

## Lack of Severe Nutrient Limitation in *Caulerpa taxifolia* (Vahl) C. Agardh, an Introduced Seaweed Spreading over the Oligotrophic Northwestern Mediterranean

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We performed a seasonal study of the importance of nitrogen (N) and phosphorus (P) as limitation to the productivity of *Caulerpa taxifolia* (Vahl) C. Agardh, a seaweed invading the western Mediterranean coasts. The study presented here indicates that *Caulerpa taxifolia* did not respond to nutrient enrichment, except for plants collected in April and September 1993, where productivity and alkaline phosphatase activity (APA) of enriched plants varied 0.5- to 3-fold relative to those of control plants. Rates of APA ranged from 9 to 52  $\mu\text{M PO}_4 \text{ odw h}^{-1}$ , close to those characteristic of P-sufficient macroalgae. Tissue nutrient concentrations were frequently above typical critical levels for species of macroalgae ranging from 1.36 to 3.13% dw, and 0.16 to 0.21% dw, for N and P, respectively. Seasonal variation was moderate and not consistent. The lack of severe nutrient limitation in Mediterranean populations of *Caulerpa taxifolia* could be an important factor enabling it to outcompete native macrophytes.

### Introduction

The alien tropical seaweed *Caulerpa taxifolia* (Vahl) C. Agardh is presently spreading over the N. W. Mediterranean Sea (Meinesz *et al.* 1993). It was first recorded in 1989, near the Oceanographic Museum of Monaco, though its presence there is believed to date from 1984 (Meinesz and Hesse 1991). Since then, *C. taxifolia* has spread to littoral areas in France, Italy, and Spain (Meinesz *et al.* 1993, Pou *et al.* 1993, Morucci *et al.* 1994), covering more than 1500 ha in 1994 (Meinesz, *pers. com.*).

The spreading capacity of *C. taxifolia* has been associated with its potential toxicity to herbivores (Guerriero *et al.* 1992, Lemée *et al.* 1993), and its perennial character and plasticity in colonizing any type of substratum from 0 to 80 m depth (Meinesz and Hesse 1991, Meinesz *et al.* 1993). *Caulerpa taxifolia* may outcompete native macrophytes such as the seagrass *Posidonia oceanica* (L.) Delile (Villèle and Verlaque 1995), and shallow-water macroalgae (Verlaque and Fritayre 1994).

Nutrients are the principal factor limiting the productivity of Mediterranean algae when light and temperature are adequate (Margalef 1974, Ballesteros 1989). The spread of *Caulerpa taxifolia* in the Mediterranean could thus reflect the adequacy of all these factors for its growth. We evaluate here the nutritional status of *Caulerpa taxifolia* and the possibility that nutrients limit its productivity. We do so by (1) testing the photosynthetic response to nutrient enrichment bioassays, and (2) quantifying the alkaline

phosphatase activity (APA), and (3) tissue nutrient concentrations.

### Materials and Methods

*Caulerpa taxifolia* was collected from a sandy bottom in a dense meadow at 9 m depth off Cap Martin (3 km E. of Monaco, France). This area supports one of the largest (19.5 ha) Mediterranean populations of *C. taxifolia* with a cover of 90% between 5 and 10 m depth (Meinesz *et al.* 1993). *Caulerpa taxifolia* plants were collected using SCUBA diving, placed immediately in dark plastic bags to prevent direct sun exposure at the surface, and carried to the laboratory in aerated seawater at constant temperature (ranging from 14 to 23 °C, depending on the ambient water temperature at the collection site). Sampling was carried out in April, July, September, November 1993, and January and April 1994.

Water samples were collected in triplicate using 250 mL acid-washed glass bottles, and quickly frozen. At the laboratory, samples were analyzed for the concentrations of soluble reactive phosphorus (SRP), nitrates, and nitrites, following the methods described in Grasshoff *et al.* (1993). Nitrite concentrations were always < 5% of nitrate concentrations and thus are not reported here.

