

Temporal variation of the biomass and structure of *Caulerpa prolifera* (Forsskål) Lamouroux meadows in the Mar Menor lagoon (SE Spain)*

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SUMMARY: The temporal changes in the structure, biomass and C, N and P content of meadows of *Caulerpa prolifera* (Forsskål) Lamouroux in the Mar Menor coastal lagoon (SE Spain) are described over the period from November 1986 to March 1989. *C. prolifera* meadows showed a unimodal pattern of vegetative development with maximum biomass values (168–173 g d.w. m⁻²) reached in summer and maintained during autumn, and minimum biomass values (0–57 g d.w. m⁻²) during late winter and early spring. Leaf area index values changed between 0.37–0.40 m² m⁻² in January–February and 2.60–7.06 m² m⁻² in July. The seasonality in the biomass and structure of the meadow was mainly related to the vegetative development of the secondary fronds. Carbon and phosphorus content of the thallus (32.5–34.8% d.w. and 0.065–0.069% d.w., respectively) had no seasonality, but nitrogen content showed a bimodal annual pattern with higher values in spring and fall (>2.5 % d.w.) than in summer and winter (<2.5 % d.w.).

Key words: Biomass, meadow structure, *Caulerpa prolifera*, coastal lagoons, Mar Menor, SE Spain.

RESUMEN: VARIACIÓN TEMPORAL DE LA BIOMASA Y ESTRUCTURA DE LAS PRADERAS DE *CAULERPA PROLIFERA* (FORSSKÅL) LAMOUROUX EN EL MAR MENOR, SE DE ESPAÑA. — Se describe la variación temporal de la estructura, biomasa y contenido de carbono, nitrógeno y fósforo de la pradera de *Caulerpa prolifera* en el Mar Menor (SE de España) desde noviembre de 1986 a marzo de 1989. La pradera muestra un ciclo anual unimodal de desarrollo vegetativo con valores máximos de biomasa (168–173 g p.s. m⁻²) durante el verano y el otoño, y mínimos (0–57 g p.s. m⁻²) durante el invierno y principios de la primavera. Los valores del índice de área foliar oscilaron entre 0.37–0.40 m² m⁻² en enero-febrero y 2.60–7.06 m² m⁻² en julio. Los cambios temporales en la biomasa y estructura de la pradera se deben principalmente a la estacionalidad en el desarrollo vegetativo de los frondes secundarios. El contenido de nitrógeno del talo mostró una pauta anual bimodal con valores mayores en primavera y otoño (>2.5 % peso seco) que en verano e invierno (<2.5 % p.s.), mientras que los contenidos de carbono (32.5–34.8 % p.s.) y fósforo (0.065–0.069 % p.s.) no mostraron una pauta temporal definida.

Palabras clave: Biomasa, estructura, *Caulerpa prolifera*, lagunas costeras, Mar Menor, SE España.

INTRODUCTION

The green alga *Caulerpa prolifera* (Forsskål) Lamouroux forms meadows which cover more than

85% of the bottom of the Mar Menor, a 135 km² hypersaline coastal lagoon located on the southeast Mediterranean coast of Spain (TERRADOS, 1991). *C. prolifera* can grow both on soft (sand, mud) and hard (rock) substrates, but its maximum vegetative development is reached on the muddy bottom of the

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lagoon's central basin. It is the dominant macrophyte in the Mar Menor and, therefore, a key species in understanding the primary production and nutrient cycling processes in the lagoon ecosystem (TERRADOS, 1991). Although there is some information regarding growth and biomass of this species in the lagoon, it is restricted to sites close to the banks (TERRADOS, 1986) or it was obtained with a low temporal frequency (BALLESTER, 1985; PÉREZ-RUZAFÁ, 1989), and might not be fully representative of the biomass cycle of *C. prolifera* in the lagoon. In this study, "meadow structure" refers to the partition of biomass among its different structural elements: stolons, primary fronds and secondary fronds. This structure may influence processes such as light distribution (PÉREZ and ROMERO, 1992) or mass transport (FONSECA and FISHER, 1986; ACKERMAN and OKUBO, 1993) within the canopy that control macrophyte physiology and, ultimately, community function. Knowledge of plant macronutrient composition is necessary to understand macrophyte growth strategies and community primary production (CHAPMAN and CRAIGIE, 1977; HATCHER *et al.*, 1977). The objective of this study is to describe the temporal changes in structure, biomass and macronutrient content of the *C. prolifera* meadow in the central basin of the Mar Menor lagoon.

