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# PRODUCTION DYNAMICS IN A MACROPHYTE-DOMINATED ECOSYSTEM: THE MAR MENOR COASTAL LAGOON (SE SPAIN)

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## SUMMARY

The greater part of the bottom of the Mar Menor, a hypersaline coastal lagoon in the south-east of the Iberian Peninsula, is covered by meadows of *Caulerpa prolifera* and *Cymodocea nodosa.* Both species show marked seasonality in their biomass cycles, reaching their highest annual values in summer-autumn and their lowest in winter-spring. The annual production of the *C. prolifera* mud-based meadows is estimated at 630-707 g dw $m^{-2}$ $y^{-1}$. Leaf production of the *C. nodosa* meadows varies between 162 and 427 g dw $m^{-2}$ $y^{-1}$, while rhizome production varies between 45 and 78 g dw $m^{-2}$ $y^{-1}$. *C. prolifera* growth seems to be limited by the availability of nitrogen in the water column, while *C. nodosa* growth is limited by the availability of nitrogen and phosphorus. Both species show adaptation in their photosynthetic characteristics ($I_c$, $I_k$, $P_{max}$) to seasonal variation in the water temperature of the lagoon. The values of these parameters for *C. prolifera* suggest that this species is adapted to life in habitats of less irradiance than *C. nodosa.* The distribution of *C. nodosa* meadows in the lagoon is controlled by the availability of light at the bottom. Overall primary production of the Mar Menor can be estimated at roughly 41270 Tm C $y^{-1}$ (some 300 g C $m^{-2}$ $y^{-1}$); 64% of the lagoon's primary production is produced by the macrophytobenthos, 11% by the microphytobenthos and 25% by the phytoplankton.

KEY WORDS: Macrophytobenthos, primary production, *Caulerpa prolifera*, *Cymodocea nodosa*, Mar Menor lagoon.

## INTRODUCTION

The Mar Menor is a coastal lagoon situated in the south-east of the Iberian peninsula (Fig. 1). Its surface area is 135 $km^2$ and its maximum depth is not more than 7 m; average depth is roughly 4 m. The bottoms are mainly soft substrates, more muddy in the central basin of the lagoon and sandy in the shallow parts, mainly of La Manga (ROS, 1987; PÉREZ RUZAFA *et al*., 1989). In areas near the bank with low hydrodynamism the substrate is also muddy. The dryness of the climate (subdesert Mediterranean dominium, CAPEL, 1981) and the absence of freshwater inputs mean that the Mar Menor, in terms of its water exchange regime with the Mediterranean Sea, functions as an antiestuarine lagoon (ROS *et al*., 1985). Now water salinity varies between 42 ‰ and 47 ‰, compared with 36-38 ‰ in the Mediterranean. Water temperature varies between 12° C in winter and 30° C in summer; at the shallow banks more extreme temperatures can be reached

(ROS & MIRACLE, 1984; TERRADOS, 1986, 1991; PÉREZ RUZAFA, A., 1989). The waters of the lagoon are always well oxygenated (TERRADOS, 1986) and nutrient concentration is low (< 1 µM $NO_3^-$, < 0.03 µM $PO_4^{3-}$; TERRADOS, 1991).

Benthic vegetation in the lagoon is predominantly made up by macrophyte meadows. The two most important species, in terms of area occupied, in the functioning of the lagoon ecosystem are the chlorophycean *Caulerpa prolifera* (Forsskal) Lamouroux and the seagrass *Cymodocea nodosa* (Ucria) Ascherson (TERRADOS, 1991). At certain shallow points with negligible hydrodynamism small patches of *Ruppia cirrhosa* (Petagna) Grande appear. In Las Encañizadas and in Santiago de la Ribera *Chaetomorpha linum* (O. F. Müll.) Kütz. may attain considerable development. Populations of photophilic algae on rocks (inner islands, El Estacio) reach high levels of biomass and local production (TERRADOS, 1986), but their contribution is small in the lagoon overall.

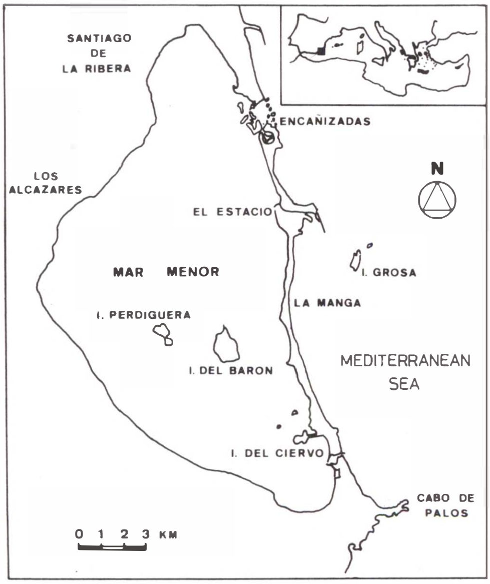

FIGURE 1. The Mar Menor lagoon and its location on the Spanish Mediterranean coast.

The great development of macrophytobenthos in the lagoon and the low phytoplanktonic density (ROS & MIRACLE, 1984) indicate that benthic primary production is more important than planktonic production in the lagoon economy (ROS, 1987). The nutrient input rate in the water mass and the extension of environments favourable to the development of submerged macrophytic vegetation (substrate stability, low hydrodynamism, sufficient light) are the main factors which determine how the primary production of the lagoon ecosystem is shared out between these two components. The present work summarizes the most important aspects of the production ecology of the two species dominant in the macrophytobenthos of the Mar Menor - *Caulerpa prolifera* and *Cymodocea nodosa.* These aspects are discussed in relation to the general functioning of the lagoon ecosystem.

## BIOMASS AND PRIMARY PRODUCTION

### *CAULERPA PROLIFERA*

The biomass of the mud-based *Caulerpa prolifera* meadow varies between 30-50 g dw $m^{-2}$ and 150-280 g dw $m^{-2}$ (BALLESTER, 1985; TERRADOS, 1986, 1991; PÉREZ RUZAFA, I.M., 1989). With small differences between areas, the meadow biomass reaches its lowest values in April-June and its highest in August-September, which are then held until the end of autumn (TERRADOS, 1986, 1991). On sand, *Caulerpa prolifera* meadows reach maximum annual biomass (97 g dw $m^{-2}$) at the end of spring; it gradually falls afterwards and is low (36-41 g dw $m^{-2}$) from January to April (TERRADOS, 1986).

