***Caulerpa taxifolia*, a beautiful, aggressive invasive tropical green alga, appeared in a harbor near San Diego in 2000. Image courtesy of the University Herbarium, UC Berkeley.**

CALIFORNIA'S NON-NATIVE SEAWEEDS

by Kathy Ann Miller

The seaweed flora of California is a world-class treasure. The magnificent diversity and abundance of seaweed populations reflect the dramatic sweep of our state's rich coastal environments and habitats–from the Pacific Northwest to the subtropics, including rocky shores and reefs, sandy beaches, and offshore islands. Our scientific knowledge of California seaweeds is young, beginning with the 1791 *Malaspina* expedition of discovery, growing through the efforts of European and east coast botanists, and coming of age with the collected works of W.A. Setchell and N. L. Gardner at the University of California at Berkeley. And yet, to this day, the delineation of species within our most common genera poses daunting challenges to phycologists, who continue to pursue field, culture, and molecular studies to unravel relationships at every taxonomic level.

The current comprehensive flora, *Marine Algae of California* (Abbott and Hollenberg 1976) lists 669 species of red, brown, and green seaweeds. The actual number is certainly much greater with the addition of recently described species, species yet to be described, and species that are currently arriving. Of those more recent introductions, some come to California naturally, through range extensions due to El Niño events and long-term climate change, but some arrive via humans who unintentionally introduce non-indigenous species on hulls of ships or, for example, by improperly disposing of aquarium plants.

Non-native or exotic species, especially those that spread like weeds, are both familiar and newsworthy. (Weeds, strictly defined, are plants that live where they are not wanted and are ecologically or economically harmful.) Since the beginning of civilization, humans have moved plants and animals to serve them, either intentionally to provide food, shelter, or companionship, or inadvertently, as hitchhikers. For hundreds of years, our terrestrial California has been gilded—and altered forever—by the unintentional introduction of European grasses; the list of introduced Mediterranean, South African, and Asian weeds is enormously long. Pampas grass! Yellow star thistle! Scotch broom! Fennel!

In the last few decades, we have come to realize that our estuaries and coastal oceans are also vulnerable to introduced species, including invasive species that can cause economic and ecological nightmares. There are an estimated 175 non-native species of plants and animals in San Francisco Bay alone, and the number continues to grow. Rapacious invertebrates and fish lead the list and grab the news—the Asian clam, Chinese mitten crab, green crab, northern pike, striped bass (an intentional introduction) are a few. But have you ever heard

of the infamous "Killer Weed," *Caulerpa taxifolia*? There are invasive seaweeds here, too.

Determining the presence of exotic seaweed species can be difficult if we have not witnessed the introduction. We consider creatures to be native when they occupy the area in which they evolved; usually there are natural barriers to the dispersal of a species. Sometimes these barriers shift through natural habitat or climate changes, allowing a species to expand its geographic range. Sometimes we are able to access new areas via new technologies, such as scuba diving or submersibles, and revise our records for the ranges of species. But to distinguish *introduced* species from those that are *native*, we must rely upon the history of collection data coupled with our understanding of species distributions and natural dispersal of populations.

When specimens from our coast were sent back to European specialists, vague collection notes ("in mare australe") and mistakes as simple as mislabeling were frequent, and have left a legacy of confusion. For example, it was recently discovered and confirmed with molecular data that the type locality (original collection) of a very common red seaweed known as *Iridaea cordata* was the tip of South America, not Vancouver Island, Canada, the provenance written on the herbarium sheet. That species name is therefore not applicable to our west coast species (now known as *Mazzaella splendens*, based on a California type specimen described by Setchell and Gardner). Similarly, the southern California rockweed *Hesperophycus californicus* was once known as *H. harveyanus*, based on a plant supposedly collected in Monterey in the 1830s—but probably collected in France and not *Hesperophycus* at all.

