

Seasonal variations in the rate of photosynthetic activity and chemical composition of the seagrass *Cymodocea nodosa* (Ucr.) Asch.*

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SUMMARY: Temporal changes in biomass, rate of photosynthetic activity and chemical composition of the seagrass *Cymodocea nodosa* (Ucr.) Asch., under the influence of various environmental factors, were followed in the Faborsa Bay, Northern Adriatic. Throughout the year the estimated average biomass was about 130 g dry wt m⁻² with annual production of 80 g C m⁻². In general, leaf length, biomass and production showed clear seasonality, with maximum values during the summer period (July-September) and clear minima in winter. Net oxygen production was closely related to biomass, leaf length, chlorophyll concentration, water temperature and incident light intensity. No clear seasonality was observed in the chemical composition (protein, fats, total phosphorus) of *C. nodosa*. Over the annual cycle, the range of measured variables was 10-16% for protein, 1.7-3.1% for fat, 0.3-0.8% for phosphorus, 1.6-2.6 for nitrogen in leaves, and 5-17% for protein, 0.9-3.2% for fat, 0.1-0.6% for phosphorus and 0.9-2.8 for nitrogen in roots.

Key words: *C. nodosa*, seasonal variations, chemical composition, production.

INTRODUCTION

The seagrass *C. nodosa* is widely distributed in the Mediterranean and the eastern Atlantic, extending along the African coast to Mauritania and to the Canary Islands (Den Hartog 1970; Vermaat *et al.*, 1993; Reyes *et al.*, 1995a). Due to local distribution patterns in shallow water, high standing crop and production, *C. nodosa* meadows are considered among the most ecologically important benthic communities in the area (Pérez and Picard, 1964). For this reason, much attention was paid recently to studies of the growth, biomass colonization, and seasonality of *C. nodosa* (Pérez and

Camp, 1986; Duarte *et al.*, 1994; Pérez and Romero, 1992, 1994; Reyes *et al.*, 1995b), to its production and relating chemical aspects of its environment and seagrass tissue (Pirc and Wollenweber 1988; Duarte, 1990; Pérez *et al.*, 1991; Pérez and Romero, 1992). Although *C. nodosa* is eurybiotic species, tolerating considerable variation in environmental salinity, oxygen content, temperature (den Hartog, 1970) sediment granulation (Pérez and Picard, 1964) and a nutrient rich substrate (Orth, 1977), limiting effects on plant physiology of several variables such as irradiance, temperature and nutrients were suggested (Duarte 1990; Pérez *et al.*, 1991; Pérez and Romero, 1992; Terrados and Ros, 1995).

C. nodosa is abundantly present in the eastern Adriatic Sea from the Gulf of Trieste (Giaccone,

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1978) and the Slovenian coast (Peduzzi and Vukovic, 1990) in the north, along the Croatian littoral (Vouk, 1914; Benacchio, 1938; Zavodnik and Zavodnik, 1982), until the area of Dubrovnik (Antolic, *et al.*, 1995; Zavodnik, 1955). A comparison with previous data (Benacchio, 1938) revealed an actual colonisation of dense *C. nodosa* meadows at areas that fifty years ago were occupied by *Posidonia oceanica* and *Zostera marina* meadows (Zavodnik, 1983; Zavodnik and Jaklin, 1990). Meanwhile, only a little information is available on the Adriatic *C. nodosa* standing crop (Peduzzi and Vukovic, 1990; Zavodnik *et al.*, 1991) and net primary production (Peduzzi and Vukovic, 1990), and no data on its chemical composition have been published.

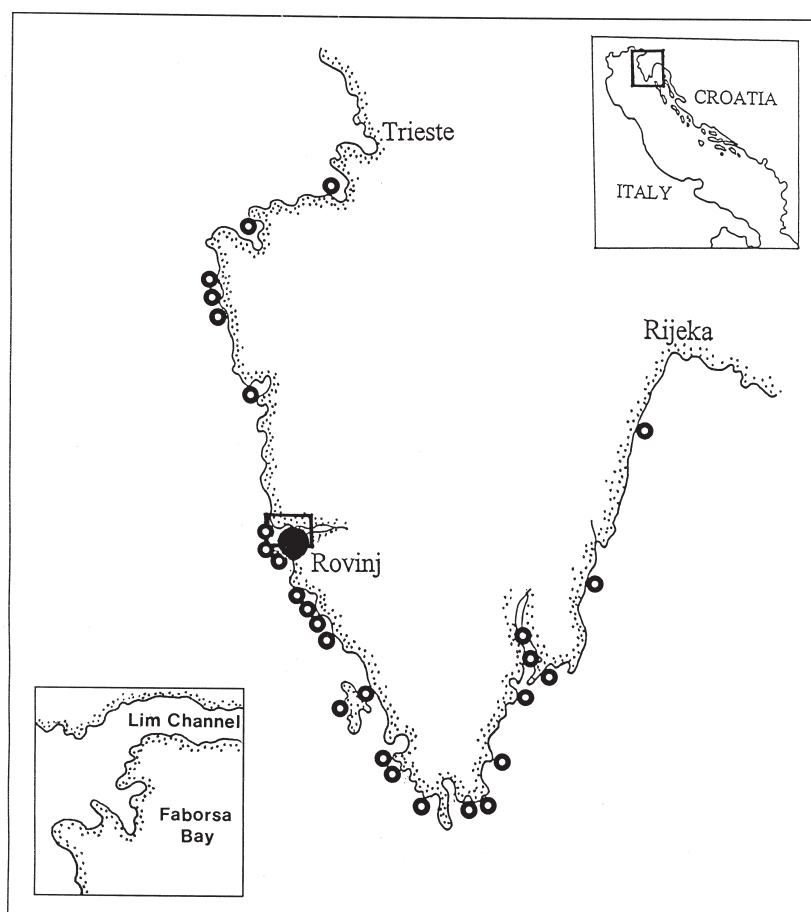
The present research was undertaken to fill gaps in existing knowledge and to contribute to a better understanding of seasonal variations in *C. nodosa* in relation to changes of some environmental factors monitored in seagrass meadow of a shallow bay. Special attention was paid to differences in: (a) leaves where photosynthetic activity is limited

