

Research Article

Life history traits of the invasive seaweed *Sargassum horneri* at Santa Catalina Island, California

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Abstract

The recent spread of the Asian seaweed, *Sargassum horneri* (Turner) C. Agardh, 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 to quantify traits that promote 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 seasonal patterns 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 to interact 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 an invasive as a non-native species introduced by humans, either intentionally or unintentionally, 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), these species can be 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 to a 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 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 are also 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 marine 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 habitats (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 broad depth range (Maggs and Stegenga 1999; Boudouresque and Verlaque 2002; Nyberg and Wallentinus 2005; South et al. 2017).

The spread of the Asian seaweed *Sargassum horneri* (Turner) C. Agardh 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). *Sargassum 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. The more widespread variant of *S. horneri* in Asia is dioecious, but 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 borne 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 substrate. Lateral branches form, followed by a single stipe that grows vertically from the holdfast prior to reproductive maturity (Sawada 1956; Yoshida 1983). Senescence follows reproduction (Terawaki 1986; Yoshida et al. 1998), completing the annual life cycle.

The *S. filicinum* variant of *S. horneri* 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). The seasonality of growth and reproduction is largely unknown, limited to a few samples collected in Japan that suggest that 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 and the potential ecological impacts of its invasion on native communities, and to develop strategies for management.

In this paper, we characterize features of the life history of the *S. filicinum* variant of *S. horneri* that contribute to its invasion success in southern California and Mexico. 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 to the extent and speed of its spread. We described 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 been well established since 2006 (Marks et al. 2015). We also evaluated its capacity for local dispersal and observed its depth range and the types of substrates occupied by different stages of its life history. Our intent is to provide a comprehensive account of the life history of this highly successful invader to guide the management of its spread.

Methods

Study Site

This study was conducted along the western portion of the leeward side of Santa Catalina Island, located off the coast of southern California, USA (Figure 1). Shallow subtidal reefs that support dense stands of *Sargassum horneri* are composed of a mixture of bedrock, boulders, cobble and sand, and extend from the intertidal to depths of 6 to 30 m where they transition to sandy bottom. Sampling was done at sites spanning 13 km of coastline between Pumpernickel Cove (33.447916; -118.479017) and the western end of the island (33.479200; -118.605733), including

many locations where *S. horneri* had previously been reported (Miller and Engle 2009).

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 relationships to convert these measurements to units of biomass.

Surveys of *S. horneri* were conducted with 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*. One transect was sampled per site, and 31 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).

Each *S. horneri* plant counted was assigned to one of five different life stage categories based on its development (Yoshida et al. 2004). Recruits were defined as ≤ 5 cm in height (Figure 2A), while all other stages (immature, fertile, senescent) were > 5 cm tall (Figure 2B–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 dark brown embryos were visible on the surface of receptacles, and “unripe” if embryos were not detected. Senescent thalli were those decaying after receptacles had been spent. Because recruits grow broader while all other life stages grow taller, we used thallus diameter as the size metric for estimating the mass of a recruit and stipe length for estimating the mass of all other stages.

We developed size to biomass relationships for each life stage (Table 1) 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 spun 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

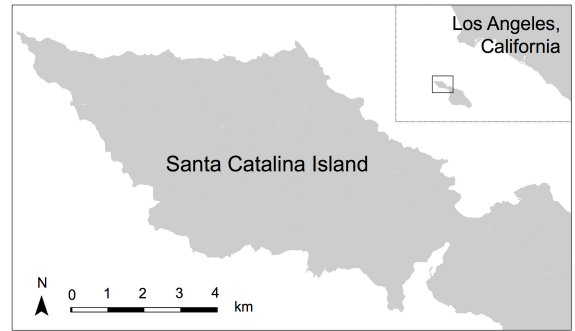


Figure 1. Map showing the study region on the leeward side of Santa Catalina Island, California, USA.

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 (see methods described below in *Habitat Affinities*).

