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Temporal variation in biomass partitioning of the seagrass *Cymodocea nodosa* at the Gulf of Thessaloniki, Greece

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The monthly variation in biomass allocated to various anatomical fractions of *Cymodocea nodosa* and the key environmental variables affecting it were studied in order that insight into this seagrass growth dynamics be provided. Samplings were conducted throughout 2007 at the Gulf of Thessaloniki, Greece. Plant biomass (annual mean: 248 g DW m^{-2}) was dominated by rhizomes and roots (rhizome plus root/leaf biomass: 1.2-9.0). Leaf biomass (mean: 60 g DW m^{-2}) displayed a unimodal annual pattern. Biomass of main axis leaves (mean: 51 g DW m^{-2}) peaked in July, while that of leaves on the additional branches (cumulative mean: 8.9 g DW m^{-2}) in August. Blades prevailed on sheaths during summer and autumn. Leaf biomass was significantly correlated (positive correlation) with water temperature, indicating that temperature is a major factor controlling leaf development. Rhizome biomass (mean: 123 g DW m^{-2}) accounted for > 50% of the total plant biomass during most of the year. Main axis biomass (mean: 96.0 g DW m^{-2}) increased sharply in October, indicating intense elongation. Biomass of various additional branches (cumulative mean: 11.2 g DW m^{-2}) peaked in October-December, suggesting intense branching. Biomass of a category of additional horizontal rhizomes bearing roots was significantly correlated (negative correlation) with water column phosphate concentrations (ranging from 0 to 3.8 μM), revealing that *C. nodosa* allocates more biomass to the development of these rhizomes possibly to increase phosphate aquisition from sediments during periods of low water column phosphate concentrations. Biomass of vertical rhizomes with short internodes (mean: 9.7 g DW m^{-2}) peaked in August, as leaf biomass did, while dead vertical shoots (mean: 5.6 g DW m^{-2}) reached their peak in October-November as a possible result of increased leaf decay. Biomass of dead vertical shoots on a category of additional horizontal rhizomes was significantly correlated (negative correlation) with phosphate concentrations, indicating increased decay rates of these branch leaves during period of low phosphate concentrations. Root biomass (mean: 65 g DW m^{-2}) peaked in August and October (max value: 123 g DW m^{-2}), while rhizome /root biomass ratio varied from 1.3 to 6.1, showing the lowest values in summer. Roots on the main axis prevailed over those of other rhizomes all year round (mean biomass: 44 and 21 g DW m^{-2}, respectively). Our findings improve the understanding of *C. nodosa* meadows growth dynamics and might contribute to their effective protection.

Key words: Seagrass, growth dynamics, biomass allocation, plant compartments, abiotic factors, temperature, nutrients.

INTRODUCTION

Seagrasses occur widely in coastal zones throughout the world, playing a multifunctional key role. These plants contribute to the productivity of the coastal zone and provide habitats and resources to rich invertebrate and fish assemblages (Guidetti *et al.*, 2002). On the other hand, seagrass decline is now a common phenomenon world-wide, and in many cases, may be attributed to anthropogenic factors (Short & Wyllie-Echeverria, 1996; Hemminga & Duarte, 2000).

In the Mediterranean Sea, five seagrass species occur, among which *Posidonia oceanica* (L.) Delile and *Cymodocea nodosa* (Ucria) Ascherson are the most important and widespread ones. *Cymodocea nodosa* extends to the Atlantic, northward of Portugal

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and southward of Senegal and it is also common in the Canary islands (Den Hartog, 1970). It is distributed from the intertidal to depths of 33-35 m (Vermaat *et al*., 1993; Reyes *et al.*, 1995; Canals & Ballesteros, 1997) and can be found from coarse sand to muddy substrates (Peduzzi & Vukonič, 1990; Pavón-Salas *et al.*, 2000). This seagrass species can colonize different environmental types, such as open coastal waters, estuaries and coastal lagoons and forms monospecific and mixed stands (Terrados & Ros, 1992; Cancemi *et al*., 2002). It is considered as a species with great phenotypic plasticity and a high capacity to adapt to environmental variability and thereby to colonize new substrates. This capacity may explain the fact that *C. nodosa* replaces *P. oceanica* in areas where environmental conditions are unfavourable for the latter seagrass species (Pergent-Martini, 1994; Cancemi *et al.*, 2002). In addition, the fact that *C. nodosa* responds faster than *P. oceanica* to environmental changes (Olesen *et al*., 2002) suggests that according to the terminology of the European Water Framework Directive (EC, 2000) it is an 'ideal' response indicator or a quality element for Mediterranean coastal habitats (Orfanidis *et al.*, 2010). *Cymodocea nodosa* has been used as an indicator of metal accumulation (Malea & Haritonidis, 1999), while recently Orfanidis *et al*. (2007, 2010) suggested that a quantitative expression of *C. nodosa* leaf length asymmetry (CymoSkew index) could be regarded as an early warning indicator of a *Cymodocea* habitat degradation.

Realization of the important role of the seagrasses in coastal ecosystems had drawn considerable attention to the study of their growth dynamics and annual productivity (Duarte *et al.*, 1994). As regards *C. nodosa*, studies on the growth and primary production have been conducted in various areas, mostly of the Medirerranean coast, both in marine (Peduzzi & Vukonič, 1990; Cancemi *et al*., 2002; Terrados *et al.*, 2006) and lagoonal environments (Terrados & Ros, 1992; Sfriso & Ghetti, 1998; Agostini *et al*., 2003; Cunha & Duarte, 2007). However, studies on seagrass biomass have paid little attention to the belowground compartment, especially to the root compartment (Duarte *et al.*, 1998) and ignored partitioning of partial fractions of the basic plant compartments. The study of temporal changes in biomass allocated to several different plant fractions and of the key environmental variables (e.g. temperature fluctuations, nutrient limitation and excess) affecting these changes could provide a better understanding of seagrass meadow dynamics and, therefore, could contribute to the effective protection and the development of reliable tools on the future status of these coastal ecosystems.

The main goal of this study is to provide new insights into *C. nodosa* growth dynamics. A description, all year long of the monthly variation in *C. nodosa* biomass at the Gulf of Thessaloniki (Northern Aegean Sea), emphasizing in biomass partitioning of various anatomical plant fractions, such as the various rhizome types (e.g. main horizontal rhizome, lateral horizontal rhizomes, vertical rhizomes with short internodes, vertical rhizomes with long internodes), the leaves produced and the adventitious roots stemming from them, is presented. The key environmental variables (e.g. temperature, nutrient concentration) affecting the monthly variation in the biomass of the various plant fractions are also investigated.

MATERIALS AND METHODS

Study area

The Gulf of Thermaikos is a water mass located in northwestern Aegean Sea at approximately 40°30′N and 23°55′E. The area, volume, maximum and minimum depths of the investigated area are 518 km^2, 11.33 km^3, 36 and 21.8 m, respectively. To the north, the Gulf becomes narrow and continues into the Gulf of Thessaloniki (Fig. 1), on the northern coast of which the city of Thessaloniki is located and which receives industrial, partially treated domestic and agricultural effluents (Nikolaidis *et al.*, 2006; Christophoridis *et al*., 2009). In the Gulf of Thessaloniki, meadows of *Posidonia oceanica* (at depths of 12 m), *Cymodocea nodosa* (at depths of 0.5-2 m) and *Zostera noltii* (at depths of 0.5 m) have been recorded (Haritonidis *et al.*, 1990; Haritonidis, 1996; Lazaridou *et al.*, 1997; Orfanidis *et al*., 2010). The growth of *C. nodosa* was studied at the eastern coast of the Gulf of Thessaloniki, at the sampling site V, in Viamyl area (x = 0413709, y = 4488799, EGSA 87 or 40°33′N, 22°58′E) (Fig. 1). This coastal area receives local effluents of a small wastewater treatment plant, direct urban discharges and freshwater inputs from a stream (Athemuntas stream) and has been considered as a polluted one (Haritonidis *et al*., 1990; Malea & Haritonidis, 1999; Orfanidis *et al.*, 2010). At Viamyl area, *C. nodosa* grows from 0.4 m to often ~2 m depth, forming a continuous monospecific meadow, in which some benthic macroalgae (e.g. *Ulva* spp., *Gracilaria verrucosa*, *Hypnea musciformis*, *Codium fragile*, *Cystoseira barbata*) or epiphytic macroalgae on the leaves of *C. nodosa* (e.g. *Ceramium diaphanum*, *C. strictum*, *Cla-*