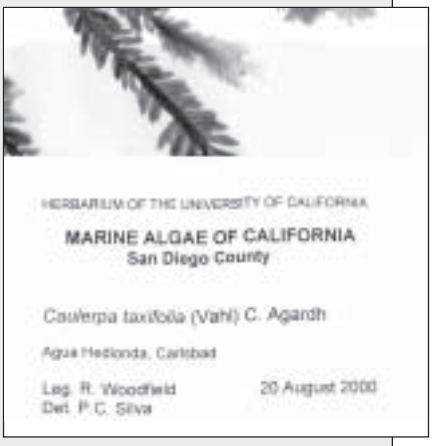
Furthermore, many of our common seaweeds have extraordinarily broad "cosmopolitan" geographic distributions and it is hard to discern their history. These species are known as "cryptogenic" because their original provenances are hidden from us. The ships that brought early explorers to our coasts were wooden reefs supporting creatures from every port visited over multiyear voyages, and were probably significant sources of introductions, long before scientists established a baseline for what is indigenous. For example, *Asparagopsis taxiformis* is a red alga, originally described from an Egyptian specimen, but considered a cosmopolitan member of subtropical and tropical communities worldwide. It occurs in southern California (San Diego, and the southern Channel Islands). Is it introduced? Has it extended its range from Baja California, Mexico? Or has it—"always" been here? We must critically revisit nomenclatural history because the basis of our knowledge of seaweed distributions is cultural as well as biological.

Finally, as every amateur and professional phycologist knows, many species look extremely similar and are difficult to tell apart, constituting complexes of what may be cryptic (hidden) or sibling (closely related) species. Learning more about our seaweed flora—and detecting interlopers—is becoming increasingly important.

The Mediterranean Sea, with 85 introduced seaweeds, including nine that are considered invasive, is a hot spot for introductions. At the Thau Lagoon, an aquaculture site on the southern coast of France, 45 species of seaweeds (23% of the flora) are exotics, probably introduced with the Japanese oyster *Crassostraea gigas*. In contrast, we've recorded a modest 12 non-native seaweed species (or 2% of the seaweed flora) from our California coast. Most of these are diminutive and easily overlooked, and several have been reported only from our

SEAWEED SCIENTIFIC NAMES, COMMON NAMES, AND AUTHORS

For this article and those that follow, common names are only provided if available. Unlike terrestrial plants, most seaweeds do not have colloquial names. For purposes of precision, a scientific name may be followed by its author(s). If a species has been retained in its original genus, the author is the person who originally described the species, for example, *Postelsia palmaeformis* Ruprecht. If a species has been transferred to another genus, the name of the describer will appear in parentheses followed by the name of the person who made the transfer. Thus, the citation *Caulerpa taxifolia* (Vahl) C. Agardh indicates that this species was originally described by Vahl (in 1802 as *Fucus taxifolius*) and transferred to *Caulerpa* by C. Agardh (in 1817).


HERBARIUM OF THE UNIVERSITY OF CALIFORNIA
MARINE ALGAE OF CALIFORNIA
San Diego County
Caulerpa taxifolia (Vahl) C. Agardh
Agua Hedionda, Carlsbad
Leg. R. Woodfield 20 August 2000
Det. P.C. Silva

Label for only California collection of *Caulerpa taxifolia* at the University Herbarium, UC Berkeley. Herbarium labels rarely include the colloquial name of the plant collected, but always include the scientific name with its author.

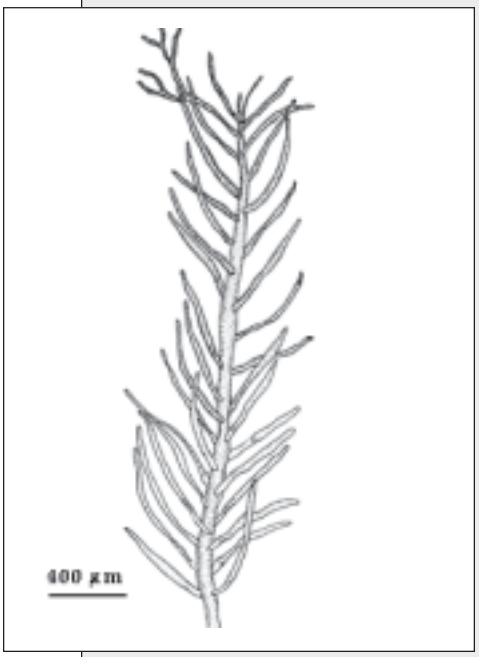
own invasion hot spot, San Francisco Bay.

