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Authors

Kaplanis, Nikolas John
Harris, Jill
Smith, Jennifer

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Research Article

Distribution patterns of the non-native seaweeds *Sargassum horneri* (Turner) C. Agardh and *Undaria pinnatifida* (Harvey) Suringar on the San Diego and Pacific coast of North America

Nikolas John Kaplanis*, Jill L. Harris and Jennifer E. Smith
Scripps Institution of Oceanography, University of California, San Diego, USA
*Corresponding author
E-mail: nikokaplanis@gmail.com

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Abstract

Here we report the occurrence of the two non-native brown macroalgal species *Sargassum horneri* (Turner) C. Agardh and *Undaria pinnatifida* (Harvey) Suringar in San Diego County and describe expansions in their ranges and new invasions on the California and Baja California coasts. Both species have exhibited characteristics of successful invaders: establishing in new areas, spreading locally, and persisting through multiple generations in areas that have been invaded. These species now occur primarily in harbors, but have also invaded open coast sites, suggesting that they can invade areas with relatively high wave action and with well-established native benthic communities. The rapid and uncontrolled spread of these species to date has serious implications for their expansion along the west coast of North America. The ecological and economic consequences of these invasions require further research.

Key words: invasive algae, macroalgae, California, Channel Islands, Cabrillo National Monument

Introduction

Marine algal invasions have become a pervasive problem. Diverse impacts include reductions in biodiversity and the abundance and performance of native species as well as changes in community structure and function (Walker and Kendrick 1998; Thresher 2000; Inderjit et al. 2006; Schaffelke et al. 2006; Valentine et al. 2007). Marine algal invasions can also threaten economically important species and industries such as aquaculture and tourism (Schaffelke et al. 2006). However, relatively few studies have comprehensively analyzed these invasions or addressed their effects (Nyberg and Wallentinus 2005; Inderjit et al. 2006; Schaffelke et al. 2006; Johnson and Chapman 2007; Schaffelke and Hewitt 2007; Valentine et al. 2007; Smith 2011). As a result, many gaps exist in our current knowledge of how specific non-native seaweeds affect indigenous ecosystems and the economies that depend on them.

Despite the fact that hundreds of species of non-native seaweeds have been documented around the world, research to date has largely focused on a small fraction of these species and a limited number of invasion locations, or has simply documented occurrence without analyzing patterns of distribution or change over time (Inderjit et al. 2006; Johnson and Chapman 2007; Williams and Smith 2007). Consequently, very little is known about the natural history of non-native algal species in their invaded environments and their interactions with recipient environments, both important elements known to influence invasion success (Valentine et al. 2007). Studies that document species-and-region-specific patterns of establishment, spread, and persistence are a crucial first step in closing major gaps in our knowledge of the invasion process. Further, because invasions often proceed rapidly it is important to gain a better understanding of how new invaders spread in the early stages of establishment.

Southern California and the surrounding coastline have received multiple high-profile invasive algal species, but little information is available about the invasion dynamics of these taxa. A recent review by Miller et al. (2011) reports 27 non-native seaweed species in California and 11 in Baja California, 9 of which are common to both areas. Most of these have been discovered in the last 30 years, and while the rate of introductions may not necessarily be increasing, climate change may increase the establishment of non-native species in Southern California and Baja California (Carlton 2000; Harley et al. 2006; Miller et al. 2011). This area has been invaded by some of the most high profile algal invaders in the world. *Caulerpa taxifolia* (M.Vahl) C.Agardh was first detected in two locations in Southern California in 2000 but was contained and successfully eradicated by 2006 (Jousson et al. 2000; Anderson 2005; Smith 2011). Other successful invaders include *Undaria pinnatifida* (Harvey) Suringar, first noted in 2000 (Silva et al. 2002), the globally invasive alga *Sargassum muticum* (Yendo) Fensholt, which was first noted in the 1970's and which has since become naturalized in this area (Norton 1981; Miller et al. 2007), and *Sargassum horneri* (Turner) C.Agardh, first noted in 2003 (Miller et al. 2007). Despite the long invasion history of this area, the dynamics and ecology of the non-native seaweeds in this region remain relatively unexplored.

Undaria pinnatifida is an aggressive invader worldwide, having colonized Argentina, New Zealand, Australia, Atlantic Europe, and the Mediterranean Sea (Silva et al. 2002; Nyberg and Wallentinus 2005). Its alarming rate of spread and ability to occupy and alter a variety of native systems have made this species one of only two algae on the International Union for the Conservation of Nature (IUCN) list of 100 most invasive species on the planet (Lowe et al. 2000). *Undaria pinnatifida* exhibits opportunistic life history traits that contribute to its successful establishment in new areas: a short, annual life span (Schaffelke et al. 2005; Miller and Engle 2009), high growth rate and fecundity, (Schaffelke et al. 2005; Valentine et al. 2007), and both a small and large dispersal shadow (Forrest et al. 2000). Serious negative ecosystem effects of this species - including reductions in native seaweed diversity- have been documented in shallow coastal communities elsewhere (Casas et al. 2004; Farrell and Fletcher 2006; Schaffelke and Hewitt 2007; Williams and Smith 2007). Because of the lack of knowledge of *U. pinnatifida* on the Pacific coast of North America and the potential for significant impacts of its further spread, we document the current distribution of this species in this region in the early stages of invasion.

In the early 20th century, *Sargassum muticum* was introduced to North America from northeast Asia and quickly spread throughout the west coast, reaching southern California in the early 1970's (Miller et al. 2007). This species is a highly successful invader worldwide and is considered to be naturalized in intertidal and subtidal communities throughout southern California (Harries et al. 2007; Miller et al. 2007). Some of the ecological effects of this species, such as reduction of native algal abundance and inhibition of native kelp recruitment have been assessed in Washington, California, and Baja California (Norton 1977; Ambrose and Nelson 1982; Espinoza 1990; Aguilar-Rosas and Machado Galindo 1990; Britton-Simmons 2004). Yet despite its widespread presence in southern California, there have been few studies examining the effects of this naturalized species in this area (Deysher and Norton 1982; Miller et al. 2011) or its current distribution.