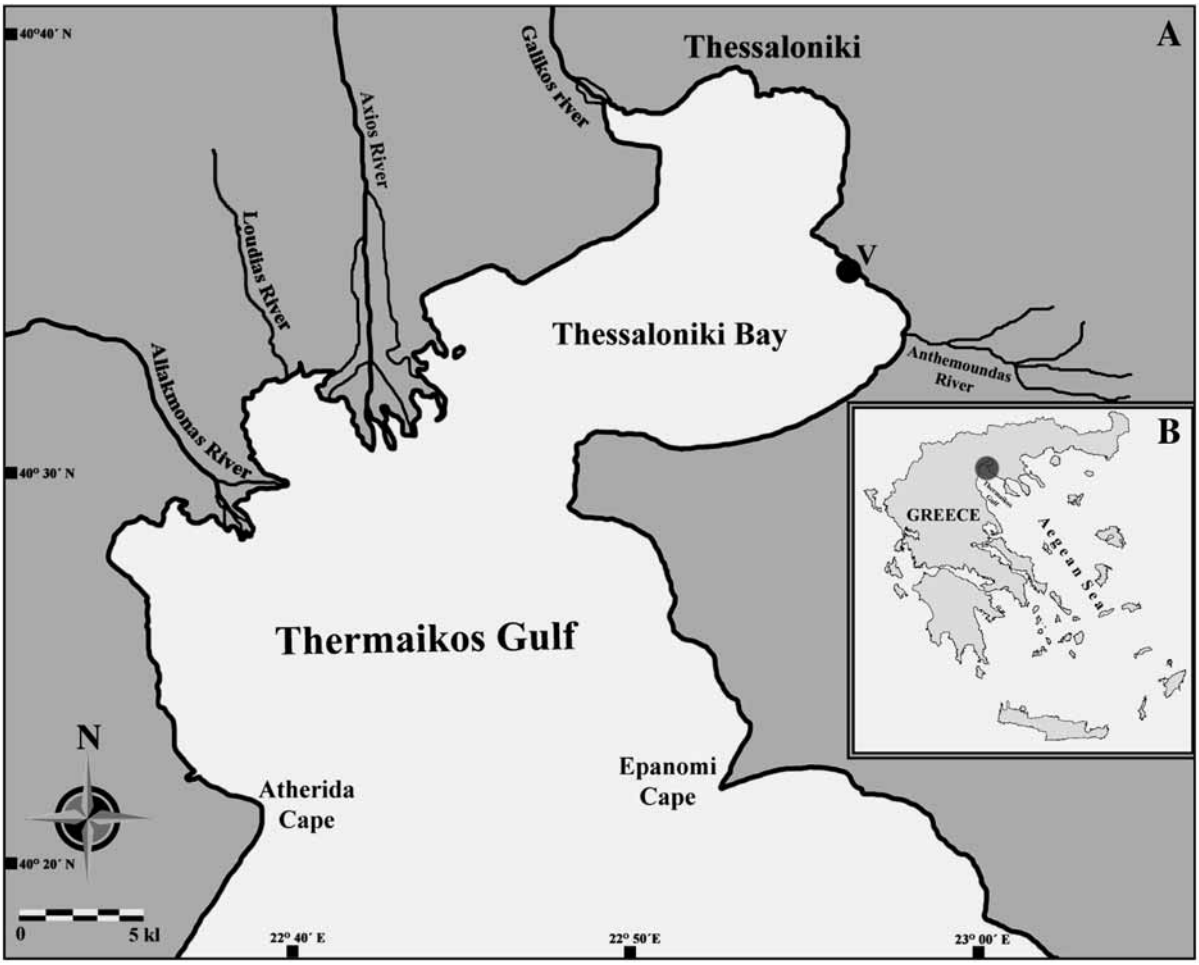

FIG. 1. (A) Geographical location of the study site. (B) Map of Thessaloniki Gulf indicating the sampling site (V).

dorhora pellucida, *Polisiphonia deusta*) were present (unpublished data). At a depth of 0.7-1 m, the sediment is fine sand, while the sediment's organic matter content varied between 0.35 and 1.51% from February to December 2007 (unpublished data). This *C. nodosa* meadow has been regarded by Orfanidis *et al*. (2010) as highly degraded.

Sampling and laboratory treatment

Monthly samples of *C. nodosa* were collected from February to December 2007 at 0.7-1 m depth at the sampling site V. Each time, three random replicate units were taken with a 20 cm diameter acrylic plastic corer penetrated to a depth of 30 cm. Seagrasses were kept in a ethylenglycol/seawater solution (40/60 v/v). Water temperature and salinity were measured at the site and water samples for the estimation of nutrient concentrations were taken.

Macroalgal epiphytes and dead plant parts were discarded in the laboratory. Plant material was subsequently partitioned into rhizomes, leaves and roots. Based on a description of the growth form of *C. nodosa* given by Terrados *et al*. (1997), rhizome material was further partitioned into the following fraction categories: (a) main horizontal rhizome or main axis, (b) lateral horizontal rhizome (termed as branch A), (c) vertical rhizome with long internodes (branch B), (d) horizontal rhizome developed from branch B (branch C), (e) vertical rhizome with short internodes on main axis (rhizome V), on branch A (rhizome VA), on branch B (rhizome VB) and on branch C (rhizome VC), and (f) dead vertical shoot on main axis (shoot D), on branch A (shoot DA), on branch B (shoot DB) and on branch C (shoot DC). Leaf material was partitioned into leaves (a) on main axis, (b) on branch A (c) on branch B and (d) on branch C and root material into adventitious roots stemming (a) from the

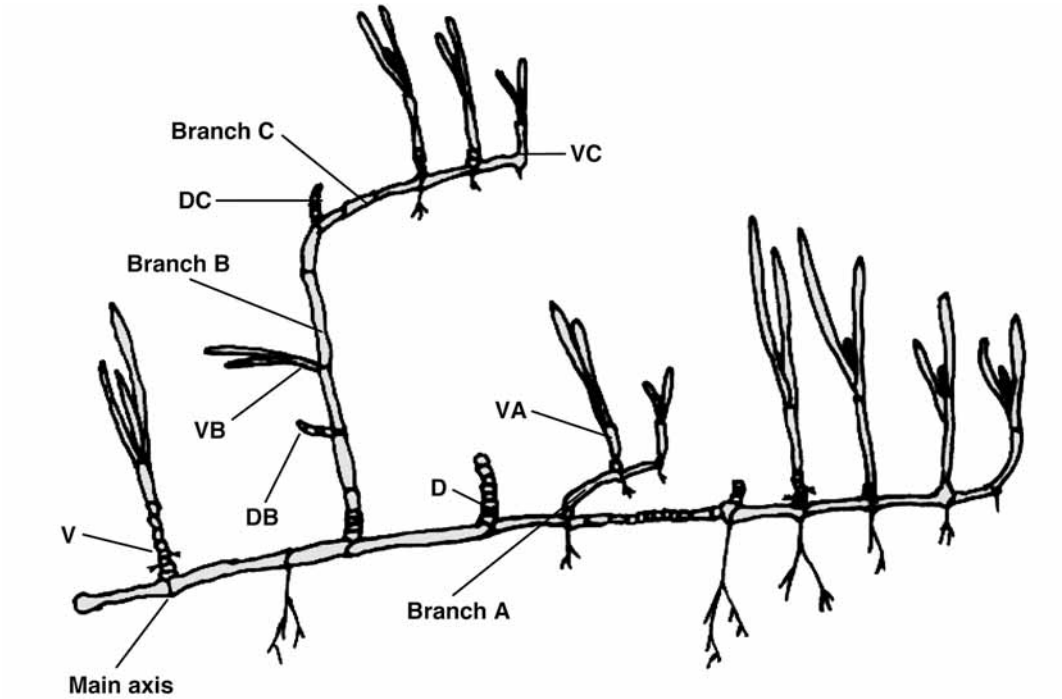

FIG. 2. A schematic depiction of the growth form of *Cymodocea nodosa* (from Terrados *et al*., 1997 modified). Main axis: main horizontal rhizome; branch A: lateral horizontal rhizome; branch B: vertical rhizome with long internodes, branch C: horizontal rhizome developed from branch B; V, VA, VB and VC: vertical rhizomes with short internodes on main axis, on branch B and on branch C respectively; D, DB and DC: dead vertical shoots on main axis, on branch B and on branch C, respectively.

main axis and (b) from the rhizomes as a total (Fig. 2). Each plant fraction was dried separately for at least 3 days at 60°C to steady weight and weighed to the nearest 0.1 mg.

Nutrients (nitrates, ammonium and phosphates) were measured using the method by Strickland & Parson (1968), by means of M501 Single Beam Scanning UV/Visible Spectrophotometry (Camspec).

Data analysis

The significance of the differences in biomass values between different plant fractions was assessed by the Wilcoxon test. The significance of the differences in biomass values of a given plant fraction between two months was tested with the Mann-Whitney U test. Spearman's rank correlation coefficient (r) was applied to identify correlations between biomass of plant fractions and abiotic variables. Non-parametric statistical tests were performed, since the sample size was usually small, leading to statistics based on ranks than on raw values (Zar, 1984).

RESULTS

Total plant biomass

Total biomass of *C. nodosa* in the study site showed an annual mean value of 247.5 g DW m^{-2} (Table 1). The coefficient of monthly variation (CV) in the total plant biomass had a value of 44.5%. This variation was mainly characterized by (a) a significant increase ($p < 0.05$) from late spring (mean: 139.8 g Dm^{-2}) to late summer (mean: 416.6 g DW m^{-2}), (b) a significant decline ($p < 0.05$) in early autumn (mean: 158.8 g DW m^{-2}) followed by a significant increase ($p < 0.05$) in mid autumn (mean: 410.9 g DW m^{-2}) and (c) a significant decline ($p < 0.05$) from mid autumn to early winter (mean: 283.7 g DW m^{-2}) (Fig. 3). Plant biomass was dominated by rhizome and root biomass, which exceeded that of leaves (Fig. 4). The rhizome plus root biomass:leaf biomass ratio varied between 1.23 and 9.00, being the lowest in July and the highest in December.