The seasonal variation in the biomass of the *Caulerpa prolifera* meadow is also reflected in a variation in its structure

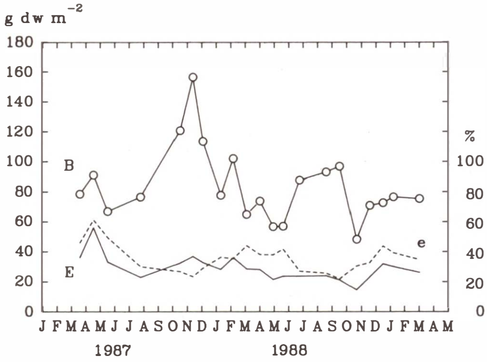

FIGURE 2. Annual variation of total biomass (B, solid line with open dots), stolon biomass (E, solid line) and the percentage of total biomass corresponding to stolons (e, dashed line; frond percentage: 100-e) in a *Caulerpa prolifera* meadow at the Mar Menor central basin (TERRADOS, 1991).

(TERRADOS, 1991). The development of the meadow is basically the consequence of the development of the fronds. The percentage of the total meadow biomass corresponding to the fronds (positive correlation, $r = 0.438$; $p < 0.05$, between the total meadow biomass and the percentage of the meadow corresponding to fronds; Fig. 2), the percentage of proliferations (negative correlation, $r = -0.848$; $p < 0.01$, between the percentages of total meadow biomass corresponding to stolons and proliferations; Figs. 2 and 3) and frond dimensions (Fig. 4) all increase. In this way the leaf area index (LAI) varies between 0.6 $m^2$ $m^{-2}$ in April and 2.9 $m^2$ $m^{-2}$ in October (TERRADOS, 1991).

From the results obtained in different laboratory experiments in which the influence of temperature on growth rates of *Caulerpa prolifera* fragments and the *in situ* annual variation in water temperature were studied (Fig. 5), TERRADOS (1991) constructed a growth model which permits estimation of the annual primary production. The annual primary production of mud-based *C. prolifera* meadows in the central part of the lagoon is estimated at 630-707 g dw $m^{-2}$ $y^{-1}$ (roughly 212-237 g C $m^{-2}$ $y^{-1}$).

The lower limit of *C. prolifera*'s survival temperature varies from 10 $^{o}$C in February to 20 $^{o}$C in June; the higher limit remains constant at around 35 $^{o}$C, while optimum growth temperature is 26-28 $^{o}$C (TERRADOS, 1991). These results suggest that growth of *C. prolifera* is practically nil during the winter, and that from the middle of May until the middle of September the water temperature allows almost optimum growth of the alga.

*Caulerpa prolifera* also grows on sand,

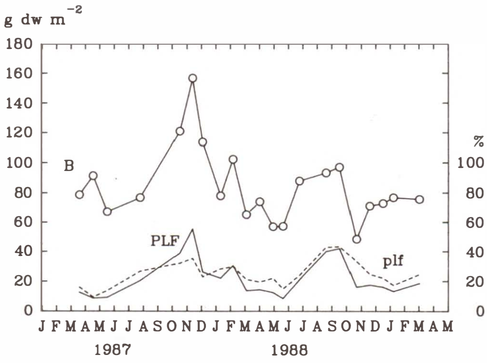

FIGURE 3. Annual variation of total biomass (B, solid line with open dots), proliferation frond biomass (PLF, solid line) and the percentage of total biomass corresponding to proliferations (fronds inserted on other fronds; plf, dashed line) in a *Caulerpa prolifera* meadow at the Mar Menor central basin (TERRADOS, 1991).

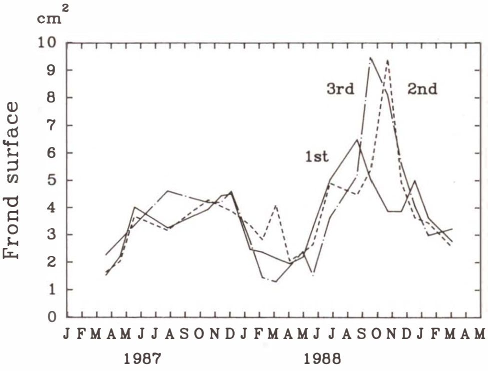

FIGURE 4. Annual variation of the surface of primary fronds (1st, solid line), secondary fronds (2nd, dashed line) and tertiary fronds (3rd, dotted-dashed line) in a *Caulerpa prolifera* meadow at the Mar Menor central basin (TERRADOS, 1991).

clay or rock, but the levels of biomass reached are much lower (TERRADOS, 1986), probably because of the lower availability of nutrients in these substrates (TERRADOS, 1991).

## *CYMODOCEA NODOSA*

*Cymodocea nodosa* meadows present an unimodal annual cycle of leaf biomass (Fig. 6; TERRADOS, 1986; TERRADOS & ROS, in press a). Leaf growth is a continuous process (Fig. 7): the highest growth rates are registered from May to July, with the result that the maximum leaf biomass values (54 g dw $m^{-2}$ in meadows on sand; 180 g dw $m^{-2}$ in meadows on mud) are recorded in July and August. Leaf biomass and leaf growth rates are minimal in January and February. Maximum total biomass registered by different *C. nodosa* meadows in the lagoon varies between 86 and 169 g dw $m^{-2}$ (BALLESTER, 1985). Shoot density in the meadow shows similar seasonal variations, with maximum values (1700-1900 shoots $m^{-2}$) in summer and minimum (1000 shoots·$m^{-2}$) at the end of winter. Maximum annual shoot density of *C. nodosa* meadows in the Mar Menor varies between 312 and 2314 shoots $m^{-2}$ (TERRADOS & ROS, in press a). The LAI varies between 0.14-0.20 $m^2$ $m^{-2}$ in January-February and 1.2-1.8 $m^2$ $m^{-2}$ in July-August; from May to September the photosynthetic surface is the same as or greater than the substrate surface.

Rhizome growth shows a seasonal variation rhythm different from that of the leaves; rhizomes grow from February to October, and the highest rates are found in May and June; growth ceases from October to January (TERRADOS & ROS, in press a).

There is a positive correlation ($p < 0.01$) between different parameters of the meadow and water temperature and incoming irradiance (Table I). "Extensive" variables, related to the quantity of photosynthetic biomass present (leaf biomass, LAI, shoot density) are linked more to water temperature. "Intensive" variables, instantaneous process rates (leaf growth, leaf P/B ratio, meadow production) are more linked to irradiance. This different degree of linking may be due to the different nature of processes involved. Intensive variables refer to short periods of

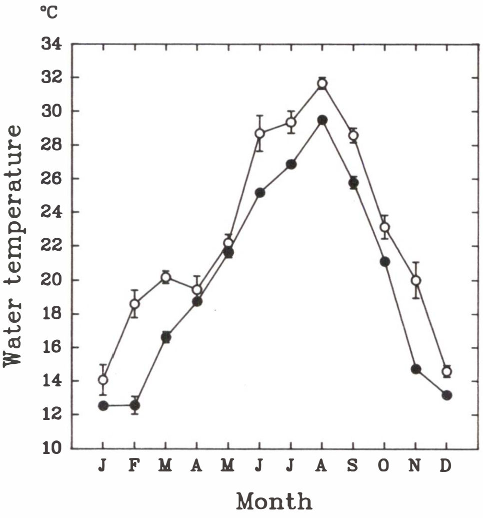

FIGURE 5. Monthly means of water temperature in the Mar Menor lagoon for the 1987/1990 period: open dots, shallow sites; full dots, central basin (TERRADOS, 1991). Vertical bars represent the standard error of mean.