Density and biomass data were summarized for each life stage individually and for all stages combined. Average density and biomass 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 (N = 31 for each season and year). One-way ANOVAs (in R, R Core Team 2017) were conducted to assess the effect of season on the density and biomass of *S. horneri*. Visual inspection of model residuals revealed deviations from normality, so we used Box-Cox transformations (Box and Cox 1964) to achieve normality of residuals. Post hoc contrasts between seasons were tested for significance with a Tukey HSD test using the *multcomp* package (Hothorn et al. 2008).

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 can change throughout a life cycle.

The depth distribution of *S. horneri* was assessed by recording its density within 1 m² quadrats placed uniformly along a transect running perpendicular to shore from the intertidal to 30 m depth or where the reef transitioned to sand, whichever came first. One transect was sampled per site, and the length of each transect ranged from 40–94 m depending upon the



Figure 2. Life stages of *Sargassum horneri*. (A) Recruit (height ≤ 5 cm), (B) Immature (height > 5 cm lacking receptacles), (C) Fertile unripe adult (receptacles present, indicated by arrow, but embryos 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 (B), Lindsay Marks (C–E).

Table 1. Regression coefficients 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 |

slope of the reef. These depths span the range within which most native species of macroalgae occur at Santa Catalina Island. The depth distributions of recruits and adults were characterized during different seasons to capture their peak abundance (eight sites were sampled for recruits in June 2012 and four sites were sampled for adults in April 2016). Measured densities were adjusted to the percent cover of hard bottom estimated within each quadrat. Measured depths were adjusted relative to Mean Lower Low Water (MLLW), and quadrats were assigned to depth intervals of 5 m ($N = 1-3$ quadrats per interval per site). We investigated the effect of depth on the density of *S. horneri* recruits and adults in separate mixed model ANOVAs (lmer function in *lme4* package for R, R Core Team 2017) using depth interval as fixed and site as random factors. Assumptions of homoscedasticity and normality were assessed through visual interpretation of the residuals, and recruit density data were log-transformed to meet model assumptions. Contrasts between depths were tested for significance with a Tukey HSD posthoc test (Hothorn et al. 2008).

We used data collected on recruit and fertile adult abundance during the seasonal surveys of the 31 sites to examine whether colonization and survivorship to reproductive maturity were disproportionately associated with particular types of bottom substrate.

During each survey we recorded the type of substrate to which each *S. horneri* plant in the 1 m² quadrats was attached ($N = 8$ quadrats per site). 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 diameter). The occurrence of recruits and adults on the different substrate types was compared to the availability of each substrate type, which we measured as percent cover in each quadrat using 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% cover.

The degree to which *S. horneri* was disproportionately associated with the five substrate types was evaluated separately for recruits and fertile adults using Manly's Alpha of selectivity (Chesson 1978, 1983):

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

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), $\alpha_i - 1/m > 0$ indicates higher

abundance and $\alpha_i - 1/m < 0$ indicates lower abundance relative to the availability of a given substrate. Manly's Alpha was calculated using the aggregate sum of all *S. horneri* and cover of substrate types within all quadrats. Analyses involving recruits were restricted to data collected during summer (June) while those involving reproductive adults were based on data collected in spring (April), which were the seasons of highest abundance for recruits and reproductive adults, respectively (see Results).

Reproductive Characteristics

We characterized the fecundity of *S. horneri* based on its reproductive allocation (RA), defined as the ratio of the biomass of reproductive vs. non-reproductive tissue (Mathieson and Guo 1992). During our sampling to develop size to biomass relationships, receptacles were separated from the thallus for all life stages possessing them: ripe and unripe fertile adults, and senescent individuals (N = 26, 31 and 28, respectively). For each thallus, RA was calculated as: (receptacle damp biomass / [total damp biomass – receptacle damp biomass]). Differences in RA among life stages were analyzed using a one-way ANOVA on log-transformed RA values. Visual inspection of model residuals revealed homoscedasticity and no deviations from normality.

