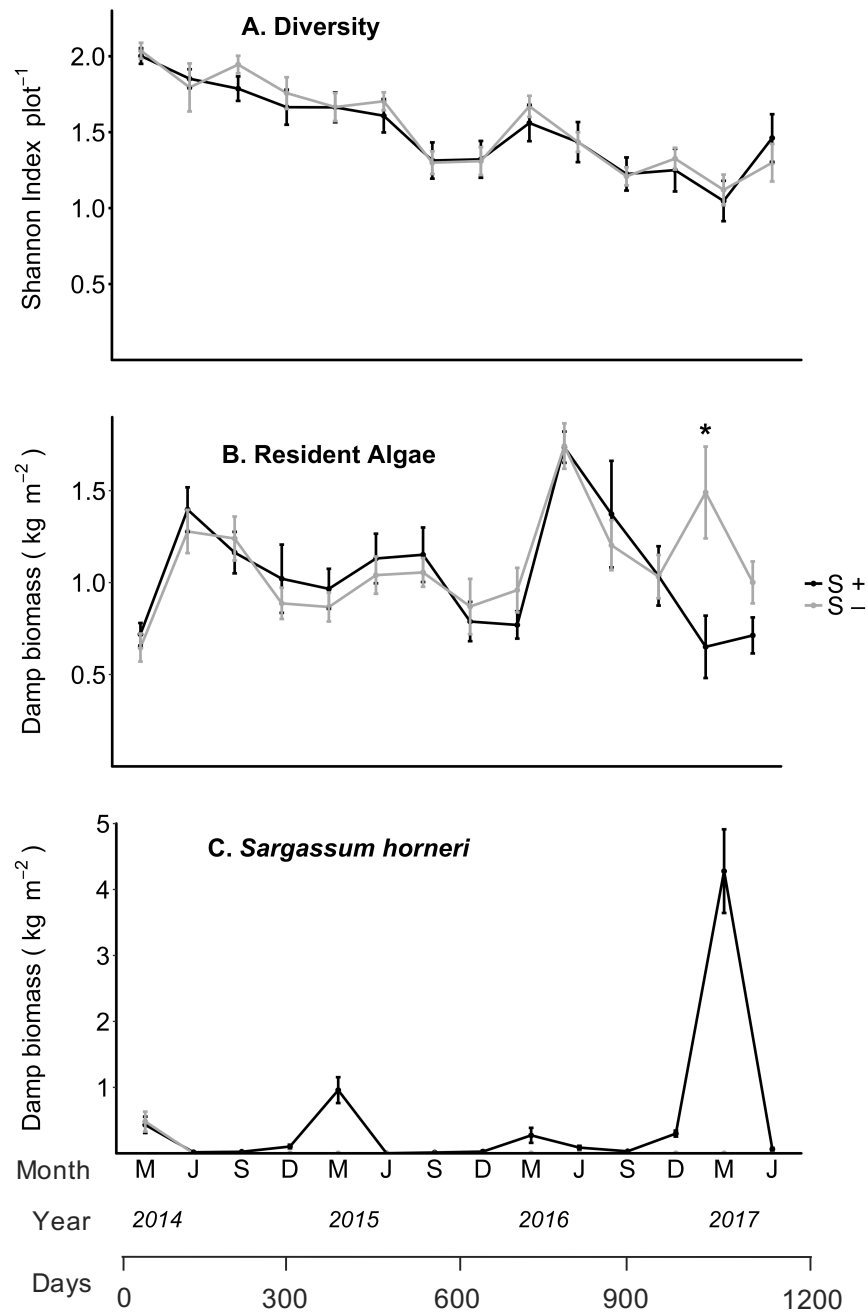


Figure 4. Results from *Sargassum horneri* removal experiment. Data are taxonomic diversity of resident algae (A), and damp biomass (mean $\pm$ SE) of resident algae (B) and *S. horneri* (C). Grey lines represent plots where *S. horneri* was removed (S-) and black lines represent control plots (S+). Significant interactions identified with multiple comparisons tests (Tukey's $\alpha < 0.05$) are indicated by *. N = 12 plots treatment⁻¹. First data point in each series is from the pre-removal census.

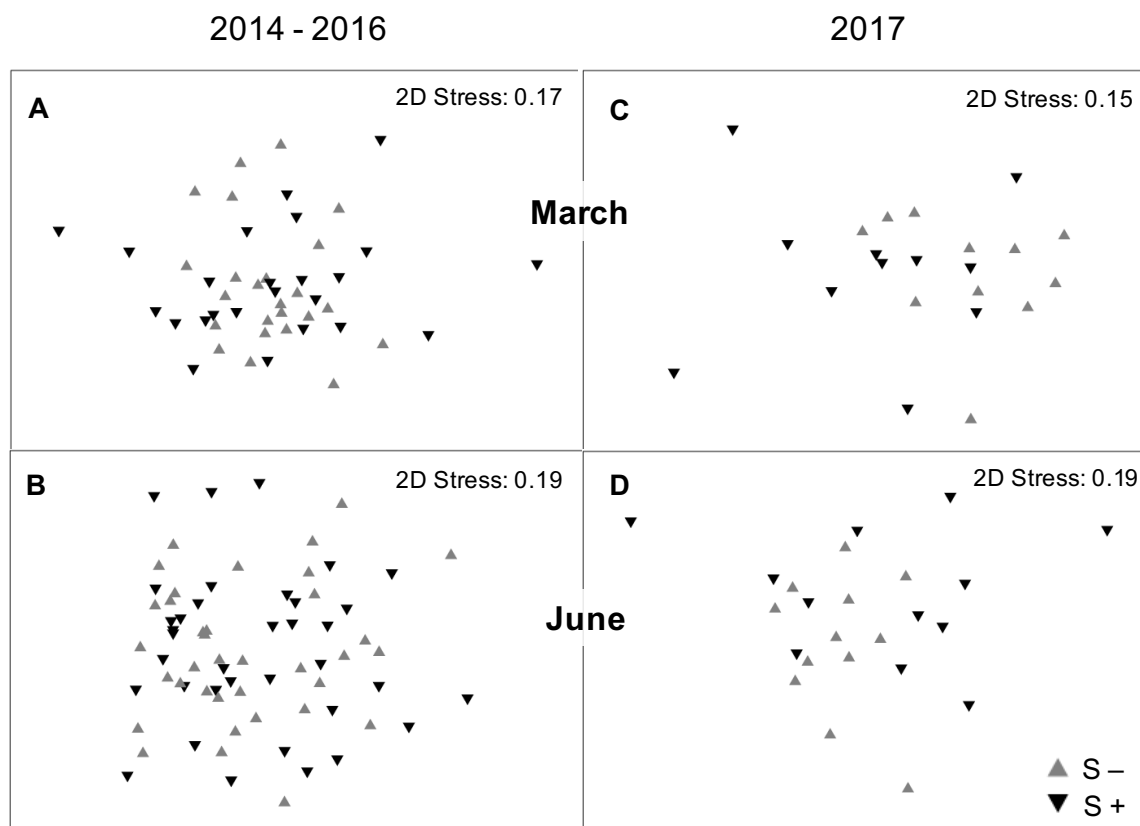


Figure 5. Non metric multidimensional scaling (nMDS) plots showing benthic algae assemblage structure in plots where *Sargassum horneri* was removed (S– in grey) and in control plots (S+ in black). Data were pooled by season and by timeframe (i.e., before and during 2017), and are presented as (A) March 2014 – 2016, (B) June 2014 – 2016, (C) March 2017, and (D) June 2017. N = 48, 72, 24 and 24 plots, respectively. Analysis used damp biomass with a square root transform and Bray Curtis similarity index. Two-dimensional (2D) stress values indicate the degree of mismatch between the predicted values from the regression of the similarity matrix and the distances between samples.

