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Short communication

Biomass seasonality of *Caulerpa taxifolia* in the Mediterranean Sea

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Abstract

The biomass of the introduced and invasive alga *Caulerpa taxifolia* was measured monthly over one year at four different sites along the French Mediterranean coast at depths of 5 and 20 m in a sheltered and an exposed area. At the 5 m depth, *C. taxifolia* mean biomass ranged from 203 to 518 g dry wt. m⁻², while at the 20 m depth, it ranged from 62 to 466 g dry wt. m⁻². The study clearly shows that a major characteristic of *C. taxifolia* is its perennial life cycle with relatively high biomass values throughout the year, in different biotopes. This could be a factor in the broad ecological impact of *C. taxifolia*.

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1. Introduction

The main vectors for introduction of alien species in the marine environment are internal oceanic canals, ballast waters, ship fouling, aquaculture, fishing baits, scientific research and aquariums (Galil, 2000). It is through the aquarium trade that *Caulerpa taxifolia* Vahl C. Agardh (Chlorophyta) was introduced into the Mediterranean in 1984 (Meinesz and Hesse, 1991; Jousson et al., 2000). This highly invasive alga, which is still

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spreading in the Mediterranean, has already affected six countries and more than 13,000 ha of sea bottom are infested (or affected) (concerned does not have that meaning in English) (Meinesz et al., 2001). Invasive strains of C. taxifolia were also discovered in California, Australia and Japan (Jousson et al., 2000; Millar, 2001; Schaffelke et al., 2002; Williams and Grosholz, 2002; Komatsu et al., 2003). In the Mediterranean, C. taxifolia which forms dense meadows, able to invade a large number of coastal benthic habitats (not an English word, maybe use habitats?) as well as sheltered and exposed locations (Boudouresque et al., 1995). The depth range of dense C. taxifolia meadows varies from few meters under the surface to over 40 m. Sparse populations can grow to 55 m deep and isolated individuals have been observed at depth of 100 m (Meinesz and Hesse, 1991; Belsher and Meinesz, 1995). A high density of C. taxifolia within an invaded area has been reported to be one of the main causes of disturbance to other flora and fauna but information concerning biomass comes only from fragmented data, collected under different conditions (Meinesz and Hesse, 1991; Pou et al., 1993; Verlaque and Fritayre, 1994; Meinesz et al., 1995; de Villèle and Verlaque, 1995) that do not give an accurate description of the invasion. Thus, it was necessary to collect these fundamental data on C. taxifolia ecology, hypothesising that the conditions of hydrodynamism and depth strongly influence the development of the alga. Also, knowledge of the annual growth pattern under different conditions is important to achieve a better understanding of the impact of C. taxifolia on the invaded ecosystems and to give information to managers attempting its control.

2. Materials and methods

C. taxifolia samples were collected from 50 cm \times 50 cm quadrats by scuba diving with a 3 m long air vacuum. Three-ten samples per site were taken monthly between March 1999 and February 2000 at four sites of the Alpes-Maritimes (France) with full coverage by *C. taxifolia*:

- (i) Cap Martin (N43°45′04″E7°29′17″), rocky substrate, 5 m deep, exposed site;
- (ii) Cap Martin, rocky substrate, 20 m deep, exposed site;
- (iii) Golfe-Juan (N43°34'08"E7°05°08"), sandy-muddy substrate, 5 m deep, sheltered site;
- (iv) Bay of Villefranche-sur-Mer (N43°42'00"E7°29'17"), sandy-muddy substrate, 20 m deep, sheltered site.

C. taxifolia grows on the steep slope of Cap Martin. This site is frequently exposed to thermic variation because of wind exposure, changing currents and upwelling of cold water (Belsher and Houlgatte, 2000). In contrast, the bays of Golfe-Juan and Villefranche-sur-Mer support dense *C. taxifolia* meadows on a flat bottom, protected from wind exposure and frequent thermic variation (Romanosky, 1955; Hentsch, 1962).

Samples were cleaned of all debris, epiphytes and sediments prior to being dried for 24 h at 80 °C, after which dry weight was measured (Ballester, 1985).