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 to estimate the maximum dispersal distance of embryos from nearby

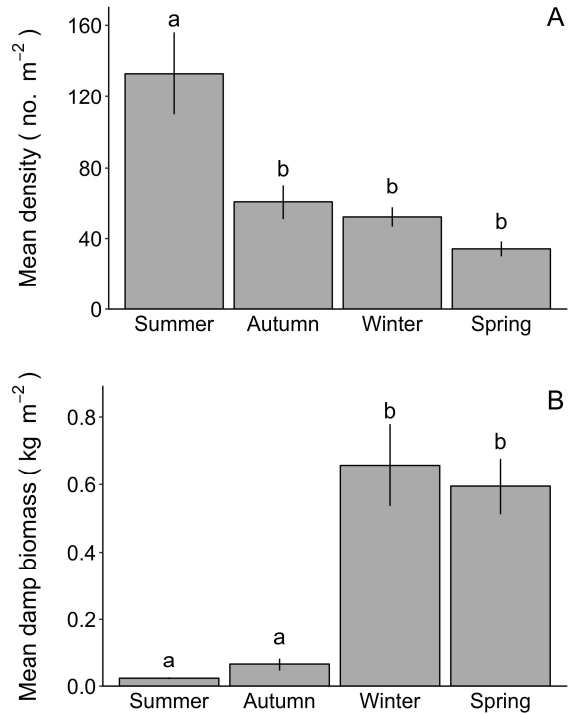


Figure 3. The mean (\pm SE) density (A) and biomass (B) of *Sargassum horneri* at Santa Catalina Island. Means are averaged over all sites surveyed within each season. N = 31 sites. Lower-case letters differentiate statistically significant differences between factors (Tukey pairwise comparison, $p < 0.05$).

naturally-occurring reproductive plants. Several possible models (including linear and non-linear) were assessed by performing a regression of recruit density on distance to reproductive plants for each plot to identify which was the best fit to the data. The linear model had the lowest Akaike Information Criterion (AIC_C) score of all those we examined (Supplementary material Table S1), so we estimated maximum dispersal distances by calculating the x-intercept from individual linear models fit to each plot (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

The mean density and biomass of *S. horneri* averaged over the 31 sites showed strong but opposite seasonal patterns (Figure 3; density: $F_{3,120} = 7.17$, $p < 0.0001$; biomass: $F_{3,120} = 74.70$, $p < 0.0001$). During the summer when density was highest (125 individuals m⁻²),

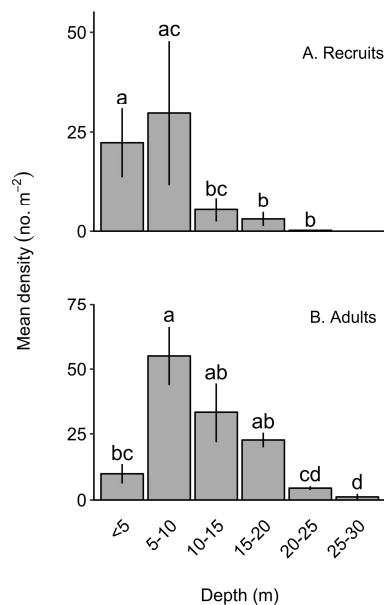
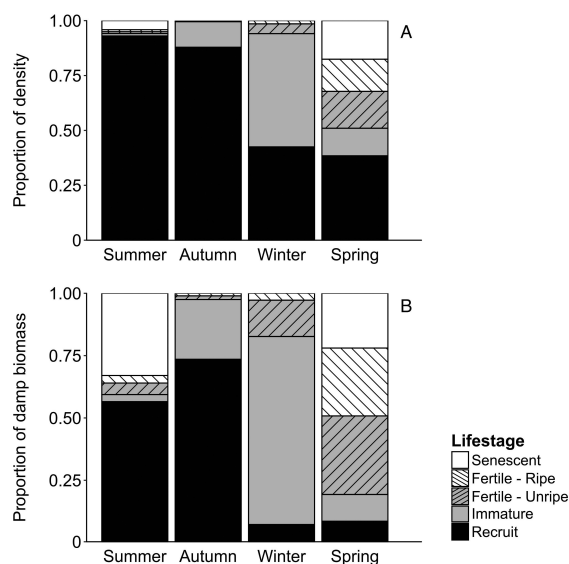