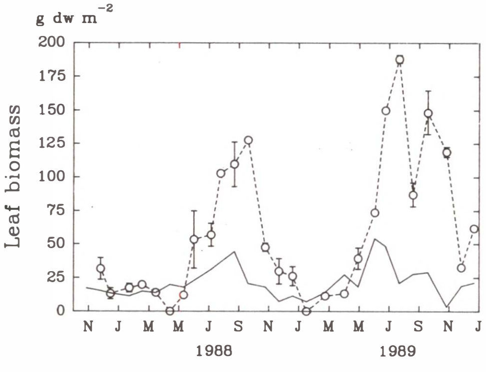

FIGURE 6. Leaf biomass annual variation of two *Cymodocea nodosa* meadows on sand (solid line) and on mud (dashed line; vertical bars, standard error of mean) in the Mar Menor (TERRADOS & ROS, in press a).

TABLE I. Values of linear correlation coefficient of Pearson (r) between some *Cymodocea nodosa* meadow variables and irradiance and water temperature (all significant at $P < 0.01$ level; TERRADOS, 1991).

| Variable | Irrad. | Temp. |
|---|---|---|
| Shoot density (shoots $m^{-2}$) | 0.592 | 0.714 |
| Leaf biomass (g dw $m^{-2}$) | 0.776 | 0.815 |
| LAI ($m^2$ $m^{-2}$) | 0.805 | 0.863 |
| Leaf growth (g dw $shoot^{-1}$ $day^{-1}$) | 0.866 | 0.698 |
| Shoot P/B ($day^{-1}$) | 0.841 | 0.599 |
| Meadow leaf production (g dw $m^{-2}$ $day^{-1}$) | 0.849 | 0.741 |

TABLE II. P-I relationship parameters of *Caulerpa prolifera* and *Cymodocea nodosa* throughout the year in the Mar Menor. Units: α, in mg $O_2$ g $dw^{-1}$ $h^{-1}$ $\mu mol^{-1}$ $m^{-2}$ $s^{-1}$; $P_{max}$ and R, in mg $O_2$ g $dw^{-1}$ $h^{-1}$; $I_c$ and $I_k$, in µmol $m^{-2}$ $s^{-1}$ (TERRADOS & ROS, in press b, c).

| | November | February | May | August |
|---|---|---|---|---|
| *Caulerpa prolifera* | | | | |
| α | 0.311 | 0.023 | 0.176 | 0.297 |
| $P_{max}$ | 3.48 | 1.21 | 3.38 | 5.63 |
| $I_c$ | 3 | 7 | 5 | 3 |
| $I_k$ | 11 | 52 | 19 | 19 |
| R | 1.06 | 0.16 | 0.90 | 0.78 |
| *Cymodocea nodosa* | | | | |
| α | 0.025 | 0.019 | 0.024 | 0.063 |
| $P_{max}$ | 1.94 | 1.32 | 9.32 | 14.02 |
| $I_c$ | 20 | 28 | 20 | 26 |
| $I_k$ | 78 | 68 | 387 | 223 |
| R | 0.50 | 0.55 | 0.49 | 1.63 |

time and depend heavily on the energy that maintains the process. Extensive variables are the organism's integrated response to the variability of the instantaneous rates, and here temperature takes on an important role, as it affects directly all the physiological processes of the organism.

Annual leaf production in meadows on sand is estimated at roughly 162 g dw $m^{-2}$ $y^{-1}$ (annual P/B: 2.46), and between 290 and 247 g dw $m^{-2}$ $y^{-1}$ in meadows on mud. A shoot produces 11-12 leaves in a year (TERRADOS & ROS, in press a). The annual rhizome production in meadows on sand is estimated at roughly 45-50 g dw $m^{-2}$ $y^{-1}$ (annual P/B: 0.29), which is equivalent to a growth in length of 39 m $m^{-2}$ $y^{-1}$. In meadows on mud, rhizome production can be estimated at roughly 66-78 g dw $m^{-2}$ $y^{-1}$ (TERRADOS & ROS, in press a).

## PHOTOSYNTHETIC FEATURES

### *CAULERPA PROLIFERA*

Compensation irradiance ($I_c$) remains constant between 3 and 7 µmol $m^{-2}$ $s^{-1}$ while saturation irradiance ($I_k$) is higher in February (52 µmol $m^{-2}$ $s^{-1}$) than in the rest

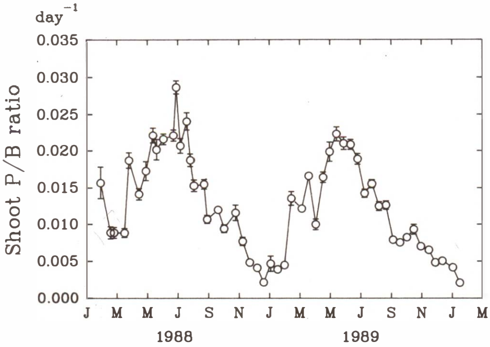

FIGURE 7. Shoot P/B ratio annual variation of a *Cymodocea nodosa* meadow on sand in the Mar Menor (vertical bars, standard error of mean) (TERRADOS & ROS, in press a).

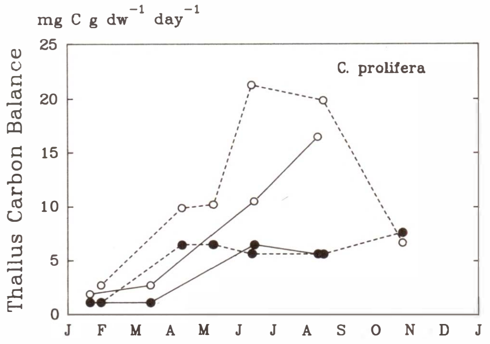

FIGURE 8. Daily carbon balances for *Caulerpa prolifera* at the central basin (solid lines) and shallow sites (dashed lines) in the Mar Menor lagoon. Net photosynthesis, open dots; dark respiration, full dots. (TERRADOS & ROS, in press b).

of the year (11-19 µmol $m^{-2}$ $s^{-1}$; TERRADOS & ROS, in press b). The light-saturated net photosynthesis rate ($P_{max}$) goes up from February (1.21 mg $O_2$ g $dw^{-1}$ $h^{-1}$) until August (5.63 mg $O_2$ g $dw^{-1}$ $h^{-1}$), and goes down in November (3.48 mg $O_2$ g $dw^{-1}$ $h^{-1}$); photosynthetic efficiency at non-saturating irradiances ($\alpha$) is minimum in February and maximum in November (Table II).