Sargassum horneri was first discovered in Long Beach Harbor in 2003 (Miller et al. 2007), the first instance of this species outside of its native range (Miller et al. 2007). *Sargassum horneri* is one of the most abundant members of the algal community in temperate areas of Japan and Korea (Choi et al. 2003; Pang et al. 2009). This alga is an ecosystem engineer in these areas, growing up to 5 m tall in dense forests that provide habitat and spawning grounds for a diverse assemblage of organisms (Choi et al. 2003; Choi et al. 2008). *Sargassum horneri* is known for its high reproductive capacity, ability to rapidly colonize new areas, and fast growth rate (3–5 m in 10 months) (Choi et al. 2003). Due to its life history characteristics and its rapid spread in the short time frame since its original introduction, *S. horneri* is recognized as having the potential to be highly invasive in Southern California, Baja California, and other areas along the west coast of North America (Nyberg and Wallentinus 2005; Miller et al. 2011). Despite the rapid invasion of *S. horneri*, little is known about its current distribution and ecological impacts in southern California and Baja California.

The goal of this study was to provide detailed information on the distribution of *S. horneri* and *U. pinnatifida* on the San Diego County coast, and to analyze patterns of establishment, spread, and persistence of these seaweeds along the California and Baja California coasts. Specifically, our first goal was to describe the distribution of these non-native algae in San Diego County. Second, we documented how the presence of these species has changed with regard to: the number of locations they have become established; spread of populations within invaded sites; and persistence of populations. Third, we compared invasion locations to ascertain whether certain habitats appear to be more invasion prone than others. Finally we assess the occurrence of these species in San Diego County within the context of the invasion of the broader California and Baja California coastlines.

Methods

We used three approaches to describe the distribution, abundance, and invasion patterns of non-native macroalgae in San Diego and the broader region: broad-scale qualitative presence/absence surveys; smaller-scale quantitative benthic community surveys; and a synthesis of published and unpublished literature.

Site selection

Thirty-two sites (10s of m in extent) in eight locations (1–10 km apart, Figure 1) in San Diego County were assessed (n=1–7 sites per location, depending on availability of suitable habitat within each location). Surveys were initially conducted in January 2012 at Mariner's Cove, Mission Bay, where the first population of *S. horneri* was discovered. Four additional sites with rip-rap substrate similar to Mariner's Cove were surveyed between February and July 2013 (Supplementary material Table S1). In July 2013, permanent sites for qualitative and quantitative surveys were established. These sites were located between Oceanside Harbor and San Diego Bay. All sites were then surveyed during summer 2013 (23 July 2013 – 7 August 2013), winter 2013 (8 December 2013 – 20 December 2013), and summer 2014 (2 July 2014 – 1 August 2014).

Survey locations were grouped into three site types based on site characteristics: harbors (n=3), open coast jetties (n=2), and natural open coast locations (n=3). Harbor locations included San Diego's three main harbors: Oceanside Harbor, Mission Bay, and San Diego Bay. The two open coast jetties, Ponto Jetty and Del Mar Rivermouth were located between Oceanside Harbor and Mission Bay. Open coast locations were La Jolla Cove in the Matlahuayl State Marine Reserve, Bird Rock in the South La Jolla State Marine Reserve, and the Cabrillo National Monument State Marine Reserve. Because it is an area of special ecological and management interest, Cabrillo National Monument was surveyed five times: fall 2013 (20 October 2013) and spring 2014 (2 April 2014) and the three survey rounds listed above.

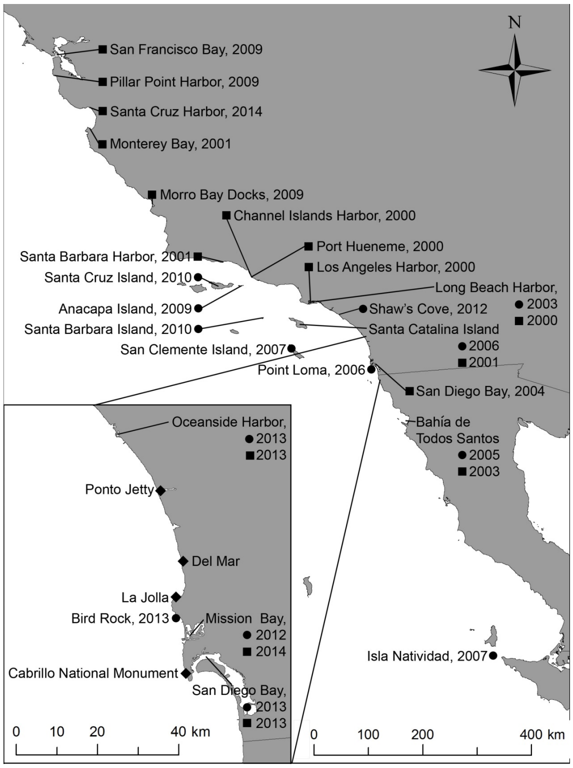

Figure 1. Map of locations where the non-native algae: *S. horneri* (circles) and *U. pinnatifida* (squares) have been documented; diamonds indicate locations where no non-native seaweeds were documented. The larger map presents results from our literature review and from herbarium collections while the inset map presents results from our survey of San Diego County. The year where each species was first documented is also shown for each location.

Within each of the eight locations, survey sites were established on hard bottom substrate suitable for the growth of macroalgae. Harbor and jetty sites were established on rip-rap rock that typically terminated in sand at maximum depths of 5 m. For open coast locations, survey sites were chosen from a habitat map generated in ArcGIS with LIDAR data. Fifteen stratified random coordinates in each open coast location were generated then ground-truthed for suitability (hard substrate, depths from 0–5m). From these, three points in each location were randomly selected as survey sites.

Qualitative surveys

Rapid qualitative surveys were conducted at 32 sites across all eight locations (Table S1) to note the establishment of populations at new sites and to describe how established populations were

Table 1. Summary information from presence-absence surveys with estimated peak abundance (# stipes / site) of non-native brown macroalgae at survey sites for all sampling rounds (Winter / Summer 2012–2014). Sites that were not sampled are shown with "ns", white indicates absence of non-native macroalgae, light grey indicates *S. horneri* was found, dark grey indicates *U. pinnatifida* was found, and black indicates both species were found concurrently. Categorical abundances are shown as follows: absent (-); 1–10 stipes (+); 11–100 stipes (++); 101–1000 stipes (+++); >1000 stipes (++++).

