Photoautotrophic metabolism of *Caulerpa taxifolia* (Chlorophyta) in the NW Mediterranean

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**Abstract:** Oxygen production and consumption by the green alga *Caulerpa taxifolia* was measured in the NW Mediterranean at Monaco using a submersible respirometer. Photosynthesis versus irradiance \( (P-I) \) curves were constructed for populations at depths of 10, 15 and 25 m in summer and 10 m in winter. *C. taxifolia* did not exhibit many of the photoadaptive responses to bathymetric changes in irradiance that have been reported in other algae. The initial slope of the \( P-I \) curve \((a)\) was inversely proportional to depth; the irradiance required for respiratory compensation \( (I_c) \), the concentrations of chlorophylls \( a \) and \( b \) and their ratios \((chl \, a/b)\) did not vary significantly with depth. Changes in the rate of dark respiration \(-R\), the gross and net photosynthetic capacities \( (P'_m, P'_n) \), \( a \), and the irradiance required for the onset of saturation \( (I_s) \) were greater between 15 and 25 m than between 10 and 15 m, despite the change in irradiance being smaller. \( P'_m \) decreased from 119 to 34 \( \mu \text{mol} \, \text{O}_2 \, \text{g}^{-1} \, \text{dry wt h}^{-1} \) between 10 and 25 m. Net \( 24 \text{ h} \) productivity \( (P_n) \), given optimum atmospheric and ocean transparency, was estimated to decrease from 790 to 89 \( \mu \text{mol} \, \text{O}_2 \, \text{g}^{-1} \, \text{dry wt d}^{-1} \) between 10 and 25 m indicating a maximum photoautotrophic growth limit of 29 m in summer. At 10 m in winter, \(-R\), \( I_c \), \( I_s \) and \( chl \, a/b \) were lower than in summer, \( P'_m \) and \( P'_n \) were similar, and the concentrations of chlorophylls \( a \) and \( b \) were higher, indicating adjustment of the photosynthetic apparatus to seasonal changes in light and/or temperature. Maximum \( P'_m \) was estimated to be 436 \( \mu \text{mol} \, \text{O}_2 \, \text{g}^{-1} \, \text{dry wt d}^{-1} \). By adjusting the \( y \)-intercept of the summer bathymetric model to fit this rate, a maximum photoautotrophic growth limit of 24 m was indicated in winter. Although these theoretical photoautotrophic limits reasonably correlate with the distribution of dense populations of *C. taxifolia* at Monaco, they are greatly inferior to its maximum reported growth depth of 99 m. This ability to grow far deeper than the photoautotrophic limit implies significant carbon acquisition by heterotrophy.

**Key Words:** Photosynthesis, Irradiance, Adaptation, Depth, Season *Caulerpa taxifolia*

**Introduction**

Over approximately a decade, the siphonaceous green alga *Caulerpa taxifolia* (Vahl) C. Agardh has spread over >30 km\(^2\) of the NW Mediterranean seabed (Meinesz et al. 1997). Its rapid expansion has been attributed to: abnormal size and growth rate (Meinesz & Hesse 1991, Meinesz et al. 1993); strong chemical defence against herbivory and epiphytic overgrowth (Guerriero et al. 1992, 1993); efficient vegetative propagation (Meinesz & Hesse 1991, Meinesz et al. 1993); enhanced tolerance of winter minimum seawater temperatures (Meinesz & Hesse 1991, Meinesz & Boudouresque 1996); an ability to colonise widely varying substrata (Meinesz et al. 1993); efficient absorption, conservation and internal recycling of nutrients (Delgado et al. 1996); and peak frond length (Meinesz et al. 1993) and productivity (Gacia et al. 1996) in autumn when the biomass of native species is at a minimum. These attributes are thought to enable the alga to outcompete native macrophytes, in particular *Posidonia oceanica* (L.) Delile (Villée & Verlaque 1995) and shallow-water macroalgae (Verlaque & Fritayre 1994). Chisholm et al. (1997) reason that growth of *C. taxifolia* may be favoured by eutrophication of substrata because the alga can take up organic N and inorganic
nutrients through its subterranean rhizoids (Chisholm et al. 1996). Rapid expansion of *C. taxifolia* may thus be a product of synergy between endogenous and exogenous factors.