MATERIAL AND METHODS

A sampling station (ST1) was selected in the north-central part of the lagoon basin at a depth of 4 m. After two months of sampling the meadow decayed completely at this point, so another sampling station (ST2) was selected not far from the former and both were followed for this study (Fig. 1). Samples ($n=4$) were collected monthly from November 1986 to March 1989 with a Van Veen grab (sediment surface retrieved: 400 cm²). Water temperature ($\pm 0.1^{\circ}\text{C}$) was measured within the meadow by a diver. The samples were washed with seawater through a 0.5 mm sieve to eliminate the mud and preserved in 4% formaldehyde seawater. In order to describe meadow structure, the thalli present in two of the samples taken each month were fractionated into three different structural elements: stolons, primary fronds (those inserted on a stolon) and secondary fronds (those inserted on a frond) (MEINESZ, 1979a). The length and biomass of stolons, and the number and biomass of primary and secondary fronds were determined for each sample.

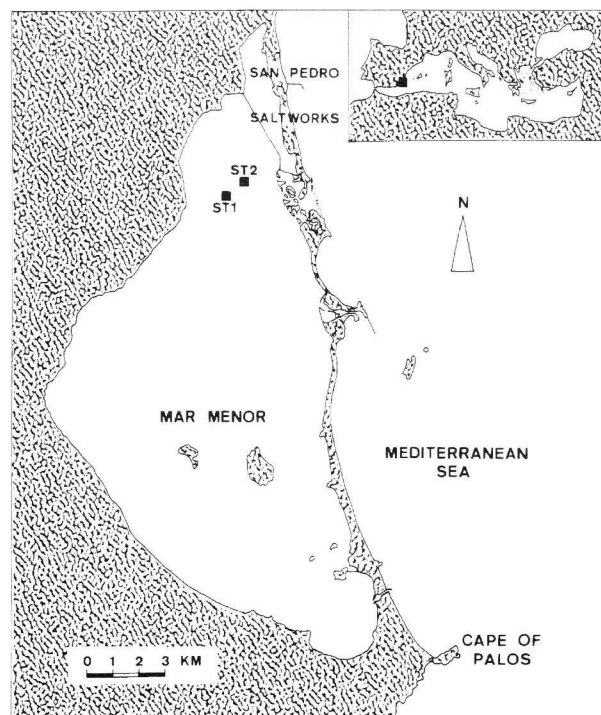


FIG. 1. – Location of the Mar Menor lagoon on the Southeast Mediterranean coast of Spain, and location of the sampling sites.

Additionally, the number of juvenile fronds (length < 2 cm; MEINESZ, 1979a), and the length and width of the fronds not broken and longer than 2 cm were determined in each frond class. Only the total biomass of *Caulerpa prolifera* was determined in the other two samples. Biomass is expressed as dry weight after drying at 105°C during 24 h (ROMERO, 1984).

The changes in the structure of the meadow were characterized by calculating the variability (coefficient of variation, V^* , SOKAL and ROHLF, 1981) of the biomass of the meadow and of each structural element (stolons, primary fronds, secondary fronds), and by quantifying how much biomass is allocated to each structural element through the year. Leaf area index (LAI) of the meadow was calculated by summing the results determined from multiplying the number of fronds in each class by their average surface area.