Location	Site	Winter 2012	Spring 2013	Summer 2013	Winter 2013	Summer 2014	*S. horneri*	*U. pinnatifida*
Oceanside Harbor	Oceanside Harbor North	ns	ns				-	+
	Oceanside Harbor, Marker 6	ns					-	++
	Oceanside Harbor, Marker 4	ns					+	++
	Oceanside Harbor Docks	ns					-	++
Ponto Jetty	Ponto Jetty	ns					-	-
Del Mar	Del Mar Rivermouth	ns					-	-
	9th Street	ns	ns				-	-
	Flat Rock, Torrey Pines	ns	ns				-	-
La Jolla	Dike Rock, Scripps	ns	ns				-	-
	La Jolla Cove East	ns					-	-
	La Jolla Cove West	ns					-	-
	La Jolla Cove Central	ns					-	-
	Boomers Cove	ns	ns				-	-
	Casa Cove	ns	ns				-	-
	Marine Street	ns	ns				-	-
Bird Rock	Bird Rock North	ns	ns				-	-
	Bird Rock Central	ns	ns				++++	-
	Bird Rock South	ns	ns				++++	-
Mission Bay	Mission Point						++++	-
	Hospitality Point	ns	ns				++++	-
	Vacation Island	ns	ns				++++	-
	Quivira Basin	ns	ns				++++	++
San Diego Bay	Harbor Island East	ns	ns			ns	-	+
	Harbor Island Central	ns	ns				-	+
	Harbor Island West	ns					-	-
	Shelter Island North	ns					++++	-
	Shelter Island South	ns	ns				++++	-
	Marina Park, Seaport Village	ns	ns				-	-
	Coronado Ferry Terminal	ns	ns				-	++
Cabrillo Natl. Monument	North Cabrillo	ns	ns				-	-
	Central Cabrillo	ns	ns				-	-
	South Cabrillo	ns	ns				-	-
	# locations where non-native seaweeds found:	1	4	3	10	13	9	8

spreading in spatial extent through time for large swaths of coastline. At each site, we searched for *S. horneri* and *U. pinnatifida* at depths of 0–5 m along as much of the coastline as possible, using SCUBA in some sites to access deeper reefs. Hard bottom substrates in harbors, including harbor breakwalls and jetties, rip-rap, and along docks and dock pilings, were searched. At open coast sites (including jetties), hard bottom substrata was searched, with a special focus on areas of low wave exposure.

Presence-absence and relative abundance (<10, 11–100, 101–1000, >1000 stipes per site) of *S. horneri* and *U. pinnatifida* were recorded. When either of these species was encountered, habitat characteristics (depth, substrate type, exposure to current and waves) and size and reproductive status of the algae also were recorded.

Quantitative surveys

Quantitative surveys were conducted at twenty sites across all eight locations (Table S1) to describe changes in non-native algal density through time and to determine if patterns of density and distribution existed with respect to benthic composition of survey locations. At each site, three 5 m transects were set 5 to 10 m apart, perpendicular to shore from 0–5 m depth. In five 1-m^2 quadrats placed on alternating sides of each transect line, brown macroalgal taxa (> 10 cm tall) were identified to species and the number of stipes was counted. In each quadrat, visual estimates of percentage of substrate covered were also made to the functional group level, which included all abiotic (bare rock, sand, shell), and biotic (articulated coralline algae, crustose coralline algae, fleshy crust, turf algae, brown, green and red fleshy macroalgae, seagrass, and sessile benthic invertebrates) components of the benthic community. Quadrats that contained substrate unsuitable for the growth of macroalgae (100% sand) were removed from the data set so that densities were reported per area of available hard bottom habitat.

Statistical analysis

Our hierarchical sampling scheme was designed to allow comparisons of non-native algal populations at the site, location, and site type (harbor versus open coast) level. To compare densities of native, non-native, and non-native naturalized brown algae (*S. muticum*) among sites, mean site-level stipe densities (# stipes / m^2) were calculated for each site and sampling round. To compare non-native algal abundance between site types, a three-factor analysis of variance (ANOVA) was used with site type and sampling round as fixed effects and location as a random effect nested within site type. Jetties were not included in the comparison among site types due to the low number of jetty sites (n=2). To explore how algae may use space in different habitats, we plotted native versus non-native site-level mean stipe densities for each sampling round.

Benthic cover data from quantitative surveys were examined using principal components analysis (PCA). Scores along the first PC axis were used to examine if densities of native, non-native naturalized or non-native taxa were related to benthic composition across our data set. Statistical analyses were performed using SigmaPlot 13 (Systat Software Inc., San Jose, California, USA) and JMP 12 (SAS Institute Inc., Cary, North Carolina, USA).

Literature review and synthesis

To provide an updated regional distribution for both species, all published and unpublished accounts of *S. horneri* and *U. pinnatifida* on the Pacific coast of North America were gathered from ISI Web of Science and Google Scholar, the University of California Herbarium database (https://webapps.cspace.berkeley.edu/ucjeps/publicsearch/publicsearch/), and personal correspondence with researchers. Web of Science and Google Scholar were searched using the key words: Baja California, California, distribution, invasive algae, *Sargassum horneri*, and *Undaria pinnatifida*. Discovery dates, identifier, location, latitude/longitude, and any depth, habitat and density information were recorded.

Results

San Diego County distribution

Sargassum horneri was found at 28% of the thirty-two sites and *U. pinnatifida* was found at 25% of the sites (Table 1). In all cases, non-native algae were found at sites where they had not previously been documented. Overall, non-native algae occurred in 43.75% of San Diego sites surveyed, and occurred disproportionately in harbor sites, with 86.7% of harbor sites having non-natives present at some point during sampling. These two invaders were found at 13.3% of open coast sites and never found to occur in jetty sites. Both species occurred together at two of San Diego's three harbors, Oceanside Harbor, and Mission Bay. In general, native brown macroalgal species dominated at our survey sites, contributing 56.7 ± 1.94% (mean ± SE) of all macroalgal stipes. The non-native naturalized alga (*S. muticum*) made up 29.1 ± 1.74%, and non-native brown macroalgae made up 14.2 ± 1.31% of stipes. For the individual non-native macroalgal species, *S. horneri* contributed 12.4 ± 1.26%, and *U. pinnatifida* made up 1.8 ± 0.47% of macroalgal stipes across all study sites.

