Community metabolism and carbon budget along a gradient of seagrass (*Cymodocea nodosa*) colonization

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Abstract

We studied the effect of seagrass (*Cymodocea nodosa*) colonization on community metabolism and sediment conditions. The biomass of *C. nodosa* increased with time after seagrass colonization. The biomass increased steadily during the 6.1 yr of colonization to 9.1 mol C m^{-2}. Gross primary production increased from 7 to 49.3 mmol C m^{-2} d^{-1} during the first stages of the colonization and then decreased to 20 mmol C m^{-2} d^{-1} at a time when the biomass was in excess of 6 mol C m^{-2}. Net dissolved organic carbon (DOC) fluxes increased with time after colonization, shifting from a net uptake in patches younger than 2 yr to a net release in older patches. Community respiration (R) increased with the seagrass colonization, leading to a shift from net autotrophy in the unvegetated sediment community to net heterotrophy after *C. nodosa* colonization. The increase in net heterotrophy with seagrass colonization was reflected in the development of reducing conditions in the sediment. To maintain a net heterotrophic benthic metabolism and net DOC release, the *C. nodosa* community must receive an input of organic matter (OM) from an allochthonous source. OM inputs from sestonic material trapped by the seagrass canopy exceed 157 mmol C m^{-2} d^{-1} in developed *C. nodosa* communities. Thus, the seagrass community acts as an important link between the pelagic and benthic communities by trapping sestonic organic carbon.

Seagrasses form highly productive ecosystems, delivering a large carbon surplus to coastal ecosystems (Duarte and Cebrián 1996; Duarte and Chiscano 1999; Hemminga and Duarte 2000). The primary production of seagrass beds is enhanced by that of epiphytic and benthic algae, which usually bring the total primary production of seagrass meadows to values twice as high as those contributed directly by the seagrasses (Hemminga and Duarte 2000). Seagrass canopies enhance organic inputs to the sediment, both directly as inputs of seagrass tissues and as sestonic particles trapped by the seagrass canopy (e.g., Ward et al. 1984; Lemmens et al. 1996; Gacia et al. 2002). These sestonic particles are defined as particulate organic matter (POM), such as plankton and organic detritus, and also as inorganic particles suspended in seawater. Moreover, the seagrass rhizosphere releases OM and oxygen (Penhale and Wetzel 1983; Pedersen et al. 1998), thereby affecting sediment properties (e.g., Kemp et al. 1984; Hemminga 1998; Marbà and Duarte 2001). These processes stimulate bacterial activity within seagrass meadows to levels well above those of adjacent unvegetated sediments (e.g., Hemminga and Duarte 2000). Hence, seagrass meadows are sites of intense metabolism, supporting both high gross primary production (GPP) and community respiration (R) rates, which are often closely balanced (Hemminga and Duarte 2000). For instance, an in situ benthic community dominated by *Thalassia testudinum* was slightly net autotrophic, as the annual GPP : respiration ratio was 1.16 (Ziegler and Benner 1998, 1999).

It would be expected that the development of seagrass meadows would increase the primary production of coastal ecosystems, but this may not result in an increased OM surplus, as respiration rates may increase accordingly. Existing evidence shows that plant biomass and detritus as well as total organic pool in the sediment (Pedersen et al. 1997; Cebrián et al. 2000) increase with time after seagrass colonization. That the organic carbon pool in the sediment increases with time after sediment colonization suggests that the meadow produces organic carbon in excess of the community's requirements. Alternatively, the increased sediment organic pool may derive from the increased retention of sestonic particles as the canopy develops during the colonization process (cf. Agawin and Duarte 2002; Gacia et al. 2002). Increases in the shoot density with the development of seagrass meadows can also alter sediment metabolism; for example, Holmer and Nielsen (1997) observed increased sulfate reduction rates in *Zostera marina* stands of increasing

shoot density. Thus, the development of the seagrass canopy along with seagrass colonization can affect the sediment composition and the rate and nature of sedimentary processes. Understanding the development of community metabolism and the associated changes in sediment composition and sedimentary processes during seagrass colonization would help clarify the role of seagrass meadows in coastal ecosystems. Unfortunately, such investigations have not been conducted to date.

In this study, we examine the effect of seagrass (*Cymodocea nodosa*) colonization on community metabolism and sediment conditions. We do so through an investigation of the relationship between *C. nodosa* patch age and plant biomass; sediment OM (particulate and stable isotope composition), redox condition, and dissolved sulfide (DS) concentration; and community metabolism and net dissolved organic carbon (DOC) production by the community.

Methods

Study site—The study was conducted in a patchy *C. nodosa* meadow growing on a tideless, 4-km-wide, shallow (<2 m) platform in Alfacs Bay (Ebro Delta, Spain, 40°36.11′N, 0°46.13′E). The *C. nodosa* patches colonized highly mobile submerged dunes, which migrate at an average velocity of 13 m yr^{-1} across the platform from the open bay toward the sand barrier that separates the bay from the Mediterranean Sea (Marbà et al. 1994). The strong coupling between dune migration and *C. nodosa* colonization dynamics has been demonstrated to maintain the patchy vegetation landscape by maintaining *C. nodosa* in a permanent state of colonization (Marbà and Duarte 1995). The patch population encompasses patches from <1 yr old (seedlings) to 10 yr old (Vidondo et al. 1997).