TABLE 1. Mean (± SE) and range of the plant biomass (g DW m^{-2}) and the biomass of various anatomical fractions of *C. nodosa* at the Gulf of Thessaloniki

		Mean ± SE	Range
Total Plant Biomass		247.503 ± 33.217	139.763-416.626
Total Leaf Biomass		60.053 ± 13.467	22.318-151.051
Main axis	Total	51.067 ± 11.960	18.296-134.643
	Blade	31.962 ± 9.943	2.597-102.879
	Sheath	19.105 ± 2.401	10.719-33.461
Branches A	Total	2.972 ± 1.799	0-20.223
	Blade	2.798 ± 1.799	0-20.223
	Sheath	0.960 ± 0.417	0-4.414
Branches B	Total	3.153 ± 1.157	0-11.054
	Blade	1.782 ± 0.745	0-7613
	Sheath	1.370 ± 0.474	0-3.954
Branches C	Total	2.886 ± 1.001	0-8.543
	Blade	1.732 ± 0.622	0-5.630
	Sheath	1.154 ± 0.408	0-3.761
Total Rhizome Biomass		122.536 ± 15.632	72.257-224.474
	Main axis	96.013 ± 10.476	55.506-160.328
	Branches A	1.299 ± 0.394	0-3.957
	Branches B	7.350 ± 2.834	0.220-29.083
	Branches C	2.545 ± 0.965	0-10.332
	Rhizomes V	8.076 ± 0.911	3.148-14.076
	Rhizomes VA	0.444 ± 0.118	0-1.110
	Rhizomes VB	0.524 ± 0.200	0-2.054
	Rhizomes VC	0.697 ± 0.304	0-2.823
	Shoots D	5.278 ± 0.694	2.184-9.514
	Shoots DA	0.009 ± 0.006	0-57.3
	Shoots DB	0.189 ± 0.079	0-0.860
	Shoots DC	0.112 ± 0.041	0-0.432
Total Root Biomass		65.016 ± 11.431	14.517-123.267
	Main axis	43.762 ± 6.554	11.234-78.833
	Other rhizomes	21.255 ± 5.799	2.879-53.042

Main axis: main horizontal rhizome; branches A: lateral horizontal rhizome; branches B: vertical rhizome with long internodes; branches C: horizontal rhizome developed from of branch B; Rhizomes V: vertical rhizome with short internodes on main axis; Rhizomes VA, VB or VC: vertical rhizome with short internodes on branch A, B or C; Shoots D: dead vertical shoot on main axis; Shoots DA, DB or DC: dead vertical shoot on branch A, B or C.

Leaf biomass

Leaf biomass had an annual mean value of 60.1 DW m^{-2} (Table 1) and showed the highest monthly variability (CV: 74.4%) among the basic plant compartments (leaves, rhizomes, roots). In particular, leaf biomass displayed an almost unimodal annual pattern (Fig. 4). It significantly increased from March (mean: 22.3 g DW m^{-2}) to August attaining a maximum mean value of 151.1 g DW m^{-2} ($p < 0.05$) and, then, it significantly decreased in September ($p < 0.05$) and from October to December (mean: 28.4 g DW m^{-2}; $p < 0.05$) (Fig. 4).

The biomass of the main axis leaves (annual mean: 51.1 g DW m^{-2}) followed a unimodal annual model; it increased significantly from early spring to mid summer (mean: 134.6 g DW m^{-2}; $p < 0.05$) and decreased not significantly ($p > 0.05$) during late summer and significantly ($p < 0.05$) from mid autumn to early winter (Table 1, Fig. 5). It was dominated by blade biomass on a yearly basis (Table 1). Blade biomass was observed to prevail over sheath biomass during late spring to late autumn, while its contribution percentage gradually increased from February (10.0%) to July (76.4%) and then gradually decreased

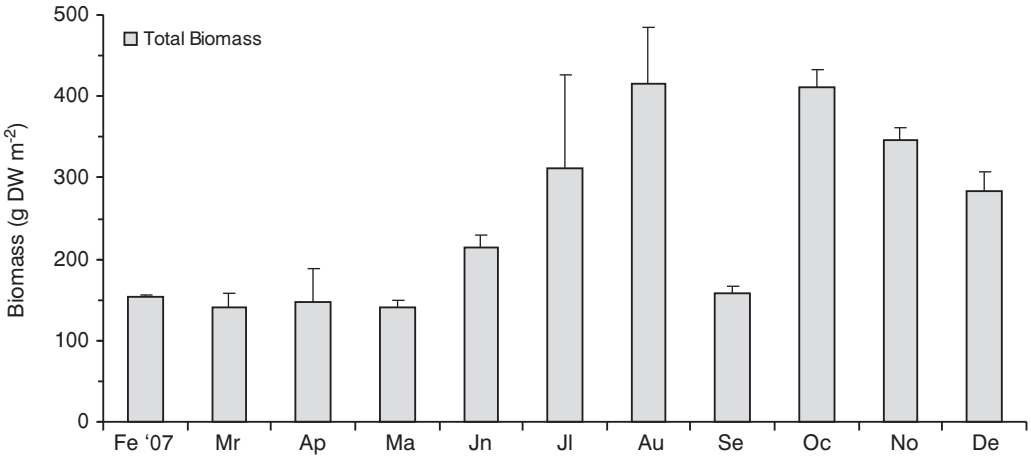

FIG. 3. Monthly variation in total plant biomass of *Cymodocea nodosa* at the Gulf of Thessaloniki. Each column represents the mean value; bars represent standard error.

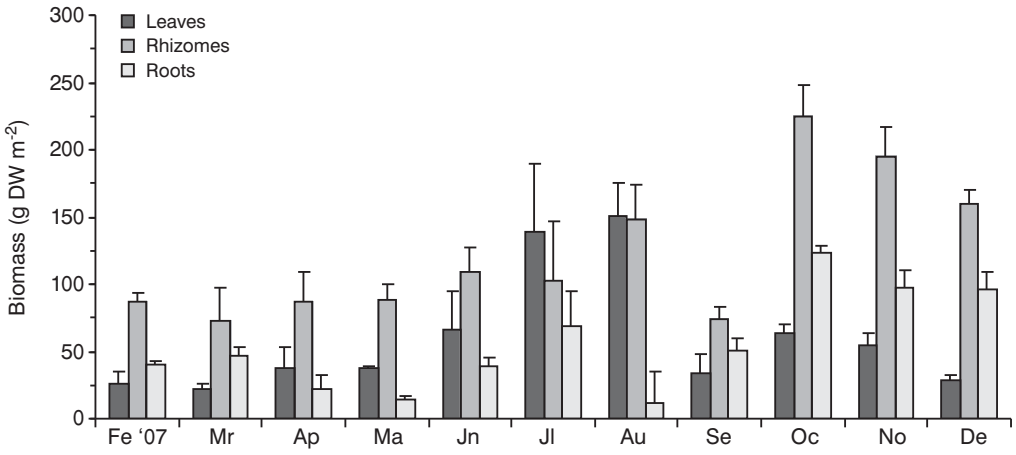

FIG. 4. Monthly variation in leaf, rhizome and root biomass of *Cymodocea nodosa* at the Gulf of Thessaloniki. Each column represents the mean value; bars represent standard error.

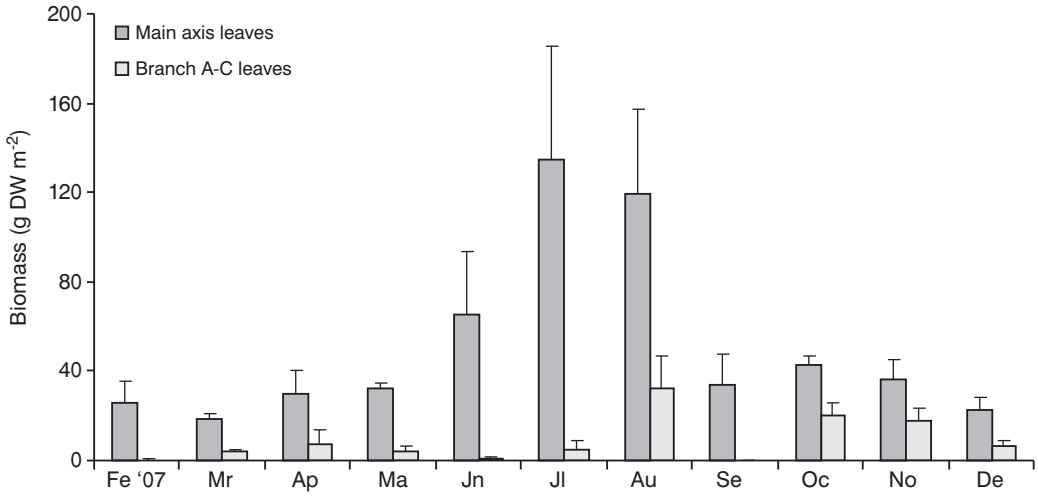

FIG. 5. Monthly variation in leaf biomass of the main axis and in total leaf biomass of branches A, B and C of *Cymodocea nodosa* at the Gulf of Thessaloniki. Each column represents the mean value; bars represent standard error.

