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Research Article

Assessment of control methods for the invasive seaweed *Sargassum horneri* in California, USA

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Editor's note:

This study was first presented at the 9th International Conference on Marine Bioinvasions held in Sydney, Australia, January 19–21, 2016 (http://www.marinebioinvasions.info/previous-conferences). Since their inception in 1999, ICMB series have provided a venue for the exchange of information on various aspects of biological invasions in marine ecosystems, including ecological research, education, management and policies tackling marine bioinvasions.

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 m^2 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 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 m^2 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, totalling 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: 33.465ºN; 118.522ºW and Lion Head: 33.453ºN; 118.502ºW) 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*.

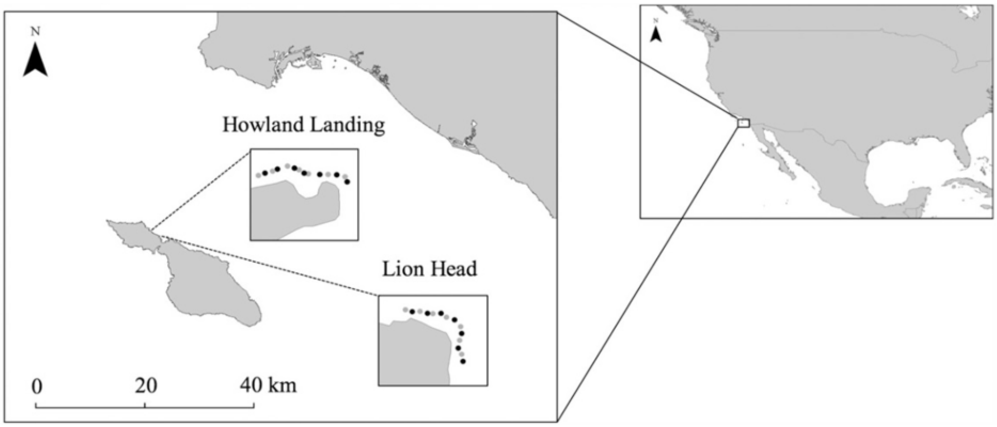

Figure 1. Map of Santa Catalina Island, located 27 km off the coast of southern California, USA. The insets show the distribution of 28 experimental plots spread across two sites: Howland Landing and Lion Head. Dark circles represent removal plots, and grey circles represent control plots.

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 m^2 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 m^2 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 ± SE = 97.9 ± 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 *S. horneri* 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 ± SE = 22.3 ± 2.9 m^{-2}).

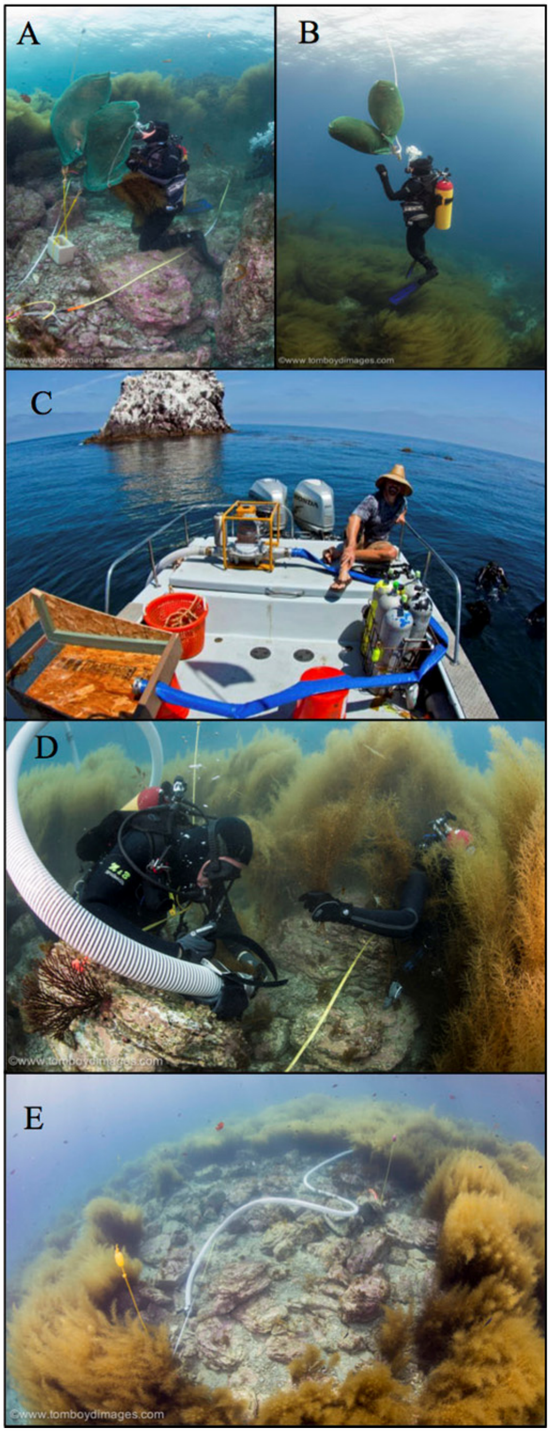

Figure 2. Two methods used to transport *Sargassum horneri* to the surface. Using the bag and line method, a diver fills bags anchored by a cinderblock (A), then clips bags to a line hanging from a boat anchored overhead (B). Using the suction device method, two divers work together to feed *S. horneri* 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-B, D-E), Adam Obaza (C).