Despite this wealth of theories on the causes and effects of *Caulerpa taxifolia* development in the NW Mediterranean, data are still lacking on fundamental aspects of the alga's biology. The rapidity of the alga's expansion in certain environments implies very high growth rates and yet laboratory measurements have indicated only moderate rates of primary production (Gayol et al. 1995, Garcia et al. 1996). Either laboratory measurements have greatly underestimated the alga's in situ primary productivity or *C. taxifolia* derive significant organic C from heterotrophy. Although Chisholm et al. (1996) have demonstrated uptake of organic C by *C. taxifolia*, the contribution of this process to growth of the alga has not been quantified. Similarly, there have been no published reports of the in situ productivity of *C. taxifolia*, thus it has not been possible to determine the relative importance of autotrophy and heterotrophy.

This study provides the first estimates of the in situ primary productivity of *Caulerpa taxifolia*. Photoautotrophic metabolism is examined as a function of bathymetry and season. Data are used to estimate the autotrophic depth limits of *C. taxifolia* in summer and winter under optimum conditions of atmospheric and oceanic transparency. These estimates are used as a basis for discussion of nutrition, growth and expansion of *C. taxifolia* in the NW Mediterranean.

**MATERIALS AND METHODS**

Scalar irradiance, seawater temperature, and net oxygen production or consumption by samples of *Caulerpa taxifolia* were measured in the sea at Monaco using a purpose-built, submersible respirometer. Measurements were made at a depth of 10 m in December 1994 and at 10, 15, and 25 m in August 1995. The respirometer included a spherical quantum sensor (Li-193SA 4π, Li-Cor) and 3 cylindrical, acrylic incubation chambers (3.5 l volume), fitted with polarographic oxygen electrodes containing built-in temperature sensors (Ponselle OXY TS, Ponselle Mesure). Acrylic was used for the incubation chambers because it is non-toxic and has a refractive index similar to seawater. After construction, the chambers were soaked in a warm solution of anionic detergent (3 h) then immersed in freshwater (1 wk) and seawater (1 wk) to remove any toxins introduced during the fabrication process. The sensors were connected by underwater electric cables to a datalogger (Li-1000, Li-Cor) secured within a pressure-resistant, waterproof housing.

The light sensor was mounted in a fixture adjacent to the sample chambers during incubations.

**Sensor calibration.** Oxygen sensors were calibrated every 2 d in 1.5 l volumes of seawater brought to air-saturation over 24 h by bubbling with humidified air while stirring. Oxygen sensors were zeroed by capping the sensor heads with small polyethylene tubes containing saturated solutions of sodium sulphite. Temperature sensors were calibrated before each set of seasonal measurements against a high precision mercury thermometer. The light sensor was pre-calibrated by the manufacturer.

**Samples.** Samples were gathered using SCUBA from locations spaced >5 m apart to avoid pseudoreplication (maximum length of stolons = 2.8 m, Meinesz et al. 1995). Samples of *Caulerpa taxifolia*, including the basal substrata to which their rhizoids were attached, of planar area similar to that of the incubation chambers, were carefully placed in each chamber (Fig. 1). The chambers were of sufficient height to enable the fronds to extend vertically without restriction. Samples of planar area approximately equal to that of the incubation chambers were selected to preserve natural frond densities.

**Field measurements.** Chambers were mixed continuously by small centrifugal pumps operating on short, external, recirculating loops connected to the upper and lower sections of each chamber (Fig. 1). Chambers were flushed with fresh seawater for 5 min in every

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**Fig. 1** One of 3 experimental incubation chambers comprising: a tall upper section (30 cm, clear acrylic) to enable fronds to extend vertically without restriction; a lower section (clear acrylic) containing a port for the fitted probe and water inlet and outlet ball-valves; a continuous circulation loop connecting upper and lower sections to provide water movement and mixing within the chamber; and a base (PVC). Sections and base were connected together with stainless steel (316 grade) spring clips and sealed with rubber O-rings.
35 min period by a timer-controlled pump. Separate electrical currents were fed to the circulation and flushing pumps through a 4-core underwater cable, connected to a shore-based power supply (240 V AC). Spring-loaded teflon ball-valves sealed the inlets and outlets of the chambers during flushings. Oxygen, temperature and irradiance were sampled every 5 s; average readings were stored by the datalogger at 5 min intervals. Each incubation lasted a total of 24 h. Six samples of Caulerpa taxifolia were measured at irradiance and modelled using a hyperbolic tangent function:

$$P = \frac{P_{im}}{\tanh(I/I_i)} + R \quad (\text{Jassby & Platt 1976}) \ (1)$$

(b) a simple exponential function:

$$P = P_0(1 - e^{-kt}) + R \quad (\text{Webb et al. 1974}) \ (2)$$

(c) a Michaelis-Menten function:

$$P = \frac{P_{im}I}{I + I_i} + R \quad (\text{Baly 1935}) \ (3)$$

Abbreviations used in these equations and elsewhere are defined in Table 1.

The accuracy with which each model simulated the data was evaluated by non-linear, least-squares regression (JMP v3 Statistics Made Visual, SAS Institute, Inc.). The function which produced the narrowest confidence intervals around the primary parameter estimates was used to characterise the light-saturation kinetics of individual algal samples.

### Analyses of variance

Variation in primary (-R, \(P_{im}\), \(I_i\)), secondary (\(a, I, P_{im}, P_{im}/-R\)) and chlorophyll (\(a, b, a/b\)) parameters as a function of depth and season was examined using 1-way analysis of variance (ANOVA; JMP v3 Statistics Made Visual). Preliminary tests for normality (Shapiro & Wilk 1965) and homogeneity of

| P-I | Curvilinear relationship between photosynthesis and irradiance |
| -R | Absolute rate of dark respiration |
| \(P\) | Gross photosynthetic capacity |
| \(P_i\) | Net photosynthetic capacity |
| \(P_i/-R\) | Ratio of gross photosynthetic capacity to respiration |
| \(P_d\) | Gross photosynthesis over a day |
| \(P_e\) | Net photosynthesis over a day |
| \(a\) | Initial slope of the P-I curve |
| \(I_i\) | Irradiance at which the initial slope intercepts the horizontal asymptote of the P-I curve |
| \(I_s\) | Irradiance at which \(P_i = -R\) |
| \(I_m\) | Irradiance at the sea surface |
| \(z\) | Depth (m) |
| \(K\) | Vertical attenuation coefficient |
| \(l\) | Time (min) |
| \(dl\) | Length of daily photoperiod (min) |
| chl a | Concentration of chl a |
| chl b | Concentration of chl b |
| chl a/b | Ratio of chl a to chl b |
| \(r^2\) | Coefficient of determination |
variance (Bartlett 1937) were carried out to ensure compliance with assumptions underlying ANOVA. Values for $I$, $k$, [chl a], [chl b], and chl a/b in tests for seasonal differences and $k$ in a test for depth differences were transformed to render variances homogeneous using the formulas indicated in Table 2. Post-hoc, multiple, pairwise comparisons of means were made at the 5% significance level using Tukey-Kramer HSD tests (Tukey 1973, Kramer 1956, JMP v3 Statistics Made Visual) when ANOVA demonstrated significant variation in parameters as a function of bathymetry.

**Regression analyses.** Parameters that varied significantly with depth in ANOVA were modelled using linear regression (JMP v3 Statistics Made Visual).

**Irradiance.** The daily irradiance profile in the study area was evaluated on the basis of measurements made on a cloud-free day in summer (25 August 1995) and a near cloud-free day in winter (6 December 1994) using:

(a) a half sine function:

$$I = I_m \sin(\pi t)$$  \hspace{1cm} (Chalker et al. 1984) \hspace{1cm} (4)

and (b) a peaked half sine function:

$$I = I_m \left[ \sin(\pi t) \right]^n$$  \hspace{1cm} (McBride 1992) \hspace{1cm} (5)

where $I_m$ was the maximum measured irradiance; $n$ was a small number $>1$, $<3$, and $t = t_0 - t_{sunrise}/dl$.

Theoretical profiles of daily irradiance under optimum conditions of atmospheric transparency (transmission coefficient = 0.67; Ashrae 1977) and ocean clarity (Type IB Oceanic Water; Jerlov 1976) were also constructed for subsequent estimation of absolute productivity. $I_m$ was calculated from:

$$I_m = I_o e^{-Kz}$$  \hspace{1cm} (Kirk 1994) \hspace{1cm} (6)

where $I_o$ was calculated for the latitude 43°45' N using the method of Drew (1983) and $K$ was calculated from data provided by Lüning & Dring (1979). $dl$ was either that calculated by the method of Drew (1983) or the measured photoperiod, whichever was longer.