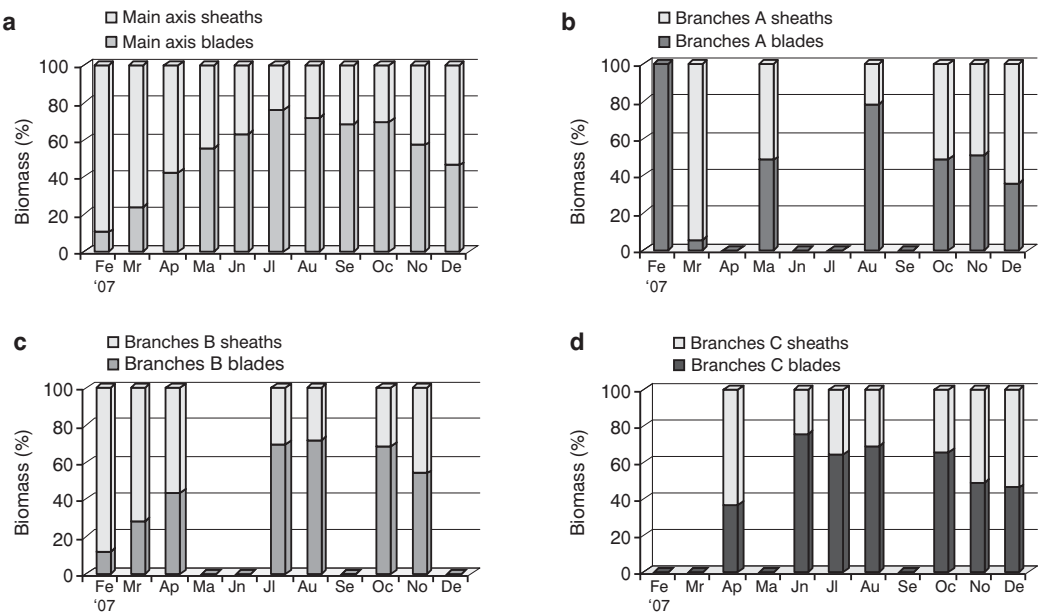

FIG. 6. Monthly variation in percentage contribution of blade and sheath biomass to leaf biomass of the main axis (a), of branch A (b), of branch B (c) and of branch C (d) of *Cymodocea nodosa* at the Gulf of Thessaloniki.

until December (46.2%) (Fig. 6a). The standing crop of the main axis leaves was significantly higher than the cumulative biomass of branches A, B and C leaves (Wilcoxon test, IzI = 3.015, N = 11, $p < 0.01$). It comprised the entire or almost the entire leaf biomass in late winter, early-mid summer and early autumn (contribution percentage: 96.5-100.0%), while it was assessed to be 78.9-86.9% of the total leaf biomass in spring and late summer and 66.9-81.1% during mid autumn to early winter.

The cumulative biomass of branches A-C leaves showed its highest values in August (31.9 g DW m^{-2}) and in October-November (17.9-20.1 g DW m^{-2}) (Fig. 5). Branch A leaf biomass did not significantly differ from branch B or C leaf biomass (Wilcoxon test, IzI = 0.666, N = 9 and IzI = 0.316, N = 10, respectively, $p > 0.05$) and biomass of branch B leaves did not significantly differ from that of branch C leaves (IzI = 0, N = 9, $p > 0.05$).

Branch A leaves were essentially observed only in April, May, August and November-December (Fig. 7). Their standing crop (annual mean: 2.9 g DW m^{-2}) (Table 1), peaked in August (mean: 20.2 g DW m^{-2})

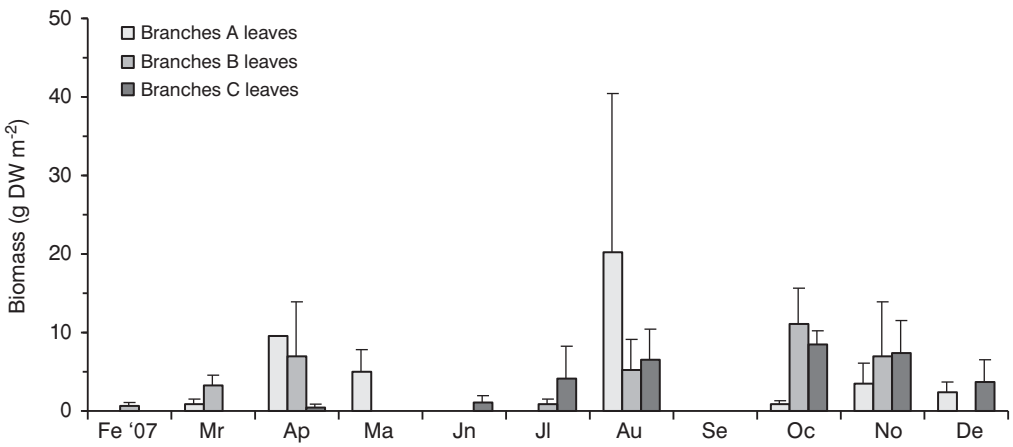

FIG. 7. Monthly variation in leaf biomass of branches A, B and C of *Cymodocea nodosa* at the Gulf of Thessaloniki. Each column represents the mean value; bars represent standard error.

(Fig. 7) and contributed to about 13% of the total leaf biomass in May and August and to 6.5-8.2% in November-December. Biomass of branch A blades prevailed over that of sheaths in August (contribution percentage: 78.2%) and sheath biomass in December (63.8%), while the biomass of branch A blades was equal (contribution percentage: 50.0%) to that of the sheaths, in May and November (Fig. 6b).

Branch B leaves were mainly observed in early-mid spring, late summer and late-mid autumn (Fig. 7), showing a remarkable contribution percentage to the total leaf biomass only in spring and autumn (13-18.5%). Their biomass (annual mean 3.2 g DW m^{-2}) peaked in October (mean: 11.1 g DW m^{-2}) (Table 1, Fig. 7). Biomass of branch B sheaths prevailed over blade biomass in late winter to mid-spring (57.0-88.1%), while blade biomass prevailed in late summer and late autumn (53.9-71.7%) (Fig. 6c).

Branch C leaves were observed in summer and mid autumn to early winter, contributing to the total leaf biomass by 1.5-4.5% during the former period and by about 14.0% during the latter one. Their standing crop (annual mean: 2.9 g DW m^{-2}) peaked in mid autumn (mean: 8.5 g DW m^{-2}) (Table 1, Fig. 7). Biomass of branch C blades prevailed over that of sheaths in summer and mid autumn (64.6-75.9%). The contribution percentage of sheath biomass increased from late autumn (50.7%) to early winter (54.0%) (Fig. 6d).

Rhizome biomass

Rhizome biomass had an annual mean value of 122.5 g DW m^{-2} (Table 1). It showed a less marked monthly variation (CV: 42.3%) than leaf biomass. This seasonal variation was mainly characterized by a significant increase from early spring (mean: 72.3 g DW m^{-2}) to late summer (mean: 148.2 g DW m^{-2}) ($p < 0.05$) and a significant decline in early autumn ($p < 0.05$) followed by a significant increase in mid autumn ($p < 0.05$) and a significant decline from mid autumn to early winter ($p < 0.05$) (Fig. 4). Rhizome biomass attained the highest mean values in October to December (159.6-224.5 g DW m^{-2}) (Fig. 4). The standing crop of this plant compartment was significantly higher than that of leaves and roots (Wilcoxon test, IzI = 2.667, N = 11, $p < 0.01$ and IzI = 2.934, N = 11, $p < 0.05$, respectively). Its percentage contribution to the total plant biomass ranged between 50.8 and 56.6% during most of the annual cycle. It was lowest in mid and late summer (33.0-35.5%) and highest in mid and late spring (59.5-63.0%).

The seasonal pattern of total rhizome biomass (Fig. 4) mainly resulted from the monthly variation of that of the main axis (Fig. 8). Main axis biomass showed an annual mean value of 96.0 g DW m^{-2} and it attained its highest values during October-November (142.2-160.3 g DW m^{-2}) (Fig. 8). Main axis biomass was significantly higher than cumulative biomass of all the remaining rhizomes (Wilcoxon test, IzI = 3.015, N = 11, $p < 0.01$). It comprised more than 70.0% of the total rhizome biomass throughout the annual cycle. Its contribution percentage was lower from October to December (71.4-75.7%) and higher from April to July (81.8-88.4%).

Total biomass of additional branches (branches A, B and C) had an annual mean value (± SE) of 11.1 (± 3.9) g DW m^{-2} and displayed elevated values

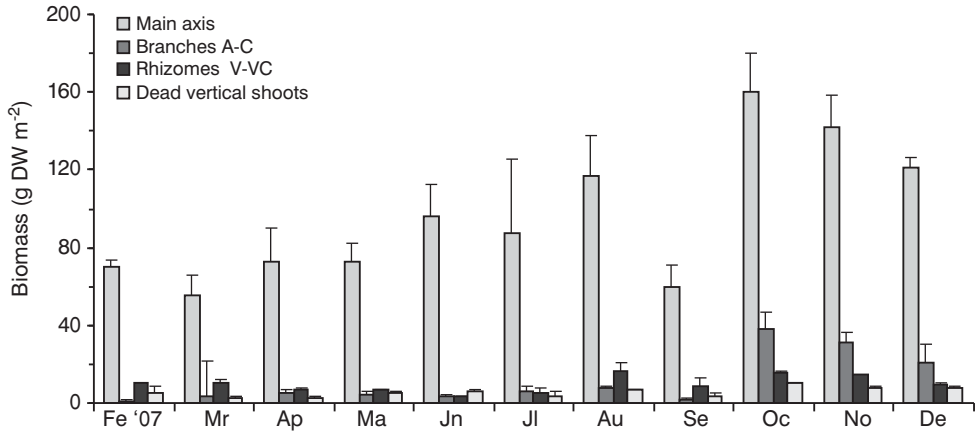

FIG. 8. Monthly variation in biomass of main axis, total biomass of branches A-C, total biomass of rhizomes V-VC and total biomass of shoots D-DC of *Cymodocea nodosa* at the Gulf of Thessaloniki. Each column represents the mean value; bars represent standard error.