Ash content of *Caulerpa prolifera* was determined monthly ($4 \leq n \leq 17$) from January 1988 to March 1989; carbon and nitrogen content were determined monthly from October 1987 to November 1988, and phosphorus content was determined

monthly from October 1987 to March 1989. The samples were frozen *in situ* with dry ice and preserved at -30°C until analysis. Prior to analysis, plant material was dried at 60°C for 24 h (ATKINSON and SMITH, 1983) and ground to fine powder. Ash content was determined after burning the samples at 450°C for 6 h (ROMERO, 1984). Carbon and nitrogen content were determined using a Perkin Elmer elemental analyzer. Phosphorus content was determined after digestion of approximately 0.1 g of sample with HNO₃:HClO₄, 5:3 v,v (SOMMERS and NELSON, 1972) using the malachite green method (FERNÁNDEZ *et al.*, 1985).

Differences in the annual average biomass allocated to the structural elements of the meadow at each station and between stations were tested using the non-parametric tests of Kruskal-Wallis (H) and Mann-Whitney (t_s) (SOKAL and ROHLF, 1981). Association between the different structural variables of the meadow was established using the product-moment correlation coefficient (SOKAL and ROHLF, 1981).

RESULTS

Water temperature of the Mar Menor lagoon varied during the period of study from minimum values in February (10.7-12.5°C) to maximum values in August (29.5°C); there were no differences between sampling sites (Fig. 2).

In terms of biomass, the primary fronds were the main element of the *C. prolifera* meadow at station

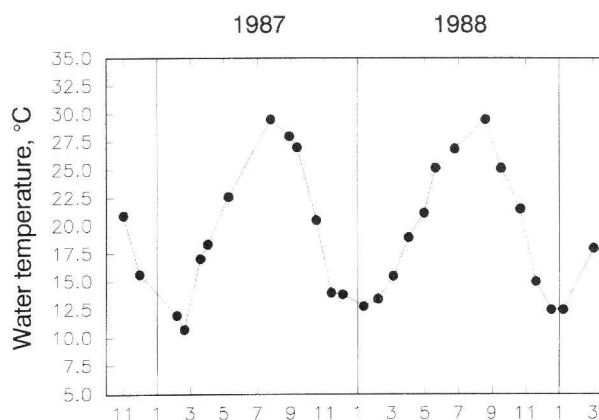


FIG. 2. – Water temperature of the Mar Menor lagoon during the period of study. All measurements are pooled together as there were no differences between stations. Bars representing the standard error of the mean are not seen because they are smaller than symbol size; n=4. The numbers on the abscissa axis indicate the beginning of the corresponding month of the year.

ST1 (H=29.4903, P<0.01) (Table 1), while stolons and secondary fronds had similar importance. At station ST2, stolons and primary fronds had similar biomass, which was higher than that of secondary fronds (H=22.0802, P<0.01). The biomass allocated to primary fronds was higher than that allocated to secondary fronds at both stations (ST1: t_s=4.354, P<0.01; ST2: t_s=4.352, P<0.01). Meadow biomass was more variable at station ST1 than at station ST2 (Table 1). The secondary fronds were the structural element with more variability, followed by stolons and primary fronds.

TABLE 1. – *Caulerpa prolifera* meadow total biomass and percent biomass of each structural element of the meadow in stations ST1 (n=22) and ST2 (n=21) during the period of study. Minimum and maximum values, mean and standard error of mean, and coefficient of variation (V*) and standard error of V*.

	Range of variation	Mean ± SE	V* ± SE
Station ST1			
Meadow biomass, g d.w. m ⁻²	2.2-168.2	73.0 ± 8.20	54 ± 10
% Stolons	13.2- 43.7	27.4 ± 1.58	27 ± 4
% Primary fronds	29.0- 48.6	44.0 ± 1.95	21 ± 3
% Secondary fronds	5.0- 47.3	28.5 ± 2.26	38 ± 6
Station ST2			
Meadow biomass, g d.w. m ⁻²	57.0-173.6	98.9 ± 6.29	29 ± 5
% Stolons	22.1- 61.5	36.2 ± 2.09	27 ± 4
% Primary fronds	29.0- 48.6	38.7 ± 1.14	14 ± 2
% Secondary fronds	9.5- 43.3	25.0 ± 1.94	36 ± 6