In July 2000, 12 *C. nodosa* patches encompassing the broadest range of patch age available in the area were located using patch size as a proxy for patch age (Duarte and Sand-Jensen 1990; Vidondo et al. 1997). At each patch, two transects, one along the longest patch axis and the other one perpendicular to it through the patch center, were laid, and one to four samples, depending on patch size (i.e., only one in the case of isolated seedlings), of *C. nodosa* were collected near the intersection of both transects using a 9.5-cm-diameter stainless steel corer that was inserted to a depth of >40 cm into the sediment. We collected the samples near the patch center, for it is the a priori most likely location of patch origin (Duarte and Sand-Jensen 1990). The age of the oldest shoot collected provides a minimum estimate of the time elapsed since the patch was established and thus an estimate of patch age (Duarte and Sand-Jensen 1990) and the location of patch origin. Shoot age was calculated as the number of leaf scars plus the number of standing leaves of the shoot divided by the average number of leaves produced annually by a *C. nodosa* shoot at this site (i.e., 14 leaves shoot^{-1} yr^{-1}) (Duarte and Sand-Jensen 1990), which yields an error of <10% on the age estimates. Patch radius (hereafter called patch size) was estimated as the average distance between the patch origin and patch edge measured along both transects for each patch studied.

Nine sediment cores taken at the origin of each patch consisted of three sediment cores with dimensions of 4.3 cm in diameter and 10 cm long, three sediment cores 4.3 cm in diameter and 2 cm long, and three sediment cores 7 cm in diameter and 50 cm long. The 7-cm-diameter cores were vertically perforated at 2-cm intervals with 1.2-cm-diameter holes, with the holes covered with tape to avoid the loss of pore water and sediment during sampling. For comparison, a similar set of sediment cores was collected at unvegetated sediment locations. The samples collected were used to estimate above- and belowground *C. nodosa* biomass, vertical distribution of *C. nodosa* root biomass, amount of OM and DS in the sediment pore water, stable carbon isotopic composition (δ^{13}C) of sediment OM and seagrass leaves, and sediment redox profiles.

In addition, community metabolism and net DOC production were quantified using in situ benthic chambers incubated at the patch origin of seven of the *C. nodosa* patches studied and one unvegetated sediment location. Community metabolism and net DOC production were estimated from the changes in the concentrations of dissolved oxygen and DOC in the benthic incubations, respectively. The chambers consisted of a polyvinyl chloride ring inserted in the sediment, avoiding damage to rhizome connections, and a polyethylene plastic bag fitted to the ring with a sampling port where water was collected. The walls of the polyethylene plastic bags are flexible structures across which turbulence propagates to the interior of the incubation chamber. Injection of a fluorescent dye (fluorescein) in the experimental chambers showed mixing times to be ~5 s within the incubation chambers. Four replicated chambers of each community examined were incubated under light and dark conditions using clear and thick dark bags, respectively.

The benthic communities studied were incubated for ~24 h, collecting samples for dissolved oxygen and DOC at the beginning of the incubation and after ~24 h. Water samples were withdrawn from the sampling port with acid-washed syringes. We elected to calculate oxygen and DOC fluxes during 24-h intervals rather than using time series, because the estimation of gross and net community production (NCP) from time-series measurements is confounded by the fact that these processes are not linear (due to changing nightlight processes) during 24-h interval; therefore, they must necessarily be integrated during 24-h periods, yielding comparable values to those derived from oxygen changes along 24-h incubations. We acknowledge that time-series measurements would have improved the estimate of respiration. We therefore considered that the allocation of effort to replicate incubation units, each sampled during a 24-h interval, would be most effective. Despite our efforts, the conditions inside the incubation chambers (e.g., light and turbulence environments) cannot fully mimic those in the unenclosed patches; hence, the rates obtained may deviate somewhat from those in the unenclosed patches, adding error to our estimates.

Sediment characteristics—All 4.3-cm-diameter and 10-cm-long sediment cores were cut longitudinally. Half of the sediment cores were kept frozen at −20°C until pore-water extraction and subsequent DS analyses. Pore water was extracted from 27 cm^3 of thawed sediment by centrifuging (at

12,000 g and room temperature for 5 min) with double centrifuge tubes, which had been previously flushed with N_2. DS concentration was analyzed following the methods of Cline (1969). The other half of the core was weighed, after overnight desiccation at 105°C, to estimate the mass of the upper 10-cm layer of sediment per unit area. A subsample of the dried sediment was burned for 3 h at 465°C, and the percentage of OM present in the sediment was estimated. The combustion temperature was lower than the 550°C recommended by Smith and Atkinson (1984) to avoid the loss of carbonates. The absolute amount of OM in the upper 10-cm layer of sediment (in g dry weight [DW] OM m^{-2}) was calculated by multiplying the percentage of OM and the mass of the upper 10-cm layer of sediment per unit area.