Figure 4. The mean proportion of the total density (A) and biomass (B) of *Sargassum horneri* accounted for by each life stage in each season. Means are averaged over all sites surveyed within each season. N = 31 sites.

biomass was negligible ($< 50 \text{ g m}^{-2}$ damp weight). In autumn, density was reduced by half, but biomass approximately doubled. In the winter, density declined slightly but biomass peaked at $\sim 600 \text{ g m}^{-2}$. Density continued to decline in the spring, while biomass remained high at $\sim 500 \text{ g m}^{-2}$.

The decline in density observed from summer through spring (Figure 3A) was driven by self-thinning as a cohort matured, while the dramatic increase in biomass between autumn and winter (Figure 3B) 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 (Figure 4A). 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 4B). 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 a low proportion (0.023) of the plants were in the immature or mature stages.

The remaining senescent individuals comprised $\sim 30\%$ of the biomass. We found that individuals of

Figure 5. 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. Lower-case letters differentiate statistically significant difference between factors (Tukey pairwise comparison, $p < 0.05$).

any size could reach maturity, including a few precocious individuals only 3 cm tall (Figure S1).

Habitat Affinities

Sargassum horneri occurred across the range of depths sampled, from the low intertidal to 30 m depth (Figure 5) and density varied significantly with depth for both recruits ($F_{5,25} = 5.07$, $p = 0.002$) and adults ($F_{5,15} = 15.04$, $p < 0.0001$). Peak densities of recruits in June and adults in April were highest between 5 and 10 m and declined with depth. Recruits were abundant in very shallow areas ($< 5 \text{ m}$) whereas adults were not. All life stages were rare below 20 m depth.

Sargassum horneri recruits and fertile adults 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 6). Recruits were also less common on bedrock and large boulders than expected, while adults occurred on these substrate types in proportion to their availability.

Reproductive Characteristics

Reproductive allocation (RA) varied significantly among the three life stages that possess receptacles ($F_{2,82} = 45.77$, $p < 0.0001$). Fertile individuals with ripe receptacles allocated a majority of their biomass

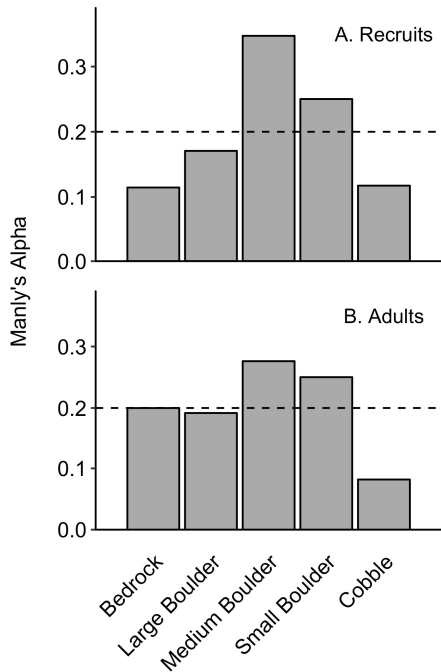


Figure 6. Occurrence of *Sargassum horneri* across substrate types relative to their availability as indicated by Manly's Alpha of selectivity for (A) recruits in June 2013, 2014 and 2015 and (B) fertile adults in April 2014 and 2015. The dashed line represents occurrence on a habitat proportional to its availability, with values $\gg 0.2$ indicating higher occurrence on a substrate type and values $\ll 0.2$ indicating a lower occurrence. See text for definitions of substrate types. $N = 744$ and 488 quadrats for recruits and adults, respectively.

to reproduction and had a mean RA of 1.2. By comparison, receptacles contributed to a much smaller proportion of the biomass in fertile individuals with unripe receptacles (RA = 0.4) and senescent individuals (RA = 0.3).