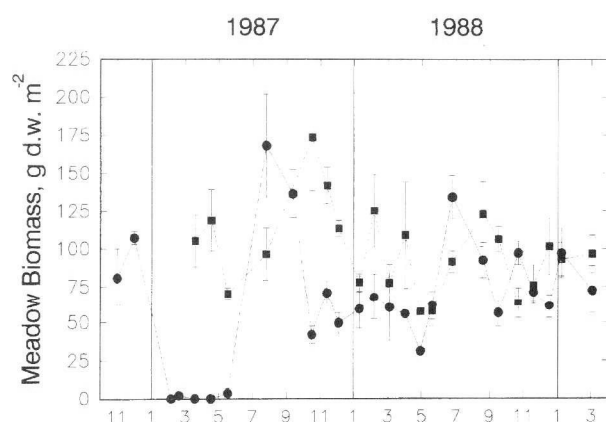


FIG. 3. – Temporal variation of *Caulerpa prolifera* meadow biomass at ST1 (circles) and ST2 (squares) sampling sites. Bars represent the standard error of the mean; $n=4$. The numbers on the abscissa axis indicate the beginning of the corresponding month of the year.

When stations ST1 and ST2 are compared, the average biomass of the *Caulerpa prolifera* meadow at ST1 was lower ($t_s=2.561$, $P=0.0104$) and more variable than that at station ST2 (Table 1). The biomass allocated to stolons was lower ($t_s=2.976$, $P=0.0029$) at ST1 than at ST2, while that allocated to primary fronds showed an opposite trend ($t_s=2.029$, $P=0.0425$) (Table 1).

The meadow decayed completely at ST1 in January 1987 (Fig. 3) and did not recover until the summer; this decay was not observed either at ST2 nor at both places during the following two winters. Although the time course of meadow biomass was rather variable in both stations, the maximum biomass values were usually reached between July and October, and the minimum ones between February and May (Fig. 3).

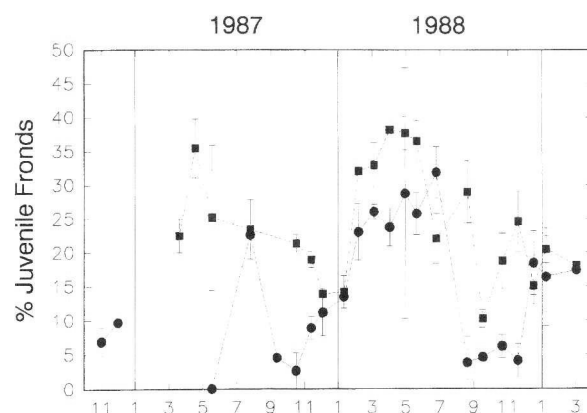


FIG. 4. – Temporal variation of the percentage of juvenile fronds (relative to the total number of fronds in the meadow) at ST1 (circles) and ST2 (squares) sampling sites. Bars represent the standard error of the mean; $n=2$. The numbers on the abscissa axis indicate the beginning of the corresponding month of the year.

At station ST1, meadow biomass was positively correlated with the percentage of biomass allocated to secondary fronds, and there were negative correlations between secondary fronds and the percentages of biomass allocated to stolons and primary fronds (Table 2). In station ST2, there were negative correlations between the meadow biomass and biomass of stolons, and between biomass of stolons and biomass of secondary fronds (Table 2).

The percentage of juvenile fronds (relative to the total number of fronds in the meadow) at station ST1 varied between 0 and 31.9% (annual average \pm SE: $11.9 \pm 2.19\%$, $V^*=86.4\%$); the values were low at the annual maxima of meadow biomass (September–November) and increased between them (Fig. 4). At station ST2, the percentage of

TABLE 2. – Linear correlation coefficients between meadow biomass and the percentages of biomass allocated to each structural element of the meadow at station ST1 (below main diagonal, $n=22$) and station ST2 (above main diagonal, $n=21$).
n.s., not significant; *, $P<0.05$; **, $P<0.01$.