The carbon isotopic composition of sediment OM was analyzed within the upper 2-cm sediment layer on samples collected with three 4.3-cm-diameter cores. Dried sediment samples were sieved to provide a sample of the fine fraction (<63 μm) for isotopic analysis. A subsample was weighed into a precombusted silver boat (500°C, 3 h), and carbonate material was removed through a combination of HCl (10%) additions and drying at 40°C. The $\delta^{13}C_{POC}$ (POC meaning particulate organic carbon) was determined on CO_2 generated by vacuum combustion in quartz tubes containing copper and precombusted copper oxide (910°C, 3 h). The CO_2 was collected by vacuum distillation and was measured on a PDZ-EUROPA GEO 20/20 mass spectrometer. Results are reported in the δ notation, calculated as

$$\delta^{13}C_{sample} = 1{,}000\left(\frac{R_{sample}}{R_{PDB}} - 1\right)$$

where R = $^{13}C/^{12}C$. Vienna Pee Dee Bellemnite (VPDB) was the reference standard, and the external measurement precision was better than ±0.1‰, based on analyses of internal laboratory standards run concurrently with all the samples. Triplicate subsamples of leaf material, including the associated epiphytes, were collected to ascertain the isotopic composition of the organic carbon of seagrasses and the associated epiphytes. The relative contribution (X) of seagrass material plus associated epiphytes to sediment OM was calculated as

$$\delta^{13}C_{sediment} = [X \cdot \delta^{13}C_{seagrass}] + [(1 - X) \cdot \delta^{13}C_{seston}]$$

by assuming that the only two major sources of sediment OM were *C. nodosa* material plus associated epiphytes (with $\delta^{13}C_{seagrass} = -11.6$) (this study) and seston (with $\delta^{13}C_{seston} = -22$) (Dauby 1989). The absolute amount of OM provided by *C. nodosa* plus associated epiphytes to the sediment (in g DW POM$_{seagrass}$ m^{-2}) was estimated as the product of the fraction of the sediment OM provided by the plant (i.e., X) and the absolute amount of OM measured in the upper 10-cm layer of sediment. To convert the g DW OM m^{-2} in the sediment to mol C m^{-2}, we used the percentage of phytoplankton carbon content of DW (34.1%) (Duarte 1992) and the percentage of seagrass carbon content of DW (33.6%) (Duarte 1990).

Sediment redox potential profiles were measured, within 20 min after collection, at 2-cm depth intervals on the 7-cm-diameter cores collected by inserting a Crison Pt electrode,

connected to a portable pH meter (Crison model 507), horizontally into the sediments. The electrode was regularly calibrated with a redox standard solution (Crison 468 mV at 25°C) and cleaned and polished to prevent accumulation of Pt oxides. Redox measurements were referred to the standard hydrogen electrode (207 mV) as described by the American Public Health Association (1992).

Seagrass biomass—Aboveground biomass was assessed by weighing, after drying at 60°C for 24 h, the leaf material collected with the stainless steel core and that enclosed within benthic incubation chambers and harvested at the end of community metabolism experiments. Belowground biomass was estimated from the total rhizome and root dry biomass harvested with the same stainless steel core. The photosynthetic and nonphotosynthetic biomass (g DW m^{-2}) was converted to mol C m^{-2} by using the percentage of photosynthetic seagrass carbon content of DW (33.6% of DW) (Duarte 1990) and the percentage of the nonphotosynthetic seagrass carbon content of DW (40% of DW) (Pérez et al. 1994).

The depth distribution of root biomass in the *C. nodosa* rhizosphere was measured by slicing those 7-cm-diameter sediment cores collected in the patches at 5-cm depth intervals and then sorting and weighing, after overnight desiccation at 60°C, the roots. The depth distribution of *C. nodosa* root biomass was summarized by fitting the model $Y = 1 - \beta^d$ (Gale and Grigal 1987), where Y is the fractional cumulative (i.e., fraction between 0 and 1) root biomass between the sediment surface to depth d (cm), d represents an "extinction coefficient," and β represents a "fitted parameter" (Jackson et al. 1996). The equation was fitted using nonparametric regression analysis (Wilkinson 1989). The centroidal depth of root biomass into the sediments was calculated, using the model, as the sediment depth composing 50% of root biomass.

Community metabolism and DOC production—Changes in dissolved oxygen concentration in the benthic chambers were used to estimate community metabolism. Dissolved oxygen concentration was measured by Winkler titration with visual end-point determination using starch indicators (Hansen 1999). The community respiration (R) was estimated using the changes in dissolved oxygen concentration in the dark chambers. Changes in dissolved oxygen concentration in the clear benthic chambers were used to calculate the NCP. The sum of R and NCP provided estimates of the GPP. Before calculating the community metabolism, the rate of change in oxygen concentration was corrected for possible oxygen diffusion across the polyethylene plastic bags using diffusion coefficients determined in laboratory experiments at in situ temperature. The diffusion of dissolved oxygen was calculated from the gradient in oxygen concentration between the enclosed water and the ambient waters and the diffusion coefficient. Oxygen units were converted to carbon units by assuming photosynthetic and respiratory quotients of 1 (Kirk 1983). Variability from these quotients about the assumed value of 1 may introduce error in the estimates (Kirk 1983).

Water samples from the benthic chambers for DOC anal-

Table 1. Mean (±SE), range, coefficients (slope ± SE, intercept ± SE), and descriptive statistics (R^2 and p) of least-squares linear regression analyses between properties of the seagrass stands and the community they support (Y) and the time since colonization (X in years). OM, organic matter; GPP, gross primary production; R, respiration; NCP, net community production; DOC, dissolved organic carbon.