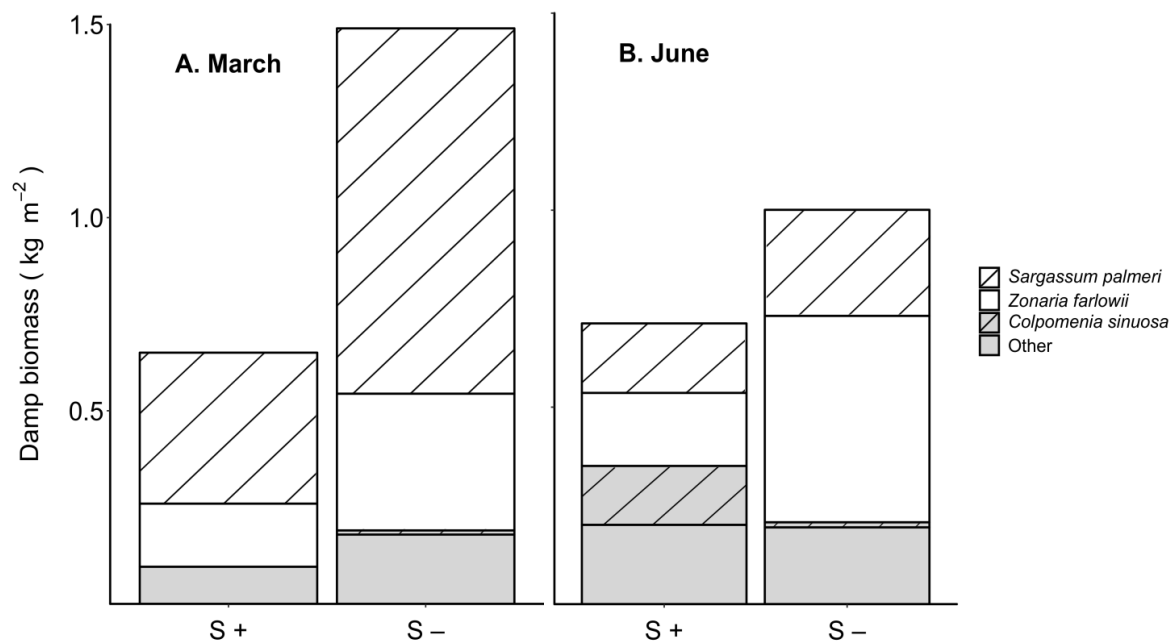


Figure 6. Damp biomass (mean only, SE not shown for clarity) of resident algae in *Sargassum horneri* removal experiment in 2017. Data are shown for March (A) and June (B) by treatment (S- removal; S+ control). The three species contributing most to the dissimilarity between treatments in SIMPER analysis are identified, and the remaining taxa are grouped as “Other”. N = 12 plots treatment⁻¹.

Tables

Table 1. Results from likelihood ratio tests (LRT) and model selection for determining the influence of experimental treatment and their interactions on the (A) Shannon Diversity Index H and (B) total biomass of resident algae. Individual parameters were tested against the null model and interactions were tested against a full model with all parameters. Models were ranked according to Akaike Information Criterion (AIC) selection with lower AIC values indicating a better fit of the data. Significance was based on chi-square test statistics.

	Model	df	AIC	χ^2	Chi df	p ($>\chi^2$)
A. Diversity of resident algae						
Individual parameters	Null	4	302.6			
	Treatment	5	304.53	0.0715	1	0.7891
	Time	5	189.34	115.26	1	< 0.0001
	Season	7	300.82	7.7784	3	0.0508
Interactions	Full	9	181.85			
	Treatment*Time	10	183.23	0.616	1	0.4325
	Treatment*Season	12	186.42	1.4246	3	0.6998
B. Biomass of resident algae						
Individual parameters	Null	4	439.72			
	Treatment	5	441.12	0.606	1	0.4363
	Time	5	440.89	0.8375	1	0.3601
	Season	7	412.22	33.507	3	0.0023
Interactions	Full	9	415.51			
	Treatment*Time	10	408.11	9.4002	1	0.0022
	Treatment*Season	12	457.8	8.6293	3	0.0347

Table 2. Composition of the resident algae present in March and June 2017 in control (S+) plots and those where *Sargassum horneri* was removed (S-). Data are damp biomass (mean $\pm$ SE kg m⁻²) and the percent contribution of individual taxa to the top 70% of the dissimilarity between S+ and S- treatments in SIMPER analysis.

