NOTE

Preliminary reports from the *Caulerpa taxifolia* invasion in southern California

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ABSTRACT: We report the first preliminary *in situ* observations of the invasive strain of the tropical green seaweed *Caulerpa taxifolia* in Huntington Harbor, California. Although patch size had regressed from the previous, presumably summer, extent, *C. taxifolia* exhibited new frond growth within patches despite low winter water temperature. The growth patterns, size of fronds, density, and biomass were similar to those reported from other invasion sites in the Mediterranean Sea and Australia. The seagrass *Ruppia maritima* also grew at the site. In patches mixed with *C. taxifolia*, the biomass of *R. maritima* was 20 times lower than in patches without *C. taxifolia*.

KEY WORDS: Invasive species · *Caulerpa taxifolia* · *Ruppia maritima*

In June 2000, the Mediterranean invasive strain of *Caulerpa taxifolia* was identified at 2 sites in southern California (Jousson et al. 2000). Since it was first discovered in the Mediterranean Sea in 1984, this invasive seaweed has continued to expand its range in the Mediterranean and Adriatic Seas (Meinesz 1999). It is considered a major ecological threat to native marine biodiversity (Académie des Sciences 1997) and one of the top 100 invasive species on earth (IUCN The World Conservation Union: http://www.issg.org/booklet.pdf). *C. taxifolia* is not native to the west coast of the USA (Abbott & Hollenberg 1976, Stewart 1991) or Baja California (Dawson 1944, Zertuche-González et al. 1995). The closest natural population of *C. taxifolia* occurs in Hawaii (Magruder & Hunt 1979).

Here we report preliminary observations made on 29 and 30 January 2001 in 1 of 2 ponds (‘west pond’, 33.72862 N, 118.06669 W digital degrees) infested by *Caulerpa taxifolia* at Huntington Harbor, Orange County, 1 of 2 invaded sites in southern California. Our observations were necessarily opportunistic and limited because access to *C. taxifolia* eradication sites in California was restricted, was difficult to arrange, and coincided with storm events that limited underwater visibility to ca. 40 cm. Our objectives were to observe the growth habit of *C. taxifolia*, without interfering with the eradication program underway (Anderson & Keppner 2001), and to make broad comparisons with *C. taxifolia* in other invasions. Although hardly exhaustive, our measurements of biomass, size structure, and density of *C. taxifolia* in Huntington Harbor are the only such data available from the western hemisphere.

The date when *Caulerpa taxifolia* first invaded Huntington Harbor is unknown, although an anecdotal account suggests *C. taxifolia* was present in 1998 (S. Murray pers. comm.). By summer 2000, *C. taxifolia* had become established in 2 artificial ponds created within a waterfront housing development adjacent to the main harbor. The ponds are largely concrete enclosures, each approximately 1.2 ha in surface area, and are surrounded by houses and lawns. Circulation is provided artificially by pumping seawater through culverts between the ponds and the main harbor. The maximum depth of the west pond is 3 m.

**Materials and methods.** Using SCUBA, we searched the pond benthos for *Caulerpa taxifolia*. We then sampled the areas covered by *C. taxifolia* to characterize the *C. taxifolia* canopy. We counted the number of upright primary fronds and stolon meristems of *C. taxifolia* in 25 × 25 cm quadrats (*n* = 4) haphazardly tossed into vegetated areas. A primary frond, which can branch into secondary fronds, was delineated by a single insertion point on the horizontal stolon. We removed above and below ground vegetation in additional quadrats (*n* = 10 with *C. taxifolia*, *n* = 5 with the seagrass *Ruppia maritima*) and counted the number of primary fronds and stolon meristems. We measured frond widths (widest point) and lengths from the insertion point on the stolon to the tip of the longest frond and compared these with canopy height measurements in the field. After removing sediments and epiphytes, we weighed *C. taxifolia* and *R. maritima* samples after drying at 70°C. We could not extrapolate to biomass in the pond because data on coverage were not available, nor could we estimate it due to time constraints and poor visibility.

