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Temporal and spatial variability in shallow- and deep-water populations of the invasive *Caulerpa racemosa* var. *cylindracea* in the Western Mediterranean

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ABSTRACT

The invasive green alga *Caulerpa racemosa* var. *cylindracea* represents an important threat to the diversity of Mediterranean benthic coastal ecosystems by interfering with native species and modifying benthic assemblages. The present study deals, for the first time, with the temporal and spatial variability of the biomass and phenology of *C. racemosa* considering both deep- and shallow-water populations. Two sampling depths (30 and 10 m) were sampled at three different rocky bottom sites every 3 months in the Archipelago of Cabrera National Park (Western Mediterranean). All morphometric variables analysed showed a spatial variation and temporal patterns depending on depth. Between depths, *C. racemosa* biomass, stolon length, number of fronds and frond length were usually significantly higher at deep-water populations, suggesting that *C. racemosa* grows better in deep-waters. Deep- and shallow-water populations displayed a high temporal variation although no evidence of seasonal patterns was found, in contrast with what has been reported by other authors. The sources of this variability are still unknown but probably both physical factors and differential herbivory pressures display a key role.

1. Introduction

In the Mediterranean Sea, invasions of the green algae of the genus *Caulerpa* represent an important threat to the diversity of benthic coastal ecosystems (Boudouresque and Verlaque, 2002), interfering with native species (Piazzi et al., 2001; Piazzi and Cinelli, 2003), and modifying benthic assemblages (Argyrou et al., 1999; Balata et al., 2004). *Caulerpa racemosa* (Forsskål) J. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque was observed for the first time off the coast of Libya (Nizamuddin, 1991) and it spread steadily to almost all of the Mediterranean (Piazzi et al., 2005), where it behaves as an invasive species (Boudouresque and Verlaque, 2002). Several studies have demonstrated macrobenthic diversity constraints due to *C. racemosa* invasion (e.g. Piazzi et al., 2001, 2005; Balata et al., 2004; Piazzi and Balata, 2008; Vázquez-Luis et al., 2008) but very few studies deal with its temporal and spatial variability. On the other hand, the scarce available information concerning *C. racemosa* biomass and phenology comes only from fragmented data, collected under different conditions and localities (Klein and Verlaque, 2008), which prevents an accurate description of the invasion dynamics of *C. racemosa*. Thus, we need more rigorous comparable studies on *C. racemosa* seasonal pattern of biomass and growth patterns including different regions, conditions and habitats, in order to provide a better understanding of the invasive capacity of this species.

Caulerpa racemosa is able to invade benthic assemblages between 0 and 70 m depth, where it behaves far more aggressively than the better known *Caulerpa taxifolia* (Klein and Verlaque, 2008). However, most studies regarding its seasonal cycle have been conducted in shallow-waters, above 20 m depth with the exception of a recent study made by Klein and Verlaque (2009) which was performed in coastal detritic bottoms at a depth of 29 m. Thus, in this study we want to widen the knowledge on the temporal and spatial variability of the biomass and morphometric features of *C. racemosa* by comparing populations thriving in shallow- and deep-waters. In particular we want to address two different but related questions: (1) is there any regular temporal pattern in the biomass and morphometric changes of *C. racemosa*; and (2) do shallow- and deep-water populations differ in these parameters?

2. Materials and methods

2.1. Study area

This study was carried out in the Archipelago of Cabrera National Park (Western Mediterranean; 39° 13′ 30″N; 2° 58′E). *Caulerpa*

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racemosa was recorded for the first time in 2003 growing at 30–35 m depth, and rapidly spread to almost all habitats present between 0 and 65 m depth. Samples to study the spatial and temporal variability in biomass and morphometric features of *C. racemosa* populations were collected every 3 months, from July 2006 to November 2007. Three rocky bottom sites were randomly chosen within the Archipelago of Cabrera National Park: Freu de la Imperial (hereafter FI), Ses Rates (SR) and Illot Foradat (IF), and two sampling depths were selected at each locality: 10 m (shallow-water) and 30 m (deep-water).

2.2. Sampling procedures

At each studied population (three sites × two depths); three replicate randomly positioned plots of 20 × 20 cm^2 were sampled every 3 months by SCUBA diving. The plots were scraped and stored in individual plastic bags and later sorted and quantified in the laboratory. Stolon length, stolon biomass, frond biomass, number of fronds, mean length of the fronds, and total biomass (dry weight) were quantified for each sample. Dry weight was obtained after drying at 60 °C to constant weight.