Y	Mean ± SE	Range	Slope ± SE	Intercept ± SE	R^2	p
Patch size (m)	8.8±1.5	3.9–17.7	2.7±1.0	0.3±3.4	0.41	0.027
Leaf biomass (mol C m^{-2})	4.3±0.8	0.1–9.1	1.6±0.3	−0.5±0.9	0.74	0.000
Rhizosphere biomass (mol C m^{-2})	12.4±2.2	0.1–25.6	3.8±0.8	0.5±2.9	0.64	0.001
Centroidal root depth (cm)	8.2±1.0	2.5–11.3	1.2±0.3	4.3±1.2	0.66	0.009
GPP (mmol C m^{-2} d^{-1})	25.7±4.7	7.0–49.3	0.3±2.5	25.0±8.7	0.00	0.918
R (mmol C m^{-2} d^{-1})	45.7±9.9	1.0–83.7	12.0±1.8	11.8±6.3	0.86	0.001
NCP (mmol C m^{-2} d^{-1})	−21.7±9.8	−71.5–14.6	−11.2±2.4	9.9±8.5	0.74	0.004
DOC flux (mmol C m^{-2} d^{-1})	8.8±19.9	−66.2–81.6	21.8±5.5	−52.9±19.1	0.68	0.007
Organic matter (mol C m^{-2})	56.2±4.3	40.3–86.5	3.7±2.1	45.6±7.2	0.17	0.113
δ^{13}C (‰)	−18.5±0.6	−21.8–−15.9	0.3±0.3	−19.2±1.1	0.00	0.416
Organic matter from seagrass (mol C m^{-2})	6.1±1.2	0.3–13.6	0.9±0.6	3.4±2.0	0.13	0.146
Redox (mV)	156.9±20.1	47.4–277.6	−22.1±9.6	219.8±32.1	0.28	0.044
Dissolved sulfide (mmol L^{-1})	0.2±0.1	0.0–0.6	0.1±0.0	0.0±0.1	0.20	0.081

yses were filtered through precombusted (450°C for 4 h) GF/ F filters. Samples were kept frozen in acid-washed material (glass vials encapsulated with silicone-Teflon caps) until analysis on a Shimadzu TOC-5000A analyzer. We used standards provided by Dennis A. Hansell and Wenhao Chen (University of Miami) of 44–45 and 2 μmol DOC. The rate of change in DOC concentration in clear and dark chambers was used to calculate the net DOC production by the communities.

The volume of the benthic chambers was estimated by injecting 0.25 M phosphate solution at the end of the experiment. Water samples from the incubations were collected after allowing the tracer to mix for 5 min and were kept

frozen until the spectrophotometric determination of the phosphate concentration (Hansen and Koroleff 1999). The volume of the incubations was calculated as the difference in phosphate concentration from the solution injected and the concentration inside the chambers; the volume ranged from 3 to 13 liters.

Results

The age of the *C. nodosa* patches studied ranged from 0.5 to 6.1 yr. The patch size ranged from 3.9 to 17.7 m and increased significantly ($p < 0.05$) with increasing time after colonization (Table 1). The *C. nodosa* patches that were examined supported photosynthetic and nonphotosynthetic biomass varying between 0.1 and 9.1 mol C m^{-2} and between 0.1 and 25.6 mol C m^{-2}, respectively (Table 1; Fig. 1). Most (74% for leaf biomass and 64% for rhizosphere biomass) (Table 1) of the variability in leaf and rhizosphere biomass observed across seagrass patches was attributable to differences in patch age. The rate of accretion of seagrass biomass during colonization was estimated at 1.6 ± 0.3 mol C m^{-2} yr^{-1} for photosynthetic biomass and 3.8 ± 0.8 mol C m^{-2} yr^{-1} for nonphotosynthetic biomass (Fig. 1; Table 1). Of the patches studied, 90% of the rhizosphere was distributed within the top 37.4 cm of the sediment, and half of the biomass was found within the upper 2.5 and 11.2 cm of the sediment layer (data not shown). However, 50% of root biomass occupied between 2.5- and 11.3-cm sediment depth, with seagrass rhizosphere reaching significantly deeper during colonization (Table 1).

The sediments in Alfacs Bay contained between 0.5% and 1.2% of OM, which represented OM loads within the upper 15-cm sediment layer ranging from 40.3 to 86.5 mol C m^{-2} (Table 1). The sediment OM content of the sediments did not increase significantly ($p > 0.05$) during the colonization process (Table 1). The δ^{13}C of sediment OM varied from −15.9‰ to −21.8‰ (Table 1), tending to become more positive, although not significantly ($p > 0.05$) (Table 1) with increasing time after colonization. The δ^{13}C of the sediment OM indicated that seagrass detritus represented between
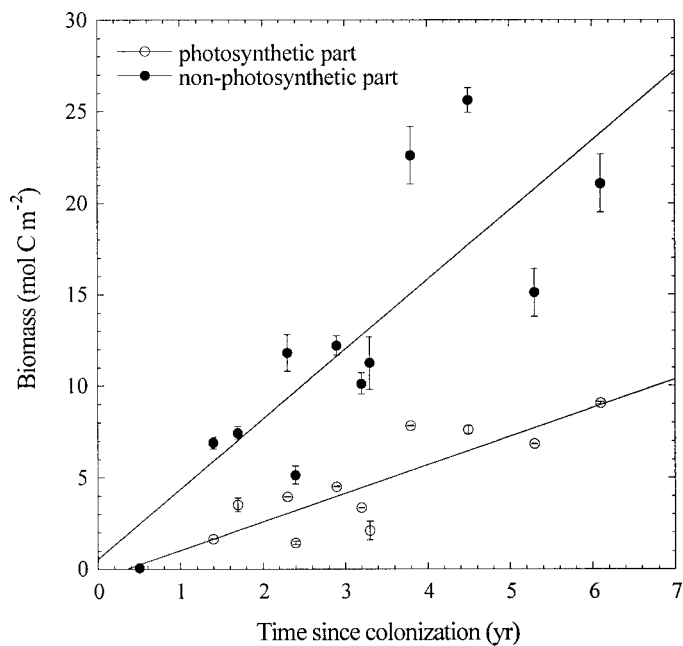