by irradiance, temperature and nutrients; and (b) rhizomes and roots buried in the ground and influenced primarily by nutrients.

MATERIAL AND METHODS

Sampling area

The sampling site was at Faborsa, a small cove in the vicinity of the entrance into Lim Channel, located 4 km north of Rovinj (Istria, Croatia) (Fig. 1). The shore is rocky to the depth of about 2 m and covered with dense settlements of *Fucus virsoides*, *Cystoseira stricta*, *C. barbata*, *Dictyota dichotoma* and other algae. Deeper, at a depth of about 5 m, the pure sandy sediment is covered with a *Cymodocea* bed. The station is partly exposed to western winds and waves. Due to the low depth and occasional fresh water inflows (commonly reduced during the summer months), the seasonal fluctuation of environmental parameters is considerable.



Sampling and field measurements

Field surveys were performed monthly from February 1988 to February 1989 and involved: sampling of plant material; measurement of relevant physical parameters (water temperature, surface light intensity) at the sampling site; sampling of sea water for subsequent chemical analyses; and experimental estimation of the *C. nodosa* productivity.

C. nodosa was collected manually by SCUBA divers. Using a quadrat sampling method, whole plants, including rhizomes (horizontal + vertical ones) and roots, were removed from two plots 50x50 cm for subsequent laboratory examination to determine the number of leaves and total biomass. At the same time, additional plant material was collected from an area adjacent to the sampling plot: leaves for photosynthetic experiments, and the whole plants for further chemical analyses. Prior to these experiments and analyses, the epiphytes were removed by scraping and washing the leaves in seawater.

Simultaneously with sampling of the seagrass, and always at the same time of the day, water temperature was measured using a limnologic thermometer with scale precision of 0.1°C. Intensity of surface light was measured with luxmeter "Zeiss" type LM every ten minutes during the incubation period.

The rates of photosynthetic activity of *C. nodosa* were estimated using the light and dark bottle method, with Winkler's titration to measure the net oxygen production and the rate of respiration. Whole leaves weighing about 3-5 g fresh weight were placed in 1000 ml wide-mouthed glass-topped bottles filled with sea water filtered through a nylon gauze No. 21 (71 μ mesh). The sealed bottles (two light and one dark for each sample) were attached horizontally to wire frames at a depth of 0.5-1 m. During experiments the bottles were agitated to prevent stagnant conditions. After one hour of incubation the water from the incubation bottles was transferred with a glass tube (device is constructed to prevent contamination with atmospheric O₂) into bottles designed for dissolved oxygen determination. The results of oxygen measurements were converted to carbon equivalents using a factor of 0.31·mg C = mg O₂, assuming a photosynthetic quotient of 1.2 (McRoy and McMillan, 1977). The rate of production is expressed in mg C g dry weight⁻¹ h⁻¹ or g C m⁻² h⁻¹.

Laboratory measurements

Chemical properties of sea water (oxygen saturation, salinity, nitrates and reactive phosphorus) were analysed according to standard methods (Strickland and Parsons, 1972).

The plant material was sorted into leaf and rhizome fractions the first for morphometric (leaf length) and biomass assessment, and the second (rhizomes with attached roots) for biomass examination. The results were expressed per m⁻² surface. The biomass of each fraction was obtained separately as dry weight (dw) after heating at 60°C for 48 hours.

For the determination of pigments, leaves were dried in a desiccator at 4°C and extracted in 90% acetone. The optical density was determined at 665 and 645 μ m with a Beckman DU spectrophotometer using 1 cm cuvettes. The corrected extinctions were calculated as mg chlorophylls g dry wt⁻¹ of the seagrass using the equations and correlation factor of Strickland and Parsons (1972).

Total nitrogen was determined by the micro-Kjeldahl procedure, and the protein content calculated using a factor of 6.25. The phosphorus content was determined following the procedure of Harvey (1953), and ether soluble substances (fats) using Soxhlet extraction. Values of the chemical composition of seagrass are given as percent of dry matter.

Statistical analyses

Seasonal differences in oxygen production and respiration were tested by one-way analysis of variance (ANOVA). Differences between treatments were tested with a multiple comparison test after Scheffé (Petz, 1985).

RESULTS

Environmental

Seasonal variations in the physical and chemical properties of the sea in Faborsá Bay are given in Fig. 2.