Once at the laboratory, plants were cleaned of epiphytes and sediment. Young, non-epiphytized blades were isolated by cutting at the stolon level, and subsequently assigned to nutrient treatments. The exper-

imental design included a control (no nutrients added), +N, +P, and +N+P, treatments. Nutrient enrichment was conducted for 10 h (from 10:00 pm to 8:00 am) (Delgado and Lapointe 1994) in 12 aerated aquaria of 20 L capacity (three replicates of one to two blades per treatment) at a constant room temperature (20 °C). Fresh ambient seawater was then used to flush residual nutrients from the aquaria. The three replicates within each treatment were assigned to tanks randomly to avoid systematic effects of shading or other gradients. Nitrogen was provided as  $\text{NaNO}_3$ , and P as  $\text{NaH}_2\text{PO}_4$ ; concentrations of N and P achieved during the pulses were 20  $\mu\text{M}$  and 2  $\mu\text{M}$ , respectively. Two subsamples from each of the replicates consisting of one whole blade of *C. taxifolia* were assayed for net productivity, dark respiration, and APA. For those bioassays, 250 mL Winkler bottles provided with magnetic stirrers were incubated either at an irradiance of 330  $\mu\text{E m}^{-2} \text{s}^{-1}$  (net productivity) or complete darkness (respiration and APA) at a constant temperature of 20 °C. Photosynthesis was saturated at the light intensity used and the temperature was optimal for *C. taxifolia* productivity in all the periods sampled (Gacia *et al.* 1994). Productivity and respiration were measured as variations in the dissolved oxygen concentration, determined to within 0.01  $\text{mg L}^{-1}$  with an Orbisphere Model 2610 oxygen measurement system, after 2 h (productivity) and 4 h (respiration) of incubation. Carbon productivity values were calculated from oxygen data using a photosynthetic quotient of 1. Alkaline phosphatase activities (APA) were determined following the spectrophotometric method of Kuenzler and Perras (1965), modified for macroalgae as described by Lapointe (1989); absorbance was measured at 410 nm on a UV-2100 Shimadzu spectrophotometer.

Productivity and nutrient tissue concentrations were reported per organic dry weight (odw) based on an average ash content of 43.1%, because seasonal variability of ash content of the thallus of *Caulerpa taxifolia* was small (< 5%).

Three replicate *C. taxifolia* plants, corresponding to a final dry weight of 1 to 2 grams per replicate, were cleaned of epiphytes in the laboratory, dried to constant weight (24 h at 70 °C), ground to a powder, and kept in sealed vials inside a desiccator containing silica gel. Total carbon and total nitrogen in tissues were determined using a 2400 Perkin Elmer CHN elemental analyzer, while total P was determined using the vanado-molybdate colorimetric method after a wet acid digestion (Jackson 1970) in a microwave oven (Mateo and Sabaté 1993).

The response in productivity, respiration, and APA to nutrient enrichment was tested using one-way ANOVA (Sokal and Rohlf 1981). Tukey's significant difference test was used to locate pairwise differences when ANOVA was significant (SYSTAT 1989). ANOVA was also used to test seasonal variations in

tissue nutrient concentration. Pearson correlation coefficients between ambient and tissue nutrients, and plant APA and productivity, were calculated for untransformed variables as recommended by Sokal and Rohlf (1981).

## Results

Nutrient concentration in the water showed relatively high nitrate and phosphorus concentrations in winter and low values from spring to autumn (Fig. 1). The SRP ranged from 0.06, close to detection level, to 0.179  $\mu\text{M PO}_4^{3-}$ . Nitrate concentrations ranged from 0.21 to 1.43  $\mu\text{M}$ . Seasonal patterns of nitrate and phosphate concentrations in the water were very similar, though they were not statistically correlated. The N : P atomic ratios of the above mentioned dissolved forms were either close to or lower, than the Redfield ratio of 16 (annual average of  $11 \pm 7$ ), falling below 5 in late summer and autumn.

No significant response of productivity of *Caulerpa taxifolia* to nutrient enrichment pulses were observed, except for plants collected in April and September 1993. The response was most noticeable in April, when productivity values for control plants were minimal (Fig. 2) ( $p < 0.05$ ). Under N-, P-, and N+P-enrichment conditions, plants collected in April 1993, increased their productivity and APA 1.5 to 3-fold compared to control plants (Figs 2, 3). In September, only N-enriched plants experienced a minor, but significant, increase in productivity and APA. A reduction of productivity (N-) and APA (N-, P-, and N+P-), with nutrient enrichment was observed in January, when APA for control plants was at its maximum. Nutrient enrichment only affected respiration rates of N-enriched plants collected in July.