Fig. 1. Relationship between the time since *Cymodocea nodosa* colonization in years and the photosynthetic and nonphotosynthetic *C. nodosa* biomass (mol C m^{-2}). Average ± SE shown. Solid lines represent the fitted linear regression.

0.5% and 18.2% of the sediment OM pool, assuming that seagrasses and seston were the only sources of sediment OM. Seagrasses, therefore, provided between 0.3 and 13.6 mol C m^{-2} of the sediment organic pool (Table 1). Sulfide concentration in sediment pore water was low (Table 1). Sulfide concentrations were below the detection limit in bare and recently colonized sediments and reached the highest values in sediments that had been colonized by *C. nodosa* for >4 yr.

Redox potential within the upper 40-cm sediment layer strongly declined with increasing sediment depth at the seagrass colonization stages examined (Fig. 2). The average redox potential within the upper 40 cm of sediment varied up to sixfold across the bare and vegetated sediments examined (Fig. 3); the average sediment redox potential decreased significantly ($p < 0.05$) with increasing time after colonization (Table 1).

The GPP of the communities ranged from 7 to 49.3 mmol C m^{-2} d^{-1} (Fig. 4a) and was independent of the time after colonization ($p > 0.05$) (Table 1). Community GPP increased during the first 2 yr after colonization, and when communities were >3 yr old, the GPP dropped to ~20 mmol C m^{-2} d^{-1} (Fig. 4a). The abrupt decline observed in GPP occurred when the communities supported photosynthetic biomass of >6 mol C m^{-2} (Fig. 5). Community respiration ranged from 1.0 to 83.7 mmol C m^{-2} d^{-1} and increased significantly ($p < 0.001$) (Table 1) with increasing time elapsed after colonization (Fig. 4b). All seagrass communities incubated were net heterotrophic, ranging from 4.6 to 71.5 mmol C m^{-2} d^{-1}, whereas bare sediments were net autotrophic with a net primary production of 14.6 mmol C m^{-2} d^{-1} (Fig. 4c). The net primary production decreased significantly ($p < 0.01$) with the time after colonization (Fig. 4c; Table 1).

Net community DOC fluxes varied from a negative flux (net uptake) of 66 mmol C m^{-2} d^{-1} in patches <2 yr old to a positive flux, net DOC release of 81.6 mmol C m^{-2} d^{-1} in the oldest patch examined (Fig. 6). The net DOC release increased significantly ($p < 0.01$) with increasing time after colonization (Fig. 6; Table 1) and with the respiration ($p < 0.05$) of the benthic communities (Fig. 7). The community metabolism and net DOC release were independent ($p > 0.05$) of the patch size.

Discussion

Our results show that, consistent with previous reports (Duarte and Sand-Jensen 1990; Pedersen et al. 1997; Cebrián et al. 2000), the photosynthetic and nonphotosynthetic biomass of *C. nodosa* increases with time after colonization. This increase in photosynthetic biomass leads to a linear increase in GPP until the biomass reaches ~6 mol C m^{-2}; when *C. nodosa* leaves exceed 6 mol C m^{-2}, the GPP decreases to ~20 mmol C m^{-2} d^{-1} (Fig. 5). This reduction in community GPP as colonization develops may be attributable to shelf-shading (Pérez and Romero 1992). Pérez and Romero (1992) reported a reduction in 25–35% of the potential production caused by shelf-shading in developed *C. nodosa* meadows, which is close to the 40% reduction of

the GPP observed in our study. In contrast, the community respiration rate increases linearly as seagrass colonization develops, shifting the benthic communities from the strongly autotrophic unvegetated sands prior to seagrass colonization to strongly heterotrophic communities associated with stands of mature *C. nodosa*. The autotrophic nature of the sediment community prior to seagrass colonization derives from the presence of an active microphytobenthic community in these sediments (Delgado 1989). The strong shading of the sediment during the colonization of *C. nodosa* (cf. Pérez and Romero 1992) may result in a shift of the benthic microbial community toward a dominance of heterotrophic processes, thereby adding to the observed shift toward heterotrophy along the colonization process. In contrast to the whole community, the seagrass component remains strongly autotrophic, as indicated by the average net rate of biomass accretion of 1.6 and 3.8 mol C m^{-2} yr^{-1} for photosynthetic and nonphotosynthetic biomass, respectively, during the colonization process. Thus, the increasing heterotrophic nature of the seagrass communities must be derived from a growing carbon demand from the heterotrophic component of the community. It is likely that, as the seagrass biomass of mature communities increases, it provides a more complex habitat, allowing the development of consumer communities, ranging from microbes to vertebrates. Indeed, Cebrián et al. (2000) reported a greater seagrass grazing rate in older patches than in younger ones, and Duarte et al. (1999) reported the development of rich microplanktonic heterotrophic communities within developing seagrass canopies. Ziegler and Benner (1999) showed that there was a strong link between the benthic community and the water-column process as the seagrass exudation fuels the bacterioplankton in the water column.