Taxonomic Group	Taxon	March			June		
		S +	S -	%	S +	S -	%
Subcanopy algae	<i>Stephanocypris neglecta</i>	25.1 $\pm$ 15	28.4 $\pm$ 11.7	7.5	26.3 $\pm$ 10.5	19.8 $\pm$ 8.5	5.8
	<i>Sargassum muticum</i>	0 $\pm$ 0	7.8 $\pm$ 5.2	.	0.5 $\pm$ 0.3	0.1 $\pm$ 0.1	.
	<i>Sargassum palmeri</i>	390.8 $\pm$ 147.2	945.7 $\pm$ 243.8	28.4	176.4 $\pm$ 46.7	269.1 $\pm$ 69.2	14.2
Understory algae	Articulated coralline spp.	0 $\pm$ 0	1.6 $\pm$ 1.6	.	0.4 $\pm$ 0.4	1.7 $\pm$ 1.7	.
	<i>Asparagopsis taxiformis</i>	0 $\pm$ 0	0 $\pm$ 0	.	0.3 $\pm$ 0.3	1.1 $\pm$ 1.1	.
	<i>Cladophora graminea</i>	0 $\pm$ 0	0 $\pm$ 0	.	0.2 $\pm$ 0.2	0 $\pm$ 0	.
	<i>Codium fragile</i>	0 $\pm$ 0	0 $\pm$ 0	.	2.1 $\pm$ 1.4	2.1 $\pm$ 1.4	.
	<i>Colpomenia sinuosa</i>	0 $\pm$ 0	10.8 $\pm$ 8.6	.	.	13 $\pm$ 5.5	12.1
	<i>Corallina chilensis</i>	19.3 $\pm$ 10.4	31.3 $\pm$ 13.1	7.1	13.9 $\pm$ 7.6	13 $\pm$ 7.3	.
	<i>Dictyopteris undulata</i>	3.7 $\pm$ 2.2	24.4 $\pm$ 6.4	6.5	15 $\pm$ 6.8	47.7 $\pm$ 13	7.2
	<i>Dictyota</i> spp.	1.1 $\pm$ 0.7	21.7 $\pm$ 8.4	.	24.5 $\pm$ 11.4	24.7 $\pm$ 12.1	5.5
	Filamentous brown spp.	0 $\pm$ 0	0 $\pm$ 0	.	0.1 $\pm$ 0.1	0 $\pm$ 0	.
	Filamentous green spp.	0 $\pm$ 0	0.2 $\pm$ 0.2	.	0.3 $\pm$ 0.3	0.5 $\pm$ 0.3	.
	Filamentous red spp.	1 $\pm$ 1	1.4 $\pm$ 1.1	.	0 $\pm$ 0	2.5 $\pm$ 2	.
	<i>Halicystis ovalis</i>	0 $\pm$ 0	0 $\pm$ 0	.	0.3 $\pm$ 0.3	0.7 $\pm$ 0.4	.
	<i>Halimnion gracile</i>	19.6 $\pm$ 11.1	21.4 $\pm$ 8.3	.	38.6 $\pm$ 21.8	29.3 $\pm$ 13.6	6.5
	<i>Hydroclathrus clathratus</i>	0 $\pm$ 0	0 $\pm$ 0	.	8.6 $\pm$ 4.3	5.3 $\pm$ 4.3	.
	<i>Laurencia pacifica</i>	0.6 $\pm$ 0.6	3.7 $\pm$ 1.1	.	7.9 $\pm$ 3	11.3 $\pm$ 5.2	.
	<i>Lithothrix aspergillum</i>	18.7 $\pm$ 9.4	21.2 $\pm$ 11.5	6.4	34 $\pm$ 20.9	25.5 $\pm$ 15	6.3
	<i>Plocamium cartilagineum</i>	2.5 $\pm$ 2.2	2.4 $\pm$ 1.6	.	17.7 $\pm$ 10.7	2.5 $\pm$ 1.5	.
	<i>Pterocladia capillacea</i>	4.5 $\pm$ 4.5	5.4 $\pm$ 4.4	.	8.8 $\pm$ 4.4	6.5 $\pm$ 4.4	.
	<i>Rhodomenia californica</i>	0 $\pm$ 0	2 $\pm$ 1.3	.	1 $\pm$ 0.5	0.6 $\pm$ 0.4	.
	<i>Scytosiphon lomentaria</i>	0 $\pm$ 0	0 $\pm$ 0	.	1 $\pm$ 0.7	0 $\pm$ 0	.
	Unidentified brown blade spp.	0 $\pm$ 0	6.1 $\pm$ 4.4	.	0 $\pm$ 0	0 $\pm$ 0	.
	Unidentified green algae spp.	0 $\pm$ 0	0.5 $\pm$ 0.5	.	0 $\pm$ 0	0 $\pm$ 0	.
	<i>Zonaria farlowii</i>	163.4 $\pm$ 36.1	354 $\pm$ 71.5	15.8	185.3 $\pm$ 47	523.8 $\pm$ 85.1	17.5
	Cumulative % contribution to dissimilarity			71.8			75.2

Appendix D: Supplemental Table S1

Table S1. List of resident algal taxa recorded in removal experiment.

Taxonomic Group	Taxon
Canopy algae	<i>Macrocystis pyrifera</i>
Subcanopy algae	<i>Eisenia arborea</i> <i>Stephanocystis neglecta</i> <i>Sargassum muticum</i> <i>Sargassum palmeri</i>
Understory algae	Algal turf spp. <i>Articulated coralline</i> spp. <i>Asparagopsis taxiformis</i> Blady red spp. Branching red algae spp. <i>Callophyllis flabellulata</i> <i>Chondria californica</i> <i>Cladophora graminea</i> <i>Codium fragile</i> <i>Codium setchelli</i> <i>Colpomenia sinuosa</i> <i>Corallina chilensis</i> <i>Corallinaspp.</i> Diatom mat <i>Dictyopteris undulata</i> <i>Dictyota</i> spp. Encrusting coralline spp. Encrusting red algae spp. Filamentous brown spp. Filamentous green spp. Filamentous red spp. <i>Halicystis ovalis</i> <i>Haliptylon gracile</i> <i>Hydroclathrus clathratus</i> <i>Laurencia pacifica</i> <i>Lithothrix aspergillum</i> <i>Plocamium cartilagineum</i> <i>Pterocladia capillacea</i> Red algal turf spp. <i>Rhodomenia californica</i> <i>Scytosiphon lomentaria</i> <i>Ulva</i> spp. Unidentified brown blade spp. Unidentified green algae spp. <i>Zonaria farlowii</i>

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Chapter V

Assessment of control methods for the invasive seaweed

Sargassum horneri in California, USA²

Abstract

Determining the feasibility of controlling marine invasive algae through removal is critical to developing a strategy to manage their spread and impact. To inform control strategies, we investigated the efficacy and efficiency of removing an invasive seaweed, *Sargassum horneri*, from rocky reefs in southern California, USA. We tested the efficacy of removal as a means of reducing colonization and survivorship by clearing *S. horneri* from 60 m² circular plots. We also examined whether *S. horneri* is able to regenerate from remnant holdfasts with severed stipes to determine whether efforts to control *S. horneri* require the complete removal of entire individuals. The experimental removal of *S. horneri* in early winter, just prior to the onset of reproduction, reduced recruitment in the next generation by an average of 54% and reduced survivorship to adulthood by an average of 25%. However, adult densities one year after clearing averaged 83% higher in removal plots and 115% higher in control plots. We attribute these higher densities to anomalously warm water associated with the 2015–16 El Niño that reduced native canopy-forming algae and enhanced the recruitment and survival of *S. horneri*. We did not find any evidence to suggest that *S. horneri* has the capacity to regenerate, indicating that its control via removal does not require

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the tedious task of ensuring the removal of all living tissue. We developed efficiency metrics for manual removal with and without the aid of an underwater suction device and found the method with maximum efficiency (biomass removed worker⁻¹ hr⁻¹) varied based on the number of divers and surface support workers. Our findings suggest that controlling *S. horneri* via removal will be most effective if done over areas much larger than 60 m² and during cool-water years that favor native algae. Such efforts should be targeted in places such as novel introduction sites or recently invaded areas of special biological or cultural significance where *S. horneri* has not yet become widely established.

Key Words: introduced species, management, marine, macroalgae, rocky reef, *Sargassum filicinum*

Introduction

Invasive species are one of the greatest agents of human-induced change to ecosystems worldwide (Pejchar and Mooney 2009). Coastal marine systems are especially vulnerable to introductions of nonindigenous species via trans-oceanic shipping, aquaculture and the aquarium trade, which have greatly extended the distribution of many marine species outside of their native ranges (Carlton 1989). Marine invasions have steadily increased over the past two centuries (Ruiz et al. 2000) and are expected to continue to rise as global trade expands. Costs associated with the impact and management of invasive species are high, totaling over \$1 billion annually in the USA (Pimentel et al. 2000), while resources available for management are limited. Therefore, agencies tasked with controlling invasions must be efficient in their management strategies. Exploration of techniques aimed at controlling the

spread and impact of marine invasive species and identification of species-specific traits that increase the efficacy of control are urgently needed.