Establishment of new populations in San Diego through time

The number of sites where *S. horneri* was found increased during our study from one to nine sites (Table 1). On 15 January 2012, *S. horneri* was discovered at a single site at Mission Point in Mission Bay. Spring 2013 surveys documented no new populations of *S. horneri,* though a second survey of Mission Point revealed a persistent, dense and localized population. All *S. horneri* populations discovered during our survey effort persisted throughout the duration of the study. During our first comprehensive survey of thirty-two sites (summer 2013), *S. horneri* was found at two new sites, in Bird Rock South, an open coast site in Bird Rock, and on the south end of Shelter Island in San Diego Bay (Table 1). At Bird Rock, juvenile *S. horneri* thalli were found in the 3–5 m depth range on cobble coated in crustose coralline algae. This was the only open coast location to have *S. horneri* throughout our survey. At Shelter Island, *S. horneri* was found growing at depths of 1–5 m along the rip-rap breakwall on the south end of the island near the marina in an area of high boat traffic.

During the winter 2013 survey, *S. horneri* was found at five new sites (Table 1). The species appeared intermingled with native algae in a small patch near the mouth of Oceanside Harbor (Oceanside Harbor North). The previously localized population at Bird Rock South spread to the Bird Rock Central site. *Sargassum horneri* was also found at three new sites in Mission Bay: at Hospitality Point, in the boat marina at Quivira Basin, and on a rip-rap breakwall near the boat ramp at Vacation Island.

During our final comprehensive sampling round, summer 2014, *S. horneri* was found at one new site, Shelter Island North. While in past surveys the species was localized at Shelter Island South, during this final survey it was observed growing along the entire length of the harbor breakwall.

Overall, we found *U. pinnatifida* at eight sites in San Diego County, and the number of sites in which it was present increased through time (Table 1). *Undaria pinnatifida* was first found at three sites in Oceanside Harbor in spring 2013: near the mouth of the harbor on a rip-rap breakwall (Oceanside Harbor, Marker 6), deeper in the harbor on rocks surrounded by soft muddy substrate, (Oceanside Harbor, Marker 4), and attached to the underside of 10–15 docks within the marina (Oceanside Harbor Docks). *Undaria pinnatifida* was not found at any site during the summer 2013 survey, including the Oceanside Harbor sites. During the winter 2013 survey, *U. pinnatifida* was found at the eastern end of Harbor Island and at the Coronado Ferry Terminal. At Harbor Island we found a group of large isolated thalli (approx. 1–2 m length) on a rip-rap breakwall, a cement breakwall, and on pilings. In Coronado, *U. pinnatifida* was observed on the underside of the ferry landing docks. In summer 2014, *U. pinnatifida* reappeared in Oceanside Harbor at the same three sites it was previously found and was found at Quivira Basin in Mission Bay and the central part of Harbor Island.

Spatial spread at sites through time

Within established sites, *S. horneri* consistently increased its spatial extent through time. At Mission Point in Mission Bay, this species was initially confined to a small section of protected rip-rap within Mariner's Cove growing on bare rock in an area sparsely populated by *S. muticum* and the native species *Dictyopteris undulata* Holmes and *Dictyota flabellata* (F.S. Collins) Setchell and N.L. Gardner. Further west on the harbor breakwall, where tidal current flows are much higher, and where native kelps (e.g. *Macrocystis pyrifera* (Linnaeus) C.Agardh, *Egregia menziesii* (Turner) Areschoug, and *Eisenia arborea* (Areschoug) occur in higher density than on the inner breakwall, no *S. horneri* was found. This population remained localized between January 2012 and spring 2013, but in summer 2013 the length of the breakwall occupied by *S. horneri* had expanded by roughly 0.33 km, with new recruits occurring in patches moving outward toward the mouth of Mission Bay. During winter 2013, these recruits developed into mature and fertile adult thalli, which then produced another cohort of recruits approximately 0.6 km further west on the breakwall in summer 2014.

A clear pattern of population expansion with each recruitment cycle was also observed at other sites. At Hospitality Point the population on the inner breakwall spread westward toward the mouth of the harbor with each recruitment cycle. At Shelter Island, the species spread from the south end of the island north, eventually reaching the north end by winter 2013. At Bird Rock, the population was discovered in a small patch at the center of the cove in summer of 2013, but eventually occupied the majority of the cove by winter 2013, again spreading with each recruitment event.

In contrast, *Undaria pinnatifida* occurred in low density populations that remained localized through time. At all sites where it was observed, densities were highest in spring to late summer, following the annual pattern of recruitment and development seen in native populations (Saito 1975) and previously observed in Santa Barbara Harbor (Thornber et al. 2004) and at Santa Catalina Island (Miller and Engle 2009). While other populations die off entirely in the late summer or early fall (Miller and Engle 2009), mature reproductive adults were observed in low densities year round in San Diego locations.