$P_{max}$ and dark respiration rate are linearly correlated with water temperature between 10 and 30°C and 10 to 35°C respectively (TERRADOS & ROS, in press b). The effect of temperature on R was smaller in May ($Q_{10}$ = 1.39) and August ($Q_{10}$ = 1.68) than in November ($Q_{10}$ = 2.54) and February ($Q_{10}$ = 2.03). In a similar way, the effect of temperature on $P_{max}$ was higher in February ($Q_{10}$ = 1.86) than in August ($Q_{10}$ = 1.46).

The time during the day that the plant receives irradiances above $I_k$ ($H_{sat}$, DENNISON & ALBERTE, 1982, 1985) varies between 7h 30' and 13h 15' in the central basin (depths of more than 4m) and between 9h 30' and 14h in the shallow areas by the bank (depths of less than 1 m; TERRADOS & ROS, in press b). Daily carbon balance (DENNISON, 1987) is always positive, and increases from January to July both in the central basin (1.9-16.5 mg $O_2$ g $dw^{-1}$ $day^{-1}$) and in the shallow areas (2.7-21.3 mg $O_2$ g $dw^{-1}$ $day^{-1}$; Fig. 8; TERRADOS & ROS, in press b).

### *CYMODOCEA NODOSA*

$I_c$ remains constant between 20 and 28 µmol $m^{-2}$ $s^{-1}$, whereas $I_k$ is greater in May (167 µmol $m^{-2}$ $s^{-1}$) and August (223 µmol $m^{-2}$ $s^{-1}$) than in November (78 µmol $m^{-2}$ $s^{-1}$) and February (68 µmol $m^{-2}$ $s^{-1}$; TERRADOS & ROS, in press c). $P_{max}$ rises from February (1.32 mg $O_2$ $dw^{-1}$ $h^{-1}$) to August (14.02 mg $O_2$ $dw^{-1}$ $h^{-1}$) and falls in November (1.94 mg $O_2$ g $dw^{-1}$ $h^{-1}$); $\alpha$ is minimum in February, maximum in August and intermediate in May and November (Table II).

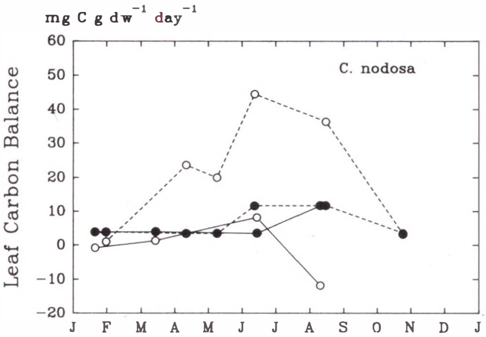

FIGURE 9. Daily leaf carbon balances for *Cymodocea nodosa* at the central basin (solid lines) and shallow sites (dashed lines) in the Mar Menor lagoon; net photosynthesis, open dots; respiration, full dots. (TERRADOS & ROS, in press c).

$P_{max}$ and R are linearly correlated with water temperature between 10 and 30°C, and 10 and 35°C respectively (TERRADOS & ROS, in press c). The effect of temperature on R is smaller in August ($Q_{10}$ = 2.07) than in November ($Q_{10}$ = 2.21) and February ($Q_{10}$ = 2.46). In contrast, the effect of temperature on $P_{max}$ is higher in August ($Q_{10}$ = 2.33) than in February ($Q_{10}$ = 2.02). The $P_{max}$/R relationship shows a shifting of the maximum from 15°C in February to 30°C in August.

$H_{sat}$ varies between 0h and 9h 30' in the central basin, and between 8h and 12h in shallow areas. The daily carbon balance in the leaves is positive throughout the year in the shallow areas, whereas it is near zero or negative in January and August in the central basin (Fig. 9; TERRADOS & ROS, in press c).

## NUTRIENT LIMITATION OF MACROPHYTE GROWTH

The average annual C:N:P ratio of thallus in *Caulerpa prolifera* is 354:21:1. The carbon, nitrogen and phosphorus content of the fronds does not show defined seasonal variation over the year

TABLE III. Growth rates, (P/B)100 $day^{-1}$ (mean, standard error of mean), of thallus fragments of *Caulerpa prolifera* (n=30) measured in aquaria with different nutrient addition treatments. $NO_3^-$ was used as nitrogen source in Experiment 1; $NH_4^+$, in Experiment 2. $PO_4^{3-}$ was used as phosphorus source in both experiments (TERRADOS, 1991).

| | Experiment 1 | Experiment 2 |
|---|---|---|
| Control | 3.39 (0.40) | 5.24 (0.29) |
| N | 6.27 (0.87) | 6.51 (0.48) |
| N+P | 6.23 (0.91) | 7.26 (0.49) |
| P | 2.42 (0.37) | 4.61 (0.36) |

(TERRADOS, 1991). Several fertilization experiments carried out in the laboratory (TERRADOS, 1991) indicate that the growth of *C. prolifera* is limited by the availability of nitrogen in the water column (Table III).

Nitrogen and phosphorus content of *Cymodocea nodosa* leaves is higher than that of the rhizomes and roots. The average annual C:N:P ratio of the leaves is 441:22:1, 672:17:1 in rhizomes, and 635:19:1 in roots (TERRADOS, 1991). Experimental additions of nitrogen and/or phosphorus to the sediment in meadows on sand indicate that the growth of *C. nodosa* is limited by the availability of nutrientes. Biomass and the growth rates of the shoots in the quadrats where phosphorus had been added were higher ($p < 0.05$) than in quadrats fertilized only with nitrogen and control (Fig. 10), whereas the P/B ratio did not change during the various treatments. The increase in shoot density in a meadow involves the growth of both leaves and rhizomes; shoot density only increased in the quadrat fertilized with both nitrogen and phosphorus (Table IV; TERRADOS & ROS, in press d).