During the observations the sea surface temperatures varied from about 10°C in winter to nearly 24°C in summer and the water was mostly supersaturated with O₂ (102-111%). Salinity ranged from 30‰ to 38‰. The seawater was poor in nutri-

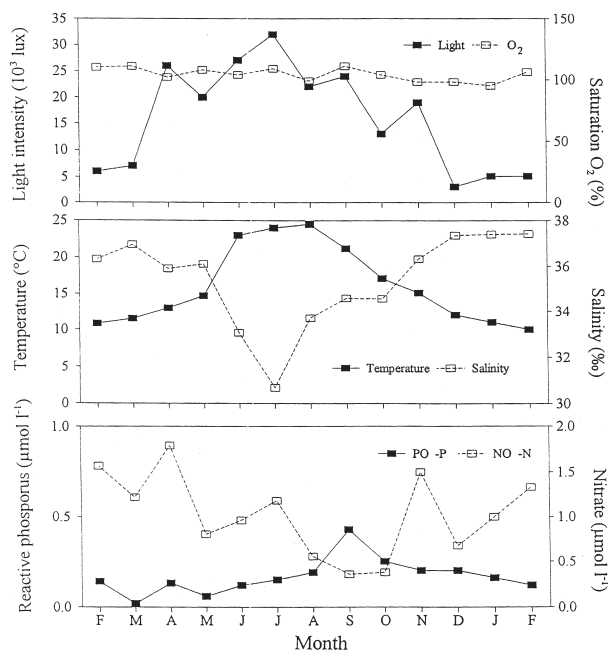


FIG. 2. – Annual variations in the light intensity, O₂ saturation, temperature, salinity, reactive phosphorus, and nitrates in seawater.

ents. Annual values fluctuated between 0.02–0.43 μmol PO₄-P/l⁻¹ and 0.36–1.79 μmol NO₃-N/l⁻¹.

Incident light intensity varied in relation to the periods of high sun or the degree of cloudiness. For these reasons, *in situ* observations of seagrass were made, whenever possible, on sunny days at 10.00 A.M. During the *in situ* measurements of photosynthesis the lowest light intensity was in winter (1900–3200 lux) and the highest in summer (up to 32000 lux).

Biomass

The biomass cycle of *C. nodosa* showed a clear unimodal annual pattern. A total biomass increase started at the end of May and reached a maximum level between 214 and 294 g (dry wt) m⁻² from July to September. Minimal values of about 13 to 23 g m⁻² occurred in the January–March period, both in leaves and roots (Fig. 3).

The leaf and root biomass showed a similar annual pattern: minimum in winter months ($B_{\text{leaves}} = 8\text{--}15$, $B_{\text{roots}} = 5\text{--}8$ dry wt m⁻²); low but somewhat higher values until the end of spring ($B_{\text{leaves}} = 13\text{--}15$, $B_{\text{roots}} = 28\text{--}36$ dry wt m⁻²); the highest values during the summer ($B_{\text{leaves}} = 118\text{--}147$ dry wt m⁻²) and summer–autumn period, respectively ($B_{\text{roots}} = 80\text{--}159$ dry wt m⁻²); and then low values in autumn ($B_{\text{leaves}} = 30\text{--}$

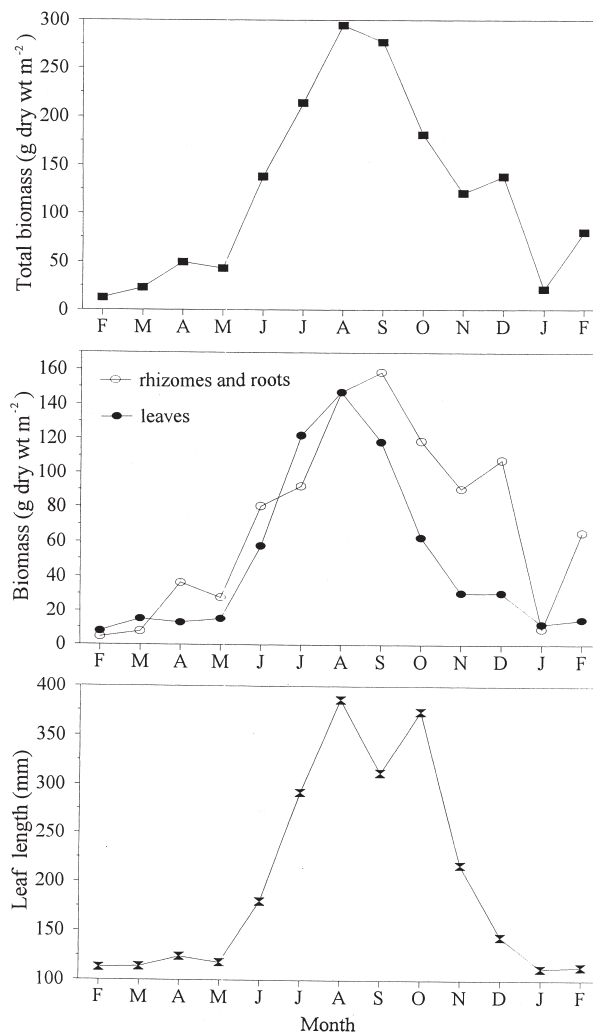


FIG. 3. – Seasonal variation in total biomass, leaf biomass and leaf length of *Cymodocea nodosa*.