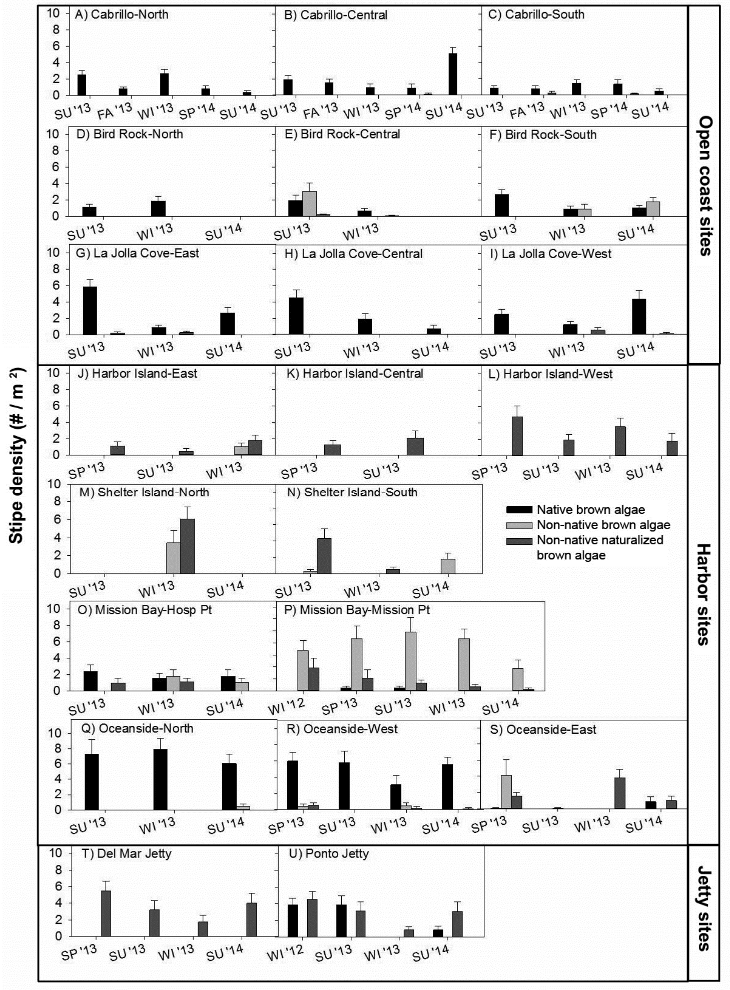

Figure 2. Mean density (± SE) of native (black), non-native (*S. horneri* and *U. pinnatifida,* light grey), and non-native naturalized (*S. muticum,* dark grey) brown macroalgae at quantitative survey sites in San Diego County during each survey round (Winter 2012, Spring 2013, Summer 2013, Fall 2013, Winter 2013, Spring 2014, Summer 2014 (abbreviated in figure)) and grouped by site type.

Changes in density through time

Despite an increase in both the number of sites where *S. horneri* and *U. pinnatifida* were present, and in the spatial extent of their populations, the density at each site did not increase for either species (Figure 2). At Bird Rock central and Bird Rock south (Figure 2E and F), the open coast sites where *S. horneri* was found, populations were patchy and densities were consistently low. Harbor sites had persistent but consistently low density populations of *S. horneri* (Shelter Island North and South, Figure 2M and N, and Hospitality Point, Figure 2O) and *U. pinnatifida* (Harbor Island East, Figure 2J). Finally, at Mission Point (Figure 2P) *S. horneri* densities were consistently higher than any other site, with the mean density ranging between 4.31 ± 1.54 stipes/m^2 (summer 2014) and 10.08 ± 1.53 stipes/m^2 (winter 2013).

Habitat type and benthic composition

Mean stipe densities of non-native species were significantly higher at harbors than at open coast sites (Table 2). Overall mean stipe densities (stipes / m^2 ± SE) for the Summer 2013, Winter 2013, and Summer 2014 survey rounds were 1.03 ± 0.97, 1.91 ± 1.10 and 1.11 ± 0.56 for harbors, and 0.0 ± 0.0, 0.47 ± 0.35, and 0.20 ± 0.20 for open coasts. There was significant variation in density of non-native species among sites within locations and among locations within site type. There were no differences in non-native species densities among sampling rounds, nor was there an interaction between site type and sampling round. Harbor sites exhibited either high native stipe densities or high non-native stipe densities, and no site had high densities of both concurrently (Figure 3). Open coast sites had low densities of non-native species and a range of densities of

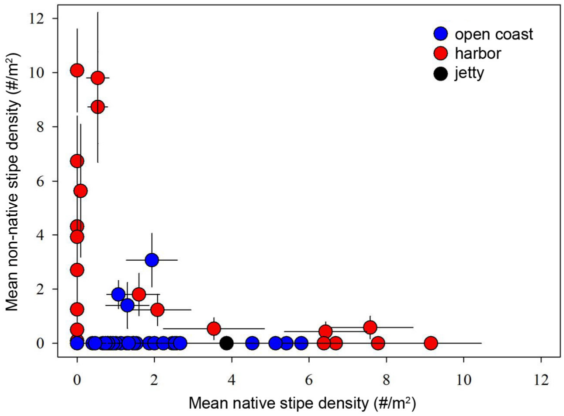

Figure 3. Mean (± SE) native vs. non-native algal stipe density (stipes/m^2) for open coast sites (blue circles), harbor sites (red circles), and jetty sites (black circles).

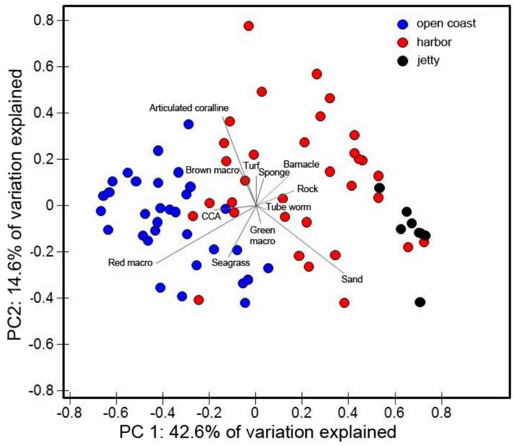

Figure 4. Principal component analysis (PCA) of major benthic groups from all sites with benthic cover survey data (n = 32 (open coast, blue), n = 34 (harbor, red), n= 8 (jetty, black)).