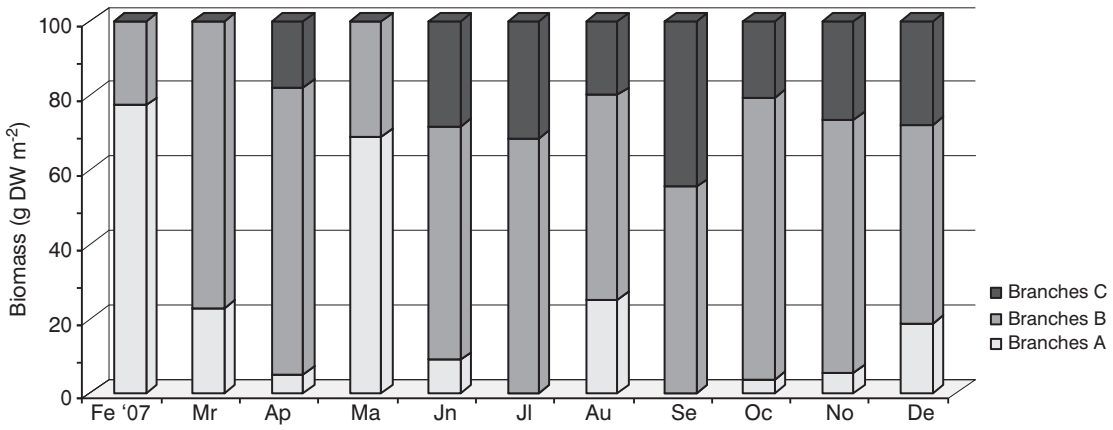

FIG. 9. Monthly variation in percentage contribution of biomass of branches A, B and C to the total biomass of these branches of *Cymodocea nodosa* at the Gulf of Thessaloniki (for more information, see Fig. 2).

mainly from October to December (20.9-38.4 g DW m^{-2}), contributing to 13-17% of the total rhizome biomass (Fig. 8). Vertical rhizomes with long internodes (branches B) showed the highest contribution to the total biomass of additional branches during most of the annual cycle (mean contribution: 66.1%), followed by branches C (22.3%) and branches A (11.0%) (Table 1, Fig. 9). Total biomass of additional branches biomass did not significantly differed from that of rhizomes V-VC and of dead vertical shoots (Wilcoxon test, $|z| = 0$ and $|z| = 1.156$, respectively, $N = 11$, $p > 0.05$).

Total biomass of vertical rhizomes with short internodes (rhizomes V-VC) showed a mean value ± SE of 9.7 ± 1.3 g DW m^{-2}, contributing to 3-14.5% of the total rhizome biomass all year long. This biomass showed the highest values in August (mean: 16.4 g DW m^{-2}) and October-November (mean: 14.3-15.2 g DW m^{-2}) (Fig. 8). Vertical rhizomes with short internodes on the main axis (rhizomes V) comprised a high fraction of the total rhizome V-VC biomass in all months (mean contribution: 85.8%) (Table 1, Fig. 10), while those on additional branches (particularly on branches C and B), mainly contributed in October-November (Fig. 10). Biomass of rhizomes V-VC was significantly higher than that of dead vertical shoots (Wilcoxon test: $|z| = 2.412$, $N = 11$, $p < 0.05$).

Biomass of dead vertical shoots showed an annual mean value ± SE of 5.6 ± 0.8 g DW m^{-2}, reaching 3-6% of the total rhizome biomass during the annual

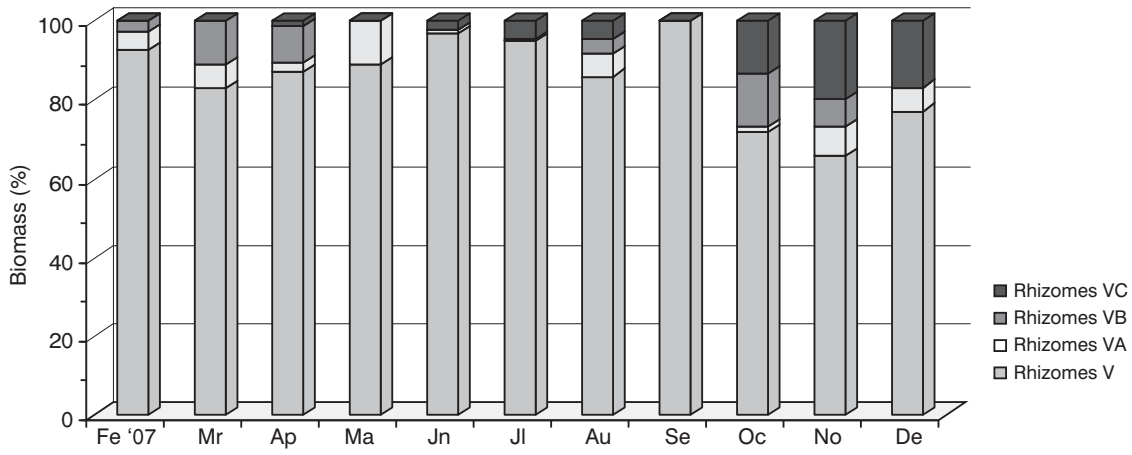

FIG. 10. Monthly variation in percentage contribution of biomass of rhizomes V, VA, VB and VC to the total biomass of these rhizomes of *Cymodocea nodosa* at the Gulf of Thessaloniki (for more information, see Fig. 2).

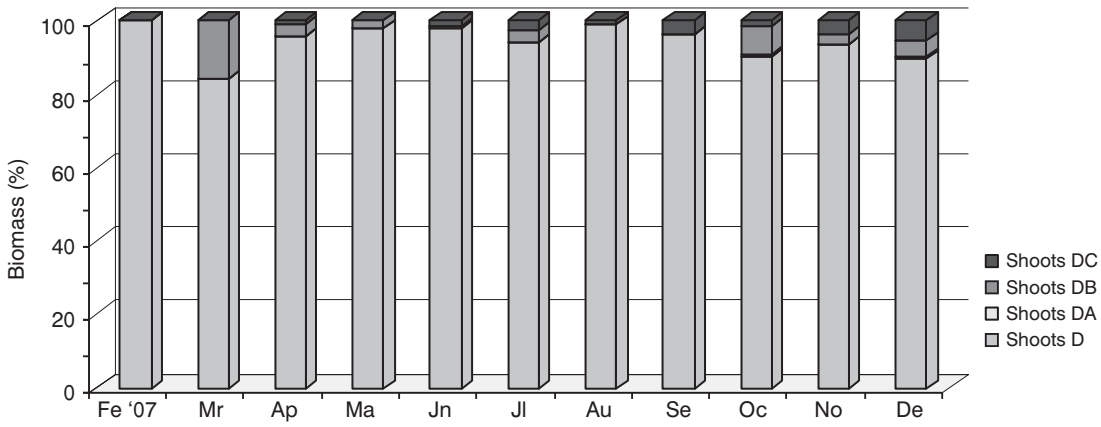

FIG. 11. Monthly variation in percentage contribution of biomass of shoots D, DA, DB and DC to the total biomass of dead vertical shoots of *Cymodocea nodosa* at the Gulf of Thessaloniki (for more information, see Fig. 2).

cycle. It displayed relatively remarkable values mainly from October to December, when it varied between 7.9 and 10.5 g DW m^{-2} (Fig. 8). Biomass of dead vertical shoots on the main axis (shoots D) contributed to 84.5-100.0% of the total dead vertical shoot biomass all year long (Table 1, Fig. 11).

Root biomass

Total root biomass (mean: 65.0 g DW m^{-2}) (Table 1) widely changed with seasons (CV: 62.9%). It significantly decreased during spring ($p < 0.01$), while during the remaining period of the annual cycle it exhibited a seasonal pattern similar to that of the total rhizome biomass, that is it significantly increased from late spring to late summer (117.4 g DW m^{-2}; $p < 0.05$), significantly decreased in early autumn (123.3 g DW m^{-2}; $p < 0.05$) and, then, significantly increased in mid autumn ($p < 0.05$) (Fig. 4). It was measured to be 10.8-14.8% of the total plant biomass in late-mid, spring, 18.2-22.2% in early-mid-summer and 28.2-33.7% during most of the sampling period, being lower than that of the rhizomes all year long (Fig. 4). The rhizome/root biomass ratio varied between 1.3 and 6.1, showing the lowest value in August and the highest in May.