64 dry wt m⁻²) and winter ($B_{\text{leaves}} = 8\text{--}12$, $B_{\text{roots}} = 6\text{--}9$ dry wt m⁻²).

The leaf biomass followed the average leaf length changes (Fig. 3). In general the leaf length was around 10–40 cm, but could reach up to 90 cm.

The rate of photosynthetic activity

Seasonal changes in the photosynthetic activity of *C. nodosa* were considerable, and the gross production varied between 0.10 in March, and 0.81 mg C g⁻¹ h⁻¹ in July. Respiration values fluctuated in the range from 0.02 to 0.38 mg C g⁻¹ h⁻¹ and the highest values were recorded in July. In spring and early summer production was greater than oxygen consumption, while in late summer and autumn the consumption was higher (Fig. 4). Analysis of vari-

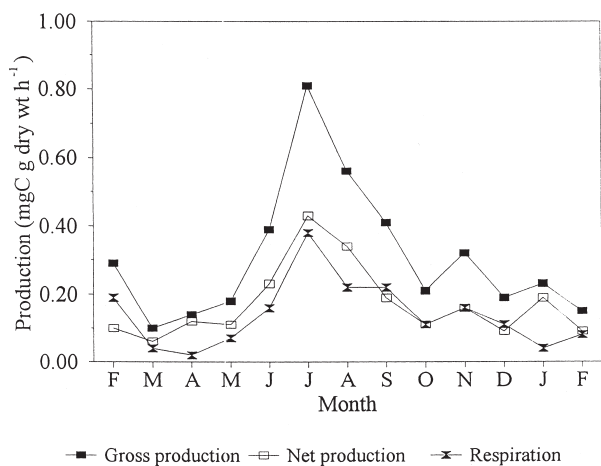


FIG. 4. – Seasonal variation in the rate of photosynthetic activity measured *in situ* in *Cymodocea nodosa*.

ance (ANOVA) revealed significant differences between seasons, both in oxygen production and respiration (Table 1). In order to test which periods differed, a multiple comparison test after Scheffé (Petz, 1985) was calculated between each pair of seasons (Table 2). Significant differences were found between the summer and all other seasons (in oxygen production) and between winter and autumn (in respiration).

TABLE 1. – One way ANOVA for differences between seasons for production and respiration. (* Significant differences at $P < 0.05$ in global tests, $p_{3,92} 0.05 = 2.70$, $p_{3,44} 0.05 = 2.82$).

Source of variation	SS	df	MS	F
PRODUCTION				
Between seasons	0.1268	3	0.0423	
Within season	0.3022	92	0.0033	12.8624 *
Total	0.4290		0.0456	
RESPIRATION				
Between seasons	0.0151	3	0.0050	
Within season	0.0350	44	0.0008	6.3345 *
Total	0.0501		0.0058	

TABLE 2. – F-ratios from multiple comparison test (after Scheffé) following ANOVA. (* Significant differences at $P < 0.05$).

Pair of samples	Production	Respiration
winter : spring	0.53	6.02
winter : summer	42.59*	1.24
winter : autumn	1.21	13.19*
spring : summer	46.09	1.57
spring : autumn	2.93*	1.22
summer : autumn	25.77*	5.55

Under field conditions a significant correlation was found between the net production of the seagrass investigated and the temperature ($r=0.85$). Somewhat lower correlation coefficient ($r=0.62$) was found between the net production of the seagrass and incident light intensity.

On the areal basis the average net production varied between 0.6 and 54 mg C m⁻² h⁻¹ with a maximum rate in June and August (Fig. 4).

Chemical composition

Variations in chemical composition of *C. nodosa* are given in Fig. 5, and the ranges in Table 3.

Dry weight of leaves varied between 19 and 29% of the wet weight, with maximum values in October. The dry weight of roots was in the range of 21-28% over the year.

The lowest amount of proteins was noted during August and September, both in leaves and roots. Protein content in roots, showed more pronounced seasonal variations and lower values than in leaves during all vegetative periods, except in February-March when they attained their maximum (17%).

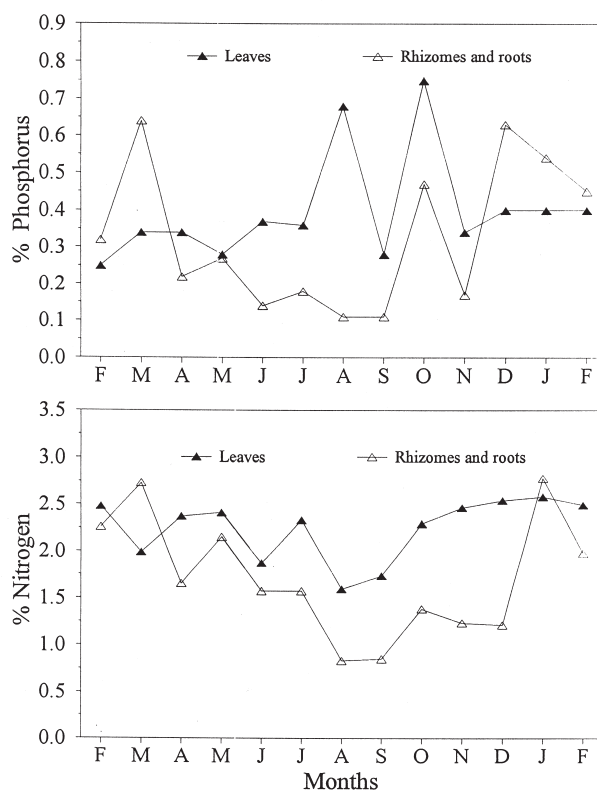


FIG. 5. – Annual cycle of nitrogen and phosphorus content in *Cymodocea* leaves and rhizomes with roots.