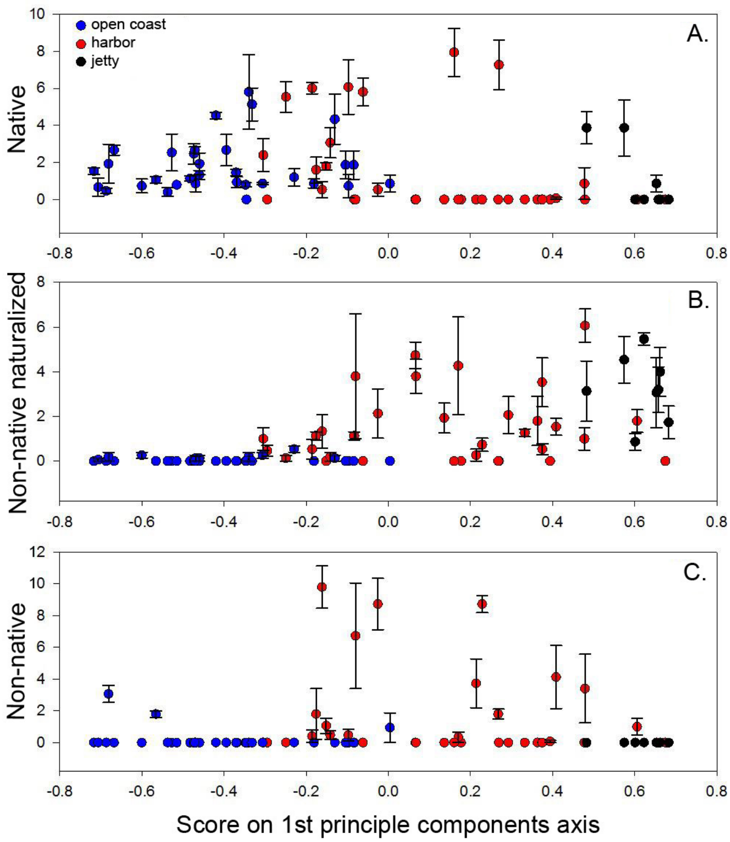

Figure 5. PC1 vs. native (A), non-native naturalized (B), and non-native (C) mean stipe densities at survey sites (n = 32 (open coast, blue), n = 34 (harbor, red), n= 8 (jetty, black).

native algae. Jetty sites had intermediate densities of native species and lacked non-natives entirely. When examining benthic community composition across all sites surveyed in this study (Figure 4), the first two principal component axes (PC1 and PC2) described over 50% of the variation in the data (with PC1 explaining 42.6% of variation). Sites within each site type clustered together along PC1 (left to right from open coast to jetty, Figure 4) suggesting that each site type was

Table 2. Results from three-way ANOVA testing for differences in mean non-native stipe densities across location nested within site type, site type (open coast versus harbor) and survey round.

Source	*df*	MS	SS	F	*p*
Site [Location, Site Type]	13	6.2331	81.0301	4.8074	0.0002
Site Type	1	26.5361	26.5361	20.4663	< 0.0001
Location [Site Type]	4	20.7358	82.9432	15.9947	< 0.0001
Site Type x Survey Round	2	0.4742	0.94833	0.3657	0.6968
Survey Round	2	1.8880	3.77605	1.4562	0.2491
Error	30	1.29658	38.8973		
Total	52				

Table 3. Summary of *S. horneri* and *U. pinnatifida* documentations on the Pacific Coast of North America from published sources and University of California Herbarium (Berkeley, California) database specimens.

Species	Year	Location	Source	Latitude	Longitude
S. horneri	2003	Long Beach Harbor	Miller 2007	33º 42.0' N	118º 14.0' W
	2005	Todos Santos Bay	Aguilar-Rosas 2007	31º 43.2' N	116º 40.2' W
	2006	Santa Catalina Island	Miller 2007	33º 24.3' N	118º 22.0' W
	2006	Point Loma	UC Herbarium	32º 41.2' N	117º 16.0' W
	2007	San Clemente Island	UC Herbarium	32º 58.7' N	118º 32.3' W
	2007	Isla Natividad	Riosmena-Rodriguez 2012	27º 27.8' N	115º 9.00' W
	2009	Anacapa Island	D. Kushner, US Natl. Park Service	34º 0.91' N	119º 22.5' W
	2010	Santa Cruz Island	D. Kushner, US Natl. Park Service	34º 2.61' N	119º 42.9' W
	2010	Santa Barbara Island	D. Kushner, US Natl. Park Service	32º 28.7' N	119º 24.2' W
	2012	Mission Bay	this study	32º 45.7' N	117º 14.8' W
	2012	Shaw's Cove	UC Herbarium	33º 32.6' N	117º 47.9' W
	2013	Oceanside Harbor	this study	33º 12.4' N	117º 23.6' W
	2013	San Diego Bay	this study	32º 42.4' N	117º 14.1' W
	2013	Bird Rock	this study	32º 48.9' N	117º 16.5' W
U. pinnatifida	2000	Los Angeles Harbor	Silva 2002	33º 42.9' N	118º 17.0' W
	2000	Long Beach Harbor	Silva 2002	33º 45.7' N	118º 12.0' W
	2000	Channel Islands Harbor	Silva 2002	34º 9.71' N	119º 13.4' W
	2000	Port Hueneme	Silva 2002	34º 9.17' N	119º 12.5' W
	2001	Santa Barbara Harbor	Silva 2002	34º 18.5' N	119º 41.4' W
	2001	Santa Catalina Island	Silva 2002	33º 24.2' N	118º 22.1' W
	2001	Monterey Bay	Silva 2002	36º 36.2' N	121º 53.3' W
	2003	Isla Todos Santos	Aguilar-Rosas 2004	31º 48.1' N	116º 47.3' W
	2004	San Diego Bay	Miller 2009	32º 42.5' N	111º 10.4' W
	2009	Morro Bay Docks	UC Herbarium	35º 22.2' N	120º 51.4' W
	2009	San Francisco Bay	Zabin 2009	37º 46.8' N	122º 23.1' W
	2009	Pillar Point Harbor	Zabin 2009	37º 30.1' N	122º 28.9' W
	2013	Oceanside Harbor	this study	33º 12.4' N	117º 23.6' W
	2014	Santa Cruz Harbor	H. Fulton- Bennett, Moss Landing Marine Laboratory	36º 57.8' N	122º 0.08' W
	2014	Mission Bay	this study	32º 45.7' N	117º 14.8' W

characterized by distinct benthic functional groups. The major loadings on PC1 were fleshy red macroalgae and crustose coralline algae in the direction of open coast sites and sand and bare rock in the direction of jetties. Sites within each classification spread along PC2, which had major loadings of articulated coralline algae, brown macroalgae, turf algae, sponges, and seagrass. This spread indicates that cover of these benthic functional groups was variable at sites within the three site types.

Densities of native, non-native naturalized, and non-native stipes were clearly grouped along PC1 based on site type (Figure 5). Native brown algal stipe densities (Figure 5A) were high in open coast sites characterized by native fleshy red macroalgae and articulated coralline algae and low in harbor and jetty sites. Harbor and jetty sites had consistently high stipe densities of non-native naturalized *S. muticum* (Figure 5B). Non-native macroalgae (Figure 5C) were found almost exclusively in harbor sites that were characterized by turf algae, articulated coralline algae, sponges, and barnacles.