Good examples are *Aglaothamnion tenuissima* (Bonnemaison) Feldmann-Mazoyer and *Polysiphonia denudata* (Dillwyn) Greville ex Harvey, both small red filaments originating in England and detected in San Francisco Bay. More recently, another small red filamentous species, *Polysiphonia harveyi* J. Bailey, once thought to be a native of the east coast of North America, has been traced through molecular methods as originating in Japan and spreading, via several introductions, to the Atlantic, including the British Isles, New Zealand, and US, including California, where it has masqueraded as *Polysiphonia acuminata* Gardner and *P. simplex* Hollenberg. A great example of a sibling/cryptic species complex!

Another example of a sibling species complex that is yet to be teased apart is the green algal genus *Bryopsis*. In addition to *Bryopsis corticulans* Setchell, three bryopsidoid entities, with different reproductive characteristics, are recorded from San Francisco Bay. One is entirely asexual, a good candidate for an introduced species (no need to find a mate). And by the way: *Bryopsis hypnoides* Lamouroux, reported from Humboldt Co. to San Pedro, was originally described from the Mediterranean. Like so many California cryptogenic species with far-flung distributions, we have to wonder: native or introduced?

The red alga *Caulacanthus ustulatus* (Mertens ex Turner) Kützing is a cosmopolitan, cryptogenic species, reported from Japan, Indonesia, South Africa, Spain, New Zealand—all places where plants have been designated as types for species now considered synonyms of *C. ustulatus*. This small, turfy species also occurs in Australia, Africa, India, and Hawaii, as well as British Columbia, Washington, and California. (As a student in 1979, I remember being shown a small population on Vancouver Island. Exotic! Exciting!) In southern California, *Caulacanthus* has been observed at numerous sites during the last decade or so, but was not recorded during extensive Bureau of Land Management surveys 30 years ago. Just last year, I spotted a large red brown patch in the intertidal as I walked my sister's dog in a park on San Francisco Bay. This proved to be the first sighting of this species at the Bay. Where did it come from? How does it disperse? Are these new introductions, or is this species extending its range due to climate change?

Lomentaria hakodatensis Yendo is an inconspicuous red alga that has quietly spread from its native Japan to the Mediterranean, Philippines, Hawaiian Islands, Australia and the west coast from British Columbia, Washington, and Oregon to California and Mexico. We assume it is an exotic because it wasn't reported in early surveys (e.g., E. Yale Dawson's surveys of the Northern coast from Cape Mendocino to Crescent City). Because many of our California spe-



ILLUSTRATIONS FROM THE DECEW WEBSITE

Throughout this article and within other articles in this *Fremontia* issue, illustrations appear from Tom DeCew's *Guide to the Seaweeds of British Columbia, Washington, Oregon, and Northern California*, a Web version of a book on northeast Pacific seaweeds conceived by the late Tom DeCew, and brought to its present state of completion with the collaboration of Paul Silva, Richard Moe, and Robert Rasmussen. DeCew planned the book as a detailed complement to *Marine Algae of California* by I.A. Abbott and G.J. Hollenberg (Stanford University Press, 1976).