We found that the density of newly settled recruits declined rapidly 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). Maximum dispersal distances estimated using linear models ranged from 3 m to 9 m except for two plots, which 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 an introduced species determine whether it will become invasive; its ability to rapidly colonize, reproduce and persist through multiple generations in a novel location will favor its spread. Highly invasive species may share

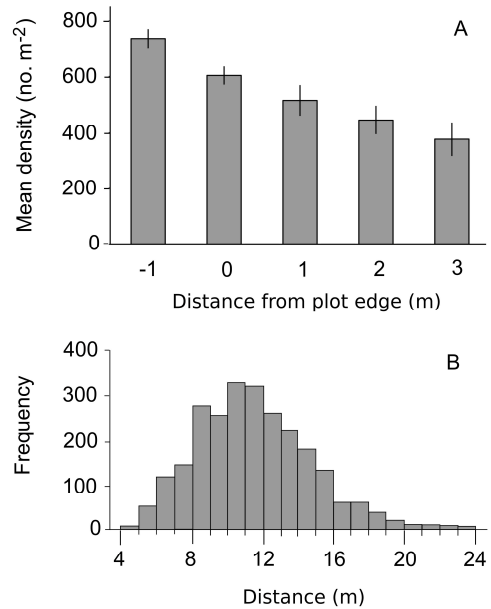


Figure 7. Dispersal of *Sargassum horneri* propagules into experimentally cleared circular plots ($N = 14$ plots). (A) Mean (\pm SE) density of *S. horneri* recruits on blocks within cleared plots at distances of 0–3 m from the plot edge and within a stand of reproductive adults 1 m outside the plot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

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 the importance of such traits for invasive marine algae is less well known. We found that *S. horneri* occurred at high densities across a broad habitat range, invested in copious reproduction, and demonstrated local dispersal that resulted in dense colonization. Many of these traits are consistent with those found for other invasive marine algae (Nyberg and Wallentinus 2005), as well as many invasive plants on land (Pyšek and Richardson 2007), and help explain the rapid population growth observed in *S. horneri* in southern California and Mexico since its discovery in 2003.

Life history traits are recognized as an important component of invasion success in plants. For example, an early, late, or extended flowering period relative to native species can enhance reproductive fitness in novel environments and promote invasion success (Crawley et al. 1996; Pyšek and Richardson 2007). As with other species, the ecological significance of the seasonality of biomass and reproduction of *S. horneri*, both in terms of facilitating its spread and dictating its impacts, is likely to depend on the seasonality of native algae competing for limiting resources such as light and attachment space in this system. In southern California, most of the dominant

native species of macroalgae are perennial, but their biomass fluctuates seasonally with their maxima occurring in the summer and autumn (Reed et al. 2009; Harrer et al. 2013; Marks 2018). Such seasonal fluctuations in biomass are near opposite of what we found for *S. horneri*, which peaked in winter in spring. The invasion of the annual Asian kelp *Undaria pinnatifida* on Australian reefs requires gaps in perennial canopies of native species in order for it to become established (Valentine and Johnson 2003, 2004; Edgar et al. 2004; South et al. 2017), and greater abundance of understory algae has been associated with reduced prevalence of *S. horneri* in the invaded range (Caselle et al. 2018). The offset seasonality in the biomass of the perennial assemblage should help facilitate the colonization and growth of *S. horneri* by increasing the availability of resources (e.g., light and space) when they are most needed.

