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Rapid Communication

Range expansion of a non-native, invasive macroalga *Sargassum horneri* (Turner) C. Agardh, 1820 in the eastern Pacific

Lindsay M. Marks[1,2]*, Paulina Salinas-Ruiz[2], Daniel C. Reed[2], Sally J. Holbrook[1,2], Carolynn S. Culver[2,3], John M. Engle[2], David J. Kushner[4], Jennifer E. Caselle[2], Jan Freiwald[5], Jonathan P. Williams[6], Jayson R. Smith[7], Luis E. Aguilar-Rosas[8] and Nikolas J. Kaplanis[9]

[1]*Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93106-6150, USA*

[2]*Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93106-6150, USA*

[3]*California Sea Grant, Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Drive, La Jolla, California 92093-0232, USA*

[4]*Channel Islands National Park, 1901 Spinnaker Drive, Ventura, California 93001, USA*

[5]*Reef Check Foundation, 13723 Fiji Way, B-2, Marina del Rey, California 90292, USA*

[6]*Moore Laboratory of Zoology, Occidental College, Los Angeles, California 90041, USA*

[7]*Department of Biological Sciences, California State Polytechnic University, Pomona, California 91768, USA*

[8]*Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Carr. Transpeninsular Ensenada-Tijuana, 3917. Frac. Playitas, Ensenada, Baja California, México. C.P. 22860*

[9]*Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Drive, La Jolla, California 92093-0202, USA*

**Corresponding author*

E-mail: marks@lifesci.ucsb.edu

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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 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

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).

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 citizen scientists, 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, government and academic groups and trained citizen scientists monitoring subtidal and intertidal reefs in California and Baja California (Supplementary material 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 (Supplemental material 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 m^{-2} and recruit densities > 1000 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% 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 fucoid 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

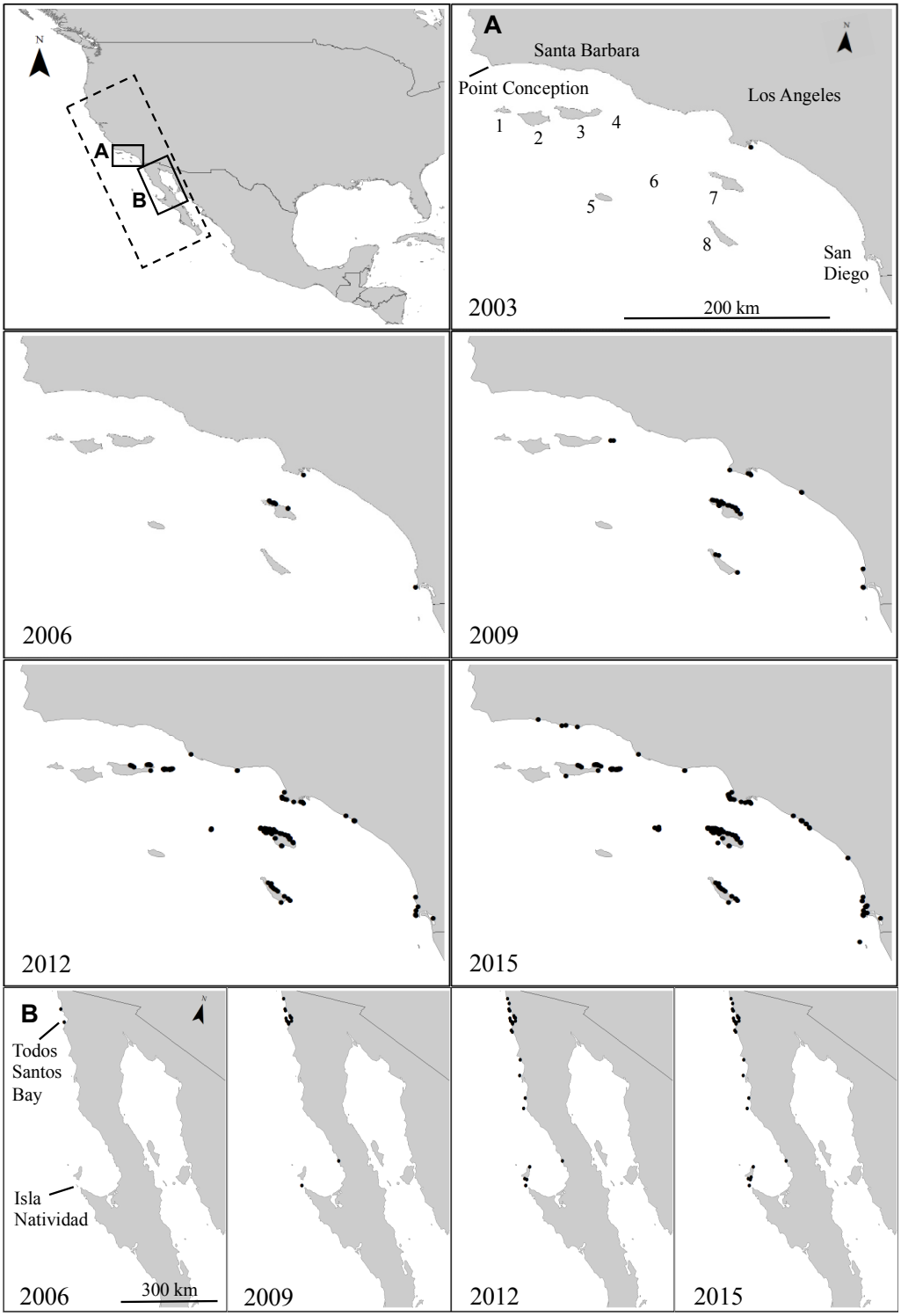

Figure 2. Chronology of geographic expansion of *S. horneri* in the southern California, USA (A) and Baja California, México (B) regions. Each dot identifies a location where *S. horneri* was found attached to the substrate at least once. Each map includes observations from all previous years to display 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 Nicolas, 6. Santa Barbara, 7. Santa Catalina, 8. San Clemente. The entire study area is outlined by the dashed line. Maps were created by P. Carlson.

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 fucoid 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.

Continued monitoring of *S. horneri* distribution is essential to identify environmental factors influencing its spread and prioritize management actions. Researchers and citizen scientists can contribute to this effort by reporting observations of *S. horneri* occurrence to an online database and map designed to help track its spread (Marine Invasive Species Tracking website 2015).

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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Supplementary material

The following supplementary material is available for this article:

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 download from Long Term Ecological Research Network Data Portal (see Marks et al. 2015, http://dx.doi.org/10.6073/pasta/63012c4e436214239ebed11ee57cbe03)