A seaweed recently introduced to southern California, USA, presented an opportunity to test the efficacy of removal in controlling invasive algae on rocky reefs. *Sargassum horneri* (Turner) C. Agardh, 1820 (Fucales) is a large, annual brown alga native to shallow reefs of eastern Asia. It was first discovered in the eastern Pacific in Long Beach Harbor in 2003 and identified as *S. filicinum* Harvey, 1860 (Miller et al. 2007), now considered a synonym of *S. horneri* (Uwai et al. 2009). The species has spread aggressively across 700 km from Santa Barbara in southern California to Isla Natividad in Baja California, Mexico (Marks et al. 2015). It occurs primarily at offshore islands though it has also been found along the mainland and in coastal embayments. In southern California we have observed *S. horneri* growing in the intertidal down to 33 m depth, with its highest densities occurring between 5–15 m. In places where *S. horneri* is established, juveniles can attain high cover with upwards of 1,000 individuals m⁻² during the summer and fall, and these grow to form thick canopies in the winter with dense stands of over 100 adults m⁻² (author's unpublished data). While definitive evidence of ecological impacts on rocky reef systems from *S. horneri* invasion is not yet available (but see Cruz-Trejo et al. 2015), the detrimental effects on native assemblages caused by other invasive seaweeds (e.g., de Villèle and Verlaque 1995; Levin et al. 2002; Casas et al. 2004; Britton-Simmons 2004) suggest management of *S. horneri* is worth exploring (Anderson 2007; Schaffelke and Hewitt 2007; Forrest and Hopkins 2013).

Several life history characteristics of *S. horneri* make it potentially suitable for control by removal. First, it is a large and conspicuous alga consisting of a single main axis with multiple lateral branches that reaches up to several meters high (Yoshida 1983). The

annual thallus is anchored by a small holdfast that gives rise to a stipe buoyed by many small gas bladders (Marks et al. 2015). The conspicuous adult thalli allow for efficient identification and removal by divers using SCUBA. Second, *S. horneri* propagates via sexual reproduction. Fertilization occurs in winter on the surface of reproductive structures born on the lateral branches of a mature thallus where embryos are developed and shed (author's unpublished data). Senescence of the thallus ensues after embryos are shed, completing the annual life cycle. *Sargassum* embryos tend to sink quickly (Gaylord et al. 2002) and the vast majority likely settle within a few meters of the parent thallus (Deysher and Norton 1982; Stiger and Payri 1999; Kendrick and Walker 1995). Clearing thalli in relatively small areas on the order of tens of square meters may therefore reduce colonization resulting from local dispersal. However, because colonization over longer distances is thought to occur via reproductively mature thalli that are dislodged and set adrift (Yatsuya 2008), any thalli removed must not be released. Asexual reproduction in *S. horneri* via fragmentation or regeneration from remnant tissue has not been studied, although it is known to occur in other fucoid species (McCook and Chapman 1992; Fletcher and Fletcher 1975). Information on the capacity of *S. horneri* to propagate asexually is needed to develop an effective management strategy for controlling its spread.

A new tool that has been developed to help control algal invasions is an underwater suction device. This type of device has been used on coral reefs in Oahu, Hawaii, to reduce densities of invasive algae (Conklin and Smith 2005), and a similar device was recently developed to aid in controlling seaweed invasions on rocky reefs in California. The device has been used to transport *S. horneri* removed from the ocean floor by divers to a platform at the sea surface, where the material can be collected for disposal on land (Meux 2013).

However, the effectiveness of this approach in controlling *S. horneri* on temperate rocky reefs and how the efficiency of this method compares to non-mechanical techniques require further investigation.

To inform efforts to manage the spread and impact of *S. horneri*, we removed it from experimental areas and followed colonization and survivorship for one year to address three questions. First, how effective is local removal in controlling populations of *S. horneri*? Second, what is the capacity of the species to regenerate from remnant holdfasts? Third, how much effort is required to remove established populations with and without the aid of an underwater suction device?

Methods

This study was performed on the leeward side of Santa Catalina Island, California, USA on two nearby reefs (Howland Landing: 33.465°N; 118.522°W and Lion Head: 33.453°N; 118.502°W) at 6–8 m depth (Figure 1). We chose these locations because they are representative of the topography of reefs in the area, and have dense populations of *S. horneri*.

Removal experiment

To evaluate the effectiveness of *S. horneri* extraction in reducing local populations, we performed a removal experiment and monitored colonization and survivorship of the next generation. We established twenty-eight 60 m² circular plots in areas where *S. horneri* was abundant and assigned plots alternately to either a removal or non-removal (i.e., control) treatment (Figure 1). Fourteen plots were located 15–20 m apart at each of the two study sites.

We extracted *S. horneri* from removal plots in the winter (February 2015) when individuals were at their largest size and lowest densities, but before the vast majority (i.e., 99%) of them became fertile so as to minimize the source of *S. horneri* propagules within the removal plots. Immediately prior to removal we counted the number of *S. horneri* adults (defined as > 5 cm tall) in sixteen 0.25 m² quadrats plot⁻¹ that were placed within each plot at 0, 1, 2 and 3 m from the edge along two perpendicular diameters. To prevent mature thalli from drifting away and starting distant populations, we captured all material removed and transported it to boats anchored at the surface. On deck, workers immediately transferred material into heavy-duty trash bags. We later emptied these bags at an upland location where we left the algae to decompose.

We removed all *S. horneri* from the substrate manually and employed one of two methods to transport it to the surface: mesh bags and lines, or an underwater suction device. The bag and line method involved divers placing *S. horneri* into weighed bags (Figure 2A). Once filled, buoyant bags were released from their weights and attached to lines hanging off the side of the boat (Figure 2B) and a worker at the surface hauled them onboard. The suction device consisted of a mechanical water pump (Subaru PTX201D Robin Pump) with 7.6 cm-diameter input and output hoses that is operated on the deck of the boat (Figure 2C). Divers fed material into the hose at depth and it was transported to the surface by the movement of a diaphragm (Figure 2D). Regardless of the method used, most individuals were completely removed from the substrate (Figure 2E). However, the holdfasts of some individuals remained after their stipes were severed.

Removal plots were resampled immediately after clearing to confirm all thalli had been removed and to quantify the density of remnant holdfasts. In September 2015, we

measured colonization by counting the number of juveniles (defined as < 5 cm tall) in all plots. In February 2016, one year after experimental removals, we counted the number of adults in each plot to assess the effects of removal on population density. Because *S. horneri* grows on rock and the percent cover of rock was consistently high but slightly variable (mean $\pm$ SE = $97.9 \pm 0.19\%$) we adjusted estimates of density within each quadrat by the percent cover of rock in that quadrat. Hence *S. horneri* is reported as number m⁻² of rock rather than number m⁻² of sea floor.