ST1 \ ST2	Biomass	Stolons	Primary fronds	Secondary fronds
Biomass	-----	0.4380*	n.s.	n.s.
Stolons	n.s.	-----	n.s.	-0.8482**
Primary fronds	n.s.	n.s.	-----	n.s.
Secondary fronds	0.5277*	-0.5282*	-0.7282**	-----

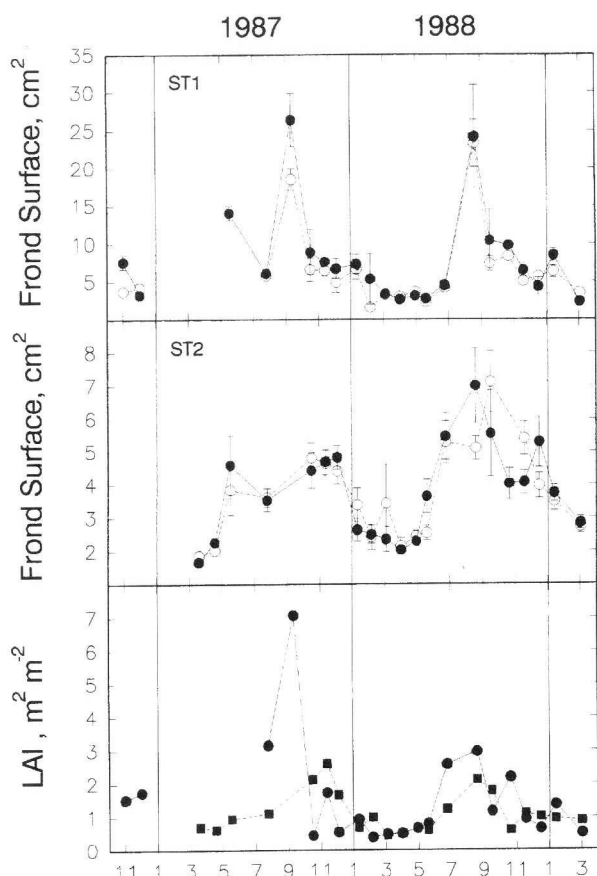


FIG. 5. – Top and middle: Temporal variation of the average surface of primary (solid circles) and secondary fronds (open circles) at sampling stations ST1 and ST2. Bars represent the standard error of the mean; $6 \leq n \leq 101$. Bottom: Temporal variation of LAI values at ST1 (circles) and ST2 (squares) sampling sites. The numbers on the abscissa axis indicate the beginning of the corresponding month of the year.

juvenile fronds varied between 10.3 and 38.2% (annual average \pm SE: $24.3 \pm 1.84\%$, $V^*=34.7\%$); higher values were reached during late winter and spring than during the rest of the year (Fig. 4).

The average surface area of the fronds showed an unimodal annual pattern at both stations, with high values during summer and early fall and low values during spring (Fig. 5). Leaf area index (LAI) values of the meadow varied between $0.37 \text{ m}^2 \text{ m}^{-2}$ and $7.06 \text{ m}^2 \text{ m}^{-2}$ at station ST1, and between $0.40 \text{ m}^2 \text{ m}^{-2}$ and $2.60 \text{ m}^2 \text{ m}^{-2}$ at station ST2 (Fig. 5). LAI showed a clear unimodal annual pattern and was positively correlated with meadow biomass at both stations (ST1: $r=0.8421$, $P<0.01$; ST2: $r=0.697$, $P<0.01$).

