THE NATURAL HISTORY OF *UNDARIA PINNATIFIDA* AND *SARGASSUM FILICINUM* AT THE CALIFORNIA CHANNEL ISLANDS: NON-NATIVE SEAWEEDS WITH DIFFERENT INVASION STYLES

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Abstract—The new millennium ushered in two prominent non-native subtidal seaweeds to southern California: Undaria pinnatifida (Harvey) Suringar (Laminariales) and Sargassum filicinum Harvey (Fucales), both originally from Asia. Our long-term and widespread survey program provided the opportunity to document their establishment and dispersal at the Channel Islands. The two species exhibit very different invasion patterns. Undaria is well known for invading a broad spectrum of habitats throughout the world; however, California is the first region outside of Asia at which little-known S. filicinum has been reported. In 2001, Undaria was discovered at a single sheltered cove on the lee side of Santa Catalina Island, on a deep (24 m) soft sediment substrate. In subsequent years, it moved onto shallow subtidal rocky habitat, mixing with the *Macrocystis* kelp forest community. By 2004, it was well established at the primary site and was found at a second adjacent site. Surprisingly, our subsequent surveys at Santa Catalina Island and the other Channel Islands, as well as alerts to the diving community, have not yielded new populations, despite this species' aggressive spread in harbors on the mainland. In contrast, S. filicinum was initially discovered in the leeward Isthmus area at the western end of Santa Catalina Island in spring 2006. In one year, it spread rapidly along the entire lee side to Avalon, forming dense groves. In 2007, we documented this species on the windward side of Santa Catalina Island and discovered populations at two locations on the lee side of San Clemente Island. We expect S. filicinum to spread further at the Channel Islands and along the southern California mainland. We report the current distribution and compare the life histories of these two invasive species.

INTRODUCTION

Seaweeds that have been introduced by human activities to regions beyond their native range, where they establish and thrive, are considered invasive species. These invaders are a focus of concern because of their potential to compete with native species and alter community composition and dynamics. A total of 277 species of invasive seaweeds have been reported worldwide, most likely dispersed via hull-fouling and aquaculture, including shellfish farming (Williams and Smith 2007). Thirteen species of non-native seaweeds have been reported from California (Miller 2004; Miller et al. 2007), accounting for about 2% of the California seaweed flora.

Perhaps the most widespread and conspicuous of these is the brown seaweed *Sargassum muticum* (Yendo) Fensholt (Fucales). Originally from northeast Asia, *S. muticum* was first reported on the

west coast of North America in the early twentieth century (Scagel 1956), reached southern California in 1970 (Setzer and Link 1971) and has become a common component of California intertidal and subtidal communities (Ambrose and Nelson 1982; Deysher and Norton 1982; Wilson 2001; Britton-Simmons 2004). In 2000, a weedy strain of the tropical green alga Caulerpa taxifolia (M. Vahl) C. Agardh (Caulerpales) was introduced to southern California and, after a multi-year and multi-milliondollar effort, was declared eradicated in 2005 (Merkel and Associates 2005). Since 1999, the Asian brown algae *Undaria pinnatifida* (Harvey) Suringar (Laminariales) (Silva et al. 2002) and Sargassum filicinum Harvey (Fucales) (Miller et al. 2007) and the cosmopolitan red alga Caulacanthus ustulatus (Turner) Kützing (Gigartinales) (Zuccarello et al. 2002; Miller 2004) have been introduced to southern and central California and continue to flourish.

In California, many of these introduced seaweeds are found in human-influenced, disturbed bays and harbors on the mainland. Undaria was discovered in southern California harbors and Monterey Harbor in 2000-2001 and Baja California, Mexico in 2003 (Silva et al. 2002; Aguilar-Rosas et al. 2004). In 2004, the Invasive Species Survey team (Moss Landing Marine Labs) reported the most recent discovery of *Undaria* in San Diego Harbor. Most of the California populations are limited to harbors and their artificial substrates, especially floats, piers, and boat hulls. However, the population at Santa Catalina Island addressed in this paper is strictly subtidal, persisting at low densities in and around a Macrocystis pyrifera community.