We tested the effects of removal on colonization (i.e., juvenile density in September 2015) and population density (i.e., adult density in February 2016) in separate two-way hierarchical ANOVAs with treatment (removal versus control) as a fixed factor and site (Howland Landing versus Lion Head) as a random factor and plots nested within sites. We considered plots independent replicates of treatment effects in cases when the random effect of site was not significant.

Fate of individuals with severed stipes

To determine whether severing a *S. horneri* stipe near its base while leaving the holdfast intact is sufficient to prevent it from regenerating, we followed the fate of individuals after cutting their stipes in March 2015. We attached identifying markers to the reef adjacent to 80 holdfasts and revisited the marked individuals monthly for four months to record whether they remained attached to the substrate and, if so, whether they regenerated new tissue. We also collected observations of the remnant holdfasts in the plots we cleared. Although we were not able to follow these holdfasts individually, we looked for perennating holdfasts when resampling the plots.

Efficiency of removal

We evaluated the efficiency of removal with and without the aid of the suction device (Figure 2) by quantifying the effort required for each method for a given quantity of *S. horneri* biomass. We did this by recording the removal method being used (i.e., suction device or bags and lines), time spent collecting, number of workers (i.e., scuba divers and surface support person) and amount of biomass removed for each dive. To estimate the biomass removed, we collected the algae into bags as soon as it was brought to the surface and weighed it to the nearest 0.5 kg using a hanging scale. In addition, we measured the rate of transport to the surface using the suction device across a range of stipe lengths to determine if size affected performance. We fed 30 pieces of several stipe lengths that are often naturally observed (30 cm, 60 cm, 100 cm and 150 cm) into the hose and recorded the time it took to bring them up to the surface.

Results

Removal experiment

The density of adult *S. horneri* prior to experimental removal in February 2015 was similar in removal and control plots ($F_{1,1} = 0.98$, $p = 0.504$) averaging 46.4 and 50.4 individuals m^{-2} , respectively (Figure 3A). Adult density differed significantly between the two sites ($F_{1,420} = 26.95$, $p < 0.001$) with density ~55% higher at Howland Landing. Quadrat sampling and visual surveys of entire plots verified that experimental clearing resulted in the removal of virtually all visible thalli in removal plots, but some holdfasts with severed stipes

remained. The density of remnant holdfasts immediately after clearing was 46.1% of the initial adult population (mean $\pm$ SE = $22.3 \pm 2.9 \text{ m}^{-2}$).

Similarly high densities of recently colonized juveniles were observed in all plots in September 2015, ~7 months after clearing (Figure 3B; $F_{1,420} = 0.08$, $p = 0.775$). Removal had a significant effect on subsequent colonization ($F_{1,26} = 12.95$, $p = 0.001$) as juvenile density was 54% lower in removal plots compared to control plots. The effects of removal of *S. horneri* on colonization by juveniles was similar at both sites (treatment $\times$ site: $F_{1,1} = 0.236$, $p = 0.125$).

The reduced densities in removal versus control plots persisted but became less pronounced over time as juveniles grew into adults (Figure 3C). By February 2016, one year after clearing, adult densities averaged 25% lower in removal plots compared to control plots. However, overall adult densities were 83% higher in removal plots and 115% higher in control plots compared to February 2015 prior to removal (Figure 3A versus 3C).

Fate of individuals with severed stipes

Significant tag loss resulted in reduced and unequal sample sizes for estimating survivorship on the different sampling dates, which compromised our ability to quantitatively evaluate the regenerative capacity of individuals with severed stipes. Nonetheless, the data that we collected indicate that *S. horneri* has little or no capacity for regenerating from remnant holdfasts as none of the individuals with severed stipes that remained tagged generated new tissue. Fifty-six of the 80 tags remained after 31 days and remnants of holdfasts were found for only 20 of these 56 individuals. Remnants of 10 of 14, 4 of 9 and 0 of 8 holdfasts remained after 54, 85 and 113 days, respectively (Figure 4). Furthermore,

when we sampled the removal experiment in September 2015, we found no remnant holdfasts, which suggests they had all senesced and disappeared within seven months.

Efficiency of removal

The efficiency of removing *S. horneri* varied by the method used to transport it to the surface and the number of workers. Three workers using the bag and line transport method yielded the slowest average removal rate of $29 \text{ kg worker}^{-1} \text{ hr}^{-1}$, while the suction device method with three workers (two divers and one surface support person) yielded an average of $38 \text{ kg worker}^{-1} \text{ hr}^{-1}$ (Figure 5). Limits on the amount of material that can be fed into the hose at any given time resulted in two divers being the optimum number to maximize the transport of algae to the surface. By contrast, the manual transportation method using bags and lines allowed for more divers to work efficiently in the same area. While the overall rate of removal using bags and lines increased with the number of workers, the maximum per capita efficiency was about $45 \text{ kg worker}^{-1} \text{ hr}^{-1}$ (Figure 5). The rate of transport using the suction device was highest at intermediate stipe lengths ($\sim 60 \text{ cm}$; Figure 6).

Discussion

Our results show that the experimental removal of *S. horneri* reduced the local population in the next generation by $\sim 25\%$ relative to control plots. However, despite this reduction, removing *S. horneri* did not lead to a decline in population density relative to the previous year as adult densities in both the removal and control plots were substantially greater in 2016 than in 2015 prior to removal. These results highlight some of the challenges associated with efforts to reduce established populations of *S. horneri* via removal.

Moreover, they suggest that measurable success using removal techniques as a means of controlling *S. horneri* will likely require that removals be done over much larger areas to ensure an adequate reduction in propagule supply, which will be costly. The effect of removing *S. horneri* on its abundance in subsequent generations (as measured by the difference in *S. horneri* density between control and removal plots in the year following removal) was most apparent during the fall when the majority of individuals were juveniles, and became less pronounced in the winter when most were adults. The order of magnitude higher densities that we observed for juveniles compared to adults is consistent with self-thinning induced by intra-specific competition, which is common in large brown algae (Schiel and Choat 1980; Schiel 1985; Dean et al. 1989; Reed 1990). The dampened effect of removal between the juvenile and adult phases suggests removal accelerated the self-thinning process.

The increased density of *S. horneri* that we observed in our removal and control plots may have been due to the unusually warm water resulting from the 2015–16 El Niño. The native canopy-forming kelps *Macrocystis pyrifera* and *Eisenia arboria* commonly found on shallow reefs of Santa Catalina Island thrive in cool, nutrient-rich water. These species largely disappeared from the leeward side of the island during our study while *S. horneri* flourished, as did other species with warm water affinities (e.g., *Zonaria farlowii*, *Dictyota* spp. and *Dictyopteris undulata*). Evidence from the nonindigenous congener *Sargassum muticum*, which became abundant at Santa Catalina Island for several years following the El Niño of 1976 (Coyer 1979), suggests that *Sargassum* spp. with warm-water affinities decline once cooler waters return and large, perennial native kelps become re-established (Ambrose and Nelson 1982) Whether *S. horneri* declines over time remains to be seen, but if the

warming observed in 2015–16 is a preview of future conditions, then tropicalization of an algal assemblage that favors *S. horneri* may be the norm.