Alkaline phosphatase activities of controls were low throughout the year, ranging from 9 to 52  $\mu\text{M PO}_4^{3-} \text{odw h}^{-1}$ , with a seasonal coefficient of vari-

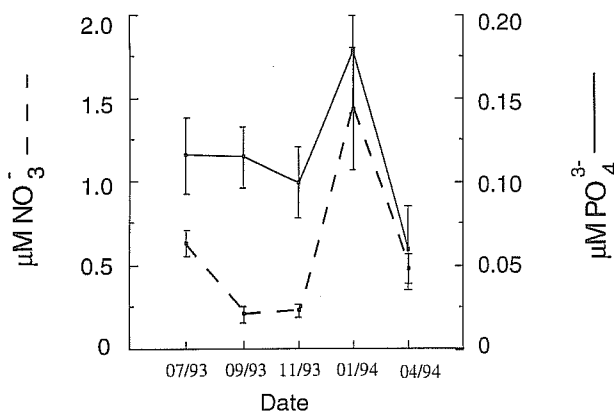


Fig. 1. Dissolved nutrient concentrations of nitrate and soluble reactive phosphorus (SRP) in the ambient seawater at Cap Martin (France), during the 13 months period (1993–1994).

ation (CV) of 50% (Fig. 3). The APA was not clearly repressed after phosphate addition, except in January when all nutrient enriched plants experienced a decrease in their APA.

Tissue N and P varied seasonally (Fig. 4, Table I;  $p < 0.01$ ). Tissue nutrient concentrations averaged  $2.27 \pm 0.61\%$  dw ( $3.39 \pm 0.98\%$  odw), and  $0.16$

$\pm 0.03\%$  dw ( $0.24 \pm 0.12\%$  odw), for N and P, respectively. Tissue nutrient concentrations were lowest in summer and highest in winter (N) and spring (P), similar to seasonal dissolved nutrient concentrations in the water. However, no significant correlation was found between tissue nutrients and dissolved nutrients and dissolved nutrients in the ambient water

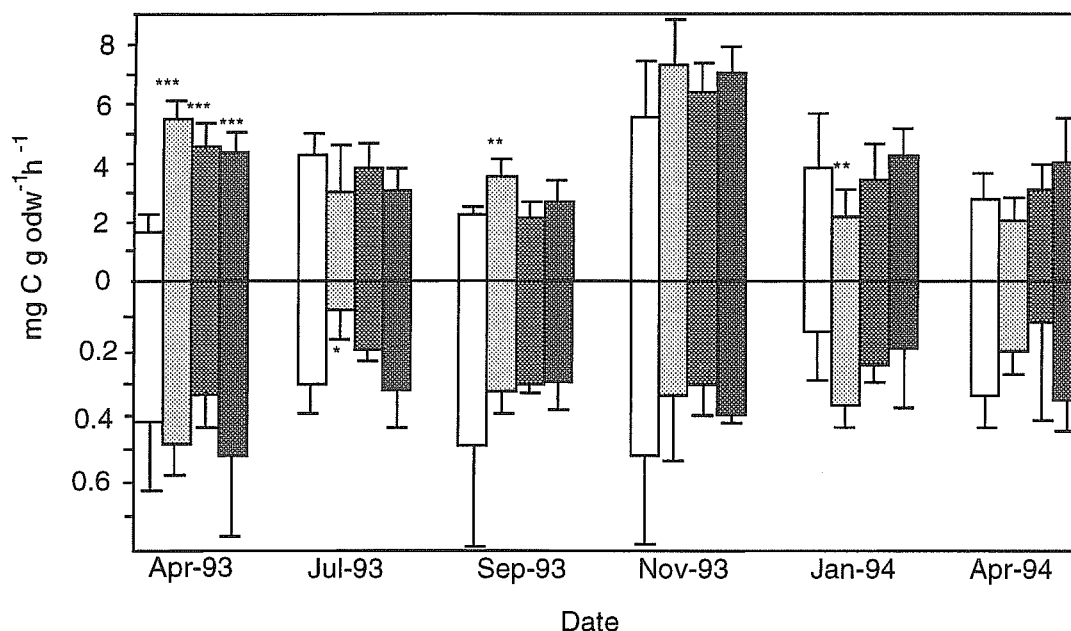


Fig. 2. Net productivity and respiration rates of *Caulerpa taxifolia* in nutrient enrichment experiments. □, control plants; □, N-enriched plants; □, P-enriched plants; ■, N+P-enriched plants, at different times of the year. Histograms are mean values  $\pm 1$  SD (N : 3 replicates and 2 subsamples per replicate). Stars indicate the level of significance, when differences are significant [one-way ANOVA ( $p < 0.05$ ), followed by Tukey's significance test]; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