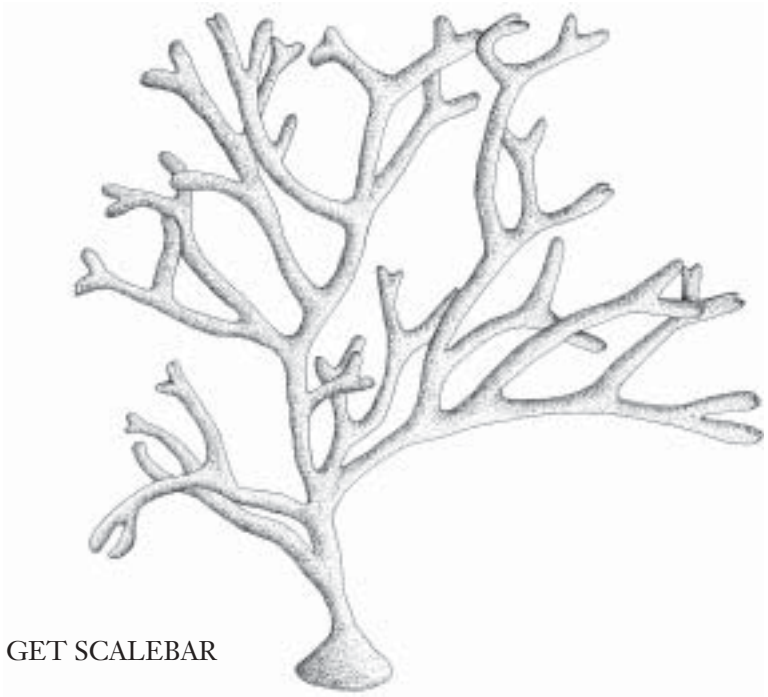
For each of the species of macroalga (seaweed) that occurs relatively commonly in British Columbia, Washington, Oregon, or northern California, Decew assembled information from specimens in West Coast herbaria and from personal collections. Each page contains a graphic depiction of distribution and reproductive status, often along with a specially commissioned original line drawing. He also compiled all published references of scientific studies for each species. The Web version, which follows the layout of the book, including all of the data and most of the illustrations for the species of brown and green algae, can be found at *http://ucjeps.berkeley.edu/guide/*.

***Bryopsis hypnoides*, a green alga, was described originally from the Mediterranean.**
Line drawing from DeCew Guide, used with permission from Paul Silva.

cies also occur in Japan, it is difficult to determine without good historical collections if a given species occurs naturally throughout the eastern and western north Pacific or if it is an introduction. *Gelidium vagum* Okamura is another small red alga, native to Japan, China, and Russia. It has a limited distribution in British Columbia and has now appeared in Tomales Bay, California. Since Tomales Bay is home to oyster mariculture, this species may have been introduced as a hitchhiker with oyster spat from Washington.

As in the Thau Lagoon, oysters have been the vector for many an introduced species, including *Sargassum muticum* (Yendo) Fensholt, a species that can be considered our first truly invasive species due to its rapid spread. Introduced to the west coast from Japan before World War II, it was detected in British Columbia in 1944, Oregon in 1947, Crescent City, California in 1963, Santa Catalina Island in southern California in 1970, and San Francisco Bay in 1973. While studies have not confirmed that *Sargassum muticum* is ecologically harmful, (e.g., displacing native species), it is certainly a conspicuous and abundant part of our intertidal and shallow subtidal communities. In 1973, when it arrived in the Solent region of southern England (possibly from a shipment of British Columbia oysters), efforts to eradicate it ended in failure, even after volunteers removed 475 tons over the course of three years. Such efforts here, if we chose to undertake them 30 years after the introduction, would surely fail as well.

Oyster mariculture may be implicated in the dispersal of the green alga *Codium fragile* subsp. *tomentosoides* (van Goor) P.C. Silva, another weed adept at asexual reproduction. *Codium fragile* comprises several well-behaved subspecies native to temperate Pacific coasts, but was lacking in the Atlantic until a weedy strain (subsp. *tomentosoides*) was introduced to the Netherlands from Japan (its presumed source) shortly before 1900. This weed has spread with increasing rapidity throughout the North Atlantic, including the Mediterranean and the North American coast from Nova Scotia to North Carolina. It is now at home in New Zealand, Australia, and California (San Francisco and Tomales bays). An herbivorous sea slug checks the growth of the weed in New Zealand. In England and Ireland, the weed has been reported to displace a native species, *Codium tomentosum*. In New England it overgrows and dislodges shellfish (thus earning the name "oyster thief") and gangs up with an introduced bryozoan to displace native kelps. To date in California it is confined to two bays and is thus separated from our native subspecies, which is well represented on the outer coast from Alaska to Baja California, Mexico.