Regional abundance and current distribution

In the relatively short invasion history of *S. horneri* and *U. pinnatifida* on the Pacific coast of North America, each species has spread rapidly to occupy a range of different habitats in multiple biogeographic regions with different environmental conditions (Figure 1, Table 3). Both species have been documented on man-made and natural substrates in protected harbors, open mainland coasts, and on offshore islands.

Since its discovery in Long Beach Harbor in 2003, *S. horneri* has shown a general southward spread, remaining in the southern California Bight and expanding southward down the coast of Baja California, Mexico (Figure 1, Table 3). In this time, it has expanded its range approximately 200 km north and 750 km south, from Santa Barbara, California to Isla Natividad, Central Baja California, Mexico.

While the first documentation of *Sargassum horneri* was in a harbor, this species has been found in few harbor locations since then. In 2010, *S. horneri* was found growing in the Port of Ensenada. In this study we report the occurrence of *S. horneri* in Oceanside Harbor, Mission Bay, and San Diego Bay. *Sargassum horneri*'s greatest invasion success has been on offshore islands along the coasts of California and Baja California. *Sargassum horneri* was first discovered at Santa Catalina Island in April 2006, and it was reported at San Clemente Island in May 2007. It has since spread to Anacapa and Santa Cruz Islands. In the south, the species has been found from the Coronado Islands in 2015 (N. Kaplanis, pers. obs.), to Isla Natividad, a small island off of the central Pacific coast of Baja California, Mexico in 2007. *S. horneri* has also successfully invaded open coast mainland locations in California and Baja California, Mexico. In 2005, *Sargassum horneri* was first reported as drift wrack at La Jolla, Baja California and growing at Rancho Packard in Todos Santos Bay, Ensenada B.C. In 2006, the first population in San Diego County was discovered at New Hope Rock, Point Loma. It has since been found in isolated populations along the southern California coast in Santa Barbara (D. Reed, University of California Santa Barbara, Santa Barbara, CA, pers. comm.), Laguna Beach, and Crystal Cove, Orange County. Our study adds a total of nine sites to the list of locations where this species is now present.

Undaria pinnatifida has primarily spread northward since its discovery in Los Angeles Harbor in March 2000, growing almost exclusively on man-made structures in protected harbor locations (Figure 1, Table 3). *Undaria pinnatifida* was reported in rapid succession at harbors throughout the California coast: Port Hueneme and Santa Barbara Harbor in November 2000 and April 2001, respectively; and as far north as Monterey Harbor by August 2001. In 2004 it was first found in San Diego Bay, and by 2009 the species was also found at Morro Bay Harbor, at Pillar Point Harbor in Half Moon Bay, and marinas in San Francisco Bay. *Undaria pinnatifida* was then found on floating structures in two marinas within the Bahía Todos Santos in April of 2012, and most recently was discovered in Santa Cruz Harbor in June of 2014 (H. Fulton-Bennett, Moss Landing Marine Lab, Moss Landing, CA, pers. comm.). In two instances *U. pinnatifida* has been found on natural substrates in island locations. In June of 2001, a deep water population was found in Button Shell Cove, an open-coast location on Santa Catalina Island. This documentation represents the first and only instance of *U. pinnatifida* occurring on a natural reef on the open coast in California. In September 2003, *U. pinnatifida* was found at Isla Todos Santos, the first documentation of this species on the Pacific coast of Mexico. *Undaria pinnatifida* has not yet been documented growing on a natural reef on the mainland Pacific coast of California. In Baja California though, populations have been observed in a natural reef setting at Punta Banda, Bahía Todos Santos (Aguilar-Rosas 2014). Here we document eight new sites from San Diego harbors where *U. pinnatifida* is present.

Discussion

We investigated the presence, establishment, spread and persistence of *S. horneri* and *U. pinnatifida* in San Diego County. Both species are well established, occurring throughout the county in multiple locations characterized by distinct habitats. Further, both species appear to be spreading locally within a short time frame to an increasing number of sites where they are found. Finally, the persistence of both species at invasion locations through multiple generations indicates that these species are established.

Sargassum horneri has proven to be a successful invader in San Diego, rapidly colonizing new areas, forming dense thickets and spreading quickly within invasion sites. This suggests that it is competitively equal to, or dominant over, native macroalgal species when conditions are right. The life history characteristics of this species may explain its success as an invasive species. Like in its native range, in invasion locations *S. horneri* grows very rapidly between November and July, reaching full size (3–5 m in length) and reproductive maturity in nine to ten months (L. Marks, University of California Santa Barbara, Santa Barbara CA, pers. comm.; N. Kaplanis pers. obs.). *Sargassum horneri* is an annual species (Gao and Hua 1997) and is capable of persisting through multiple generations because it is monoecious and extremely fecund (Miller and Engle 2007). Once released, *S. horneri* eggs have the potential to be fertilized for up to 48 hours, a window of viability much longer than related species (Pang et al. 2009). In San Diego, mature senescent thalli bearing reproductive conceptacles have been observed in spring of 2014 and 2015 throughout the county as beach wrack and as drift (N. Kaplanis, pers. obs.). Whether these drifting thalli are capable of releasing viable embryos is unknown, but it appears likely that *S. horneri* is capable of local dispersal even without a human transport vector.

Undaria pinnatifida has remained a relatively inconspicuous invader in San Diego. Its spread has been slow, has been mostly confined to man-made substrates, and no obvious ecological effects of its colonization have yet been observed. However, this survey provides only a snapshot of *U. pinnatifida* in a relatively early stage of a potential invasion. More detailed studies that investigate the interactions of this invader with the native benthic community are needed to better understand and track the progress of this invasion along the Pacific coast of North America.