The efficacy of removing invasive algae could be strengthened by selecting conditions under which native species can exert biotic control on the remaining population, or even by enhancing these controls. Researchers in Hawaii attributed their success in controlling invasive *Eucheuma* spp. and *Kappaphycus* spp. on patch reefs to introducing urchins after performing removals (Conklin and Smith 2005). Once divers reduced the algae below a critical threshold, the herbivores were able to prevent it from growing back. While this is an effective strategy on coral reefs where indiscriminant grazing is acceptable, introducing generalist herbivores is not a viable strategy to control invasive algae on temperate rocky reefs, which are often dominated by a diversity of macroalgae.

An alternative strategy to enhance biological resistance to the regrowth of invasive algae on rocky reefs is to perform removals under conditions favoring the colonization of native species of macro-algae and sessile invertebrates that compete for space and/or light. Resource competition is recognized as an important mechanism structuring communities (MacArthur 1970; Levine and D'Antonio 1999; Tilman 2004), and competition for space and light plays a key role in organizing the benthic community on rocky reefs (Miller and Etter 2008; Arkema et al. 2009). The invasion of a community is thought to be inversely related to species richness due to the enhanced ability of resident species to preempt resources (Elton 1958), and manipulative field experiments have shown that decreasing native diversity increases limited resources and the abundance and survivorship of non-native species in subtidal benthic communities. For example, Stachowicz et al. (2002) found that experimentally increasing sessile invertebrate species richness decreased both the availability

of space, the limiting resource in this system, and the abundance of non-indigenous ascidians by buffering against temporal fluctuations in the cover of individual native species. Furthermore, multiple resources might be limiting the success of a non-native species throughout its life cycle, and higher functional diversity may allow a community to preempt multiple resources more effectively. A native algal community with crustose and turfing algae preempting space and understory and canopy-forming algae preempting light sequentially suppressed the recruitment and survivorship of the nonindigenous seaweed *Sargassum muticum* (Britton-Simmons 2006). The preemption of limited resources by native species of algae and invertebrates in areas where *S. horneri* has been removed could likewise limit *S. horneri*'s ability to re-establish.

Another important factor to consider when controlling invasive algae through removal is the mechanisms by which it recolonizes cleared areas. Many species of invasive algae have the ability to regenerate from miniscule amounts of tissue (e.g., Fletcher and Fletcher 1975; McCook and Chapman 1992) and this characteristic presents a challenge when considering control via removal (Smith 2015). We found no evidence that *S. horneri* has the capacity to regenerate from remnant holdfasts. This suggests that severing stipes, which is far less time consuming than carefully scraping all tissue from the reef, would be an effective and efficient means of reducing *S. horneri* abundance.

Whether an underwater suction device, such as the one tested in this study, would be the preferred method for invasive algae control depends on staff and budget limitations. The bag and lines method is optimal when many workers (i.e., > two divers and one surface support worker) are available. It also requires minimal training and material costs, and so may be preferred with constrictive budgets. A suction device minimizes surface support

effort, particularly associated with lifting heavy bags, and offers increased efficiency with a limited number of workers (< 3 divers). Drawbacks of using a suction device include increased start-up costs, logistical challenges associated with equipment transportation and maintenance, and limitations on working depths. In addition, significant time can be spent troubleshooting, such as identifying appropriately sized pieces of algae to reduce the frequency of clogs. However, removal efficiency is likely to improve as operators become more familiar with the device and alter equipment to better suit the target species. Workers in Hawaii designed several models using different kinds of pumps until they identified the optimal configuration for their target species (Conklin personal communication). Therefore, long-term efficiency gains may make a suction device preferable if an extended control effort is expected.

Eradicating problematic species from their novel habitats is most likely to be successful if attempted before they become widely established (Myers et al. 2000; Bax et al. 2003; Hulme 2006). *Caulerpa taxifolia*, a green alga native to the Indo-Pacific region, was introduced in two protected embayments in southern California in 2000 and a rapid response effort successfully eradicated this species (Anderson 2005). The appearance of *S. horneri* off the open coast of North America is the first record of this species outside of its native range in Asia (Marks et al. 2015). While the aggressive spread of *S. horneri* throughout southern California and Baja California, Mexico makes total eradication in this region highly unlikely, *S. horneri* has the potential to spread to other temperate reefs around the globe. Knowledge about the life history and effective methods for controlling *S. horneri* abundance will prepare resource managers in other regions to eradicate new populations before they become widely established. Our study is one of the first on targeted control of an invasive species on the

open coast of California. Development of a removal protocol along with awareness generated by this work will better prepare resource managers and the general public for future invasions of *S. horneri* in other regions.

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Figures

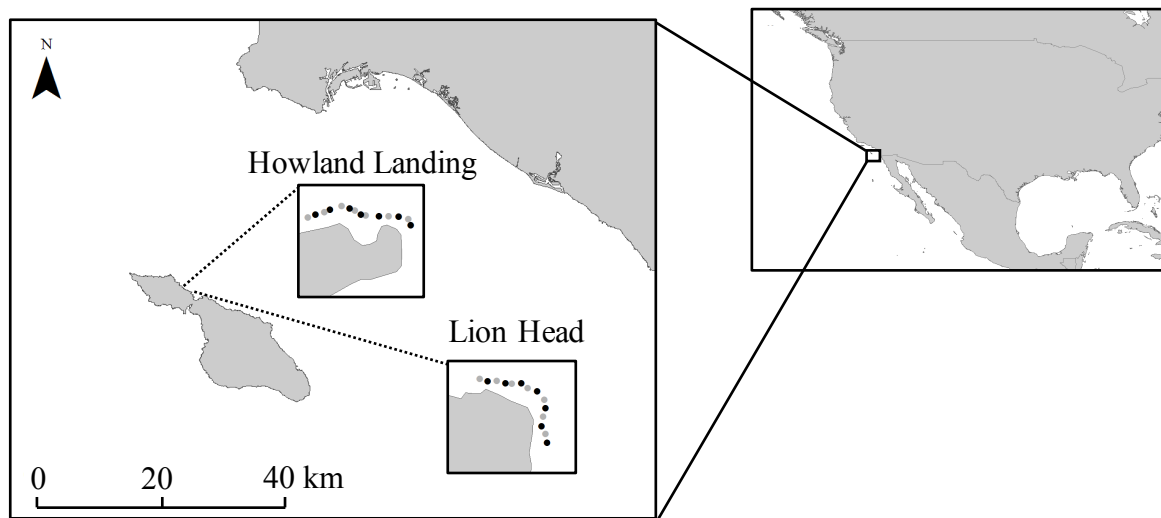


Figure 1. Map of Santa Catalina Island, located 27 km off the coast of southern California, USA. The insets show the distribution of 28 experimental plots spread across two sites: Howland Landing and Lion Head. Dark circles represent removal plots, and grey circles represent control plots.