**Depth limits to growth.** The lower depth limit for photoautotrophic growth in summer was estimated by fitting an exponential function to a plot of $P_o/D$ versus depth and determining, by extrapolation, the depth at which $P_o/D$ became $\leq 0$. The same parameter was estimated in winter by adjusting the $y$-intercept of the summer model to obtain the estimated value for $P_o/D$ at 10 m and then extrapolating the curve to find the depth at which $P_o/D$ became $\leq 0$.

**RESULTS**

**Field observations.** Frond densities tended to be higher at 10 and 15 m than at 25 m; frond length tended to be greater at 15 m. The substratum consisted of limestone rocks and rubble at 10 and 15 m and a mixture of fine silt and mud at 25 m. Buried several cm beneath the sediment horizon at 25 m were the organic remains of a former seagrass bed (Ollivier 1929). Sea-water temperature varied between 17 and 18°C during measurements in December 1994 and between 23 and 25°C during measurements in August 1995.
Parameters defining the mean features of the P-I curves, together with tissue chlorophyll concentrations and ratios, are provided in Table 2. The gross and net photosynthetic capacities of populations at 10 m were equal in summer and winter. Dark respiration consumed 4% of $P_{\text{m}}$ at 10 m in winter and 7 to 13% of $P_{\text{m}}$ between 10 and 25 m in summer.

**Variation in parameters.** Except for $P_{\text{m}}$ and $P_{\text{n}}$, parameters varied more between the 2 seasons than with depth (Table 2). $P_{\text{m}}$ and $P_{\text{n}}$ were almost identical in summer and winter. In summer, $-R$, $I$, $I_a$, and chl a/b increased, whereas $\alpha$, $P_{\text{m}}$/-$R$ and the concentrations of chl a and chl b decreased. Neither $I$, nor the concentrations of chl a and chl b or their ratios altered significantly as a function of bathymetry (Table 2). $-R$, $P_{\text{m}}$, $P_{\text{n}}$, $\alpha$, $P_{\text{m}}$/-$R$ and $I_a$ were inversely proportional to depth (Fig. 4, Table 3). Larger differences in parameters occurred between 15 m and 25 m than between 10 m and 15 m (Tables 2 & 3), despite the change in irradiance being smaller (Table 4).

**Irradiance.** Data gathered on a cloudless day in summer (25 August 1995) at a depth of 25 m demonstrated that irradiance followed a peaked half sine curve (Eq. 5, $r^2 = 1.00$):

**Flux rates.** Comparison of net oxygen flux with irradiance under near cloudless conditions on 6 December 1994 indicated that changes in photosynthetic rate marginally lagged changes in irradiance, i.e. maximum photosynthetic rate was attained approximately 30 to 40 min after the solar zenith (Fig. 2). The combined oxygen demand of microscopic organisms associated with the basal substratum and water column made negligible contribution to the overall flux rate of oxygen in both the light (0.1 to 0.5%) and the dark (0.8 to 3%). No correction was applied to estimates of productivity or respiration for *Caulerpa taxifolia*.

**P-I curves.** On average, the simple exponential function (Eq. 2) produced the narrowest confidence intervals around the primary parameter ($P_{\text{a}}$, $I_a$, $-R$) estimates and was therefore selected for characterisation of the P-I response in *Caulerpa taxifolia*. At natural frond densities, photosynthesis did not reach light-saturation in any of the populations measured (Fig. 3). Productivity per µmol irradiance decreased with depth and was slightly higher in winter (Fig. 3).
rather than a half sinusoid (Eq. 4, $r^2 = 0.77$) (Fig. 5). This relationship also held in winter (Fig. 2, $r^2 = 0.99$), except for a small change in $n$, the power of the sine term:

$$I = 263 \times [\sin(\pi \times (t - t_{\text{sunrise}})) / 816)]^{1.085} \quad (7)$$

Peaked half-sinusoid irradiance profiles were thus used for calculation of daily primary production. The irradiance profiles indicated a daily photoperiod of 13 h 30 min on 25 August 1995 and 9 h 10 min on 6 December 1994; these photoperiods were, respectively, 6 min shorter and 22 min longer than those calculated using the method of Drew (1983) for 21 August and 6 December. 14.6% of $I_0$ penetrated to a depth of 25 m on 25 August 1995 indicating that the seawater was slightly more transparent than Type II Oceanic Water (Jerlov 1976). The optical transparency of the seawater during measurements in winter was between Type II and Type III Oceanic Water (Jerlov 1976).