Both non-native species investigated here were found almost exclusively in harbors in San Diego County. In these harbors, densities of non-native macroalgae are high when densities of native macroalgae are low and vice-versa. This pattern may result from occupation by the non-native species of an open niche that is not suitable for the growth of native macroalgae, or may be due to competitive displacement by the invaders. The disproportionate presence of these species in harbors may be a result of these locations being initial points of introduction, suggesting boats as a vector for long distance transport. Once present in harbors, the invaders may remain restricted to these habitats or they may spread into adjacent open coast sites. Whether the rocky reefs of our study area are more resistant to invasion than harbors, or whether they have simply not been exposed to propagules of the non-native species remains to be determined. However, it appears that several offshore islands in southern California and in Baja California are highly susceptible to invasion. Whether these new open coast invasions are the result of El Niño associated conditions that have negatively impacted kelp communities, potentially opening space for invader colonization, is yet to be determined. More long-term monitoring in conjunction with experimental manipulations are needed to better understand the dynamics and potential impacts of these invaders along the Pacific coast of North America.

The results of our surveys also provide valuable insight into the distribution of the naturalized invader *S. muticum*, which was abundant at nearly every survey site. Unlike *S. horneri* and *U. pinnatifida, S. muticum* was abundant on open-coast jetties year round. *Sargassum muticum* was also abundant in low energy environments throughout San Diego's harbors, as well as high energy wave-swept intertidal and subtidal areas along the open coast. Further, *S. muticum* was found both in areas devoid of other macroalgae and intermingled with native macroalgal species. While *S. muticum* was ubiquitous, it was never found in dense canopy-forming stands, as it is observed in its native range (Deysher and Norton 1982) and was observed during its initial invasion of San Diego in the 1970's (P. Dayton, Scripps Institution of Oceanography, San Diego, CA, pers. comm., Ambrose and Nelson 1982). At present, it appears as though *S. muticum* has become naturalized in San Diego but little is known about how this species interacts with native benthic communities or the new invaders over time. Continued monitoring is needed to better understand the invasion ecology of these three non-native species.

Comparing patterns of invasion of these macroalgal species along the San Diego County coast to the broader coastal region provides important context to understanding patterns of spread. In San Diego County, *S. horneri* grows in large meadows in the local harbors. These harbor populations are similar to the extensive populations now observed on the leeward side of Santa Catalina Island, though their spatial extent is more confined by limited availability of suitable hard substrate. On the open coast of San Diego, *S. horneri* remains contained in small localized populations with small spatial coverage and lower densities. In the wave and current exposed areas along the west and southern coasts of Santa

Catalina, the Northern Channel Islands, and the southern California mainland, *S. horneri* has also not yet been observed to form large or persistent meadows. The mechanisms driving these patterns of establishment remain unclear but may be tied to wave and current exposure.

Despite *U. pinnatifida*'s reputation as an aggressive invader, the colonization pattern for San Diego, as with the rest of the Pacific coast of North America, has shown that *U. pinnatifida* is largely restricted to man-made structures in harbors. This is strikingly different from other invasion locations such as Australia and New Zealand, where widespread invasion on the open coast has prompted aggressive removal and control programs (Lonhart and Bunzel 2009). Instances where *U. pinnatifida* has invaded natural substrates on the open coast of California and Baja California remain rare despite fears that these observed populations are the beginning of a widespread and devastating invasion. The pattern of colonization along the Pacific coast of North America may be a result of a limited temperature tolerance (Aguilar-Rosas et al 2004; Miller and Engle 2009), an inability to become established in areas of high wave exposure (Miller and Engle 2009), or an inability to compete with native macroalgae for settlement space on the benthos – but these mechanisms have yet to be explored.

The spread of *S. horneri* and *U. pinnatifida* along the Pacific Coast of North America in the past two decades has been swift and reveals that these two species are capable of becoming invasive in a range of habitats within this region. Colonization of areas far from their native ranges indicates that these species are capable of utilizing a human-mediated transport vector. Distribution patterns suggest hull fouling of large commercial vessels as a likely vector for initial introduction and fouling of smaller recreational vessels as a vector for secondary spread. Further, their capability to spread locally from these initial points of introduction may also suggest secondary spread through sexual and asexual propagation. These two species have also proven to be highly versatile. While *S. horneri* has remained confined to the southern California Bight and the Baja California Coast, it has successfully colonized a wide range of habitat types in this region. *Undaria pinnatifida* has also proven capable of invading a variety of habitat types, and has expanded its range from Baja California to northern California, spanning across multiple distinct biogeographic provinces. Finally, the persistence of both species since their initial introductions indicates they are also able to withstand competition and with native algal species and grazing pressure from native herbivores.

The ecological and economic impacts of these seaweed invaders have yet to be explored. In its native range, *S. horneri* is known to influence a variety of different coastal environmental parameters including dissolved oxygen concentration, water flow, pH, and light conditions (Komatsu et al. 2007). It is also known to play an important ecological role in offshore waters, forming large, dense, drifting mats (Komatsu et al. 2007). In its native range, this species is an important biofilter that removes inorganic nutrients from mainland effluent discharges (Pang et al. 2009). The impacts of the large invasive stands and drifting mats of this species on the Pacific coast of North America on coastal environmental conditions and nutrient distributions remains unknown. Few studies have assessed the impacts of *U. pinnatifida* on native communities in other areas, and ecological effects of *U. pinnatifida* on native species have been variable based on invasion location. Further, little is known about how this species may affect the rocky reef communities of the Pacific coast of North America if it spreads further (Lonhart and Bunzel 2009).

The coastal communities of the Californias are currently undergoing invasion by multiple non-native macroalgae. The majority of these species have appeared in the past 30 years, and species such as *S. horneri* and *U. pinnatifida* are still in the early stages of the invasion process, providing the opportunity to gain insight into the early stages of algal invasions. Further, environmental shifts associated with climate change, including increases in the frequency and intensity of ENSO events, may be making the California and Baja California coasts more susceptible to invasion by non-native algal species through creating more space and reducing natural resistance (Miller et al. 2011). While the current distributions of these species may be confined by latitudinal temperature barriers, with the North Equatorial Current possibly confining the spread of *U. pinnatifida* south, and the California Current possibly confining the spread of *S. horneri* north, temperature shifts associated with climate change could potentially alter these barriers and allow for further spread of these species. Identifying the underlying mechanisms that facilitate or inhibit further spread is the next logical step in advancing our knowledge of the invasion ecology of these species.

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The following supplementary material is available for this article:

Table S1. Summary of surveys in San Diego County.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2016/Supplements/AI_2016_Kaplanis_etal_Supplement.xls