The ash content of *Caulerpa prolifera* varied between $7.6 \pm 0.74\%$ (mean \pm SE) of dry weight

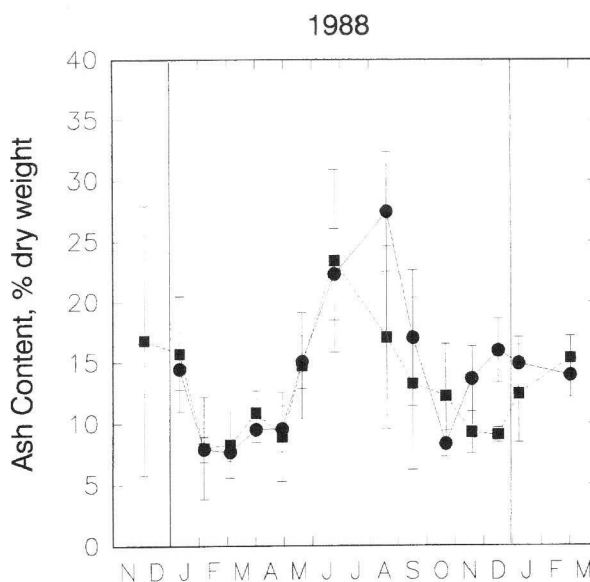


FIG. 6. – Temporal variation of the ash content of *C. prolifera* during 1988 at ST1 (circles) and ST2 (squares) sampling sites. Bars represent the standard error of the mean; $4 \leq n \leq 17$.

(% d.w.) and $27.4 \pm 4.92\%$ d.w. at station ST1, and between $7.9 \pm 4.19\%$ d.w. and $23.37 \pm 7.53\%$ d.w. at station ST2. During 1988 ash content showed an unimodal annual pattern with high values in summer and low values in winter (Fig. 6). The carbon content of *C. prolifera* varied between 27.9 and 37.6% of d.w. at station ST1, and between 30.5 and 42.4% d.w. at station ST2. Thallus phosphorus content varied between 0.016 and 0.156% d.w. at station ST1, and between 0.012 and 0.106% d.w. at station ST2. Neither carbon nor phosphorus showed a clear temporal pattern (Fig. 7). The changes in the nitrogen content, however, suggested a bimodal annual pattern in both stations, with lower values in winter and summer than in spring and fall (Fig. 7). Nitrogen content varied between 1.22 and 2.93% d.w. at station ST1, and between 1.00 and 3.11% d.w. at station ST2. Differences between stations in the ash or macronutrient content were not significant (Mann-Whitney U-test, $P>0.05$).

DISCUSSION

The biomass values of the *Caulerpa prolifera* meadow found in this study are similar, both in value and in annual range of variation, to those