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Results and discussion. *Caulerpa taxifolia* grew in discrete patches in the soft clay sediments in 2 to 3 m water depth in Huntington Harbor. The salinity was 34‰ (R. Woodfield pers. comm.). We found 3 major patches with smaller patches (20 × 20 cm) scattered around the major patches. Visibility was too poor to measure the size of major patches, but they were estimated to be over several meters in diameter. The smaller patches apparently had receded from their former extent because, swimming away from their perimeters, we found single thalli, then decomposed thalli at a maximum of 150 cm from the perimeter, then mud. Although the water temperature was 10 to 12°C, which limits the growth of the invasive strain of *C. taxifolia* (Komatsu et al. 1997), some frond tips exhibited new growth within the patches. We also observed over 20 unattached fragments of *C. taxifolia* consisting of stolons with fronds and rhizoids intertwined in the canopy.

The biomass, frond density, and size of *Caulerpa taxifolia* from different invasion sites are similar (Table 1). Although not all mean or extreme values from other sites fell within the 95% confidence intervals for the Huntington Harbor means, we do not want to overinterpret results based on small samples collected in different manners, seasons, habitats, and invasions of different ages. Instead, we focus on new observations and point out that there is a paucity of published data for quantitative comparisons.

*Caulerpa taxifolia* exhibited growth strategies typical for the genus *Caulerpa* (Williams et al. 1985, Smith & Walters 1999) that enable the various species to propagate prolifically. For example, upright fronds had developed adventitious rhizoids and stolons when lying decumbent on sediments, and stolons when entwined within the canopy. Rhizoids growing down from a stolon pillar generated fronds at the distal end. One growth feature not previously observed in any *Caulerpa* species was the profuse production of proliferations (Fig. 1) arising from upright primary fronds and higher order branches, with a radial arrangement of branchlets, which are typically planar on native *C. taxifolia*. A frond had to achieve a minimum length of 1.5 cm, but typically 4.5 cm, to develop proliferations. We assume that these proliferations produce higher-order branches. The number of primary fronds of *C. taxifolia* (240 to 4046 m⁻²) was within the range exhibited at other invasion sites (Table 1). If 20% of primary fronds (including branches) had >5 proliferative tips (Fig. 2A) and they produced secondary branches, a very dense canopy could develop.

The mean ± standard error (SE) number of stolon meristems was 555 ± 182 m⁻² (n = 10). We believe this is the first account of meristem density for an invasive population of *Caulerpa taxifolia*. This high meristem density highlights the potential for proliferation both across the sediment and by growing upwards and over

<table>
<thead>
<tr>
<th>Site</th>
<th>Reference</th>
<th>No. primary fronds m⁻²</th>
<th>Biomass (g dry wt m⁻²)</th>
<th>Mean length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Huntington Harbor 95% CI</td>
<td>This study</td>
<td>1478 ± 1296 (14)</td>
<td>102 ± 97 (10)</td>
<td>10.4 (197)</td>
</tr>
<tr>
<td>Moreton Bay, Australia</td>
<td>Pillen et al. (1998)</td>
<td>4138 ± 1370 (nd)</td>
<td>86 ± 7.2 (nd)</td>
<td>6 ± 3.1 (nd)</td>
</tr>
<tr>
<td>Cap Martin, France</td>
<td>Meinesz et al. (1995)</td>
<td>5100 to 13 920 (14)</td>
<td>500 (nd)</td>
<td>mostly &lt;20</td>
</tr>
<tr>
<td>Elba Island, Italy</td>
<td>Ceccherelli &amp; Cinelli (1998)</td>
<td>250 to 2700 (4 monthly)</td>
<td>nd</td>
<td>3 to 16</td>
</tr>
<tr>
<td>New Caledonia</td>
<td>Garrigue (1994)</td>
<td>≤37 (nd)</td>
<td>1836 (nd)</td>
<td>2 to 10</td>
</tr>
</tbody>
</table>