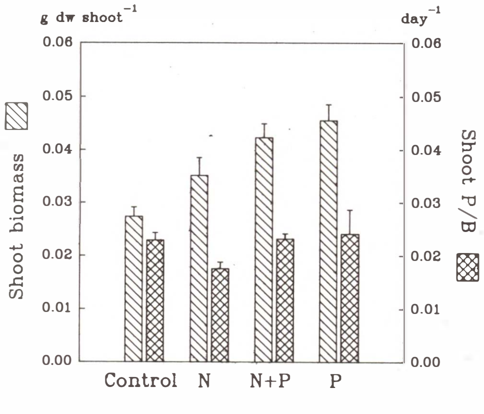

FIGURE 10. Biomass and P/B ratio of *Cymodocea nodosa* shoots after long-term fertilization of the sediment (sand). Vertical bars, standard error of mean. (TERRADOS & ROS, in press d).

TABLE IV. Effect of the long-term fertilization (monthly nutrient additions from April to July) of the sediment with nitrogen ($NH_4^+$) and/or phosphorus ($PO_4^{3-}$) on the shoot density of a *Cymodocea nodosa* meadow on sand. Mean (standard error of mean) of the number of shoots in 25 permanent quadrats (100 $cm^2$) before and after treatments (TERRADOS & ROS, in press d).

| Treatment | Number of shoots per quadrat | |
|---|---|---|
| | Initial | Final |
| Control | 18.2 (0.9) | 37.7 (1.4) |
| N | 16.6 (0.9) | 27.2 (1.2) |
| N+P | 19.6 (0.8) | 60.1 (2.7) |
| P | 17.6 (0.7) | 35.3 (1.2) |

## TOTAL LAGOON PRIMARY PRODUCTION ESTIMATE

Following the bionomic mapping made by PÉREZ RUZAFA *et al.* (1989) and by studying aerial colour photographs taken on a flight in 1986, we have calculated that of the 135 $km^2$ of the lagoon's surface area approximately 85% of the bottom is muddy, 14% sandy and 1% rocky (TERRADOS, 1986, 1991). The shallow sandy bottom is covered by vegetation in approximately 18% of its area, making up 2.5% of the lagoon total. Similarly the area of the *Caulerpa prolifera* meadow on mud can be estimated at roughly 115 $km^2$, and the macrophyte meadows on sand at 3.5 $km^2$. The presence of communities of photophilic algae on rock is not important in the ecosystem as a whole.

With these data, supposing that half the meadows of macrophytes on sand are made up by *Caulerpa prolifera* and the other half by *Cymodocea nodosa* and with the

TABLE V. Biomass, primary production and surface covered by different plant communities in the Mar Menor lagoon (Data from BALLESTER, 1985; TERRADOS, 1986, 1991; PÉREZ RUZAFA,A., 1989 and Gilabert, pers. comm.). [1] isla del Ciervo, [2] El Estacio.,

| | Biomass g dw m$^{-2}$ | Annual production g dw m$^{-2}$ y$^{-1}$ | Annual production g C m$^{-2}$ y$^{-1}$ | Surface km$^{2}$ | Total prod. Tm C | Production % of total |
|---|---|---|---|---|---|---|
| *Caulerpa prolifera* (mud) | 31-157 | 630-707 | 211.7-237.5 | 115 | 24343-27318 | 63.18 |
| *Caulerpa prolifera* (sand) | 16-97 | 388-446 | 130.4-149.8 | 1.75 | 228-262 | |
| *Cymodocea nodosa*, leaves | 3-170 | 166-360 | 49.8-108.0 | 1.75 | 87-189 | 0.42 |
| rhizomes | 65-157 | 47-72 | 15.5-23.8 | 1.75 | 27-42 | |
| Photophilic algae[1] | 20-152 | 389 | 74 | 0.67 | 50 | 0.12 |
| Photophilic algae[2] | 0-956 | 1040 | 71 | 0.67 | 48 | 0.12 |
| Microphytobenthos (mud) | | | 36 | 115 | 4117 | 10.00 |
| Microphytobenthos (sand) | | | 23.5-44.6 | 20 | 470-892 | 1.62 |
| Phytoplankton | | | 75 | 135 | 10125 | 24.53 |
| | | | TOTAL | | 41269.3 Tm C y$^{-1}$ | |
| | | | | | ≈ 306 g C m$^{-2}$ y$^{-1}$ | |

estimates for annual production of the meadows of *C. prolifera* (TERRADOS, 1991), *C. nodosa* (TERRADOS & ROS, in press a), and the communities of photophilic algae, it is possible in turn to estimate the total primary production of macrophytobenthos in the lagoon (Table V).

The estimates for primary production of the phytoplankton and microphytobenthos are approximate and are based on carbon uptake rates measured at midday, using the $^{14}C$ method, during incubation periods of two hours, by Gilabert (pers. comm.) and PÉREZ RUZAFA, A. (1989), respectively. These authors took these measurements during the second half of 1987 and along all 1988 on a weekly basis (Gilabert, pers. comm.) or on a monthly basis (PÉREZ RUZAFA, A., 1989).

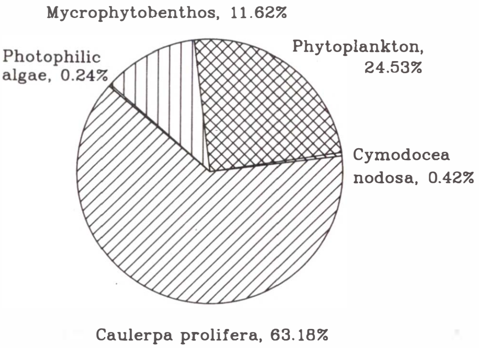

FIGURE 11. Percentage of annual primary production achieved by the different plant communities of the Mar Menor lagoon.

These estimates were calculated by multiplying the assimilation rates measured in one day by the number of hours of daylight on that particular day, and considering the daily assimilation as representative of the time period between sampling (one week for phytoplankton; one month for microphytobenthos). The annual estimate is the sum of the weekly or monthly estimates. As a result, and with all the limitations of the extrapolation method used, the production values obtained for these two compartments are considered maximum estimates.

Overall primary production of the Mar Menor lagoon can be estimated to be at least 41,269 Tm of carbon a year, which is equivalent to about 300 g C m$^{-2}$ y$^{-1}$. Macrophytobenthos production is two to three times higher than phytoplankton production (Fig. 11). Microphytobenthos production makes up 11% of total lagoon production, whereas macrophytobenthos production makes up slightly less than 64%.

## ENVIRONMENTAL CONTROL OF MACROPHYTE DISTRIBUTION IN THE LAGOON BY LIGHT AVAILABILITY

Secchi disk depth values ($D_{sd}$) measured by Gilabert (pers. comm.) on a weekly basis at a point situated in the northern part of the central basin in 1988 can be used to calculate the light extinction coefficient (k) through the relation $k = 1.7 / D_{sd}$ (POOLE & ATKINS, 1929; GIESEN *et al.*, 1990). The average annual value obtained is $k = 0.35$, but during August and September k may reach 0.57. In these conditions the quantity of light reaching the bottom of the lagoon is small and in fact irradiances measured at the bottom of the Mar Menor at midday in summer ($< 200\ \mu mol\ m^{-2}\ s^{-1}$) are lower than those measured during the rest of the year, even winter (TERRADOS, 1991).