TABLE 3. – Chemical composition of *Cymodocea nodosa* - maximal (max), minimal (min) and mean (\bar{x}) values.

COMPOUND	max		min		\bar{x}		Remark
	leaves	roots	leaves	roots	leaves	roots	
Protein	16.1	5.2	17.4	5.2	14.1	10.8	% dry wt.
Fat	3.1	3.2	1.7	0.5	2.5	1.8	% dry wt.
Chlorophyll <i>a</i>	5.2	-	1.9	-	3.0	-	mg/g dry wt.
Chlorophyll <i>b</i>	2.1	-	0.6	-	1.2	-	mg/g dry wt.

The average amount of protein in *C. nodosa* leaves was 14%, and 10% in the roots.

Variations in fat levels of *C. nodosa* were appreciable from month to month in both leaves (1.7-4.0%) and roots (0.5-3.3%), with a clear tendency to attain maximum values in the summer season.

High temporal variations of phosphorus and nitrogen contents in the *C. nodosa* leaves and roots, with somewhat lower values in the roots, were observed (Fig. 5). It was not possible to establish a significant correlation between the phosphorus content in *C. nodosa*, and its concentration in seawater. On average, the total phosphorus content in the leaves was 0.39% of dry weight, and 0.34% in the roots. The total nitrogen content was 2.24% dry wt in the leaves, and 1.71% in the roots.

During the vegetative cycle pronounced variations in chlorophyll content occurred in *C. nodosa* leaves. The seasonal variation in chlorophyll *b* mostly followed the variation in chlorophyll *a*, but the values for chlorophyll *b* were always lower (Fig. 6). The highest concentration of chlorophylls per square meter in a *Cymodocea* bed was noted in

September (169 mg dry wt⁻¹ m⁻²). From then on a rapid simultaneous decline in content of chlorophylls and leaf biomass was observed, coupled with decreased levels of environmental parameters (temperature, reactive phosphorus and partially light intensity). In *Cymodocea* leaves, the minimum chlorophylls content was recorded in January (6 mg m⁻²).

DISCUSSION

The primary production of *C. nodosa* is relatively low in comparison with other seagrass species (Mazzella and Alberte, 1986; Lindeboom and Sandee, 1989; Hillman *et al.*, 1989), and when compared with tropical conditions (Pérez and Romero, 1994) shows a decreasing trend in a moderate climate. In the Mediterranean, lower ambient temperatures seem to be responsible for a slower metabolism, leading to very low production values during winter (Reyes *et al.*, 1995b). Somewhat shorter growing seasons at lower latitudes, could probably affect primary production in a similar way (Pérez and Romero, 1994).

In certain parts of the Mediterranean comparatively higher primary production of *C. nodosa* was recorded than that reported in the present study. The photosynthetic activity increased from low rates during the winter-spring period to maximal rates (significantly higher than in other seasons) during summer, followed by a decline in autumn-winter. Such a trend - coincident with changes in temperature, daylight and illumination - has been reported from several seagrass communities (Penhale, 1977; Drew, 1978; Sand-Jensen 1975; Ott, 1980; Peduzzi and Vukovic, 1990; Reyes *et al.*, 1995b). Values closest to ours were reported by Terrados from Mar Menor (Reyes *et al.*, 1995b), while results obtained in Alfacs Bay (Pérez *et al.*, 1991), Ebro Delta (Pérez, 1989), Gulf of Trieste (Peduzzi and Vukovic, 1990) and El Médano

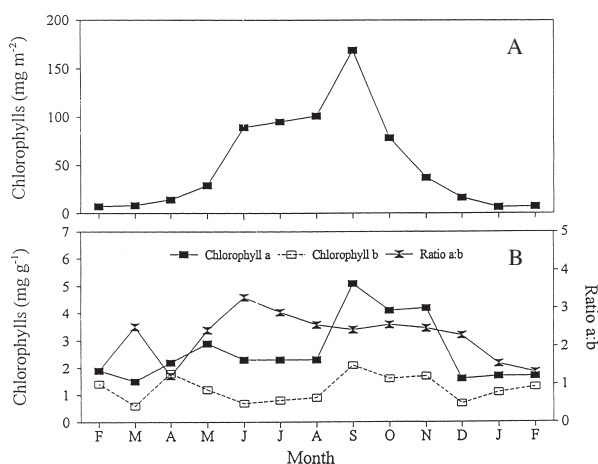


FIG. 6. – A, Seasonal variation in chlorophyll content in *Cymodocea nodosa* on areal basis; B, seasonal variation of chlorophylls *a* and *b* (mg/g dry wt) and values of the *a*:*b* ratio.

TABLE 4. – Leaf biomass and production of some species of seagrasses.