Substitution of empirically determined irradiance maxima with values calculated for idealised conditions of atmospheric and oceanic transparency (clear sky, Type IB Oceanic Water) yielded irradiance profiles described by:

$$I = I_m \times [\sin(\pi \times (t - t_{\text{sunrise}})) / 555)]^{1.052} \quad (9)$$
in winter; and

$$I = I_m \times [\sin(\pi \times (t - t_{\text{sunrise}})) / 816)]^{1.052} \quad (10)$$
in summer. Values for $I_m$ are given in Table 4; $dl$ in Eq. (9) was the empirically determined photoperiod.
Table 3. Linear regression of parameters (Y) vs depth (X in m), r² is the coefficient of determination. p is the probability that the slope is not significantly different from 0. For principal variation, > indicates 1 or more population means significantly larger than another (Tukey-Kramer, α = 0.05).

<table>
<thead>
<tr>
<th>Y</th>
<th>Y =</th>
<th>r²</th>
<th>p</th>
<th>Principal variation</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>-R</td>
<td>0.242X - 11.8</td>
<td>0.31</td>
<td>0.0159</td>
<td>15 &gt; 25 m</td>
<td>( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1} )</td>
</tr>
<tr>
<td>( P^\rho )</td>
<td>190.5 - 3.955X</td>
<td>0.72</td>
<td>0.0000</td>
<td>10, 15 &gt; 25 m</td>
<td>( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1} )</td>
</tr>
<tr>
<td>( P^\delta )</td>
<td>178.7 - 5.712X</td>
<td>0.73</td>
<td>0.0000</td>
<td>10, 15 &gt; 25 m</td>
<td>( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1} )</td>
</tr>
<tr>
<td>( \alpha )</td>
<td>0.578 - 0.015X</td>
<td>0.67</td>
<td>0.0000</td>
<td>10, 15 &gt; 25 m</td>
<td>( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1} )</td>
</tr>
<tr>
<td>( P^{\alpha - R} )</td>
<td>20.6 - 0.538X</td>
<td>0.55</td>
<td>0.0004</td>
<td>10 &gt; 25 m</td>
<td>No units</td>
</tr>
</tbody>
</table>

Table 4. Estimated mean 24 h primary productivity of *Caulerpa taxifolia* near Monaco under clear atmospheric conditions; theoretical values for \( d/ \) and \( L^e \) calculated from Drew (1983), the latter assuming Type IB Oceanic Water (Jerlov 1976).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>10 m winter Actual</th>
<th>10 m summer Actual</th>
<th>15 m summer Actual</th>
<th>25 m summer Actual</th>
</tr>
</thead>
<tbody>
<tr>
<td>( d/ )</td>
<td>min</td>
<td>555</td>
<td>533</td>
<td>810</td>
<td>816</td>
</tr>
<tr>
<td>( L^e )</td>
<td>( \mu \text{mol m}^{-2} \text{s}^{-1} )</td>
<td>296</td>
<td>417</td>
<td>589</td>
<td>983</td>
</tr>
<tr>
<td>( P^\rho )</td>
<td>( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt d}^{-1} )</td>
<td>439</td>
<td>560</td>
<td>782</td>
<td>994</td>
</tr>
<tr>
<td>( P^\delta )</td>
<td>( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt d}^{-1} )</td>
<td>314</td>
<td>436</td>
<td>578</td>
<td>790</td>
</tr>
</tbody>
</table>

because this was longer than the interval from sunrise to sunset (see Chalker et al. 1984)

**Daily production.** Whole day net productivity (\( P^\delta \)) using measured dimensions for \( L^e \) and \( d/ \) was estimated to range from 578 \( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt} \) at 10 m to 35 \( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt} \) at 25 m in summer; \( P^\rho \) in winter was estimated to be 54% of that calculated for 10 m populations in summer (Table 4). Respiration consumed an increasing proportion of \( P^\delta \) as depth increased in summer (26 to 78% between 10 and 25 m) and 28% of \( P^\rho \) at 10 m in winter.