2.3. Statistical analyses

Total biomass of *Caulerpa racemosa* was strongly and significantly correlated with frond ($r^2 = 0.920$; $p < 0.0001$) and stolon ($r^2 = 0.967$; $p < 0.0001$) biomass. Thus, in order to avoid redundancy on the results section, total biomass, stolon length, number of fronds and frond length of *C. racemosa* are the only variables used in the permutational univariate analyses. The data were considered to represent a fully three-way design of samples (replicates) within sampling time (random factor Ti), within sites (random factor Si) and within depths (fixed factor De). These data were subjected to a three factorial univariate PERMANOVA based on Euclidean distance. Although variables were univariate a PERMANOVA has been employed because the null distribution of the test statistic in PERMANOVA is produced by permutation, thus avoiding the usual normality assumptions of ANOVA, and also permitting interpretation of interaction terms within random factors (Anderson, 2001). These analyses, and others described subsequently, were carried out using the Primer v6 statistical package (Clarke and Gorley, 2006), in conjunction with the Windows PERMANOVA+ module (Anderson et al., 2008).

3. Results

At 10 m depth, *Caulerpa racemosa* total biomass ranged between 0 (SR and FI, in July 2006) and 5.5 ± 4.5 (mean ± SD) g dw sample^{-1} (FI in July 2007) and stolon length ranged from 0 to 975 ± 544 cm (mean ± SD). The number of fronds ranged between 0 at FI in July 2006 and SR at the beginning of the study period to 184 ± 17.1

Table 1
Details of the three-factor PERMANOVA test (with time six levels, site three levels as random factors and depth two levels as a fixed factor) for all variables analysed in *Caulerpa racemosa* (biomass dw sample^{-1}, stolon length cm sample^{-1}, number of fronds sample^{-1} and mean fronds length cm).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Pseudo *F*	*p* Value	Estimates of components of variation
Biomass						
Time	5	47.48	9.496	2.0737	0.181	0.2731
Site	2	0.62	0.310	6.78e-2	0.927	−0.1185
Depth	1	54.05	54.055	1.2704	0.371	0.2251
TixSi	10	45.79	4.579	2.6784	0.012	0.4783
TixDe	5	114.53	22.905	7.4618	0.006	2.2040
SixDe	2	44.12	22.062	7.1871	0.018	1.0551
TixSixDe	10	30.69	3.069	1.7953	0.074	0.4532
Residual	72	123.11	1.709			1.7098
Total	107	460.41				
Stolon length						
Time	5	5.19e6	1.03e6	4.2824	0.028	44251
Site	2	4.80e5	2.404e5	0.9908	0.408	−61.37
Depth	1	5.13e6	5.13e6	1.5516	0.289	35238
TixSi	10	2.42e6	2.42e5	2.108	0.032	21258
TixDe	5	8.19e6	1.63e6	7.4025	0.005	1.57e5
SixDe	2	3.61e6	1.80e6	8.17	0.015	88235
TixSixDe	10	2.21e6	2.21e5	1.9243	0.058	35466
Residual	72	8.28e6	1.15e5			1.15e5
Total	107	3.55e7				
Number of fronds						
Ti	5	60935	12187	1.2627	0.373	−122.22
Si	2	10503	5251.6	0.5441	0.603	−596.75
De	1	49837	49837	0.6287	0.689	1130.3
TixSi	10	96516	9651.6	3.3635	0.002	2453.3
TixDe	5	1.340e5	26810	5.6679	0.009	3069.5
SixDe	2	1.199e5	59982	12.681	0.002	620.2
TixSixDe	10	47301	4730.1	1.6484	0.109	2869.5
Res	72	2.066e5	2869.5			
Total	107	7.257e5				
Frond length						
Ti	5	13.792	2.7584	5.3537	0.005	0.3533
Si	2	1.6271	0.8135	1.579	0.263	9.1e-2
De	1	186.88	186.88	49.055	0.001	1.8437
TixSi	10	5.1524	0.5152	3.6324	0.002	0.2494
TixDe	5	14.36	2.8719	5.7346	0.011	0.5132
SixDe	2	1.8956	0.9477	1.8925	0.202	0.1575
TixSixDe	10	5.0081	0.5008	3.5307	0.001	0.3459
Res	72	10.213	0.1418			0.3766
Total	107	238.92				