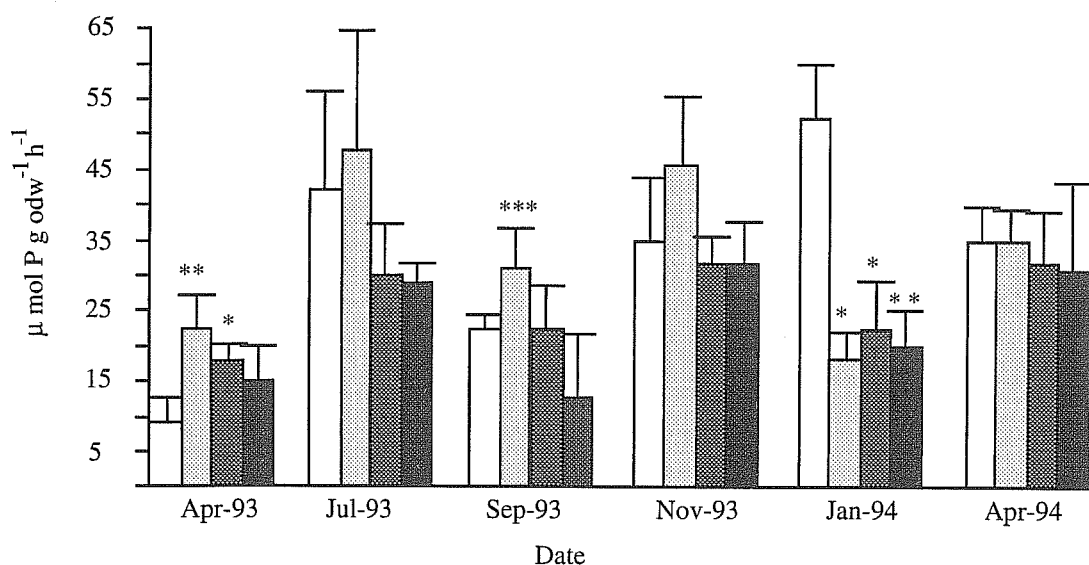


Fig. 3. Alkaline phosphatase activity (APA) of *Caulerpa taxifolia* in nutrient enrichment experiments. □, control plants; □, N-enriched plants; □, P-enriched plants; ■, N+P-enriched plants, a different times of the year. Histograms are mean values  $\pm 1$  SD (N = 3 replicates and 2 subsamples per replicate). Stars indicate the level of significance, when differences are significant [one-way ANOVA ( $p < 0.05$ ), followed by Tukey's significance test]; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

( $p \leq 0.05$ ). Tissue carbon averaged  $52.04 (\pm 2.82)\%$  odw and varied very little throughout the year (Table I).

The N : P atomic ratios in tissues always exceeded the Redfield ratio of 16 (average of  $32 \pm 9$ ), with relatively high N : P values in winter (46) and low values (22) in late summer.