Mean *C. taxifolia* biomass in g dry wt. m^{-2} (Standard Error), [*n*], collected in Cap Martin 5 m (CM5), Cap Martin 20 m (CM20), Golfe-Juan 5 m (G5), Villefranche 20 m (V20) between March 1999 and February 2000

| Depth | Substrate | Winter | | | Spring | | | Summer | | | Autumn | | | Station |
|-----------|-----------|-------------|-------------|--------------|--------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|---------|
| | | January | February | March | April | May | June | July | August | September | October | November | December | |
| Exposed | | | | | | | | | | | | | | |
| 5 m | Rock | 336.6; | 269.2; | 233.6; | 269.6; | 281.6; | 336.4; | 291.6; | 386.8; | 396; | 406; | 427.6; | 322.4; | CM5 |
| | | (14.8); [5] | (26.4); [5] | (18.8); [10] | (20.8); [10] | (36.8); [7] | (36.4); [6] | (93.6); [5] | (24.8); [6] | (46.4); [4] | (102); [5] | (16); [5] | (47.6); [4] | |
| 20 m | Rock | 258; | 224; | 250; | 203.6; | 234; | 154.4; | 158.4; | 235.6; | 244.8; | 203.6; | 256.8; | 219.6; | CM20 |
| | | (36.4); [5] | (14); [5] | (21.6); [10] | (17.2); [10] | (35.5); [8] | (25.2); [8] | (16.4); [6] | (26.4); [6] | (41.6); [4] | (11.6); [4] | (26.8); [5] | (29.2); [5] | |
| Sheltered | | | | | | | | | | | | | | |
| 5 m | Muddy- | 220; | 242.4; | 122.8; | 170; | 198.6; | 276.8; | 466.1; | 518.4; | 466; | 442.8; | 352.5; | 220; | G5 |
| | sandy | (19.6); [5] | (21.2); [5] | (12.8); [4] | (11.6); [5] | (21.2); [5] | (30); [5] | (16.8); [5] | (8.4); [4] | (10); [3] | (32.8); [4] | (44.4); [5] | (22.8); [5] | |
| 20 m | Muddy- | 88; | 63.6; | 62.4; | 54.8; | 88.6; | 85.6; | 82; | 95.2; | 100; | 96.5; | 101.2; | 82.4; | V20 |
| | sandy | (12.4); [5] | (2.4); [5] | (6.8); [10] | (5.6); [9] | (15.6); [6] | (10.4); [6] | (7.6); [6] | (8.4); [4] | (11.6); [5] | (14); [5] | (11.2); [5] | (12.4); [5] | |

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Because the biomass values, after a $(\sqrt{x})^{-1}$ transformation, matched the conditions of normality (Kolmogorov–Smirnoff's test) and homoscedasticity (Leven's test), a one-way ANOVA followed by a SNK test was performed to compare the seasonal biomass of *C. taxifolia* between the four sampled sites (see Table 1).

3. Results

At all sites, *C. taxifolia* contribute considerable biomass throughout the year (between 55 and 518 g dry wt. m⁻²), with maximum values reached between summer and autumn (Table 1). Clear differences between the sites were only apparent in summer. During spring, winter and autumn, the difference between the sites was not clear, except for the biomass values recorded in Villefranche (20 m) which were lower all year. In a sheltered environment the monthly biomass was higher at 5 m than at 20 m and biomass values measured at Golfe-Juan showed the highest annual variation in amplitude. In the exposed environment, the range of variation was narrow and biomass was only significatively higher at 5 m depth in summer and autumn (Table 2).

4. Discussion

C. taxifolia can cover most of the substrate, forming a dense meadow that appears stable and homogeneous over time. However, the quantity of *C. taxifolia* varies with time, and maximum biomass occurs in summer and autumn. Shallow waters are more suitable for *C. taxifolia* development and the highest biomass was measured within the 6–10 m depth (from 470 to 800 g dry wt. m⁻²) (Meinesz et al., 1995; Verlaque and Fritayre, 1994; de Villèle and Verlaque, 1995). Changes in biomass are sudden in exposed areas due to frequent thermic variation whereas biomass variations are progressive in sheltered environments. The development of the alga depends strongly on the substrate. The maximum biomass previously recorded, 600–800 g dry wt. m⁻², was measured inside a *Posidonia oceanica* bed (de Villèle and Verlaque, 1995), and was much higher than our biomass measurements. Because *C. taxifolia* is not water nutrient limited (Delgado et al., 1995), it is able to create its own substrate with its root-like rhizoids (Finzer and Poizat, 1996; Chisholm et al., 1996), thus we can