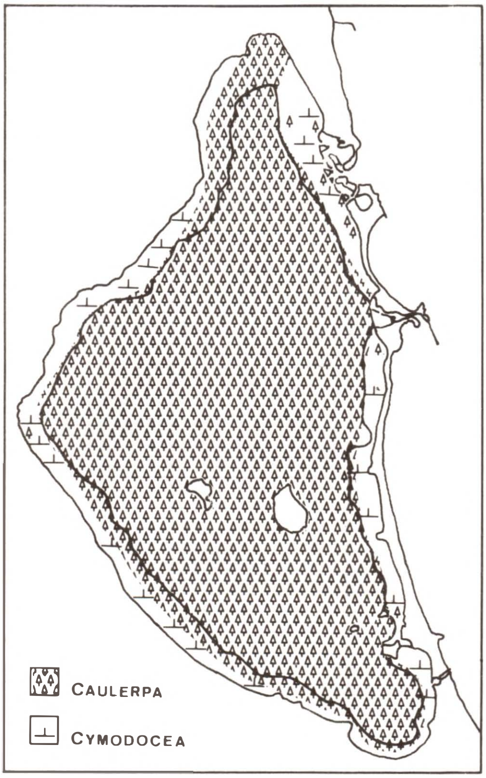

FIGURE 12. Distribution of *Caulerpa prolifera* and *Cymodocea nodosa* meadows in the Mar Menor lagoon, according to all information available. Compare with the map in PÉREZ RUZAFA *et al.* (1989); the 3.3 m isobath is shown (TERRADOS, 1991).

DENNISON (1987) used $H_{comp}$ values (the period of time during the day that the plant receives irradiances of more than $I_c$; DENNISON & ALBERTE, 1982, 1985) to predict the depth limit of distribution of *Zostera marina* in Woods Hole, and obtained the empirical relation between the light extinction coefficient and depth limit of distribution $Z_c = 1.62/k$, similar to that found by NIELSEN *et al.* (1989; in DUARTE, in prep.) in Danish estuaries ($Z_c = 1.53/k$). VICENTE & RIBERA (1982; in DUARTE, in prep.) obtained the relation $Z_c = 1.36/k$ for *Thalassia testudinum* on Puerto Rican coasts. Starting from a thorough bibliographical study DUARTE (in prep.), calculates an average relation for marine seagrasses of $Z_c = 1.86/k$, which is equivalent to the depth reached by 11% of the light incident on the surface.

If we apply this last relation to k values calculated for 1988 in the Mar Menor (Gilabert, pers. comm.) we find the annual variation of critical depth ($Z_c$) of seagrasses vertical distribution which, for the months of August and September, varies between 3.3 and 5.5 m.

Currently *Cymodocea nodosa* only forms dense meadows in the outer areas - the shallower areas - of the lagoon; at depths of more than 4 m only isolated shoots are observed, never a meadow (TERRADOS, 1991). Therefore it is necessary to modify the bionomic charting of the lagoon made by PÉREZ RUZAFA *et al.* (1989); we should extend the distribution of the monospecific meadow of *Caulerpa prolifera* to the area occupied by the *C. nodosa-C. prolifera* mixed meadow (Fig.

12). The distribution of the *C. prolifera* monospecific meadow in the lagoon coincides almost perfectly with the 3.3 m isobath and with the results of a dredging campaign carried out in April 1987 (PÉREZ-RUZAFA, unpublished data), in which the dominance of *C. prolifera* throughout the lagoon is shown.

Daily carbon balances calculated for *Caulerpa prolifera* and *Cymodocea nodosa* in different months of the year (Figs. 8 and 9) indicate that during certain periods of winter and summer not enough light reaches the bottom of the central basin to ensure a positive daily balance for *C. nodosa.* This is caused by the shorter day and the smaller angle of incidence of the sun's rays in winter, and mainly by the extinction of light in the water column in summer. *C. prolifera*, in contrast, maintains a positive carbon balance at the bottom of the central basin througout the year.

All these findings suggest that insufficient light reaches the bottom of the central basin of the Mar Menor in August and September for meadows of *Cymodocea nodosa* to develop. Light availability at depth appears therefore to be the main factor in determining the distribution of meadows of *C. nodosa* in the lagoon.

## *CYMODOCEA NODOSA* REGRESSION

PÉREZ RUZAFA *et al.* (1987, 1989) and ROS (1987) indicate that after dredging and enlargement of the El Estacio channel at the beginning of the seventies, *Caulerpa prolifera* began to colonize the Mar Menor; as a result *Cymodocea nodosa* meadows were gradually replaced by *Caulerpa prolifera* meadows. If we check the biomass data for both species obtained by dredging in 1982/3 (BALLESTER, 1985) and 1987 (PÉREZ RUZAFA *et al.*, unpublished data) this replacement is not clearly seen - rather, we see the consistency over the past few years of a basically monospecific meadow of *C. prolifera.*

The only charted information available about macrophytobenthos prior to the enlargement of the El Estacio channel is the work carried out by LOZANO (1954; Fig. 13). The places where this author found "very abundant Zostera" (probably meadows of *Cymodocea nodosa*) coincide with the areas where today we find meadows of *C. nodosa* (shallow sandy bottoms), while the places where this author found "negligible Zostera" (in the central part of the northern basin) are also areas where today we find isolated shoots of *C. nodosa* (TERRADOS, 1991). Although we do not have information about all the areas of the lagoon, the comparison of these data with the situation today suggests that the distribution of *C. nodosa* in the lagoon has not changed significantly since 1953.

The colonization of the lagoon by *Caulerpa prolifera* is beyond all possible doubt; if it had been present before in its current quantity, this alga would have been

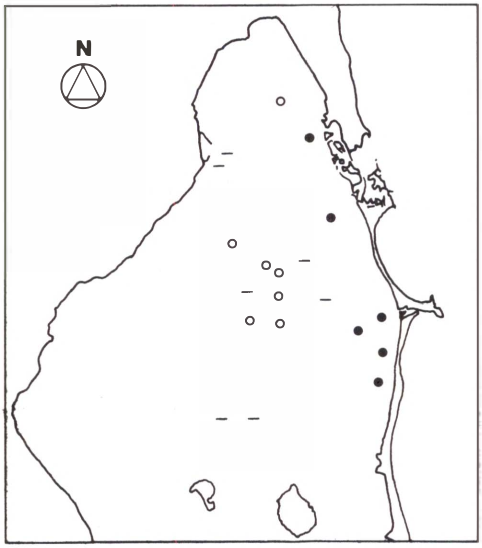

FIGURE 13. Distribution of submerged vegetation in the Mar Menor before dredging and enlargement of the El Estacio channel: solid circles, abundant "Zostera" (likely, *Cymodocea nodosa*); hollow circles, scarce "Zostera"; dashes, no vegetation (redrawn from LOZANO, 1954).

mentioned in the studies prior to the dredging of the El Estacio channel (LOZANO, 1954; SIMMONEAU, 1973). As we have said above, it is not altogether certain that the recent colonization by *C. prolifera* has meant that *C. nodosa* has been displaced.