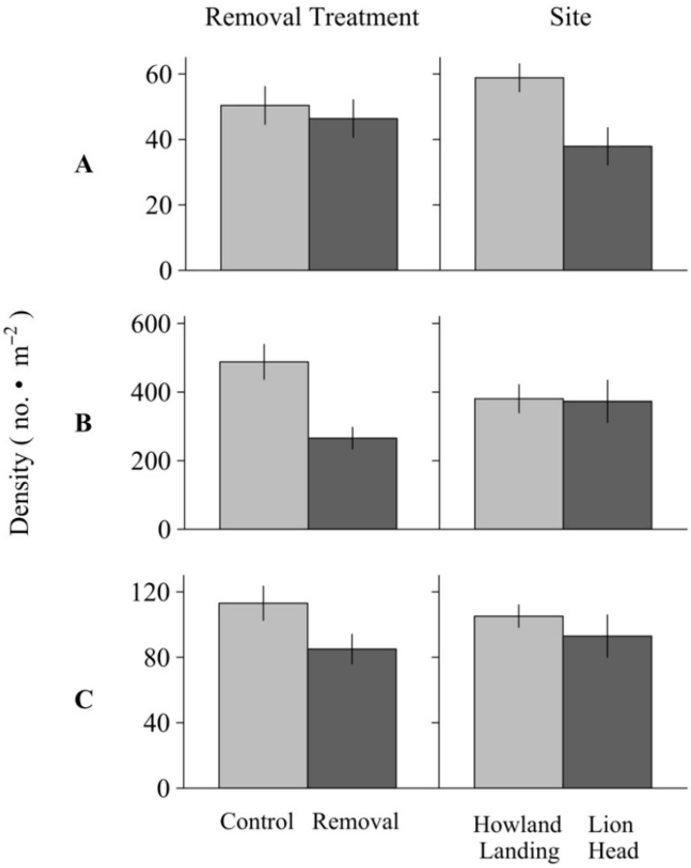

Figure 3. Results of removal experiment showing the average density ± SE of *Sargassum horneri* (A) adults prior to their removal, (B) juveniles ~220 days after removal, and (C) adults ~366 days after removal (N = 14 plots).

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 effect of removing *S. horneri* on colonization by juveniles was similar at both sites (treatment x 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 kg worker^{-1} hr^{-1}, while the suction device method with three workers (two divers and one surface support person) yielded an average of 38 kg worker^{-1} 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 kg worker^{-1} hr^{-1} (Figure 5). The rate of transport using the suction device was highest at intermediate stipe lengths (~60 cm; Figure 6).

Discussion

Our results show that the experimental removal of *S. horneri* reduced the local population in the next generation by ~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.,

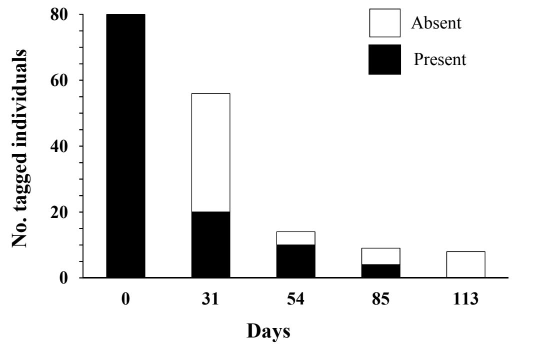

Figure 4. Survivorship of *Sargassum horneri* with severed stipes. Solid bars represent the number of thalli with remnant tissue remaining. Open bars represent the number of tags relocated where holdfasts had senesced. Combined, the bars represent the total number of tags found, and the number of individuals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

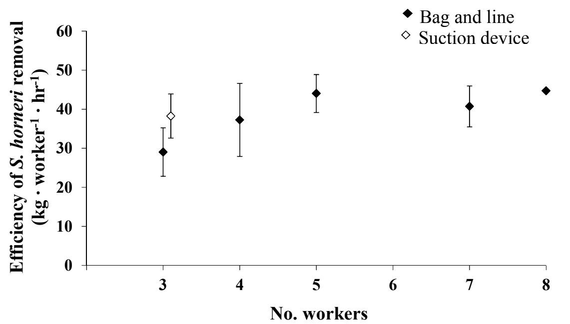

Figure 5. *Sargassum horneri* average removal rate (kg wet biomass worker^{-1} hr^{-1}) ± SE reported for each removal method. Replication varies by the number of dives with each given number of workers using each method. N = 15 dives with 3 workers using the suction device, and N = 6, 4, 6, 6 and 1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

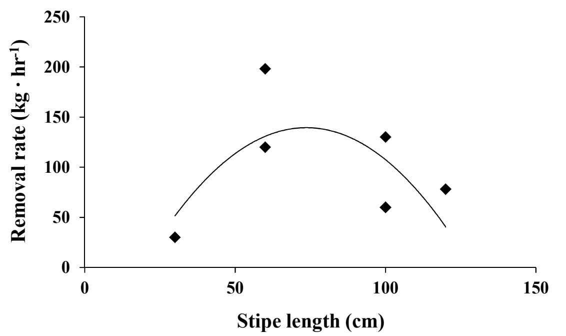

Figure 6. The rate (kg wet biomass hr^{-1}) at which stipes of *Sargassum horneri* were transported by workers using the suction device as a function of stipe length.

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 macroalgae 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 nonindigenous 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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Supplemental material

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