Table 2 Analysis of variance on seasonal C. taxifolia biomass (g dry wt. m^{-2})

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|--------|--|------|-------|-------|-----------------|--|
| Season | Source of variation | d.f. | MS | F | <i>p</i> -value | SNK test of the interaction between the stations |
| Winter | Stations (CM5 \times CM20 \times G5 \times V20) | 3 | 89.2 | 74.55 | 0.00 | CM5 = G5 = CM20 > V20 |
| Spring | | 3 | 60.3 | 31.46 | 0.00 | CM5 = G5 = CM20 > V20 |
| Summer | | 3 | 109.4 | 59.56 | 0.00 | G5 > CM 5 > CM20 > V20 |
| Autumn | | 3 | 84.5 | 45.81 | 0.00 | CM5 = G5 > CM20 > V20 |

hypothesis that the main factors driving *C. taxifolia* development are temperature, light and physical disturbance.

Among all the *C. taxifolia* population in the world (introduced or natural), the Mediterranean populations exhibit the highest biomass. Thus, Williams and Grosholz (2002) reported 102 g dry wt. m⁻² in Huntington Harbor (3 m depth on mud) (California, USA), which is much lower than our data obtained in Golfe-Juan (shallow sheltered site). Pillen et al. (1998) recorded in the sheltered and shallow part of Moreton Bay (Brisbane, Australia) a biomass value of 86 ± 7.2 g dry wt. m⁻², which is lower than all the biomass values in the Mediterranean. In a tropical regions, autochthonous stands of *C. taxifolia* are isolated or of patchy distribution. Garrigue (1994) measured a very low mean biomass value in the lagoons of New Caledonia: 0.073 g dry wt. m⁻² (maximum 1.8 g dry wt. m⁻²).

The biomass of *C. taxifolia* is often greater than the biomass of other species of *Caulerpa* in the Mediterranean. Thus, throughout the year, the biomass values of *C. taxifolia* are always greater than those of *Caulerpa prolifera* (Forsskål) Lamouroux [from <5 g dry wt. m⁻² to 289 g dry wt. m⁻²] (Ballesteros 1989–1990; Pérez, 1989; Meinesz, 1979; Perez-Ruzafa et al., 1989; Terrados and Ros, 1995). Only Gessner and Hammer (1960) recorded at Villefranche-sur-Mer, in October, biomass values (360–375 g dry wt. m⁻²) close to those of the *C. taxifolia* meadows at the same depth (442.8 ± 32.8 g dry wt. m⁻²). The biomass of the introduced *Caulerpa racemosa* (J. Agardh) Borgesen changes greatly throughout the year. According to Piazzi et al. (2001) biomass values of *C. racemosa* (447 g dry wt. m⁻² on dead mat of *P. oceanica* and 250 g dry wt. m⁻² on rocks, growing in Livorno, Italy, between 2 and 5 m deep in Autumn) are close to those of *C. taxifolia* under similar conditions. In spring the biomass of *C. racemosa* is much lower than that of *C. taxifolia* (19–20 g dry wt. m⁻² on rock and dead matt) (Piazzi et al., 2001).

The main difference between the life cycle of *C. taxifolia* and the other Mediterranean macrophytes is that this species exhibits its highest biomass in autumn, when autochthonous algal productivity is decreased (Ballesteros, 1989) facilitating competition in the photophilic algal communities (Verlaque and Fritayre, 1994). During the winter drop, the minimal biomass is made up of a dense web of thick stolons bearing short highly ramified primary axes (Meinesz et al., 1995) still fully covering the substrate and assuring the re-growth of the alga in spring (Komatsu et al., 1997). These characteristics lead to the modification of the habitat structure, with various direct or indirect consequences impacting the flora and fauna (Boudouresque et al., 1995).

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