Sargassum filicinum, native to the warmer parts of Japan and Korea, has not been reported as an invasive species prior to its arrival in California. In contrast, Undaria pinnatifida, native to southeastern Russia, Japan, northern China, and Korea, is an aggressive invasive species in the Mediterranean Sea, England, Atlantic Europe (where it was accidentally introduced and then propagated as a crop), New Zealand, Australia, Argentina, and Baja California, Mexico (Silva et al. 2002; Aguilar-Rosas et al. 2004). A variety of dispersal events (single introductions, multiple introductions, local site-to-site dispersal) as well as various microevolutionary processes (founder's

effect, bottlenecks, selection for novel, locally adapted gene combinations) are responsible for *U. pinnatifida*'s worldwide success (Voisin et al. 2005). Uwai et al. (2006) traced the multiple Japanese origins of worldwide populations using molecular methods and speculated that the California (their study included populations from San Pedro, Santa Barbara, and Monterey but not Santa Catalina Island) and Mexican populations were introduced via shipping vectors.

Since 1980, we have conducted 180 multi-day subtidal survey expeditions throughout the eight California Channel Islands with the Tatman Foundation's Channel Islands Research Program (CIRP). During these trips, teams of biologists and volunteers carried out reconnaissance surveys at a broad spectrum of locations to evaluate the distribution and abundance of marine plant and animal species. Our combined experience and network of biologist contacts have provided early documentation of the arrival of *Undaria pinnatifida* and *Sargassum filicinum* at the Channel Islands. Here we report what we have learned from our focused surveys of these non-native seaweeds.

MATERIALS AND METHODS

Following the initial record of *U. pinnatifida* at Button Shell Cove in May 2001, we distributed e-

	Number of sites per year								
Island	2001	2002	2003	2004	2005	2006	2007		
San Clemente	17	8	10	9	4	0	10		
Santa Catalina	19	12	12	15	11	22	14		
Santa Barbara	0	6	0	0	7	3	0		
San Nicolas	0	6	0	0	0	0	0		
Anacapa	4	3	2	5	7	5	8		
Santa Cruz	2	1	13	15	7	11	10		
Santa Rosa	0	5	5	5	5	3	0		
San Miguel	0	6	0	8	6	0	0		

mail messages and posters to alert southern California scientific and recreational divers about this new island invader, requesting notice if this species is encountered. From 2001-2007, our reconnaissance surveys covered representative sites around the eight Channel Islands (Table 1), including sheltered coves where we predicted that U. pinnatifida might establish. We also carried out a series of population surveys at Button Shell Cove, initially in June and September 2001, then annually in April and May from 2002 through 2007, with occasional other visits. Surveys consisted of three diver-pairs searching throughout this small cove, in both rocky and soft-bottom habitats, at depths ranging from 2 to 25 m. All U. pinnatifida encountered was collected to the extent feasible. Collected plants were categorized as recruit (<20 cm blade without lobes and midrib in evidence only near base), juvenile (blade with full midrib, but no evidence of sporophyll), immature (blade with developing sporophyll) or mature (blade with fully formed sporophyll).

After our discovery of the initial specimen of *S. filicinum* at Santa Catalina Island in April 2006, we once again spread the word to divers to watch for this invasive species and report observations to us. We carried out reconnaissance surveys during 2006–2007 at representative locations at Santa Catalina and five other islands (Table 1). Wherever *S. filicinum* was found, we estimated abundances and recorded distribution patterns and life history information.

RESULTS

Undaria pinnatifida

Initial discovery. On May 10, 2001, Steve Madaras, a dive boat operator and his friend Koji Ozaki, an underwater photographer from Japan, were diving for halibut at Button Shell Cove, a cove east of Long Point, Santa Catalina Island (Fig. 1).

Mr. Ozaki recognized kelp growing at 20 m as *Undaria pinnatifida* (Harvey) Suringar, or wakame. Mr. Madaras contacted the first author and provided a specimen on May 23, 2001.

Subsequent surveys. On June 10–11, 2001, six divers descended at the Button Shell Cove site to 20 m and immediately found the reported population.

We also explored shallow water in the vicinity and adjacent sites near White's Landing and Hen Rock.

The majority of the population at Button Shell Cove grew on *Chaetopterus* worm tubes in soft sediment, at depths between 19 and 26 m. Other seaweeds present on worm tubes were *Pelagophycus porra* (Leman) Setchell, *Agarum fimbriatum* Harvey, *Laminaria farlowii* Setchell, *Dictyopteris undulata* Holmes and juvenile *Eisenia arborea* Areschoug. We collected 121 individuals from this depth. Most plants bore sporophylls, and many blades were truncated due to apical erosion. We also collected 11 small individuals of *U. pinnatifida* (< 60 cm blade length) in depths of less than 6 m under the pier. Despite a diversity of substrates available under the pier, they grew only on tires. Eight out of the 11 bore sporophylls.