The distinctive "Dead man's fingers", *Codium fragile* subsp. *tomentosoides*, has the second, well-earned, name of "oyster thief". Our native subspecies lives on the outer coast, while the invasive *C. fragile* subsp. *tomentosoides* has been found only in San Francisco and Tomales bays. Line drawing from DeCew Guide, used with permission from P. Silva.

The next two non-native seaweeds are infamous aggressors, though how they will play in California is yet to be seen. In 2000, both the green alga *Caulerpa taxifolia* (M. Vahl) C. Agardh, and the brown kelp *Undaria pinnatifida* (Harvey) Suringar showed up in southern California. News of the first has swamped interest in the second, because *Caulerpa* had proven itself to be a devastating plague in the Mediterranean. Distasteful to herbivores, it has covered acres of seafloor, out-competing native seagrasses and smothering native fauna.

The culprit is an escaped invasive aquarium strain, identified as originating in Australia and subsequently hybridizing with other strains, creating a strain tolerant of temperate waters. During eelgrass surveys, *Caulerpa* was discovered in a shallow lagoon, Agua Hedionda, near San Diego and in Huntington Harbor, California. Because the plant fragments and regenerates, it cannot be manually removed.

***Undaria pinnatifida*, native to Japan, Korea, and China, is known as wakame in Japanese cooking. Photograph by K.A. Miller.**

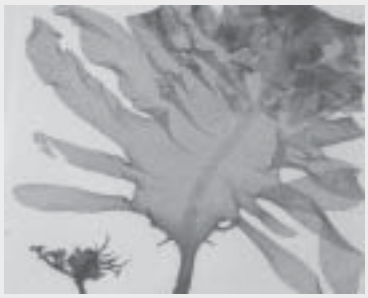
Protect Our Coast from An Invasive Kelp

Undaria pinnatifida originated in Asia and has spread around the world to Australia, New Zealand, South America, Europe—and now California. *Undaria* is unlike any other California kelp. Its blade is delicate (thin), elaborately lobed along the margin, and has a prominent midrib. It can be three to five feet long, and if you look closely, you'll see tiny dots scattered over the surface, formed by tufts of microscopic hairs. The reproductive structure (sporophyll) develops below the blade, just above the holdfast, and is unique in that it is deeply frilled, like old-fashioned ribbon candy. The blade persists from spring through summer, and then erodes back to the holdfast and sporophyll.

If you find this species, take a picture of it underwater. If this is not possible, collect a specimen for a photograph *but do not* throw it back into the water! Rather, dispose of it on land, and contact Dr. Kathy Ann Miller, Wrigley Marine Science Center, Santa Catalina Island, (310) 510-4012 (*kam@usc.edu*).

There are several websites with useful additional information about this seaweed (search the Web for *Undaria pinnatifida*). For example, the site at *biology.ucsc.edu/people/potts/lonhart/undaria.html* includes many images of this plant.

Holdfast of *Undaria pinnatifida.*



Blade of *Undaria pinnatifida.*

Caulerpa patches were covered with tarp and bleach was injected beneath. A couple of years of this treatment (and several million dollars) resulted in a tentative victory: *Caulerpa* has not been seen at these sites in more than a year, and has not been reported from new sites. Quarterly monitoring continues until complete eradication can be declared.

Ten species and four subspecies of *Caulerpa* are sold in aquarium stores in southern California. Of these, 12 are capable of surviving in the temperate zone, and are potential escapees.Because of difficulties identifying the invasive strain, the chance of a new introduction is very real until all species of *Caulerpa* are banned from the aquarium trade.