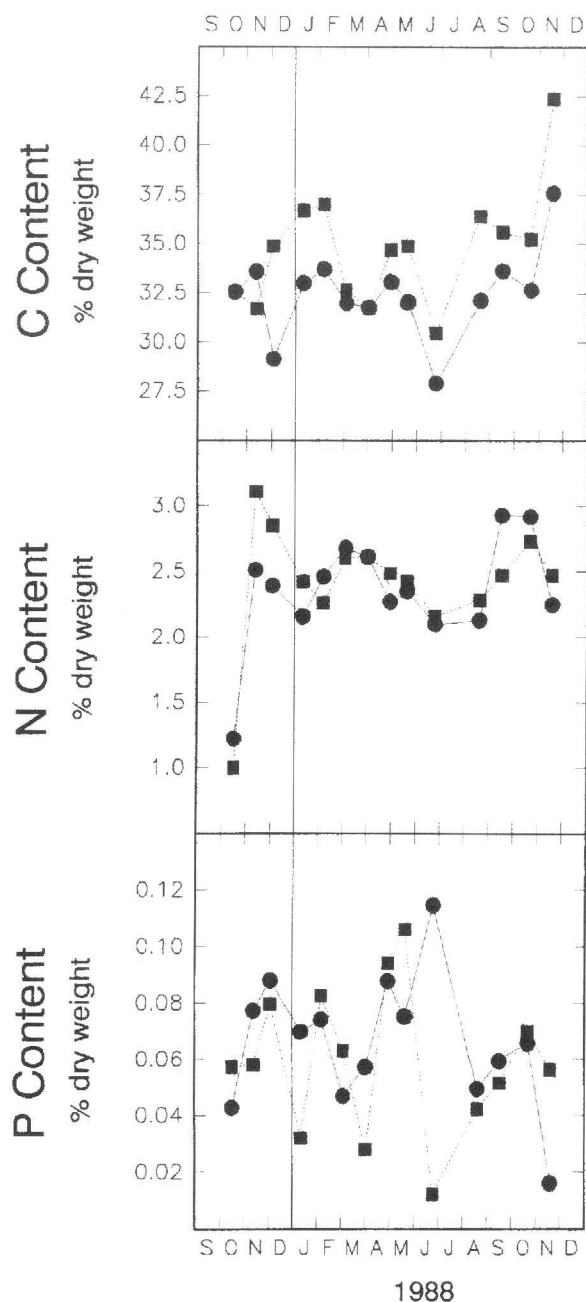


FIG. 7. — Temporal variation of the carbon, nitrogen and phosphorus content of *C. prolifera* during 1988 at ST1 (circles) and ST2 (squares) sampling sites.

previously obtained by BALLESTER (1985), TERRADOS (1986) and PÉREZ-RUZAFA (1989) in the Mar Menor, and to those found in other places of the Western Mediterranean (MEINESZ, 1979b; BALLESTEROS, 1989). Only GESSNER and HAMMER (1960) found higher biomass values (360–375 g d.w. m⁻²) in Villefranche-sur-Mer, France.

The annual cycle of meadow biomass showed an unimodal pattern, with high values reached in summer and maintained during autumn, and low values during spring (Fig. 3). This pattern in the biomass cycle suggests that a great part of the annual growth of the alga is concentrated during late spring and early summer. The similarity between this temporal pattern and those described by BALLESTER (1985), TERRADOS (1986) and PÉREZ-RUZAFA (1989) suggests that the *Caulerpa prolifera* meadow has an homogeneous cycle of vegetative growth throughout the Mar Menor. In addition, this pattern is relatively similar to that found by MEINESZ (1979 a, b) in Crouton Bay, France, where *C. prolifera* reached the maximum biomass values in November-December and the minimum ones in June.

Although there were differences in the structure of the meadow between stations it is not clear if they were just caused by the exceptional complete decay of the meadow at station ST1 in 1987. The cause of this decay remains unknown. Environmental features of both places seemed fairly similar (TERRADOS, 1991) and did not appear to be responsible for the decay. However, the study of some aerial photographs of the area during the last forty years might give a clue to this decay. Some photographs show patches likely devoid of macrophyte vegetation (pers. observ.) connected to places where brines have been drained from large saltworks which extend along the northeast coast of the lagoon (Fig. 1). These brines could cause the mortality of *C. prolifera* plants in the sites where the effluent remained undiluted. In this later regard, TERRADOS (1991) showed that salinities above 50‰ reduced the growth rate of *C. prolifera* thalli held in aquaria, and at a salinity of 60‰ the algae died.

The seasonality in the biomass and structure of the *C. prolifera* meadow seems to be a consequence of the vegetative development of the secondary fronds. The variability of the percentage of biomass allocated to secondary fronds was higher than the variability of those allocated to stolons and primary fronds, and even higher than the variability of the whole biomass meadow at station ST2 (Table 1).

At station ST1 meadow biomass was positively correlated with biomass of secondary fronds, and this was negatively correlated with biomass of stolons and biomass of primary fronds (Table 2). In station ST2 meadow biomass was not correlated with biomass of secondary fronds but with biomass of stolons, and these last two variables were negatively correlated (Table 2). These results suggest that the

changes in biomass and structure of the meadow were driven mainly by the development of the secondary fronds. In a somewhat similar trend, MEINESZ (1979 a, b) also found this alternating seasonality in the development of stolons and fronds, although the primary fronds were the main source of temporal variation in the biomass of the *C. prolifera* meadow he studied.