In September 2001, plants were collected at depths between 22 and 24 m (Table 2). Most blades were deteriorated, leaving midribs, sporophylls (some flabby and "spawned out"; others dark and healthy), and holdfasts. No juvenile sporophytes were observed. In April and May 2002, we collected *U. pinnatifida* on rocky substrates in the

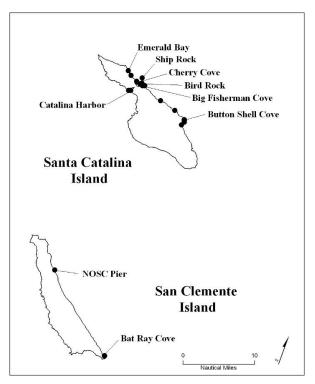


Figure 1. Map showing selected survey sites at Santa Catalina and San Clemente islands to the south and Italian Gardens to the north of Long Point. *Undaria pinnatifida* was absent at these sites, at all depths.

Table 2. Undaria pinnatifida population surveys at Santa Catalina Island.

Site	Date	Substrate	Undaria depth (m)	# Divers	# Undaria	Notes
Button Shell	5/10/2001	Worm tubes on sand	20	2	No data	Initial discovery by Steve Madaras & Koji Ozaki. Voucher collected.
	6/10– 11/2001	Worm tubes on sand	19–26	6	121	First survey of rock & sand habitats throughout cove.
		Car tires under pier	6	6	11	Young Undaria.
	9/6/2001	Worm tubes on sand	22–24	24	33	CA Dept. Fish & Game divers aided surveys.
	9/25/2001	Worm tubes on sand	24	7	54	This single patch of <i>Undaria</i> apparently was missed on prior survey.
	4/19/2002	Worm tubes & snail shells on sand; metal & plastic debris; cobble/rock w/kelp plastic debris; cobble/rock w/ kelp	6–26	6	559	Undaria not counted by habitat. Most on worm tubes at 15–26 m. Few on cobble/rock at 10–15 m. Juveniles predominated.
	5/10/2002	Cobble/rock w/ kelp	6–20	10	482	
	5/13/2003	Worm tubes & snail shells on sand; metal debris; pier pilings; cobble-rock w/kelp debris; pier pilings; cobble/rock w/ kelp	6–25	6	638	Undaria not counted by habitat. Most on worm tubes at 15–22 m. or on cobble/rock at 10–15 m. Juveniles predominated.
	5/14/2004	Cobble/rock w/kelp	5–15	6	63	Undaria mostly on main kelp reef.
		Worm tubes & snail shells on sand	8–23	6	16	<i>Undaria</i> in shallow eelgrass bed.
		Car tires under pier	6	6	3	Young Undaria.
	5/1/2005	Cobble/rock w/ kelp	3–12	5	234	Few mature adult <i>Undaria</i> .
	4/23/2006	Cobble/rock w/ kelp	5–14	6	90	Earlier in April, USC class collected undetermined # of <i>Undaria</i> .
	5/14/2007	Cobble/rock w/ kelp	6–16	6	203	96% of <i>Undaria</i> found at 6–13 m depths on kelp reef.
White's Landing	5/14/2004	Metal debris on sand	12	6	83	Single patch of <i>Undaria</i> was directly offshore from pier.

Macrocystis pyrifera (C. Agardh) Linnaeus forest at Button Shell Cove at 6–12 m depth, and observed that it was less common at greater depths. In subsequent years, *U. pinnatifida* has not been found in the deep kelp community (Table 3). Undaria recruits in late winter (February-March) with the native kelps, is reproductive in spring and summer, when it begins to deteriorate, and disappears by late October. From 2001 through 2007, we tracked

recruits, juveniles, and immature and mature plants (Tables 2, 3; Fig. 2). The population size and timing of development fluctuates. For example, the phenological pattern in 2002, 2003, and 2005 was similar, with 10–20% mature individuals in May, but 90% of the individuals were mature in June 2001 and May 2007. These results also indicate that the population as a whole is stable year to year, despite

Table 3. Sites at Santa Catalina (SCA) and San Clemente (SCL) islands where Undaria and S. filicinum were observed. Abundances: absent (-); 1–10 plants (+); 11–100 plants (+++); 101–1000 plants (++++); >1000 plants (+++++); not determined (X).