Biomass of roots stemming from the main axis showed a mean value of 43.8 g DW m^{-2} (Table 1). It significantly prevailed over that of roots on other rhizomes (mean: 21.3 g DW m^{-2}) (Table 1) (Wilcoxon test, $|z| = 3.015$, $N = 11$, $p < 0.01$). Both displayed a similar seasonal trend and showed their highest mean values in December (78.8 g DW m^{-2}) and August (53.0 g DW m^{-2}), respectively (Fig. 12). Biomass val-

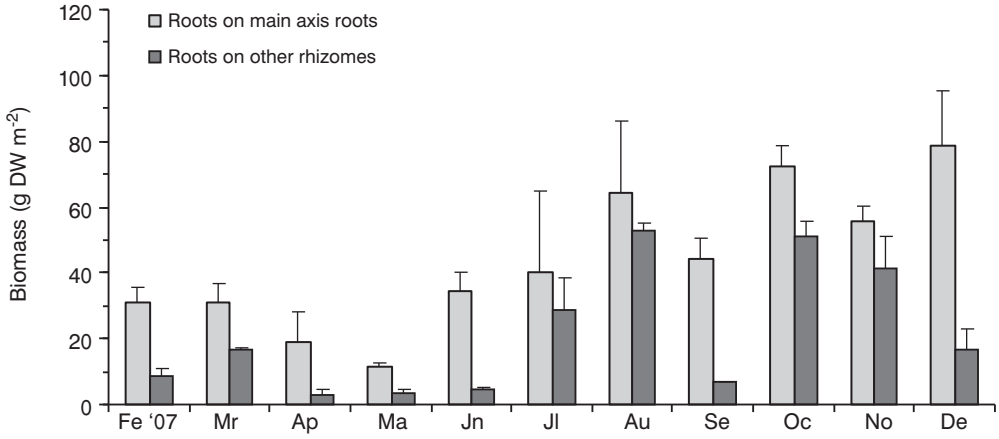

FIG. 12. Monthly variation in biomass of roots stemming from the main axis and from other rhizomes of *Cymodocea nodosa* at the Gulf of Thessaloniki. Each column represents the mean value; bars represent standard error.

ues of roots on the main axis varied from 54.5 to 87.8% of the total root biomass during the sampling period.

Associated environmental variables

Water temperature ranged from 10.9°C in February to 27.1°C in August; it was highly correlated with water salinity, which varied from 33.2 psu in February to 36.9 psu in August ($r = 0.827$, $n = 11$, $p < 0.01$). Nutrient concentrations were in the range of 0.10-25.69 μM for the nitrates, 0.22-9.47 μM for the ammonium and 0-3.81 μM for the phosphates. Nitrate concentrations showed the lowest value in September and the highest one in February, while ammonium concentrations presented the lowest values in February, April and December and the highest in March. Phosphate concentrations were below detectable limit during June-July and from September to December, and peaked in March. The mean nitrate concentration was 4.48 μM, the mean ammonium concentration 1.19 μM and the mean phosphate one 0.36 μM. Mean nitrate concentration value was higher, that of ammonium was lower and that of phosphate was similar to the average water column nitrate, ammonium and phosphate concentrations in seagrass beds (2.7 μM, 3.1 μM and 0.35 μM, respectively, according to Hemminga & Duarte, 2000). The correlation values between the biomass of the various examined plant fractions (Table 1) and the environmental variables (water temperature, water column nitrate, ammonium and phosphate concentrations) were examined; significant correlations were found only with temperature and phosphate concentrations (Table 2).

DISCUSSION

Leaf biomass of *C. nodosa* in Gulf of Thessaloniki showed a unimodal annual model with higher values in summer, similar to that described for the species by other authors at various coastal Mediterranean locations (Peduzzi & Vukovič, 1990; Terrados & Ros, 1992; Pérez & Romero, 1994; Rismondo *et al.*, 1997; Sfriso & Ghetti, 1998; Cancemi *et al.*, 2002; Zharova *et al.*, 2008). The seasonal variability observed reflects changes both in leaf size and leaf density (unpublished data; Marbà *et al.*, 1996), while in larger seagrass species, seasonal variability in leaf biomass mainly reflects changes in leaf size (Marbà *et al.*, 1996). This variability was mainly derived from the seasonal fluctuation in the biomass of the leaves on the main horizontal rhizome (main axis), which accounted for a large fraction of the total leaf biomass in all seasons. The biomass of leaves on the additional branches contributed to some extent mainly in late summer as well as in autumn, when the biomass of these branches reached its peak. The observation that blades mainly contributed to the total leaf biomass from late spring to late autumn, most probably was due both to the high occurrence of undifferentiated leaves (Cunha & Duarte, 2007) and the comparatively large size of the adult leaf blades (Agostini *et al.*, 2003). On the other hand, sheath biomass was dominant during winter and early spring, since sheaths remain attached to the rhizome for a long time even after blade falling (Hemminga & Duarte, 2000).

Our results indicate that water temperature is a major factor controlling annual variability in *C. nodosa* leaf biomass, particularly in that of the main axis leaves (see Table 2). Increasing temperature during spring possibly triggered growth, high late summer temperatures (27°C) caused rapid biomass drop and reduced temperatures in autumn and winter contributed to biomass decline (Pérez & Romero, 1992; Rismondo *et al.*, 1997; Cancemi *et al.*, 2002; Zharova *et al.*, 2008). According to Marbà *et al.* (1996), among the seagrass species growing in western Mediterranean, *C. nodosa* is the most sensitive to seasonal fluctuations, while *P. oceanica* the least one. The season-

TABLE 2. Significant Spearman's (r) coefficient values, showing correlations between biomass of *Cymodocea nodosa* anatomical fractions and the corresponding environmental factors ($n = 11$)

	Temperature	Phosphate concentrations
Total leaf biomass	0.811^{**}	–
Main axis leaf biomass	0.811^{**}	–
Main axis Blade biomass	0.866^{**}	–
Branches C biomass	–	-0.657^{*}
Shoot DC biomass	–	-0.828^{**}

$^{*}p < 0.05$, $^{**}p < 0.01$

al growth pattern of *C. nodosa* is primarily associated with temperature changes, reflecting the tropical origin of the genus *Cymodocea* (Marbà *et al*., 1996). A reduction in light availability, at least partly resulted from shelf-shading and shading by macroalgae, possibly contributed along with thermal stress in late summer-early autumn to growth depression (e.g. Rismondo *et al*., 1997; Cunha & Duarte, 2005; Zharova *et al.*, 2008; Orfanidis *et al*., 2010).

Leaf biomass values of *C. nodosa* in the sampling site of Thessaloniki Gulf were comparable to those reported for the same seagrass species in other, marine and lagoonal Mediterranean environments (Table 3). However, both lower and higher values have been also recorded (Table 3), probably in relation to different local environmental factors (e.g. water temperature, light, depth, hydrodynamic force, nutrient load, competition) (Cancemi *et al.*, 2002; Olesen *et al.*, 2002; Terrados *et al.*, 2006) and the patchy (mosaic) distribution of the species (Barberá *et al.*, 2005; Orfanidis *et al*., 2010). Low leaf biomass values were observed in a low nutrient habitat, the Mar Memor, SE Mediterranean coast of Spain (Terrados & Ros, 1992), while the high ones found in the Bay of Piran, the Gulf of Trieste and in the Venice lagoon (Peduzzi & Vukonič, 1990; Rismondo *et al.*, 1997) were associated with the high nutrient availability in these habitats (Cunha & Duarte, 2007). Increased nutrient inputs in the Ria Formosa Lagoon, S Portugal, have been shown to enhance *C. nodosa* shoot length, shoot biomass (up to 945 g DW m^{-2}) and leaf production, but were also associated with increased shoot mortality and low horizontal rhizome elongation rate. The latter were attributed to both direct nutrient effects and indirect effects because of shelf-shading, shading by fast-growing algae and sediment anoxia (Cunha & Duarte, 2005; 2007).

The fact that the rhizome-root compartment of *C. nodosa* in the study area represented the largest part of the total biomass all year long (with the lowest contribution in summer when leaf development was at its maximum), is consistent with the findings by other authors in various plant stands (Pérez & Romero, 1994; Rismondo *et al.*, 1997; Cancemi *et al*., 2002; Guidetti *et al*., 2002). This reveals that the rhizome-root compartment is well developed and plays an important structural role by anchoring the plant to the substrate and, thereby, by accounting for its stability and persistence (Sfriso & Ghetti, 1998; Guidetti *et al*., 2002). The rhizome plus root/leaf biomass ratio in our stand was comparable to those reported for *C. nodosa* at some other locations (Pérez & Romero, 1994; Rismondo *et al*., 1997), possibly reflecting similar environmental conditions particularly those (degree of hydrodynamism and nature of the sediment or its nutritional capacity) that have been linked with this ratio values (Zieman & Wetzel, 1980; Peduzzi & Vukovič, 1990). On the other hand, both higher and lower ratio values have been also observed in other *C. nodosa* stands (Sfriso & Ghetti, 1998; Guidetti *et al*., 2002).