The increased respiration of the community as colonization proceeds is associated with changes in the sediment conditions, particularly reducing conditions, as the vegetated sediment has been reported to increase the sulfate reduction rates (Holmer and Nielsen 1997; Hansen et al. 2000). Whereas the development of the *C. nodosa* rhizosphere has been shown to lead to more positive redox conditions (Marbà and Duarte 2001) through the diffusion of oxygen across the seagrass roots (Penhale and Wetzel 1983; Pedersen et al. 1998), this is not sufficient to prevent the development of reducing conditions in the bulk sediment, derived from the rapidly increasing respiration in the developed stands of *C. nodosa*.

The finding that *C. nodosa* communities become highly heterotrophic during the colonization process implies that these communities must receive allochthonous OM inputs to support the high respiratory rates observed and that the magnitude of these allochthonous inputs must increase with time after colonization. Moreover, as the developing *C. nodosa* community becomes strongly heterotrophic, it acts as a net source of dissolved OM to the water column. The net release of DOC from developed seagrass communities exceeds by far the GPP and must be, therefore, partially maintained by allochthonous carbon inputs. The allochthonous inputs of organic carbon must be sufficient to satisfy the excess respiration of the communities and the net release of DOC, the possible losses of POC, and the increased storage of OM in
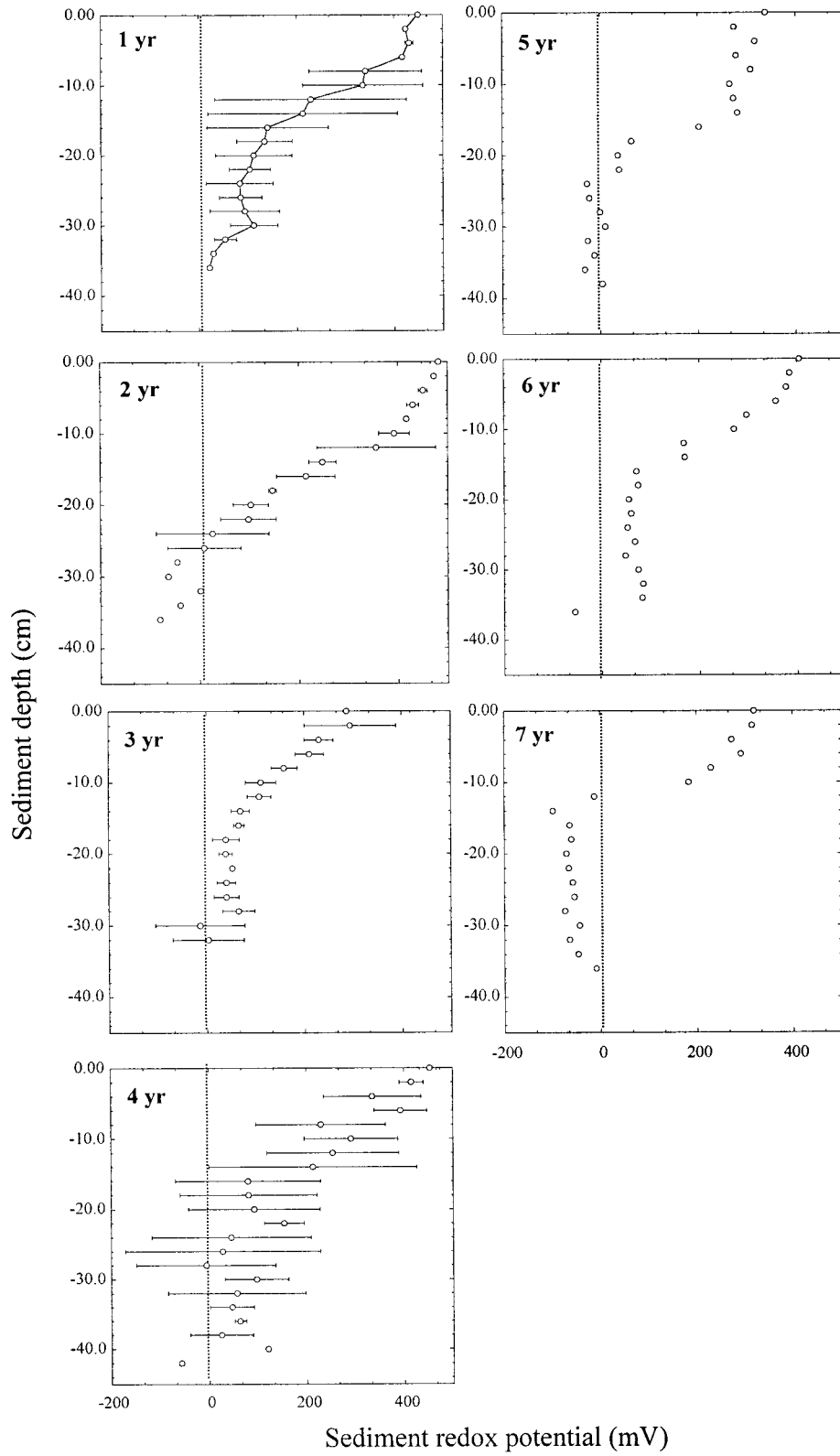
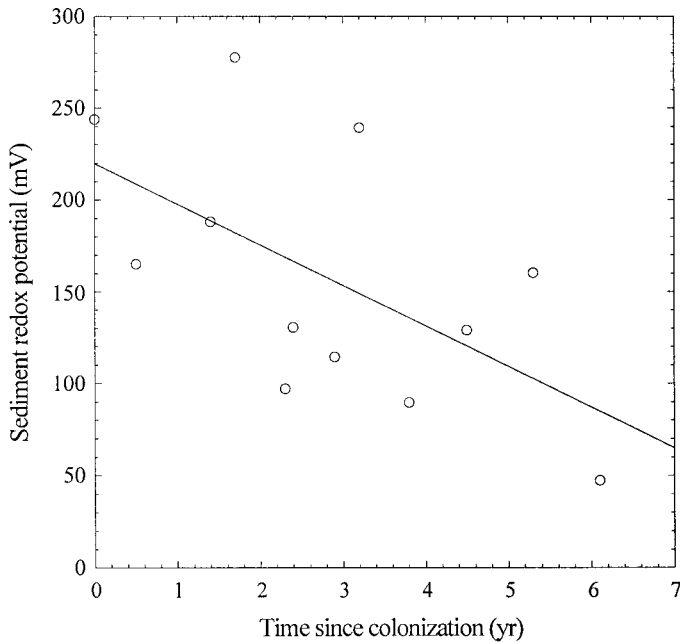Fig. 2. Profiles of redox potential in *Cymodocea nodosa* sediments.