Island	Site	Latitude	Longitude	Date	Undaria	S. filicinum
SCA	Button Shell Cove	33° 24.3N	118° 22.0W	6/10/01	+++	-
	"	"	دد	9/6/01	++	-
	"	"	دد	9/25/01	++	-
	"	"	دد	4/19/02	+++	-
	"	44	cc	10/21/02	-	-
	"	"	۲۲	5/13/03	+++	-
	"	"	۲۲	5/14/04	+++	-
	White's Landing	33° 23.5N	118° 22.1W	5/14/04	++	-
	Button Shell Cove	33° 24.3N	118° 22.0W	2/10/05	++	-
				4/30/05	+++	-
	WMSC Intake Pipes	33° 26.8N	118° 29.1W	4/20/06	-	++
	West Cherry Cove	33° 27.1N	118° 30.1W	4/21/06	-	+
	Button Shell Cove	33° 24.3N	118° 22.0W	4/23/06	+++	-
	West Emerald Bay	33° 28.1N	118° 31.7W	4/24/06	-	+
	Hen Rock	33° 24.0N	118° 21.9W	9/12/06	-	++
	Button Shell Cove	33° 24.3N	118° 22.0W	9/12/06	-	-
	Pumpernickel Cove	33° 26.9N	118° 28.8W	11/1/06	-	+++
	WMSC Intake Pipes	33° 26.8N	118° 29.1W	11/1/06	-	+++
	Isthmus Reef	33° 26.9N	118° 29.5W	11/2/06	-	++
	Bird Rock	33° 27.1N	118° 29.3W	11/2/06	-	+++
	Big Geiger Cove	33° 27.6N	118° 31.1W	11/4/06	-	+++
	Empire Landing*	33° 26.4N	118° 27.8W	11/4/06	-	X
	Twin Rocks*	33° 25.1N	118° 23.4W	11/4/06	-	X
	E of East End Quarry*	33° 19.3N	118° 18.2W	11/25/06	-	X
	Casino Point*	33° 20.9N	118° 19.5W	12/9/06	-	X
	Button Shell Cove	33° 24.3N	118° 22.0W	5/14/07	+++	-
	Hen Rock	33° 24.0N	118° 21.9W	5/14/07	-	+
	Goat Harbor	33° 25.1N	118° 23.7W	5/14/07	-	+++
	Ripper's Cove	33° 25.7N	118° 26.0W	5/14/07	-	+++
	Button Shell Cove	33° 24.3N	118° 22.0W	7/10/07	++	-
	East Cherry Cove	33° 27.0N	118° 30.0W	7/12/07	-	+++
	Bird Rock	33° 27.1N	118° 29.3W	10/25/07	-	++++
	Pumpernickel Cove	33° 26.9N	118° 28.8W	10/25/07	-	++++
	Pin Rock, Catalina Hbr	33° 25.6N	118° 30.4W	10/26/07	-	+++
	West Catalina Hbr	33° 25.5N	118° 30.7W	10/26/07	-	++++
	Button Shell Cove	33° 24.3N	118° 22.0'W	10/27/07	+	+++
	Ship Rock	33° 27.8N	118° 29.5W	10/28/07	-	+++
SCL	South of NOSC Pier	32° 58.4N	118° 31.8W	5/12/07	-	+
	Bat Ray Cove	32° 49.2N	118° 21.05W	5/13/07	-	+++

^{*}Record from W. Bushing, Avalon, CA

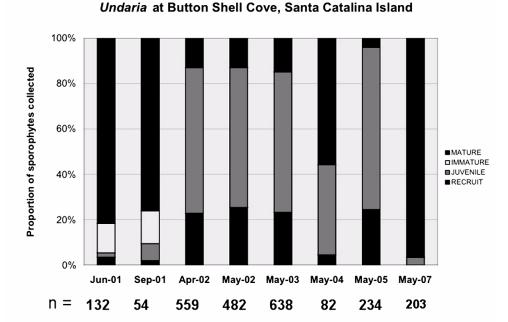


Figure 2. Age distribution of *Undaria pinnatifida* sporophytes at Button Shell Cove, Santa Catalina Island, 2001–2007. Bars represent proportion of collections in each age class (recruit, juvenile, immature, mature; see Materials and Methods for criteria). Total number collected each year (n) is presented below the graph.

removal of plants that we encounter in our surveys each year.

Annually, we searched for *U. pinnatifida* at Santa Catalina Island and throughout the Channel Islands during a series of CIRP cruises (Tables 1, 2, 3). Although we alerted scientists and divers, we have received no reports of *U. pinnatifida*, nor have we discovered any other populations in the course of our surveys at the eight Channel Islands.