This seasonality in the development of the fronds affected not only the biomass allocated to each element of the meadow but also the dimensions of the fronds, which were bigger during the summer months (Fig. 5). As a result, LAI values showed a clear unimodal pattern along the year at both stations. The observation that juvenile fronds were less abundant (Fig. 4) during the months when the vegetative development of the meadow was high (Figs. 3 and 5) is consistent with the observed seasonality in the dimensions of the fronds. The highest percentages of juvenile fronds were found in spring (Fig. 4), just before the period of maximum development of the meadow (Figs. 3 and 5), which suggests that it is in late spring/early summer when an important part of frond development takes place.

Previous data of LAI values for *Caulerpa prolifera* in the Mar Menor establish a range of annual variation from 0.004 to 0.535 m² m⁻². These values are lower than those found in this study likely because they were obtained from a meadow of smaller biomass (54.9 g d.w. m⁻²; BALLESTER, 1985). At the annual maximum of vegetative development (365 g d.w. m⁻²) of a *C. prolifera* meadow in Ville-franche-sur-Mer (France), GESSNER and HAMMER (1960) calculated LAI values of 7.7–7.9 m² m⁻², which, except for station ST1 in 1987, are higher than those found in this study. When compared with Mediterranean seagrasses, LAI values of *C. prolifera* meadows in the Mar Menor are within the range of those reported for shallow *Cymodocea nodosa* meadows (0.15–4 m² m⁻²; GESSNER and HAMMER, 1960; BALLESTER, 1985; CAYE and MEINESZ, 1985; PÉREZ, 1989; TERRADOS and ROS, 1992), but smaller than those found in *Posidonia oceanica* meadows (1.1–14.7 m² m⁻²; OTT, 1980; WITTMANN, 1984; ROMERO, 1985).

The changes in the nitrogen content of *Caulerpa prolifera* suggested a bimodal annual pattern, with higher values in spring and fall than in summer and winter (Fig. 7). The decrease in nitrogen content of the plants during summer, a period of fast vegetative growth, could be explained by a “dilution effect” (LEWEY and GORHAM, 1984) if nitrogen uptake does not match nitrogen growth requirements. The low

values also found in winter could be due to the stress caused to the plants by the low water temperatures and a higher dominance of degradative processes; MEINESZ (1979a) found that the vegetative growth of *C. prolifera* was halted at water temperatures below 13°C. However, from the observed seasonality in the nitrogen content of the thallus it must not be concluded directly that nitrogen availability may limit the vegetative growth of *C. prolifera* during the period of highest biomass growth.

If the nutrient content of *Caulerpa prolifera* in the Mar Menor is compared with that of other macrophytes (ATKINSON and SMITH, 1983; DUARTE, 1990), it seems that *C. prolifera* has an average content of nitrogen but a very low content of phosphorus. The average contents of carbon, nitrogen and phosphorus (as % d.w.) during the period of the study were 32.5%, 2.35% and 0.069%, respectively, at station ST1, and 34.8%, 2.42% and 0.065% at station ST2. These results give average atomic C:N:P ratios of 1214:75:1 at ST1, and 1380:82:1 at ST2, which deviate greatly from the median ratio that ATKINSON and SMITH (1983) proposed for benthic macrophytes (550:30:1). On the other hand, DUARTE (1990) showed that nitrogen and phosphorus contents of 1.8% and 0.2 % d.w., respectively, discriminated between seagrass meadows that responded to nutrient enrichment. These comparisons suggest, although in an indirect way, that the growth of *C. prolifera* in the Mar Menor might be more limited by the availability of phosphorus than by that of nitrogen. Some preliminary experiments developed by TERRADOS (1991) suggest that it is nitrogen and not phosphorus the macronutrient limiting the growth of this alga. However, *C. prolifera* plants in those experiments were grown in aquaria without sediment, and the results may not reflect the situation of the alga in the field. WILLIAMS (1984) has shown in *Caulerpa cupressoides* that ammonium can be taken up from the sediment by the rhizoids and translocated to the fronds; *C. prolifera* might also be able to do that. Whether it is nitrogen, phosphorus or both that limit the vegetative development of *Caulerpa prolifera* in the Mar Menor is, therefore, a question still not answered and one that requires direct experimental testing.

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