Species	Locality	Leaf dry wt (g m ⁻²)	Productivity		Authors
			(gC m ⁻² day ⁻¹)	(mgC g dry wt ⁻¹ h ⁻¹)	
<i>Cymodocea nodosa</i>	Adriatic Sea	8-147	0.07-0.60	0.06-0.43	Present study Gessner and Hammer, 1960
	Mediterranean	13-342	5.4-18.7	0.82-2.90	
	Mediterranean	206-215			Pérez, 1989 Drew, 1978
	Malta	165	3.6	1.75-2.35	
<i>Posidonia oceanica</i>	Tyrrhenian Sea	1296-1680	1.52-4.51		Ott, 1980
<i>Halophila decipiens</i>	Virgin Islands	5-12*	0.10-0.50	0.25-1.45	Joselyn <i>et al.</i> , 1986
<i>Zostera marina</i>	Alaska	62-1840	3.3-3.8	0.3-0.4	Penhale, 1977
	North Carolina	48-162	0.90	0.88	Jacobs, 1979
	Roscoff	61-131			

*leaves, roots and rhizomes biomass

(Reyes *et al.*, 1995b) indicated fairly higher photosynthetic activity. With regard to other seagrass species, primary production of *C. nodosa* in Faborisa Bay is comparable to data for *Zostera marina* from North Carolina (Penhale, 1977) and *Halophila decipiens* from the Virgin Islands (Joselyn *et al.*, 1986) (Table 4).

The production of *C. nodosa* during the spring-summer period in Alfacs Bay significantly failed compared with the values expected from the irradiance reaching the plants, but still was substantial (> 400 g dry wt m⁻²) despite acute nutrient deficiency (Pérez *et al.*, 1991). Such findings were explained by partial nutrient depletion (low P and sufficient N content in leaves tissue) that may result in rapid leaf growth if the P necessary to produce new leaves is supplied by reabsorption of P before abscission of old leaves during exponential seagrass growth.

At our study site protein content showed great variations during the growth of *C. nodosa*, both in leaves and roots. The higher N-content in *C. nodosa* leaves than in other plant organs was also reported by Pirc and Wollenweber (1988) and Peduzzi and Vukovic (1990). The protein maximum in leaves occurred during fall, and in winter showed a higher protein content than in the roots, except in early spring before the leaves started to grow. In Faborisa Bay, P content in *C. nodosa* tissue exceeded the critical value (0.2 %) proposed by Duarte (1990), and was fairly higher than P measured in tissue of the above-mentioned population. On the other hand, the N content of leaves was substantial during the whole investigated period, but in roots and rhizomes during an intensive growth season it was very close to the proposed critical value (1.8%) (Fig.5). Contrary to total phosphorus, nitrogen content in roots and rhizomes was evidently reduced

during the period of maximal growth, which might be the reason for low photosynthetic activity in our samples. As could be deduced from results obtained in Alfacs Bay, such nitrogen limitation, due to its typically large effect on photosynthetic activity (Chapin *et al.*, 1987), rather than limitation by P, may have resulted in reduced primary production in our observations.

The nutrient limitation discussed above may be responsible for comparatively low biomass of *C. nodosa* and may influence its reproductive success. Namely, in the study area, during the present study, we have never observed flowers and seeds. The scarce germination of *C. nodosa* in the Venice Lagoon (Curiel *et al.*, 1996), the absence of germination in the Gulf of Trieste (Peduzzi and Vukovic, 1990) and at our sampling area, imply a reduced viability of northern Adriatic populations, despite an obvious tendency for expansion of its areals. Environmental factors (e.g. salinity, temperature, nutrients) known to influence the reproductive success of *C. nodosa* (Buia and Mazzella, 1991), fluctuate in the northern Adriatic in ranges close to those established for areas characterized by well-displayed sexual reproduction. Although, temperatures in the northern Adriatic are slightly lower than those around the Iberian Peninsula and the Canary Islands -they are in the range of 19-20°C which is considered indispensable for flowering *C. nodosa* (Reyes *et al.*, 1995a)- they could not account for lack of sexual reproduction of *C. nodosa* at the studied site.

There are different opinions concerning the factors influencing leaf biomass and leaf length (Sand Jensen, 1975; Jacobs, 1979, 1983; Lindeboom *et al.*, 1982). Contrary to Orth (1977) and Iizumi *et al.* (1980), who emphasized the importance of nutrient content in seawater, our results indicate a

more distinctive influence of temperature and light intensity on total biomass, leaf biomass and leaf length. These results are similar to the results of Peduzzi and Vukovic (1990), Pérez and Romero (1992), and Reyes *et al.* (1995b). The leaf length and annual biomass of *C. nodosa* fluctuated seasonally, with a maximum during summer and minimum during a winter, showing clear unimodal annual pattern, similar to those reported by other authors from different localities of inland seas and ocean coastal areas (Jacobs, 1979; Ott, 1980; Bulthuis and Woelkerling, 1983; Reyes *et al.*, 1995b).

Chlorophyll *a* and *b* content were considerably higher in fall, when the ratio of chlorophyll *a* to *b* was 2.4. Drew (1978) reported a similar summer ratio in *Cymodocea* (2.3) but a considerably higher spring value (3.7). In the present study, chlorophyll content was closely correlated with seasonal cycles of biomass, net production and temperature. Consequently, during its growth season *C. nodosa* can be considered as a producer similar to seaweeds growing at the same site (Zavodnik, 1973).