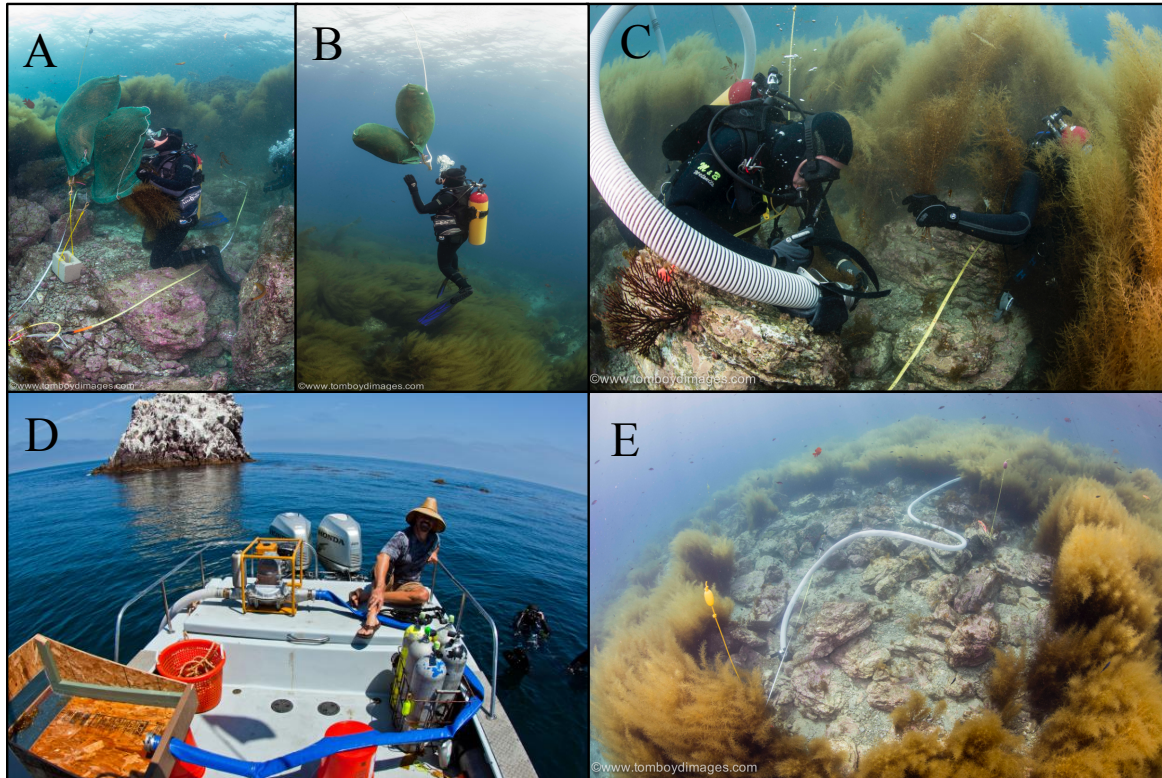


Figure 2. Two methods used to transport *Sargassum horneri* to the surface. Using the bag and line method, a diver fills bags anchored by a cinderblock (A), then clips bags to a line hanging from a boat anchored overhead (B). Using the suction device method, two divers work together to feed *S. horneri* into the hose (C), and a person at the surface collects the material from a sorting table after inspecting it for bycatch (D). After clearing using both methods, plots were left barren of *S. horneri* (E). Photo credits: Tom Boyd (A-C, E), Adam Obaza (D).

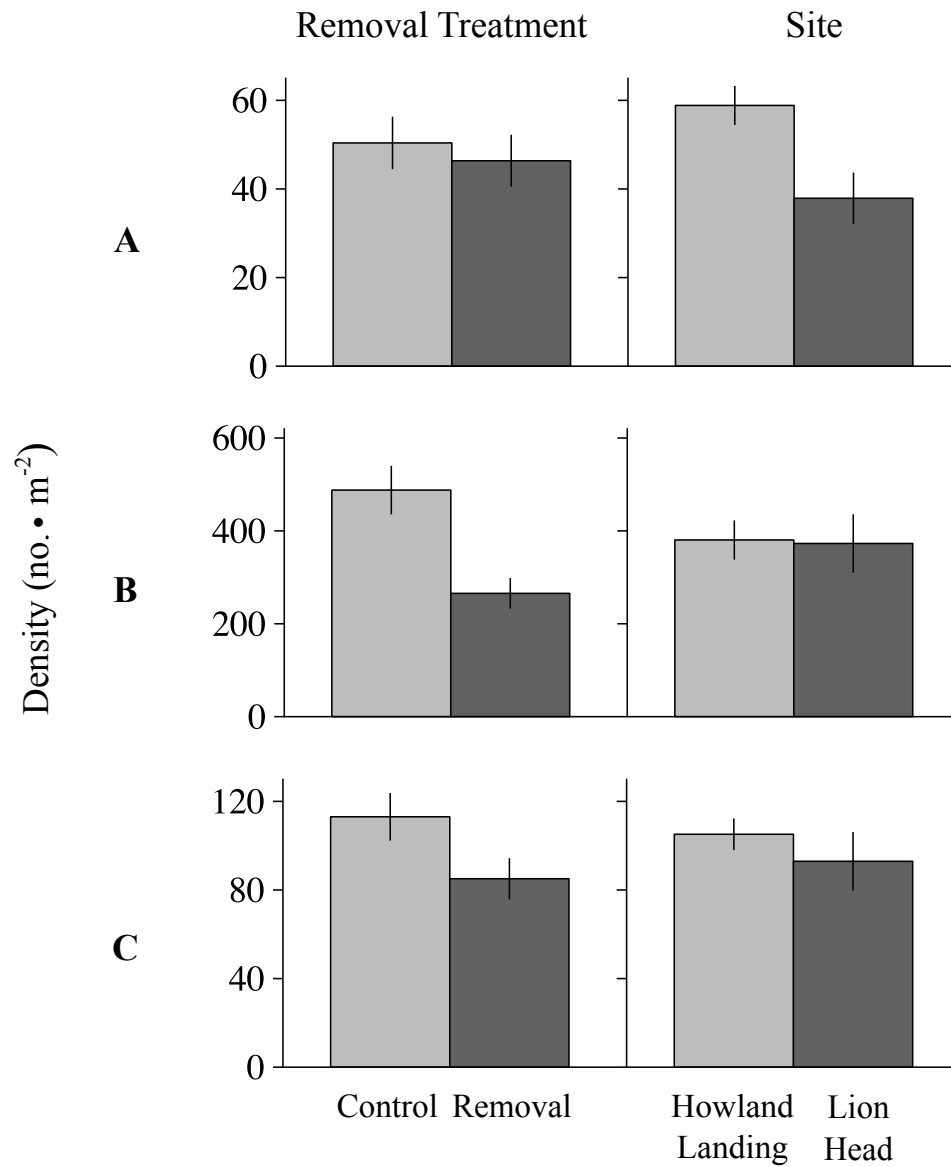


Figure 3. Results of removal experiment showing the average density $\pm$ SE of *Sargassum horneri* (A) adults prior to their removal, (B) juveniles ~220 days after removal, and (C) adults ~366 days after removal (N = 14 plots).