Sargassum filicinum

Initial discovery. On April 8, 2006, we discovered a population of Sargassum filicinum at the Intake Pipes, a rocky point north of Big Fisherman Cove near the Wrigley Marine Science Center and the town of Two Harbors, on Santa Catalina Island, CA (Miller et al. 2007, Fig. 1). Discovery of the initial specimen of S. filicinum by the first author occurred less than two weeks prior to a CIRP survey trip to the island that included Japanese phycologist Dr. Hiroshi Kawai, who confirmed the species identity and collected specimens for molecular analysis, allowing us to pinpoint its likely origin as the Seto Inland Sea, Japan (Miller et al. 2007). In April 2006, there were

more than 30 plants (0.3–1.5 m tall) at depths between 4 and 12 m at the Intake Pipes site. Some individuals were young, with rosettes of fern-like, spiny leaves, but most were mature, bearing elongate receptacles and the characteristic spherical-elliptical vesicles of *S. filicinum*. We also observed plants in sheltered habitats at Cherry Cove (2 plants at 4 m and 13 m depths) and Emerald Bay (4 plants at 7 m depth), both nearby sites on the leeward west end of the island (1.8 km and 3.0 km NW of Intake Pipes; Fig. 1). These three populations at Santa Catalina Island may have been the result of a single introduction and subsequent local dispersal.

In the year following its discovery on the west end of Santa Catalina Island, *S. filicinum* spread rapidly along the leeward (north) side of Santa Catalina to the east end (Table 3). In 2007, *S. filicinum* was confirmed at more sites along the leeward (north) side of Santa Catalina Island. In May, juvenile plants densely carpeted shallow horizontal rock surfaces at these sites (Fig. 3). In October 2007, we documented populations at Button Shell Cove and Ship Rock (Fig. 1) that were absent during surveys in May and July 2007. Within



Figure 3. Juvenile *Sargassum filicinum* covering available substrate at 6 m depth, Goat Harbor, Santa Catalina Island. Photo by Dan Richards.

one year, *S. filicinum* spread at Bird Rock (Fig. 1) from a single patch at the east end to scattered dense patches along the entire west side. In April 2007, drift specimens of *S. filicinum* were observed at Catalina Harbor, on the windward (south) side of Santa Catalina Island (Fig. 1). Dives in October 2007 at both sides of the outer mouth of the harbor confirmed the presence of patchy populations of *S. filicinum*. The pattern of large plants surrounded by juveniles suggests an early stage of invasion at these sites. During these 12 dives in October, with 2 observers spending a total of 8 hours underwater at 6 sites, we counted approximately 5000 plants.



Figure 4. Mature *Sargassum filicinum* at 6 m depth, Bat Ray Cove, San Clemente Island. Photo by Dan Richards.

In May 2007, we surveyed 10 sites along the leeward coast of San Clemente Island, from Northwest Harbor to Pyramid Cove. We found a single plant south of the NOSC Pier, about midisland (Table 3, Fig. 1). At Bat Ray Cove just north of Pyramid Head (Fig. 1), we found a 10 m by 20 m patch of reproductive, senescent *S. filicinum* at 6–13 m depth in an open, sandy habitat (Table 3, Fig. 4). During May-September 2007, we surveyed 8 sites at Anacapa Island and 10 sites at Santa Cruz Island; *S. filicinum* was absent (Table 1).

DISCUSSION AND CONCLUSIONS

The pattern of spread of these two species at the Channel Islands is unexpected. Undaria pinnatifida was reported at harbors throughout the southern California Bight, and at Santa Catalina Island and Monterey Harbor, within a year of its discovery in Los Angeles Harbor (Silva et al. 2002). Since its initial introduction to Monterey, U. pinnatifida has not spread in central and northern California, despite predictions that it would do so (Silva et al. 2002; Thornber et al. 2004). On the other hand, S. filicinum was discovered in Long Beach Harbor in 2003 but was not reported again until 2006 (Aguilar-Rosas et al. 2007; Miller et al. 2007). It then spread explosively on Santa Catalina Island and has been observed at San Clemente Island, a popular fishing destination, where we predict it too will spread rapidly. The subtidal habitats at Anacapa Island and the southeast portion of Santa Cruz Island are similar to those in the southern islands and probably suitable for the establishment of S. filicinum. However, despite extensive boat traffic, a potential vector for establishment, we have yet to observe it at those locations.