Variation in oceanic conditions could alter the phenology of invasive algae. For example, *Undaria pinnatifida* has only one pulse of reproduction in its native Japan (Morita et al. 2003), but can have biannual cohorts of recruits in southern California (Thornber et al. 2004) and New Zealand (Schiel and Thompson 2012). Shifts of *U. pinnatifida* in New Zealand from a strictly annual species to one with overlapping generations (e.g., Hay and Villouta 1993; Schiel and Thompson 2012; James et al. 2015) is thought to be due to a smaller, more favorable temperature range (South et al. 2017). It is worth noting that our research coincided with a prolonged period of anomalously warm water that extended from 2014 to 2016 (Reed et al. 2016) and the three-year duration of our study did not allow us to investigate the degree to which the seasonality of *S. horneri*'s life history traits are influenced by interannual variability in oceanographic conditions. Observations of *S. horneri* during cooler years from elsewhere in the invaded region indicate the seasonal cycle that we documented for *S. horneri* is consistent under a range of environmental conditions (Miller and Engle 2009; Cruz-Trejo et al. 2015; Kaplanis et al. 2016; Caselle et al. 2018). However, more detailed multi-year comparisons involving sites that span a wide latitudinal gradient are needed to provide greater insight into the role of environmental variation in altering seasonality in the life history of *S. horneri*.

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). *Sargassum horneri* may serve a similar role during winter and spring in the kelp forests of southern California because 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). It also has the potential to outcompete native macroalgae for limited resources in the same manner as an invasive congener, *Sargassum muticum*, which limits the growth of native kelp through shading by its canopy (e.g., Britton-Simmons 2004). However, a potentially important distinction between *S. horneri* and *S. muticum* is that *S. muticum* is pseudo-perennial, in that it regenerates from remnant holdfasts after its reproductive stipes senesce, while *S. horneri* has an obligate annual life cycle that is incapable of regenerating from remnant holdfasts (Marks et al. 2017). Hence, any competitive impacts of *S. horneri* may be temporary; the ephemeral presence of *S. horneri* could allow native perennial species to reclaim vacated space following its senescent phase. Nevertheless, rapid growth to a large size and the suppression of native species 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 (down to 30 m). However, recruitment was highest at depths < 10 m while densities of adults peaked in the 5–10 m depth range. These patterns suggest recruits take advantage of high irradiance and disturbed substrates in shallow water. As individuals grow tall, however, 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 canopy-forming species span the entire range as *S. horneri* does. Because our results on the depth distributions of recruits and adults were derived from data collected in different years, it is possible this pattern also reflects differences in oceanic conditions. 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* was able to colonize and survive on all types of consolidated

hard substrate. However, it was more likely to recruit and reach maturity on small to medium boulders, while smaller cobble was a less frequent substrate for both recruits and adults. Recruits were also less common on bedrock and large boulders, but adults were found on these substrate types in proportion to their availability. The higher than predicted occurrence of *S. horneri* recruits on 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. We found that *S. horneri* can reach reproductive maturity independent of size, and allocates > 60% of its biomass to reproductive structures during the period of peak fertility. This value is within the upper range of other furoid 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). Like its invasive congener, *S. muticum*, the *S. filicinum* 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 furoids (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 to hundreds of square meters in size. High fecundity coupled with a short dispersal distance could enable *S. horneri* to persist in patches through multiple generations. Studies of *S. muticum* showed that embryos sink rapidly to

the bottom when shed from receptacles (Norton and Fetter 1981) and most disperse less 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. 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 (Marks et al. 2015).

Sargassum horneri possesses life history traits that likely contribute to its spread and persistence in California and Mexico. We found that traits related to habitat affinity and reproduction were consistent with 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 promote the 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 in the context of the invaded community. Information presented here, paired with knowledge of the life histories of resident species are essential for understanding potential interactions with *S. horneri* and generating hypotheses that may be tested with experiments. Additional comparative and experimental studies will further our understanding of how invader traits and environmental factors interact to promote marine invasions. This information will be critical for developing best practices for managing marine invasive species by identifying the most effective times and places to target for control or mitigation of their impacts.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. The mean and inter-quartile range of the heights of all fertile (i.e., ripe and unripe) *Sargassum horneri* individuals sampled at all sites (N = 31) during the entire study period (June 2013–June 2015) shown by season.

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.

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 $x = -\alpha / \beta$.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Marks_etal_Figure_S1.pdf

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Marks_etal_SupplementaryTables.xlsx

Data are available online for download from the Long Term Ecological Research Network Data Portal, <https://doi.org/10.6073/pasta/d684a982c9154fbcc70805ad360534d9>