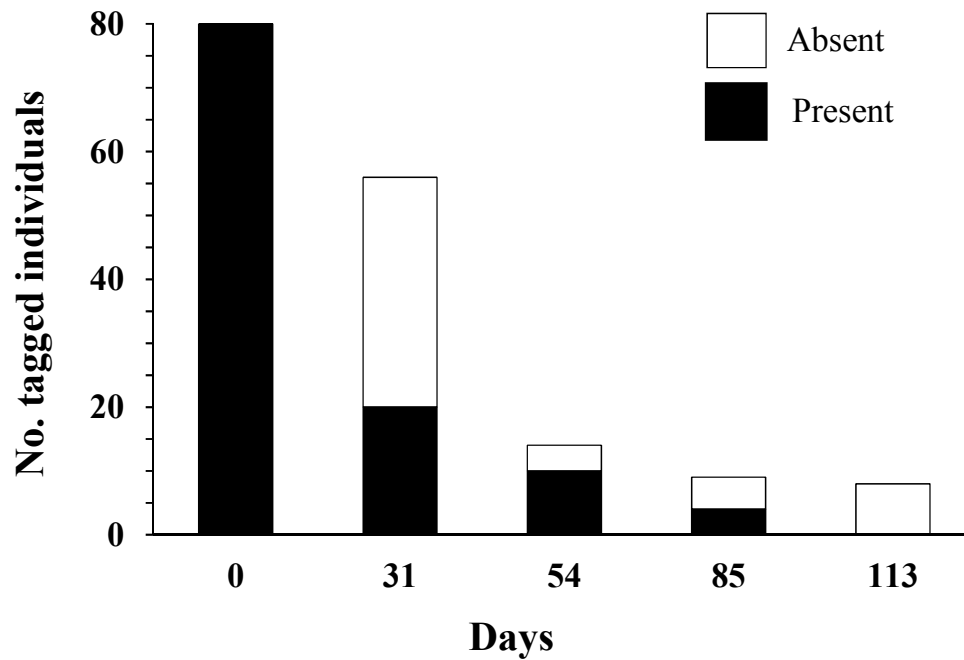


Figure 4. Survivorship of *Sargassum horneri* with severed stipes. Solid bars represent the number of thalli with remnant tissue remaining. Open bars represent the number of tags relocated where holdfasts had senesced. Combined, the bars represent the total number of tags found, and the number of individuals upon which survivorship was based for each sampling period.

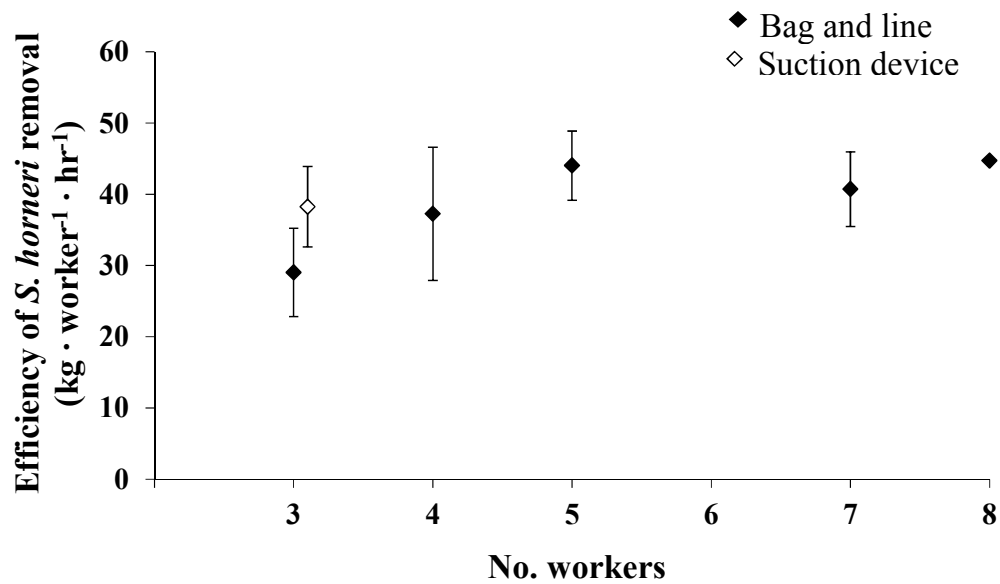


Figure 5. *Sargassum horneri* average removal rate (kg wet biomass worker⁻¹ hr⁻¹) ± SE reported for each removal method. Replication varies by the number of dives with each given number of workers using each method. N = 15 dives with 3 workers using the suction device, and N = 6, 4, 6, 6 and 1 dives with 3, 4, 5, 6, and 8 workers using the bag and line removal method, respectively.

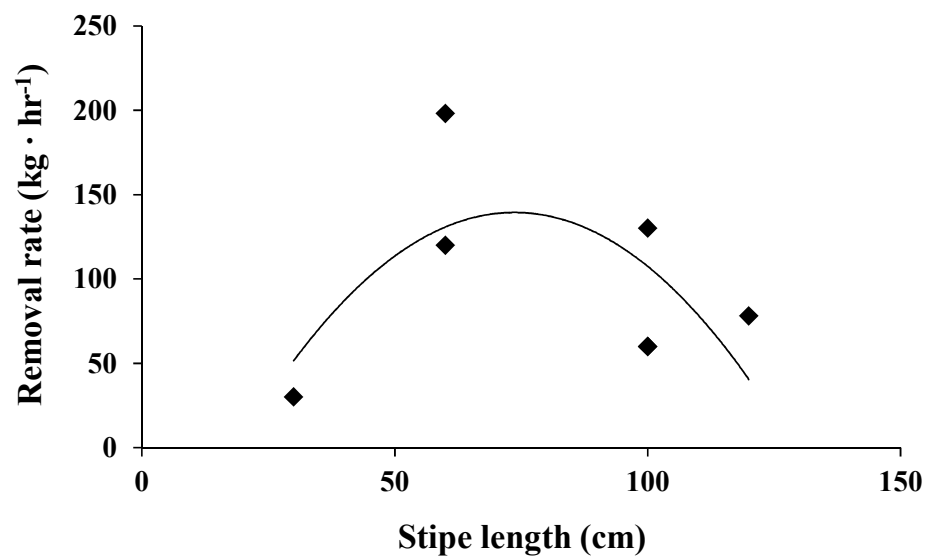


Figure 6. The rate (kg wet biomass hr⁻¹) at which stipes of *Sargassum horneri* were transported by workers using the suction device as a function of stipe length.

Appendix E: Electronic Supplements S1-S4

The following supplementary material is available for this article:

Table S1. Recruitment and survivorship of *Sargassum horneri* following removal

Table S2. Survivorship of *Sargassum horneri* with severed stipes

Table S3. Per capita removal rate of *Sargassum horneri*

Table S4. Transport rate of *Sargassum horneri* using suction device

This material is available online for download from the Long Term Ecological Research

Network Data Portal, <http://dx.doi.org/10.6073/pasta/a812d149f4d6e9cd5662d4c44eaedd22>

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