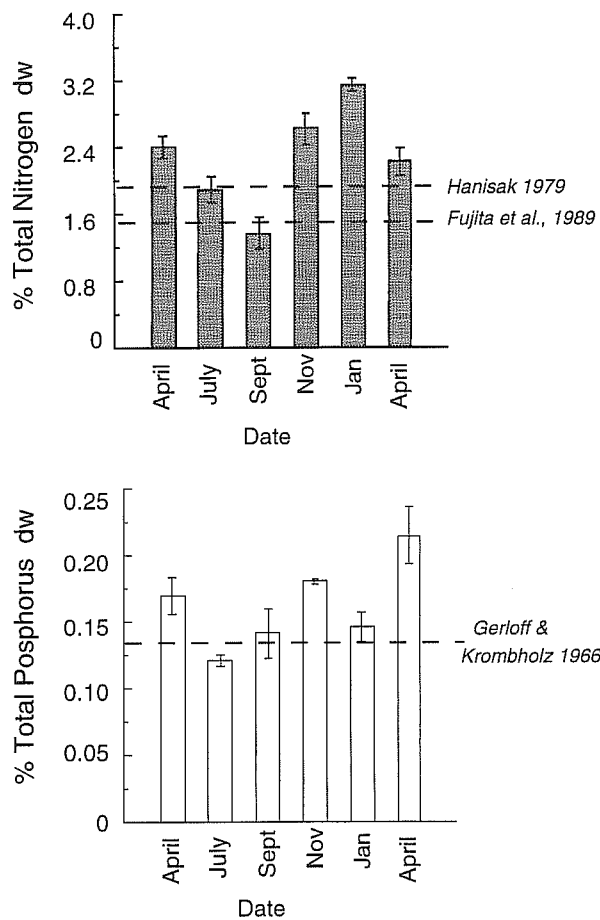


Fig. 4. Nutrient content in tissues of *Caulerpa taxifolia* at different times of the year and critical levels reported for other macroalgae. Histograms are mean  $\pm$  SD of three replicates.

## Discussion

The data presented here indicates that the productivity of *Caulerpa taxifolia* is unlikely to be severely limited by nutrients throughout the year, because,

(1) a non-significant increase of productivity due to nutrient enrichment, was the common response in all the periods assayed, except for April 93, when *Caulerpa taxifolia* productivity was about two-fold enhanced by N, P, and N+P enrichments and in September 93 when N-enriched plants had their productivity enhanced;

(2) the measured alkaline phosphatase activity (APA) of *Caulerpa taxifolia* is relatively low, close to those for P-sufficient macroalgae (Lapointe *et al.* 1992, Delgado and Lapointe 1994); and

(3), tissue N and P of *Caulerpa taxifolia* were usually above the critical levels for growth, reported for other aquatic plants (Gerloff and Kromholz 1966, Hanisak 1979, Fujita *et al.* 1989).

Low APA values and the absence of a short-term productivity enhancement to P-enrichment found for *Caulerpa taxifolia*, have also been observed for other macroalgae in the order Caulerpales (O'Neal and Prince 1988, Delgado and Lapointe 1994). For calcareous species this response was believed to be associated to their adaptation to tropical waters having low SRP concentrations (Delgado and Lapointe 1994). Moreover, although the seasonal variation of tissue nutrients of *C. taxifolia* in control plants (CV of about 50%) could influence APA, these variations were more similar (though not statistically significant) to changes in productivity rather than to those of phosphate concentration in the water. This suggests that seasonal APA changes reflect metabolic variations linked to productivity, which behaves independently from ambient conditions. It would also explain why increasing phosphate concentration in the water did not have an inhibitory effect on APA of *C. taxifolia*, as one would expect from inducible enzymes such as the phosphatases and as occurs in the majority of marine plants (Kuenzler and Perras 1965, Lapointe *et al.* 1987, Delgado and Lapointe 1994). Only in January did *C. taxifolia* plants show about a

Table I. Nutrient content in tissues of *Caulerpa taxifolia* and atomic ratios at different times of the year. Values are mean  $\pm$  sd in % per organic dry weight. Ash content of 43.1% dry weight.

|       | Date             |                  |                  |                  |                  |                  |
|-------|------------------|------------------|------------------|------------------|------------------|------------------|
|       | 4-20-93          | 7-5-93           | 9-14-93          | 11-9-93          | 1-19-94          | 4-19-94          |
| % N   | 4.22 $\pm$ 0.23  | 3.32 $\pm$ 0.28  | 2.39 $\pm$ 0.34  | 4.59 $\pm$ 0.33  | 5.50 $\pm$ 0.14  | 3.89 $\pm$ 0.28  |
| % P   | 0.30 $\pm$ 0.025 | 0.21 $\pm$ 0.007 | 0.25 $\pm$ 0.034 | 0.32 $\pm$ 0.003 | 0.26 $\pm$ 0.020 | 0.37 $\pm$ 0.039 |
| % C   | 48.74 $\pm$ 1.16 | 48.05 $\pm$ 3.89 | 55.25 $\pm$ 5.96 | 51.52 $\pm$ 2.58 | 53.96 $\pm$ 0.52 | 54.70 $\pm$ 1.16 |
| N : P | 31               | 35               | 22               | 32               | 46               | 23               |
| C : N | 13               | 17               | 27               | 13               | 11               | 16               |
| C : P | 420              | 610              | 571              | 415              | 536              | 382              |

60% reduction in their APA, and that was for all three nutrient treatments, coinciding with maximal values of APA in control plants (Fig. 3).