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REFERENCES

Antolic, B., A. Span, and E. Draganovic. – 1995. In : Durbesic P., and A. Benovic (eds), Mljet (Priopcenja), Hrvatsko ekolosko drustvo etc., Zagreb. *Ekoloske monografije* 6: 531-542.

Benacchio, N. – 1938. Osservazioni sistematiche e biologiche sulle *Zosteraceae* dell'AltoAdriatico. *Thalassia*, 3(3): 1-41.

Bulthuis, D.A. and W.J. Woelkerling. – 1983. Seasonal variations in standing crop, density and leaf growth rate of the seagrass *Heterozostera tasmanica* in Western Port and Port Phillip Bay, Victoria, Australia. *Aquat. Bot.*, 16: 111-136.

Buia, M.C. and L. Mazzella. – 1991. Reproductive phenology of the mediterranean seagrasses *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Aschers., and *Zostera noltii* Hornem. *Aquat. Bot.*, 40: 343-362.

Chapin, F.S. III, A.J. Blomm, C.B. Field and R.H. Waring. – 1987. Plant response to multiple environmental factors. *BioSci.*, 37: 49-57.

Curiel, D., A. Bellato, A. Rismondo, and M. Marzocchi. – 1996. Sexual reproduction of *Zostera noltii* Hornemann in the lagoon of Venice (Italy, north Adriatic). *Aquat. Bot.*, 52: 313-318.

Den Hartog, C. – 1970. *The Sea-grasses of the World*. North-Holand, Amsterdam, 275 pp.

Drew, E. – 1978. Factors affecting photosynthesis and its seasonal variation in the seagrasses *Cymodocea nodosa* (Ucria) Aschers., and *Posidonia oceanica* Delile in the Mediterranean. *J. exp. mar. Biol. Ecol.*, 31: 173-194.

Duarte, C.M. – 1990. Seagrass nutrient content. *Mar. Ecol. Prog. Ser.*, 67: 201-207.

Duarte, C.M., N. Marbá, N. Agawin, J. Cebrián, S. Enriquez, M.D. Fortes, M.E. Gallegos, M. Merino, B. Olesen, K. Sand-Jensen, J. Uri, and J. Vermaat. – 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Mar. Ecol. Prog. Ser.* 107: 195-209.

Giaccone, G. – 1978. Revisione della flora marina del mare Adriatico Parco marino Miramare, Suppl. ann. 1977, 6 (19): 5-118.

Gessner, F. and L. Hammer. – 1960. Die Primärproduktion in mediterranen *Caulerpa-C.*-Wiesen. *Bot. Mar.*, 2: 158-163.

Harvey, H.W. – 1953. Microdetermination of phosphorus in biological material. *Analyst.*, 78: 110-114.

Iizumi, H., A. Hattori and C.P. McRoy. – 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. *J. exp. mar. Biol. Ecol.*, 47: 191-201.

Jacobs, R.P.W.M. – 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquat. Bot.*, 7: 151-172.

Jacobs, R.P.W.M., H.H. Hegger and A. Ras-Willems. – 1983. Seasonal variations in the structure of a *Zostera* community on tidal flats in the SW Netherlands, with special reference to the benthic fauna. *Proc. K. ned. Akad. Wet. C.*, 86: 347-375.

Josselyn, M., M. Fonseca, T. Niesen, and R. Larson. – 1986. Biomass, production and decomposition of a deep water seagrass, *Halophila decipiens* Ostenf. *Aquat. Bot.*, 25: 47-61.

Lindeboom, H.J. and A.J.J. Sandee. – 1989. Production and consumption of tropical eelgrass fields in eastern Indonesia measured with bell jars and microelectrodes. *Neth. J. Sea Res.*, 23:181-190.

Lindeboom, H.J., H.A.J.De Klerk, V.D. Driessche and A.J.J. Sandee. – 1982. Production and decomposition of eelgrass (*Zostera marina*) in saline Lake Grevelingen. *Hydrobiol. Bull.*, 16: 93-102.

Mazzella, L. and R.S. Alberte. – 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. *J. exp. mar. Biol. Ecol.*, 100: 165-180.

McRoy, C.R. and C. McMillan. – 1977. Production ecology and physiology of seagrasses. In: McRoy, C.P., C. Helfferich (eds.), *Seagrass ecosystems: a scientific perspective*, pp.53-87. Marcel Dekker, New York.

Merino, B. Olesen, K. Sand-Jensen, J. Uri and J. Vermaat. – 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Mar. Ecol. Prog. Ser.*, 107:195-209.

Orth, R.J. – 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Mar. Biol.*, 44: 187-194.

Ott, J.A. – 1980. Growth and production in *Posidonia oceanica* (L.) Delile. *P.S.Z.N. I: Mar.Ecol.*, 1: 47-64.

Peduzzi, P. and A. Vukovic. – 1990. Primary production of *Cymodocea nodosa* in the Gulf of Trieste (Northern Adriatic Sea): a comparison of methods. *Mar. Ecol. Prog. Ser.*, 64:197-207.

Penhale, P.A. – 1977. Macrophyte-epiphyte biomass and in an eelgrass (*Zostera marina* L.) community. *J. exp. mar. Biol. Ecol.*, 26: 211-224.