Rhizome biomass of *C. nodosa* in the study area showed values which were similar to those reported for this species at some other Mediterranean coastal environments (Table 3). It displayed a clear seasonal trend, although the monthly variation of rhizome biomass was less marked than that of the root and of the leaf biomass. In general, *C. nodosa* shows seasonal fluctuations both in above- and belowground modules growth, while larger seagrass species (e.g. *P. oceanica*) exhibit seasonal fluctuation mainly in shoot growth (Marbà *et al.*, 1996). The seasonal pattern of the rhizome biomass in the study site was generally similar to that observed for the same species in other coastal Mediterranean environments (Rismondo *et al.*, 1997; Cancemi *et al*., 2002). An increase in biomass values during spring and summer was followed by a reduction in late summer-early autumn and a second increase in autumn. On the other hand, more or less different seasonal patterns have been also reported by other authors. For instance, no seasonality has been observed by Terrados & Ros (1992), while an almost unimodal annual model with the highest values in summer has been described by Agostini *et al*. (2003). This variability is most probably related to different local environmental factors, thus confirming reports by other authors that this seagrass is a species with phenotypic plasticity and a great capability of adapting to environmental changes (Pergent-Martini, 1994; Cancemi *et al*., 2002).

The observation that the increase in the rhizome biomass of *C. nodosa* during spring and summer coincided with an increase in the leaf biomass is consistent with the findings reported by other authors (Duarte & Sand-Jensen, 1990). The increase in the belowground biomass of this seagrass species has been assumed to be proportional to the aboveground production biomass (Duarte & Sand-Jensen, 1990; Zharova *et al*., 2008), since the organic carbon fixed by the leaves is translocated, in part, to the belowground compartment (Zharova *et al.*, 2008). The fact that the rhizome biomass peaked in autumn when the leaf

TABLE 3. Literature data on mean annual and maximum monthly or maximum seasonal biomass (in g DW m^{-2}) of *Cymodocea nodosa* stands from Mediterranean Sea; *: values estimated from figures

Geographical area	Coordinates	Total		Leaves		Rhizomes		Roots		Authors
		mean	max	mean	max	mean	max	mean	max	
Mar Menor Lagoon, SW Mediterranean Sea, Site E_1	37N 00W				68		172			Terrados & Ros, 1992
Mar Menor lagoon, SW Mediterranean Sea, Site E_2	37N 00W				171		269			Terrados & Ros, 1992
Alfacs Bay, Ebro Delta, W Mediterranean Sea	40N 00E				208		248		148	Pérez & Romero, 1994
Blanes Bay, W Mediterranean Sea	41N 02E				124		94		121	Marbà & Duarte, 2001
Cala Jonquet Bay, W Mediterranean Sea	42N 03E				88		331		105*	Cebrián *et al.,* 1997
Urbinu Lagoon, Corsica, N Mediterranean Sea	42N 09E	777	1090	332		280		165		Agostini *et al*., 2003
Ischia, Naples Bay, Tyrrhenian Sea	40N 13E				159		450*		270*	Cancemi *et al*., 2002
Venice Lagoon, N Adriatic	45N 12E				810		741		290	Rismondo *et al*., 1997
Grado Lagoon, N. Adriatic	45N 13E	410			155*		300*		200*	Guidetti *et al.,* 2002
Piran Bay, Trieste Gulf, N Adriatic, Site R1	45N 14E		1020		230*					Peduzzi & Vukovič, 1990
Piran Bay, Trieste Gulf, N Adriatic, Site R2	45N 14E		323		130*					Peduzzi & Vukovič, 1990
Piran Bay, Trieste Gulf, N Adriatic, Site R3	45N 14E		341		150*					Peduzzi & Vukovič, 1990
Bardawil Lagoon, SE Mediterranean Sea	31N 33E		359							Geneid & El-Hady, 2006
Thessaloniki Gulf, N Aegean Sea	40N 22E	248	417	60	151	123	225	65	123	present study

biomass decreased, could be explained by a more intense translocation of the fixed organic carbon from the old parts of the leaves to the belowground compartment (Zharova *et al*., 2008).

The observed seasonal pattern of the total rhizome biomass mainly resulted from the variation in the main horizontal rhizome biomass, which represented a large fraction of the total rhizome biomass all year long. The fact that the biomass of the additional branches (vertical rhizomes with long internodes and less of the lateral horizontal rhizomes) showed relatively high values during autumn, indicates a comparatively intense branching. In addition, this possibly suggests that a marked part of the fixed organic carbon is translocated from the old leaves to these plant fractions (Zharova *et al*., 2008). The finding that the biomass of the C branches is negatively correlated (Table 2) with the water column phosphate concentrations (ranging between 0 and 3.8 μM) suggests that *C. nodosa* allocates more biomass to the development of these bearing roots horizontal rhizomes during periods of low phosphate concentrations possibly in order to increase phosphate acquisition from the sediment pool (Peréz *et al*., 1994). The seasonal fluctuation in the biomass of the vertical rhizomes with short internodes should reflect changes both in rhizome size and rhizome density (Marbà *et al*., 1996). Thereby, the low biomass values recorded in spring and summer were mainly due to the small rhizome size, the peak value in late summer both to the large size and the high density, while the relatively high or moderate values in autumn and winter to the large rhizome size. The *C. nodosa* vertical axes grow approximately 13 mm yr^{-1}, while the horizontal rhizomes from a few centimeters per year in dense beds to 2 m yr^{-1} in low density beds (Caye & Meinesz, 1985). Horizontal rhizome growth permits a vegetative expansion, while vertical axes assure the occurrence of sexual reproduction (Caye & Meinesz, 1985). The observed variability in the biomass of the dead vertical shoots mainly found on the main axis in late summer, autumn and winter with very low biomass values, should reflect the seasonal variability in the decay rates of seagrass leaves. The finding that the biomass of the dead vertical shoots on branches C is significantly correlated (negative correlation) with water column phosphate concentrations (Table 2), indicates increased decay rates of those branch leaves during periods of low phosphate concentrations.

The root biomass of *C. nodosa* in the study area displayed values in the range of those recorded for this seagrass species at some other coastal Mediterranean locations (Table 3). The finding that the total root biomass in our stand was lower than that of rhizomes all year round but accounted for a remarkable fraction of the total plant biomass, is consistent with those by other authors (Rismondo *et al.*, 1997; Cancemi *et al.*, 2002). Duarte *et al*. (1998) found that the root production of *C. nodosa* from the W Mediterranean represents a marked component (20%) of the total plant production. Seagrass root growth may receive a sizeable amount of the carbon fixed by the plants to maintain their ability to acquire nutrients, particularly when production is nutrient-limited (Pérez *et al*., 1994).

Roots stemming from the main axis prevailed over those stemming from other rhizomes probably as a result of higher density and larger size. Duarte *et al.* (1998) observed that the average length as well as the average number and weight per node of roots produced at nodes of horizontal rhizomes exceeded those of roots of vertical rhizomes. The total root biomass of *C. nodosa* in the study site displayed a seasonal model similar to that observed for this species in some other coastal Mediterranean environments (Rismondo *et al*., 1997; Cancemi *et al*., 2002). Adventitious roots stemming from both the main axis and the other rhizomes showed an identical seasonal trend, which was coupled with that of the rhizome biomass, indicating that the variability in rhizome elongation and branching induces changes in root biomass. The reduction in root biomass during spring, when rhizome biomass increased, may reflect a partial death of roots (Agostini *et al*., 2003; Zharova *et al*., 2008). The highest root biomass and the lowest rhizome / root biomass ratio occurred in summer (the period of greatest nutrient demands), indicating that *C. nodosa* allocates more biomass for root development in order to increase the capacity of roots to acquire nutrients from the sediment (Pérez *et al*., 1994).

In conclusion, the biomass of *C. nodosa* is generally dominated by rhizome and root material all year long. Leaf biomass shows a unimodal annual pattern with the highest values in summer. In the study site, leaves on the main axis accounted for a large fraction of the total leaf biomass during all seasons, while leaves on the additional branches mainly contributed during late summer and autumn. Blades prevailed over sheaths mainly during summer and autumn. Leaf biomass is significantly correlated (positive correlation) with water temperature, suggesting that temperature is a major factor controlling leaf develop-

ment. *Cymodocea nodosa* generally displays a variability in rhizome biomass seasonality. The main axis biomass greatly exceeded the cumulative biomass of the remaining rhizomes all year long. It increased during spring and summer and sharply in mid autumn, indicating an intense elongation, while additional branches contributed to mainly in autumn, resulting in intense branching. Branches C biomass is significantly correlated (negative correlation) with water column phosphate concentrations, indicating that the seagrass allocates more biomass for the development of these horizontal rhizomes during low phosphate periods possibly in order to increase phosphate acquisition from the sediment. Biomass of vertical rhizomes with short internodes peaked in August (as leaf biomass did), while dead vertical shoots mainly in October-November as a possible result of increased leaf decay. Rhizome biomass of *C. nodosa* generally exceeds that of roots. Roots on the main axis prevailed over those stemming from other rhizomes, while both types of roots showed an identical seasonal trend in biomass values, which was generally coupled with that of rhizome biomass. Our findings improve the understanding of *C. nodosa* meadows growth dynamics and along with those of future comperative studies and controlled experiments could be utilized for the monitoring and conservation of *C. nodosa* coastal habitats.

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REFERENCES

Agostini S, Pergent G, Marchand B, 2003. Growth and primary production of *Cymodocea nodosa* in a coastal lagoon. *Aquatic Botany*, 76: 185-193.