Changes in salinity - a fall from 50-60‰ in the sixties to 45‰ today - and in water temperature - in the sense of damping off the extreme values - caused by the dredging and enlargement of the El Estacio channel, have not had a negative effect on the viability of the seagrass inside the lagoon - indeed, its development has been favoured. The increase in organic material in the sediment of the bottom areas colonized by *Caulerpa prolifera* and consequently the increase in the levels of the sediment's anoxia (PÉREZ RUZAFA *et al.*, 1987) is not in itself harmful to *C. nodosa* since seagrasses are capable of supplying enough oxygen to the rhizomes and roots through the lagunar air system to keep up their activity (PENHALE & WETZEL, 1983; DeLAUNE *et al.*, 1984; SMITH *et al.*, 1984; SORREL & DROMGOOLE, 1988; LARKUM *et al.*, 1990). Furthermore, the higher level of organic material in the sediment ensures greater availability of nutrients for the plant (TERRADOS, 1991).

There does not seem to be a direct interaction between *Caulerpa prolifera* and *Cymodocea nodosa.* The colonization of the lagoon by *C. prolifera* may simply have been the occupation of an empty niche in the ecosystem after the changes in temperature and salinity caused by the works in El Estacio, and not a process of competitive exclusion at the expense of *C. nodosa.*

Whereas the colonization of muddy substrates, with low hydrodynamism, by *Caulerpa prolifera* is a relatively fast process (ROS *et al.*, 1988), the consistency of some of the meadows of this alga on sand since 1985 (TERRADOS, 1991) leads us to suppose that the muddying and the formation of a meadow of high biomass in relatively shallow sandy substrates (less than 2 m deep) is a much slower process, indeed, a dense meadow on sandy sediment may not finally be created. We may put forward the hypothesis that the lower availability of nutrients in the sandy bottoms hampers the development of a dense meadow of *C. prolifera* (TERRADOS, 1991).

## DISCUSSION

The maximum biomass attained by the meadows of *Caulerpa prolifera* in the Mar Menor is equivalent to the maximum leaf biomass attained by meadows of *Cymodocea nodosa* in shallow muddy areas; it is higher than the leaf biomass of the meadows of *C. nodosa* on sand, which are the most extended in the lagoon. Obviously, the total biomass attained by *C. nodosa*, including rhizomes and roots, is greater than that of *C. prolifera.*

The biomass cycle of both species show a certain time lag. *Caulerpa prolifera* reaches maximum biomass in summer and maintains it until November-December; *Cymodocea nodosa* also reaches maximum biomass in summer, but in autumn it already begins to fall. *C. nodosa* reaches minimum biomass in winter, while *C. prolifera* reaches its minimum biomass in spring.

The meadows of *Caulerpa prolifera* have an average annual LAI between 1.40 and 1.88 $m^2\ m^{-2}$, higher than that of the meadows of *Cymodocea nodosa* on sand (0.71 $m^2\ m^{-2}$). The presence of *C. prolifera* in the lagoon would seem to suppose an increase in the surface of the substrate available for the settlement of epiphytes. However, field observations carried out indicate that the presence of macroepiphytes on *C. prolifera* is negligible; the old leaves of *C. nodosa* usually have a fair number of epiphytes. This may be due to the higher rate of renovation of the biomass of *C. prolifera* compared with *C. nodosa*'s leaf biomass, or to the alga's use of defensive substances (PAUL & FENICAL, 1986).

In accordance with the estimates we have made, both annual primary production and the annual P/B ratio are higher in *Caulerpa prolifera* (211.7-237.5 g C $m^{-2}$ $y^{-1}$; P/B = 4) than in *Cymodocea nodosa* (leaves: 49.8-108 g C $m^{-2}$ $y^{-1}$; P/B = 2.5; rhizomes: 15.5-23.8 g C $m^{-2}$ $y^{-1}$; P/B = 0.29). Light and temperature appear to be the main environmental factors which control meadow production of macrophytes, for the amounts of nutrient available.

N and P content in *Caulerpa prolifera* is higher than in *Cymodocea nodosa.* Both species have a similar N:P ratio. *C prolifera* growth seems to be limited by the availability of nitrogen, whereas *C. nodosa* growth seems to be limited by the availability of both nitrogen and phosphorus.

*Caulerpa prolifera* presents lower $I_c$ and $I_k$ figures than *Cymodocea nodosa.* $\alpha$ is higher in *C. prolifera* than in *C. nodosa,* whereas the $P_{max}$ reached by the seagrass, especially in spring and summer, was higher than that of the chlorophycean. All this suggests that *C. prolifera* can live in conditions of less irradiance than *C. nodosa,* as shown by the daily carbon balances calculated for both species throughout the year. *C. nodosa* has a larger fraction of non-photosynthetic biomass than *C. prolifera*; therefore energy requirements for the maintenance of the plant are higher. Water temperature exerts a linear influence on the $P_{max}$ and R rates in both species between 10 and 30 $^{o}$C and 10 and 35 $^{o}$C, respectively. Both species show adaptation in their photosynthetic characteristics to the seasonal variation of the water temperature.

The capacity for vegetative expansion and dispersion of *Caulerpa prolifera* is higher than that of *Cymodocea nodosa* (TERRADOS, 1991). After the dredging and enlargement of the El Estacio channel in 1972, *C. prolifera* carried out a spectacular colonization process in the Mar Menor, and today it can be found all over the lagoon. It is capable of implanting itself on rock (El Ciervo island and Los Alcázares), but where it reaches its greatest biomass is on mud and sand. Biological features such as almost continuous growth throughout the year or the capacity of generating vegetatively a new thallus from any fragment swept away by the water have enabled it to spread out rapidly throughout the lagoon.