Table 1. Comparison of *Caulerpa taxifolia* between invasion and native (New Caledonia) sites. 95% confidence interval (CI) provided for Huntington Harbor data. Dimensions are for live material, except for Cap Martin (herbarium material). Data are mean ± standard deviation (SD) with number in parentheses. nd: no data

Fig. 1. Portion of a frond of *Caulerpa taxifolia* with many proliferative tips. Arrows point to several examples. Scale in cm
other organisms. The stolon meristems of various species of Caulerpa, including Caulerpa taxifolia in its native habitat (S. L. Williams unpubl. data from St. Croix, U.S. Virgin Islands) and the invasive Mediterranean strain, can grow at least 1 cm d⁻¹ in the field (O’Neal & Prince 1982, Williams et al. 1985, Williams & Dennison 1990, Boudouresque 1997). Stolon growth rates together with meristem density provide a basis for modeling spread rates.

Gigantism is considered a characteristic of the genetically differentiated aquarium strain of Caulerpa taxifolia (Jousson et al. 2000, Wiedenmann et al. 2001). Fronds of Caulerpa taxifolia in its native habitats are reported to grow to 15 cm (Taylor 1972, Magruder 1979, Garrique 1994, Littler & Littler 2000), but means and variances have not been reported. Published data on the mean size of the invasive Caulerpa taxifolia do not greatly exceed 15 cm (Table 1), although the maximum size can be up to 60 cm (Meinesz et al. 1995). The majority of the Caulerpa taxifolia fronds in Huntington Harbor were within the size range in the native habitat (Fig. 2B), but the longest frond was 24.6 cm. By proliferating over the top of the highest-order branches, Caulerpa taxifolia attained a mean canopy height of at least 20 cm in Huntington Harbor. The mean ± standard deviation (SD) frond width was 1.36 ± 0.38 cm (maximum 2.1 cm, n = 76), with 70% of the fronds <1.8 cm. Frond width data are not available for other populations. The entire genus is notorious for remarkable morphological plasticity in response to the environment (Jaubert & Meinesz 1981, Carruthers et al. 1993, Meinesz et al. 1995, Ceccherelli & Cinelli 1999, Collado-Vides & Robledo 1999). Frond size-frequency data from native and other invasive populations would be useful for a rigorous assessment of population differences. If found, such differences could be the result of genetic differentiation in the aquarium-invasive strains, morphological plasticity in response to the environment, or some other factor, e.g. differences in epiphytes, pathogens, or grazers.

Ruppia maritima, a submerged aquatic vascular plant protected under the USA Clean Water Act, grew over large areas of the study pond, a feature of the invaded habitat not previously reported. Ruppia maritima provides important habitat for waterfowl (Kantrud 1991), which were present in the invaded ponds at Huntington Harbor. Most, but not all, of the R. maritima had a collapsed, senescent canopy of flowering shoots, its typical winter state in southern California (S. L. Williams et al. unpubl. data). Caulerpa taxifolia grew intermingled with Ruppia maritima in some of these patches. In the non-senescent patches sampled, the biomass of Ruppia maritima was reduced where it grew with Caulerpa taxifolia compared with where it grew alone (Fig. 3); the 95% confidence intervals for the biomass means did not overlap. Although our data are few and correlative, lower seagrass biomass in the presence of Caulerpa taxifolia is consistent with the observations that Caulerpa taxifolia is overgrowing the native seagrass (Zostera marina) in Agua Hedionda, California (R. Woodfield pers. comm.) and that it can outcompete native seagrasses in the Mediterranean (Ceccherelli & Cinelli 1997, 1998, 1999). If this is true, then Caulerpa taxifolia,
together with Musculista senhousia and Bunodeopsis sp., forms a trio of non-native species having deleterious effects on native seagrasses in southern California (Reusch & Williams 1998, 1999, Williams & Heck 2001).

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