Pérez, J.M. and J. Picard. – 1964. Nouveau manuel de bionomie benthique de la Mer Méditerranée. *Recl Trav. Stn mar. Endoume*, 31: 5-137.

Pérez, M. – 1989. *Fanerógamas marinas en sistemas estuáricos: producción, factores limitantes y algunos aspectos del ciclo de nutrientes*. Ph. D. thesis, Univ. Barcelona.

Pérez, M. and J. Camp. – 1986. Distribution especial y biomass de las fanerógamas marinas de las bahías del Delta del Ebro. *Invest. Pesq.*, 50: 519-530.

Pérez, M. and J. Romero. – 1992. Photosynthetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. *Aquat. Bot.* 43: 51-62.

Pérez, M. and J. Romero. – 1994. Growth dynamics, production, and nutrient status of the seagrass *Cymodocea nodosa* in a

- Mediterranean semi-estuarine environment. *P.S.Z.N.I: Mar. Ecol.*, 15: 51-64.
- Pérez M., J. Romero, C.M. Duarte and K. Sand-Jensen. – 1991. Phosphorus limitation of *C. nodosa* (Ucria) Ascherson in the Canary Islands. *Mar. Biol.*, 109: 129-133.
- Petz, B. – 1985. Osnovne statističke metode za nematematičare. Sveučilišna naklada Liber, Zagreb, 409 pp.
- Pirc, H. and B. Wollenweber. – 1988. Seasonal changes in nitrogen, free amino-acids and C/N ratio in the Mediterranean seagrasses. *P.S.Z.N.I: Mar. Ecol.*, 9: 167-179.
- Reyes, J., M. Sansón and J. A. Carillo. – 1995a. Distribution and reproductive phenology of the seagrass *Cymodocea nodosa* (Ucria) Ascherson in the Canary Islands. *Aquat. Bot.*, 50: 171-180.
- Reyes, J., M. Sansón and J. A. Carillo. – 1995b. Leaf phenology, growth and production of the seagrass *Cymodocea nodosa* at El Médano (South of Tenerife, Canary Islands). *Bot. Mar.*, 38: 457-465.
- Sand-Jensen, K. – 1975. Biomass, net production and growth dynamics in eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Ophelia*, 14: 185-201.
- Schwarzenbach, G. – 1957. *Complexometric Titrations*. Interscience Publishers, New York, 119pp
- Strickland, J.D.H. and T.R. Parsons. – 1972. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd Can.*, 167: 311 pp.
- Terrados, J. and J.D. Ros. – 1995. Temperature effects on photosynthesis and depth distribution of seagrass *Cymodocea nodosa* (Ucria) Ascherson in the Mediterranean coastal lagoon: the Mar Menor (SE Spain). *P.S.-Z.N.I: Mar. Ecol.* 16: 133-144.
- Vermaat, J. – 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Mar. Ecol. Prog. Ser.*, 107: 195-209.
- Vermaat, J.E. and F.C.A. Verhagen. – 1996. Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. *Aquat. Bot.*, 52: 259- 281.
- Vermaat, J.E, J.A.J. Beijer, R. Gijlstra, M.J.M. Hootsmans, C.J.M. Philippart, N.W. van den Brink and W. van Vierssen. – 1993. Leaf dynamics and standing stocks of intertidal *Zostera noltii* Hornem. and *Cymodocea nodosa* (Ucria) Ascherson on the Banc d'Arguin (Mauritania). *Hydrobiologia* 258: 59-72.
- Vouk, V.-1914. O istraživanju fitobentosa u Kvarnerskom zavalju. *Prir. istr. Hrv. Slav.*, 2: 20-30.
- Zavodnik, D. – 1995. Podmorje otoka Mljeta u Jadranskoj znanstvenoj literaturi in: Durbesic P., and Benovic A (eds), Mljet (Priopćenja), Hrvatsko ekološko društvo etc., Zagreb. *Ekoloske monografije* 6: 523-529.
- Zavodnik, D. and N. Zavodnik. – 1982. Survey of benthic communities in the area of Osor (North Adriatic Sea). *Acta Adriatic.*, 23: 259-270.
- Zavodnik, N. – 1973. Seasonal variations in rate of photosynthetic activity and chemical composition of littoral seaweeds common to North Adriatic. I. *Fucus virsoides* (Don) J. Ag. *Bot. Mar.*, 16: 155-165.
- Zavodnik, N. – 1983. Observations on the flora of seaweeds and seagrasses on the western coast of Istria (North Adriatic) (in Croatian). *Biosistematika*, 9: 1-13.
- Zavodnik, N. – 1992. Prilozi morskoj flori i fauni losinjske otocne skupine. II. Morske cvjetnice (Spermatophyta). *Otocni ljetopis Cres-Losinj*, 8: 215-220.
- Zavodnik, N. and A. Jaklin. – 1990. Long-term changes in the Northern Adriatic marine Phanerogam beds. *Rapp. Comm. int. Mer. Médit.*, 32: 15.
- Zavodnik, D., A. Span, N. Zavodnik, A. Simunovic and B. Antolic. – 1991. Benthos of the western coast of the island Krk (Rijeka Bay, the North Adriatic Sea). *Thalassia Jugosl.*, 17(3/4): 285-337.

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