Fig. 3.   Average redox potential in *C. nodosa* rhizosphere during seagrass colonization.

the sediment and as seagrass biomass (Fig. 8). The imports must be highest in developed patches, when the metabolism is highly heterotrophic (51 mmol C m^{-2} d^{-1}) and the community exports large amounts of DOC (81 mmol C m^{-2} d^{-1}) (Fig. 6). The POC export, which we did not measure, must be at least equal to the 0.3 mmol C m^{-2} d^{-1} removed through grazing and leaf shedding (Cebrián et al. 2000). Developed patches accumulate material as detrital organic material in the sediments at a rate of 10 mmol C m^{-2} d^{-1}, and seagrass biomass accretes at a rate of 15 mmol C m^{-2} d^{-1}. Thus, the import of organic material should be at least 157 mmol C m^{-2} d^{-1}.

The conclusion is that there must be a significant input of allochthonous OM inputs (>157 mmol C m^{-2} d^{-1}) to the developed patches of *C. nodosa* communities, which is consistent with the finding, derived from the examination of the stable isotope composition of the OM present in the sediments, that sestonic inputs account for >80% of the OM present in the sediment in *C. nodosa* communities. Seagrass canopies have been shown to increase sedimentary inputs of organic carbon (Kemp et al. 1984; Ward et al. 1984; Lemmens et al. 1996; Gacia et al. 2002). Agawin and Duarte (2002) provided evidence of active trapping of sestonic particles (such as planktonic organisms and latex beads) by seagrass canopies, able to remove the entire sestonic load of the water column each day. Similarly, the examination of the organic carbon budget of a *Posidonia oceanica* meadow revealed that >70% of the carbon deposition was derived from sestonic particles (Gacia et al. 2002). The colonizing *C. nodosa* patches in Alfacs Bay have also been reported to import nitrogen (Pedersen et al. 1997). The remarkable capacity of seagrass canopies to trap sestonic materials depends on the development of the canopy (Gacia et al. 1999). This is therefore expected to increase with time after colonization and
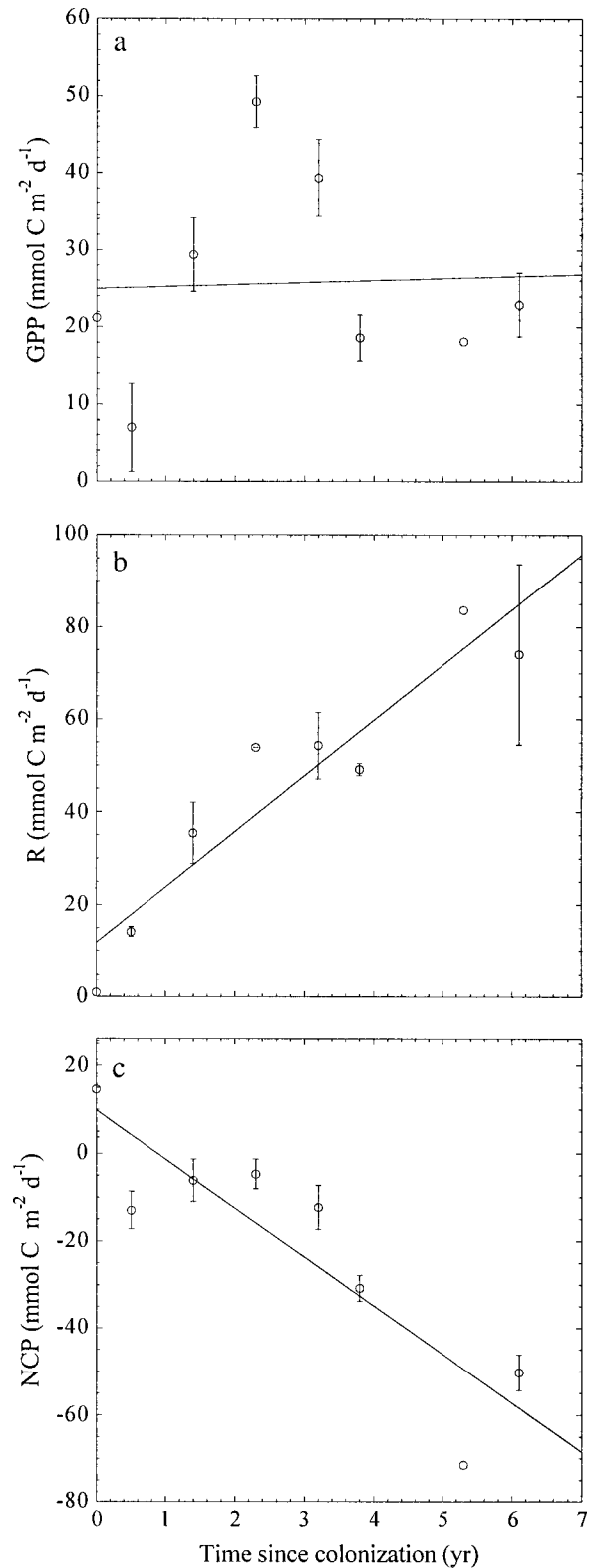