It is interesting that both *U. pinnatifida* and *S. filicinum* established at Todos Santos Island in Baja California, Mexico as well as Santa Catalina Island in California. Neither of these sites are major harbors with international shipping. We hypothesize that *S. filicinum* arrived in California via international shipping, but has spread to Santa Catalina and San Clemente islands via pleasure boats (both are frequented by boats berthed in Los Angeles and San Diego area harbors). This may be the case for *U. pinnatifida* as well.

Undaria pinnatifida has demonstrated a broad ecological tolerance, having established itself globally. It is a fast-growing, extremely fecund opportunist that is precociously fertile, with a microscopic, cryptic gametophytic stage in its life history (Saito 1975; Thornber et al. 2004). These traits make it difficult to eradicate once it has established. Still, its growth and longevity are controlled by temperature (Oh and Koh 1996), which may limit its spread in southern California.

The depths at which *Undaria* initially established itself at Button Shell Cove far exceed 15 m reported as a maximum depth for other populations, both native and introduced (Saito 1975; Silva et al. 2002; Russell et al. 2008) and may reflect a refuge from warmer surface waters. Undaria pinnatifida is also sensitive to wave exposure, which may limit it to harbors and sheltered coves (like Button Shell Cove), although it exhibits a very different pattern in New Zealand, where it is spreading aggressively to the open coast (Russell et al. 2008). We would predict that U. pinnatifida would establish at sheltered coves at Anacapa and Santa Cruz islands, with pleasure boats from U. pinnatifida-infested berths in Long Beach, Los Angeles, Santa Barbara, Ventura, and Channel Islands harbors as its vectors. But this has not been the case.

Populations of *U. pinnatifida* at Santa Catalina Island are strictly annual, with a pattern of development similar to that in its native habitat (Fig. 2; Saito 1975). *Undaria pinnatifida* and *S. filicinum* share similar phenologies, recruiting in late winter, growing quickly, becoming reproductive early, and dying in late summer or fall. The Santa Catalina Island population of *U. pinnatifida* does not exhibit a burst of recruitment in the fall (Thornber et al. 2004) and overlapping generations as in New Zealand (Hay and Villouta 1993), and we have not observed extensive herbivory by kelp crabs, as reported in Santa Barbara Harbor (Thornber et al. 2004).

Sargassum filicinum, like S. muticum, is well adapted for widespread dispersal to and rapid colonization of new areas (Nyberg and Wallentinus 2005). Like S. muticum, this species is monoecious, bearing both male and female conceptacles; individuals are thus capable of self-fertilization. It is

extremely fecund, with large and abundant reproductive receptacles. Fertile fragments are buoyant due to air-filled vesicles and can readily disperse locally. Its establishment, like that of S. muticum and U. pinnatifida, may be promoted by its precocious fertility, which is presumably related to its essentially annual growth pattern (Miller et al. 2007). Again like S. muticum, it is a fast-growing opportunist, producing copious recruits in overlapping generations and colonizing a variety of habitats. Unlike S. muticum, it occupies a relatively narrow depth range (6-19 m) and apparently has a narrower temperature tolerance, since so far it has invaded only the warmest habitats in California. We speculate that S. filicinum is adept at local dispersal but that long range dispersal is episodic. This would account for its slow progress on the mainland coast, which is interrupted by stretches of sand and manmade structures, unlike the uninterrupted habitat available around Santa Catalina Island.

Although we did not find *U. pinnatifida* dispersing to new sites and observed that S. filicinum is spreading rapidly at Santa Catalina Island and has reached San Clemente Island, we also predict that the situation could change. It may require repeated introductions of *U. pinnatifida* under a narrow set of conditions to initiate the establishment of a population in the subtidal habitats around the Channel Islands. We speculate that changes in the cover and density of Macrocystis, due to changes in ocean climate, e.g., ENSO events and climate change (Stachowicz et al. 2002) and biotic interactions, e.g., domination by herbivores like urchins, could create conditions conducive to introduction (Valentine and Johnson 2003, 2004)—or not (Valentine and Johnson 2005). The current boom of S. filicinum could continue, or equilibrate with populations of native species, much as S. muticum has at Santa Catalina Island relative to its explosive growth (Ambrose and Nelson 1982) after an ENSO event. It remains to be seen how U. pinnatifida and S. filicinum populations will interact with those of native species (seaweeds and herbivores) and the non-native S. muticum over time. We hope that our observations stimulate detailed ecological studies of these new members of the community.

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