Barberá C, Tuya F, Boyra A, Sanchez-Jerez P, Blanch I, Haroun RJ, 2005. Spatial variation in the structural parameters of *Cymodocea nodosa* seagrass meadows in the Canary Islands: a multiscaled approach. *Botanica Marina*, 48: 122-126.

Canals M, Ballesteros E, 1997. Production of carbonate particles by phytobenthic communities on the Mallorca-Mecorca shelf, northewestern Mediterranean Sea. *Deep-sea Research II*, 44: 611-629.

Cancemi G, Buia MC, Mazzella L, 2002. Structure and growth dynamics of *Cymodocea nodosa* meadows. *Scientia Marina*, 66: 365-373.

Caye G, Meinesz A, 1985. Observations on the vegetative development, flowering and seeding of *Cymodocea nodosa* (Ucia) Ascerson on the Mediterranean coasts of France. *Aquatic Botany*, 22: 277-289.

Cebrián J, Duarte CM, Marbà N, Enríquez S, 1997. Magnitude and the fate of the production of four co-occurring Western Mediterranean seagrass species. *Marine Ecology Progress Series*, 155: 29-44.

Christophoridis C, Dedepsidis D, Fytianos K, 2009. Occurrence and distribution of selected heavy metals in the surface sediments of Thermaikos Gulf, N. Greece. Assessment using pollution indicators. *Journal of Hazardous Materials*, 168: 1082-1091.

Cunha AH, Duarte CM, 2005. Population age structure and rhizome growth of *Cymodocea nodosa* in the Ria Formosa (southern Portugal). *Marine Biology*, 146: 841-847.

Cunha AH, Duarte CM, 2007. Biomass and leaf dynamics of *Cymodocea nodosa* in the Ria Formosa lagoon, South Portugal. *Botanica Marina*, 50:1-7.

Den Hartog C, 1970. *The seagrasses of the world*. North Holland Publication, Amsterdam.

Duarte CM, Sand-Jensen K, 1990. Seagrass colonization: biomass development and shoot demography in *Cymodocea nodosa* patches. *Marine Ecology Progress Series*, 67: 97-103.

Duarte CM, Marbà N, Agawin N, Cebrián J, Enríquez S, Fortes MD, Gallegos ME, Merino M, Olesen B, Sand-Jensen K, Uri J, Vermaat J, 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series*, 107: 195-209.

Duarte CM, Merino M, Agawin NSR, Uri J, Fortes MD, Gallegos ME, Marbà N, Hemminga MA, 1998. Root production and belowground seagrass biomass. *Marine Ecology Progress Series*, 171: 97-108.

EC, 2000. *Directive 2000/60/EC, Establishing a framework for community action in the field of water policy.* European Commission, Luxemburg.

Geneid YA, El-Hady HH, 2006. Distribution, biomass and biochemical contents of the seagrass species of lake Bardawil, Mediterranean sea, Egypt. *Biologia Marina Mediterranea*, 13: 225-229.

Guidetti P, Lorenti M, Buia M C, Mazzella L, 2002. Temporal dynamics and biomass partitioning in three Adriatic seagrass species: *Posidonia oceanica, Cymodocea nodosa, Zostera marina*. *P.S.Z.N.: Marine Ecology*, 23: 51-67.

Haritonidis S, 1996. Greece. In: Schramm W, Nienhuis PH, eds. *Marine benthic vegetation. Recent changes and the effects of eutrophication.* Springer, Berlin: 403-410.

Haritonidis S, Diapoulis A, Nikolaidis G, 1990. First results on the localisation of the herbiers of marine phanerogams in the Gulf of Thermaikos. *Posidonia Newsletter*, 3: 11-18.

Hemminga MA, Duarte CM, 2000. *Seagrass ecology.* Cambridge University Press, Cambridge.

Lazaridou E, Orfanidis S, Haritonidis S, Seferlis M, 1997. Impact of eutrophication on species composition of macrophytes in the gulf of Thessaloniki, Macedonia, Greece: first evaluation of the results of one year study. *Fresenius Environmental Bulletin*, 6: 054-059.

Malea P, Haritonidis S, 1999. *Cymodocea nodosa* (Ucria) Aschers. as a bioindicator of metals in Thermaikos Gulf, Greece, during monthly samplings. *Botanica Marina*, 42: 419-430.

Marbà N, Duarte CM, 2001. Growth and sediment space occupation by seagrass *Cymodocea nodosa* roots. *Marine Ecology Progress Series*, 224: 291-298.

Marbà N, Cebrián J, Enriquez S, Duarte CM, 1996. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. *Marine Ecology Progress Series*, 133: 203-215.

Nikolaidis NP, Karageorgis AP, Kapsimalis V, Marconis G, Drakopoulou P, Kontoyiannis V, Krasakopoulou E, Pavlidou A, Pagou K, 2006. Circulation and nutrient modelling of Thermaikos Gulf, Greece. *Journal of Marine Systems*, 60: 51-62.

Olesen B, Enríquez S, Duarte CM, Sand-Jensen K, 2002. Depth-acclimation of photosynthesis. Morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea. *Marine Ecology Progress Series*, 236: 89-97.

Orfanidis S, Papathanasiou V, Gounaris S, 2007. Body size descriptor of *Cymodocea nodosa* indicates anthropogenic stress in coastal ecosystems. *Transitional Waters Bulletin*, 2: 1-7.

Orfanidis S, Papathanasiou V, Gounaris S, Theodosiou T, 2010. Size distribution approaches for monitoring and conservation of coastal *Cymodocea* habitats. *Aquatic Conservation. Marine and Freshwater Ecosystems*, 20: 177-188.

Pavón-Salas N, Herrera R, Hernández-Guerra A, Harou R, 2000. Distribution pattern of seagrasses in the Canary Islands (central-east Atlantic Ocean). *Journal of Coastal Research*, 6: 329-335.

Peduzzi P, Vukonič A, 1990. Primary production of *Cymodocea nodosa* in the Gulf of Trieste (Northern Adriatic Sea): a comparison of methods. *Marine Ecology Progress Series*, 64: 197-207.

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

Pérez M, Romero J, 1994. Growth dynamics, production, and nutrient status of the seagrass *Cymodocea nodosa* in a Mediterranean semi-estuarine environment. *P.S.Z.N.I.: Marine Ecology*, 15: 51-64.

Pérez M, Duarte CM, Romero J, Sand-Jensen K, Alcoverro T, 1994. Growth plasticity in *Cymodocea nodosa* stands: the importance of nutrient supply. *Aquatic Botany*, 47: 249-264.

Pergent-Martini C, 1994. *Impact d'un rejet d'eaux usées urbaines syr l'herbier à Posidonia oceanica, avant et après la mise en service d'une station d'épuration*. Ph. D. Thesis, University of Corse, France.

Reyes J, Sansón M, Afonso-Carrillo J, 1995. Distribution and reproductive phenology of the seagrass *Cymodocea nodosa* (Ucria) Ascherson in the Canary Islands. *Aquatic Botany*, 50: 171-180.

Rismondo A, Curiel D, Marzocchi M, Scattolin M, 1997. Seasonal pattern of *Cymodocea nodosa* biomass and production in the lagoon of Venice. *Aquatic Botany*, 58: 55-64.

Sfriso A, Ghetti PF, 1998. Seasonal variation in biomass, morphometric parameters and production of seagrasses in the lagoon of Venice. *Aquatic Botany*, 61: 207-223.

Short FT, Wyllie-Echeverria S, 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation*, 23: 17-27.

Strickland JDH, Parson TR, 1968. *A practical handbook of seawater analysis*. Fisheries Research Board of Canada, Ottawa.

Terrados J, Ros JD, 1992. Growth and primary production of *Cymodocea nodosa* (Ucria) Ascherson in a Mediterranean coastal lagoon: the Mar Menor (SE Spain). *Aquatic Botany*, 43: 63-74.

Terrados J, Duarte CM, Kenworthy, 1997. Experimental evidence for apical dominance in the seagrass *Cymodocea nodosa. Marine Ecology Progress Series*, 148: 263-268.

Terrados J, Grau-Castella M, Piñol-Santiña D, Riera-Fernández P, 2006. Biomass and primary production of a 8-11 m depth meadow versus < 3 m depth meadows of the seagrass *Cymodocea nodosa* (Ucria) Ascherson. *Aquatic Botany*, 84: 324-332.

Vermaat JE, Beijer JAJ, Gijlstra R, Hootsmans MJM, Philippart CJM, van den Brink NW, van Vierssen W, 1993. Leaf dynamics and standing stocks of the intertidal *Zostera noltii* Hornem. and *Cymodocea nodosa* (Ucria) Ascherson on the Banc d'Arguin (Mauritania). *Hydrobiologia*, 258: 59-72.

Zar JH, 1984. *Biostatistical analysis. 2nd edition*. Prentice-Hall Inc, NJ.

Zharova N, Sfriso A, Pavoni B, Voinov A, 2008. Analysis of annual fluctuations of *C. nodosa* in the Venice lagoon: Modeling approach. *Ecological Modelling*, 216: 134-144.

Zieman JC, Wetzel RG, 1980. Productivity in seagrasses: methods and rates. In: Phillips RC, McRoy CP, eds. *Handbook of seagrass biology: an ecosystem perspective*. Garland STPM, New York: 87-116.