Surprisingly, indications of N- and P-limitation of productivity of *C. taxifolia* (April 1993) coincided with relatively high nutrient concentrations in tissues and water column. This contrasts with the nutrient limitation, particularly P, reported for Mediterranean seaweeds and seagrasses in summer when light and temperature are adequate for growth (Ballesteros 1989, Pérez *et al.* 1994, Delgado *et al.* 1994). Independence of *C. taxifolia* from nutrient concentrations in the water, has been partly shown in this study. Little is known about the nutrient dynamics of *C. taxifolia* such as its possible high affinity for nutrients (high ratio of  $V_{\max} : K_s$ , *sensu* Healey 1980), its ability to take up nutrients from the sediments via rhizoids, and its capacity to store nutrients. Studies on other species of Caulerpales indicate the existence of some of these features. For example, they have been shown to be able to obtain nutrients from the sediment pool through their extensive root-rhizoid system (Williams 1984a, Littler *et al.* 1988), and carbohydrate utilization has been shown to maintain winter growth in *Caulerpa paspaloides* (Bory) Greville (O'Neal and Prince 1982).

The persistently high biomass stands of *Caulerpa taxifolia*, up to 613 g dw m<sup>-2</sup> in dense meadows (Meinesz and Hesse 1991), are an important nutrient trap, holding about 1 ( $\pm 0.2$ ) g P m<sup>-2</sup> and 14 ( $\pm 3.7$ ) g N m<sup>-2</sup>. These figures are two-fold higher than the P contained in a seagrass bed of *Posidonia oceanica*, including rhizomes (Delgado 1986, Delgado and Vidal 1989), though frequently lower than the amount estimated for populations of the sublittoral alga *Cystoseira mediterranea* Sauvageau (Delgado *et al.* 1994). If 1/3 of the total nutrients contained in the meadow (equivalent to the observed 30% seasonal variation in the tissue nutrient) were used in the synthesis of new organic matter through nutrient reallocation, an amount of approximately 50 g C of new *Caulerpa taxifolia* per year could be supported. In this regard, the siphonaceous nature of the thallus of *C. taxifolia* could facilitate the nutrient translocation of the stored nutrients, as well as the reallocation of nutrients taken up from either the water column or the sediment, within a given patch. Also, nutrient recycling inside *C. taxifolia* meadows may have a pre-enrichment role in nutrient availability to the

plant through nutrient reabsorption from dead and decomposing parts, excreted by resident animals, and bacterial activity (Williams 1984b, Williams and Carpenter 1988).

The success of Mediterranean populations of *C. taxifolia* in waters so different from their original tropical ones is especially striking. In response to changes in light, temperature and nutrients (Zabala and Ballesteros 1989), most of the Mediterranean seaweeds and seagrasses have distinct annual cycles of biomass and productivity (Ott 1980, Ballesteros 1991, Pérez and Romero 1992). Seasonal variation of the productivity of *Caulerpa prolifera* (Forsskål) Lamouroux, the widest distributed species of the genus *Caulerpa* throughout the Mediterranean (Meinesz 1980), has been related to changes in water temperature (Terrados and Ros 1992). All this contrasts with Mediterranean populations of *C. taxifolia* which do not show a clear annual cycle of biomass, despite presenting seasonal variations of their growth and productivity (Komatsu *et al.* 1994, Gacia *et al.* 1994). In this regard *C. taxifolia* is similar to its tropical relatives (Mathieson and Dawes 1975). Our results indicate the spread of *Caulerpa taxifolia* in Mediterranean ecosystems to be related with its ability to meet its nutrient requirements in the nutrient-poor Mediterranean waters. This ability may be enhanced by its perennial and siphonaceous nature, and its high persistent biomass. Therefore, we suggest that the lack of severe nutrient limited productivity of Mediterranean specimens of *Caulerpa taxifolia*, could be an important factor accounting for its outcompetition with native macrophytes.

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