The colonization of the Mar Menor by *Caulerpa prolifera* has brought about an increase in macrophytobenthic primary production and thus in the lagoon's primary production. On the one hand, the annual production of the meadow of *C. prolifera* on mud (212-235 g C $m^{-2}$ $y^{-1}$) is higher than that of meadows of *Cymodocea nodosa* (65-130 g C $m^{-2}$ $y^{-1}$); on the other hand, the presence of macrophytes in the lagoon is now much higher than before the opening of the El Estacio channel. The importance of the change in the Mar Menor caused by the enlargement of the El Estacio channel is obvious, since a species that colonized the lagoon after the project now accounts for 63% of the autotrophic incorporation of carbon into the ecosystem.

The colonization has, predictably, had other effects.

The establishment of a meadow of *Caulerpa prolifera* protects the sediment, increasing sedimentation rates and reducing sediment resuspension rates in situations of high hydrodynamism, especially in shallow bodies of water such as the Mar Menor; therefore water turbidity is probably now less. This process has been identified in other systems where there is significant macrophyte presence (SHORT & SHORT, 1984).

The decomposition rates of *Caulerpa prolifera* are higher than those of *Cymodocea nodosa*: experiments on decomposition of *C. nodosa* leaves carried out by PÉREZ (1989) show that after 140 days 40% of the initial dead material remains, while with *Caulerpa cupressoides*

(WILLIAMS, 1984a), which must have decomposition rates similar to those of *C. prolifera*, after seven days 50% of the initial dead material is lost. Although these differences are probably less with relation to nitrogen and phosphorus, the matter cycling in the macrophytobenthos is faster now that it is dominated by *C. prolifera* than when the dominant macrophyte was *C. nodosa*. However, the lower biomass turnover of macrophytes in comparison with phytoplankton causes the inflow of energy into the ecosystem to be slower now that the macrophytobenthos is dominant. For the lagunar ecosystem, the presence of macrophytes has meant the acquisition of compartments which have greater inertia and are stabilizing factors of both primary and secondary production (HARRISON & MANN, 1975; FENCHEL, 1977; KENWORTHY & THAYER, 1984).

As they are fixed to the substrate, aquatic macrophytes are capable of using the movement of the water to acquire dissolved inorganic nutrients more efficiently than phytoplankton (MANN, 1982). A moderate degree of hydrodynamism increases the volume of water used by the macrophytes and breaks the difussion gradients, facilitating the assimilation of nutrients (LOBBAN *et al.*, 1985). Furthermore, if they are on soft substrates, they can use the nutrients present in the sediment (McROY & McMILLAN, 1977; THURSBY & HARLIN, 1982; SHORT & McROY, 1984; BRIX & LYNGBY, 1985).

The relative importance of root and leaf assimilation depends on the level of availability of nutrients in the water or in the sediment (McROY & McMILLAN, 1977; THURSBY & HARLIN, 1982; BRIX & LYNGBY, 1985; BORUM *et al.*, 1989; HILLMAN *et al.*, 1990). It is generally accepted that the sediment is the main source of nutrients both for freshwater macrophytes (BARKO & SMART, 1980, 1981; DUARTE & KALFF, 1987; CHAMBERS *et al.*, 1988) and for marine phanerogames (SHORT, 1983 a, b, 1987; SHORT & McROY, 194; THURSBY & HARLIN, 1984; SHORT *et al.*, 1985; WILLIAMS, 1987, 1990; HILLMAN *et al.*, 1990).

The dominance of *Caulerpa prolifera* and *Cymodocea nodosa* in the lagoon determines, on the one hand, the consumption of the nutrients present in the sediment (which cannot be utilized directly by phytoplankton); and on the other hand, the competition with the phytoplankton in the acquisition of nutrients, as ROS & MIRACLE (1984) and ROS (1987) have suggested.

Although the concentrations of inorganic compounds of nitrogen and phosphorus dissolved in the water of the Mar Menor are very low, *Caulerpa prolifera* is probably capable of meeting its requirements of nitrogen and phosphorus from the nutrients available in the sediment. WILLIAMS (1984 b) showed that *Caulerpa cupressoides* was capable of assimilating $NH_4^+$ through the rhizoids and transporting it to the fronds. The values for the semisaturation constant for the absorption of $NH_4^+$ that this author obtained indicate that *C. cupressoides* is better adapted to use sediment than water as a nitrogen source. The experiments in sediment fertilization carried out in the Mar Menor (TERRADOS & ROS, in press d) and in other places (PÉREZ *et al.*, 1991) indicate that *Cymodocea nodosa* is capable of using nutrients present in the sediment.

As we have seen, nitrogen and phosphorus content in *Caulerpa prolifera* is greater than in *Cymodocea nodosa*. Because of this, the presence of the alga in the lagoon has probably increased the capacity of the macrophytobenthos to absorb the nutrients that enter the lagoon, in competition with the phytoplanktonic populations. This - together with the lower $I_c$ and $I_k$ of *C. prolifera*, the proposed reduction in water turbidity in the lagoon due to the greater presence of macrophytes and the channelling of the nutrient input towards the macrophytes - make us suppose that the colonization by the chlorophycean has probably increased the Mar Menor's resistance to eutrophication processes.

The participation of macrophytobenthos in the overall production of the Mar Menor is high compared with that in other places, such as the bays of the Ebro delta (PÉREZ, 1989). These bays constitute an estuarine environment where the inflow of freshwater and nutrients is important and where phytoplanktonic production predominates. In contrast, in the Mar Menor there is no marked inflow of freshwater, the interchange with the Mediterranean Sea is less, and although the amount of nutrient input from land sources has not been evaluated, it must be less than in the bays of the Ebro Delta. In these conditions of relative scarcity of nutrients in the water column, the light reaches the bottom in sufficient quantities to allow the development of submerged vegetation, capable of using the nutrients present in the sediment.

Summer seems to be a critical time of year for the functioning of the Mar Menor. It is then that development of the phytoplanktonic populations is at its highest (Gilabert, pers. comm.); therefore light extinction in the water column increases in such a way that at the bottom of the central basin there is insufficient light for *Cymodocea nodosa* to grow. The high water temperatures cause the metabolic cost of maintaining the vegetation to be higher. Furthermore, it has been suggested that the increase in the resident human population on the banks of the lagoon at this time of year, and the shortcomings of the sanitation network in the villages around the lagoon probably cause more nutrients to enter (TERRADOS, 1986), which may be one of the reasons for the proliferation of phytoplankton in summer.

This greater development of phytoplankton in summer causes a reduction in the quantity of light that reaches the bottom. If this reduction increased, the development of *Caulerpa prolifera* and other types of submerged vegetation would be hindered, thus triggering a process of eutrophication which would alter completely the functioning and environmental characteristics of the lagunar ecosystem. The relations between phytoplankton and macrophytes as far as the nutrient cycle and production-consumption of detritus are concerned require special attention in the future, because of their implications for the overall functioning of the Mar Menor lagoon ecosystem.

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