Maximum theoretical \( P^\delta \), assuming zero cloud cover and light attenuation by Type IB Oceanic Water, was estimated to range from 790 to 89 \( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt} \) between 10 and 25 m in summer and to be 436 \( \mu \text{mol O}_2 \text{ g}^{-1} \text{ dry wt} \) at 10 m in winter (Table 4).

**Depth limits to growth.** Exponential models of the change in maximum theoretical \( P^\delta \) with depth indicated that there was insufficient primary production to meet respiratory demand at depths greater than 29 m in summer and 24 m in winter (Fig. 6).

**DISCUSSION**

Drew & Abel (1990) had difficulty determining the light-saturation characteristics of *Halimeda* because the position of the chloroplasts within segments changed as a function of irradiance and photoperiod. Movement of chloroplasts has been observed in other siphonaceous algae, including *Bryopsis* (Steinecke 1925), *Caulerpa prolifera* (Dawes & Barlotti 1969). *C. taxifolia*...
Fritayre (1994) in so far as C taxi-prevailed during the study, data indicate that Gacia et al. (1996) may have misconstrued the bio-
tum. Assuming that normal environmental conditions
8.57 g C m\(^{-2}\) d\(^{-1}\) at a depth of 9 m. However, we believe
concentrations of organic compounds in the substra-
t could fix 1.95 to
Caulerpa taxifolia
linked to urban waste-water discharge and/or high
and
N
has the ability to take up organic C and
suggested that rapid expansion of
has not been quantified. Chisholm et al. (1997) have
that maximum photosynthesis occurred for 6 h d\(^{-1}\) in
November when the biomass and productivity of
C, taxifolia
native marine plants are most reduced may provide
depth of occurrence of 99 m (Belsher
Meinesz 1995).
Effect on overall productivity than solar angle and
Titlyanov 1981, Dring 1990). The only significant response to
declared inorganic P directly from substrata, but the degree to
this study used attached samples with high natural
frond densities. Comparison of the parameter dimen-
sions reported by these 3 studies indicates a degree of
correlation between the tissue biomass and the est-
mated values of \(a, l_1\), and \(k_2\) (Table 5). Highest overall
efficiencies and rates of photosynthesis were deter-
mined on excised fronds (Gacia et al. 1996), suggesting
that stolon and rhizoid tissues contribute less to pro-
ductivity. Lowest efficiencies and rates of photosynthe-
sis were determined for the high biomass samples
measured in this study. Photoautotrophic growth of
Caulerpa taxifolia in the field may thus be self-limited
by tissue biomass. By corollary, if populations are sig-
nificantly more efficient in their use of irradiance at
low tissue biomass and biomass decreases with depth,
then the true limits of photoautotrophic survival may
be greater than predicted by this study.

Except for data obtained by Gacia et al. (1996) in
November 1993, all measured \(P_{a0}\) for Caulerpa taxifolia
fall within the range of values reported for other
Caulerpa species: 20 to 207 \(\mu\)mol O\(_2\) g\(^{-1}\) dry wt h\(^{-1}\)
(O’Neal & Prince 1982, 1988, Gattuso & Jaubert 1985,
(1996) argued that maximum photosynthetic capacity
in November when the biomass and productivity of
native marine plants are most reduced may provide
C. taxifolia with a competitive advantage. Data pro-
vided here indicate photosynthetic capacity has less
influence on overall productivity than solar angle and
length of daily photoperiod (cf. Tables 3 & 4).