While news of *Caulerpa* reached the public in newspapers, television, and Internet reports, *Undaria pinnatifida*, a two meter long kelp native to Japan, Korea, and China silently skipped its way up the California coast from harbor to harbor, from Los Angeles to Santa Barbara. In 2001, it leaped to Monterey Harbor and a small cove on the leeside of Santa Catalina Island. Over the past several decades, *Undaria* has invaded Europe, the Mediterranean, South America, and Australia and New Zealand, through deliberate introductions (it is a prized food) and probably by hitchhiking on the hulls of ships. Like many invaders, it has a broad tolerance for temperature and thrives in quiet water, especially in the presence of the nitrogen enrichment typical of harbors. In California harbors, it is a short-lived annual, recruiting in the early spring, and with a smaller pulse of new sporophytes in the fall at some sites, and then disappearing for the winter. Santa Catalina Island, one of the California Channel Islands, is the only site at which it co-occurs with native seaweeds in a relatively natural (non-harbor) setting. There it lives at record-setting depths (up to 24 m) in the clear offshore waters. In three years of observation at Catalina, *Undaria* has spread within the site, moving into shallower depths (including the understory of a giant kelp bed), but it has not extended its range to other sites around the island or other islands.

Because it is an annual, *Undaria* does not appear to compete with perennial native kelps, but it certainly warrants status as a potential pest, capable of usurping habitat for much of the summer. The California Department of Fish and Game is making efforts to eradicate it from Santa Barbara harbor, and volunteer groups are chipping away at the Catalina and Monterey populations. However, many predict that

any effort to remove *Undaria* at this point is too little and too late. The kelp life history promotes long-term survival of the species through highly variable conditions. Each kelp plant is capable of dispersing millions of spores and establishing populations of the microscopic, filamentous sexual phase. *Undaria* is probably here to stay, although we should make every effort to eradicate it. Whether it will continue its march up the coast remains to be seen.

A final species deserves mention, because there is evidence that it may be establishing itself in California after years of unsuccessful introductions. This is the brown alga *Ascophyllum nodosum* (Linnaeus) Le Jolis, the knotted wrack native to the Atlantic, used to steam clams and lobsters or pack bait. It has been sighted floating in the Bay on many occasions over the years, surely as discarded packing material, but only this year has a sample been collected that might indicate that it has settled in. This too was floating, like the ecad (ecological form) of *Ascophyllum* called *scorpioides*; attached plants have not yet been observed.

The brown alga *Ascophyllum nodosum*, native to the Atlantic, is used to pack bait. It may be establishing itself in California after many years of unsuccessful introductions. Image courtesy of University Herbarium, UC Berkeley.

This example reminds us that the establishment of a non-native species is not a simple slam dunk. Those species blessed with a peculiar suite of attributes (broad physiological tolerances, copious reproductive abilities, and facile dispersal mechanisms) still require a large dose of luck to establish on foreign shores.

To date *Sargassum muticum*, *Caulerpa taxifolia*, *Undaria pinnatifida*, and perhaps *Caulacanthus ustulatus* can be considered invasive weeds as well as non-native components of the California flora. What will the future hold? Introductions seem to be increasing (*Caulerpa* and *Undaria* arrived simultaneously in the new millennium), and the consequences of this global homogenization of species are mixed. Some, or perhaps most, introductions are benign or neutral, but others are disastrous, setting the scene for "invasional meltdowns," facilitating other invasions and sometimes increasing the impact of subsequent invaders. I've often thought that the urchin-dominated habitats that have replaced some of our kelp forests in southern California are fine settings for the invasion of seaweed species distasteful to urchins, who could really challenge our native kelps to a run for their money. But luck has been with us, so far. It's clearly more important than ever to continue to study our shores and to train our students to recognize our native California seaweeds—and the new arrivals.

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