Using a photosynthetic quotient (\(PQ\)) of 1, biomass
data of Verlaque & Fritayre (1994) and an assumption
that maximum photosynthesis occurred for 6 h d\(^{-1}\) in
winter and 10 h d\(^{-1}\) in summer, Gacia et al. (1996) esti-
mated that Caulerpa taxifolia could fix 1.95 to
8.57 g C m\(^{-2}\) d\(^{-1}\) at a depth of 9 m. However, we believe
that Gacia et al. (1996) may have misconstrued the bio-
mass data of Verlaque & Fritayre (1994) in so far as
they presented essentially the same data1 for organic dry weight ('ODW') as Verlaque & Fritayre (1994) provided for total dry weight. Unless we have misinterpreted Gacia et al. (1996), they calculated organic dry weight by subtracting a mean annual ash content of 43.1% from total dry weight. If this is correct, their estimates should be reduced by the same proportion, yielding a range of 1.11 to 4.88 g C m⁻² d⁻¹. Using their chosen value of 1 for P/Q and the biomass data of Verlaque & Fritayre (1994), we obtained very similar estimates of P₂ at 10 m: 1.81 g C m⁻² d⁻¹ in December and 4.24 g C m⁻² d⁻¹ in August. A value of 1 for P/Q is probably too low for most marine algae (Ryther 1956, Strickland 1960, Littler & Murray 1974, Buesa 1980); using a more realistic value of 1.21 (Buesa 1980) decreases estimates of net organic carbon productivity to 1.5 g C m⁻² d⁻¹ in winter and 4 g C m⁻² d⁻¹ in summer.

Multiplying these rates of carbon production by Gacia et al.'s (1996) ratio of dry wt:ODW (1.757) indicates biomass productivities at a depth of 10 m of 2.6 g dry wt m⁻² d⁻¹ in winter and 7 g dry wt m⁻² d⁻¹ in summer. Crudely assuming that winter and summer rates each apply for half of the year and that the ratio of winter to summer production does not alter with bathymetry indicates annual biomass production rates of 1760 g dry wt m⁻² yr⁻¹ at 10 m, 1100 g dry wt m⁻² yr⁻¹ at 15 m and 210 g dry wt m⁻² yr⁻¹ at 25 m. Measurements made by Verlaque & Fritayre (1994) indicate an annual mean biomass of 411 g dry wt m⁻² at 10 m at Cap Martin, France, 5 km east of Monaco, in 1992. Between November 1996 and April 1997, we estimated mean biomasses of 221 g dry wt m⁻² at 15 m and 160 g dry wt m⁻² at 25 m in the study area at Monaco (calculated using a ratio of 1:10 dry weight to wet weight). Providing there is no loss of tissue, these estimates very roughly suggest that Caulerpa taxifolia could increase its surface cover annually by a factor of 4 at 10 and 15 m but only by a factor of 1.3 at 25 m assuming maintenance of uniform biomass. Meinesz et al. (1997) document an expansion factor of about 10 until population growth becomes limited, presumably by substratum availability. They also provide data which indicate that the depth interval most widely colonised by the alga in the Monaco region is 20 to 50 m (their Table 1). Although these data do not consider differences in biomass between one area and another, nor the possibility of higher photosynthetic rates at the leading edges of populations due to lower tissue biomass (see earlier discussion), or of the possibility of periodic nutrient events, they strongly suggest that rapid growth of the alga in parts of the NW Mediterranean cannot be explained solely on the basis of autotrophy.


1But Verlaque & Fritayre (1994) reported biomasses of 345 g dry wt m⁻² in winter and 448 g dry wt m⁻² in summer, not 332 g dry wt m⁻² in winter and 447 g dry wt m⁻² in summer as stated by Gacia et al. (1996).
Terrestrial plants, growing in nutrient-poor or organically rich soils, satisfy much of their N requirement by uptake of dissolved organic compounds (Chaplin et al. 1993, Kielland 1994, Northrup et al. 1995). While heterotrophy has not been studied extensively in macroalgal species, certain species are able to assimilate organic C and/or N directly (see Kremer 1981) or by association with symbiotic fungi (Kingham & Evans 1986). Although Kremer (1981) considers it unlikely that uptake of organic C plays a significant role in the carbon balance of seaweeds, the supplementation of photoautotrophic metabolism with heterotrophy might explain certain anomalies reported in the literature. Assimilation of organic compounds could, for example, account for the paradoxical growth of *Laminaria ochroleuca* at a depth of 50 m in the Straits of Messina (Drew et al. 1982), decoupling of photosynthetic rate and stolon elongation in *Caulerpa paspaleoides* during winter (O’Neal & Prince 1988), and why newly collected samples of *C. racemosa* var. *uvitiera* consumed organic carbon faster than they produced it (Riechert & Dawes 1986).

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