Fig. 4.   Relationship between the time since seagrass colonization (years) and the (a) gross primary production (GPP), (b) respiration (R), and (c) net community production (NCP) in mmol C m^{-2} d^{-1} in the benthic communities studied. Solid lines represent the fitted linear regression.

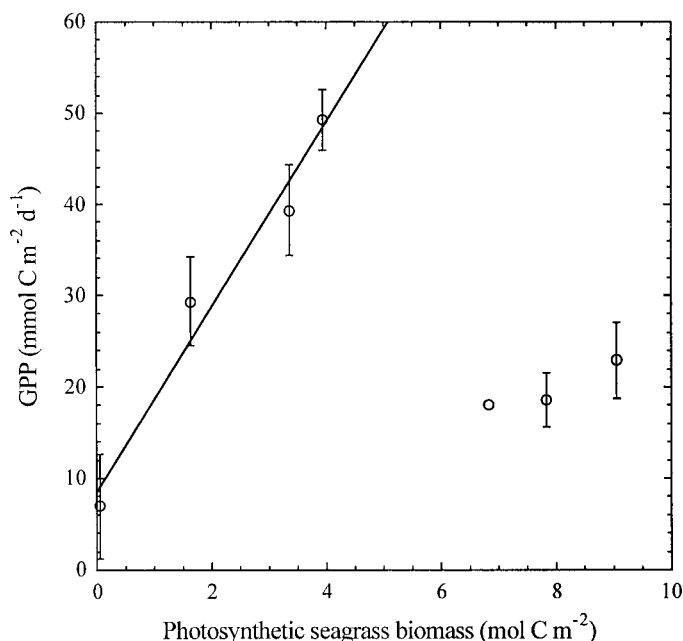Fig. 5. Relationship between the photosynthetic seagrass bio-mass (mol C m⁻²) and the gross primary production (mmol C m⁻² d⁻¹). Solid line shows the fitted linear regression for the first four points.

Fig. 7. Relationship between the respiration (mmol C m⁻² d⁻¹) and the net DOC flux from the benthic incubations (mmol C m⁻² d⁻¹). Negative values represent net DOC consumption. Solid line shows the fitted linear regression.

allows the seagrass community to support an intense hetero-trophic activity that far exceeds the gross production of the *C. nodosa* meadow.

The results reported are subject to uncertainties derived from possible artifacts associated with the experimental
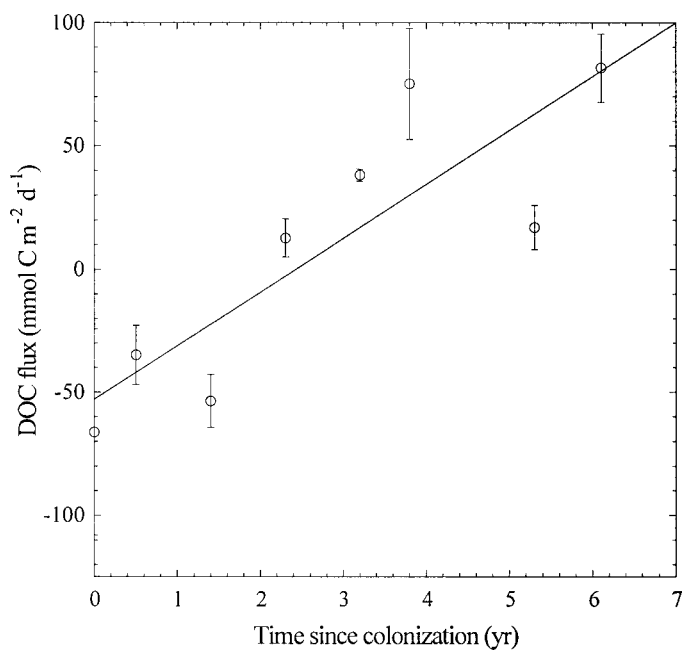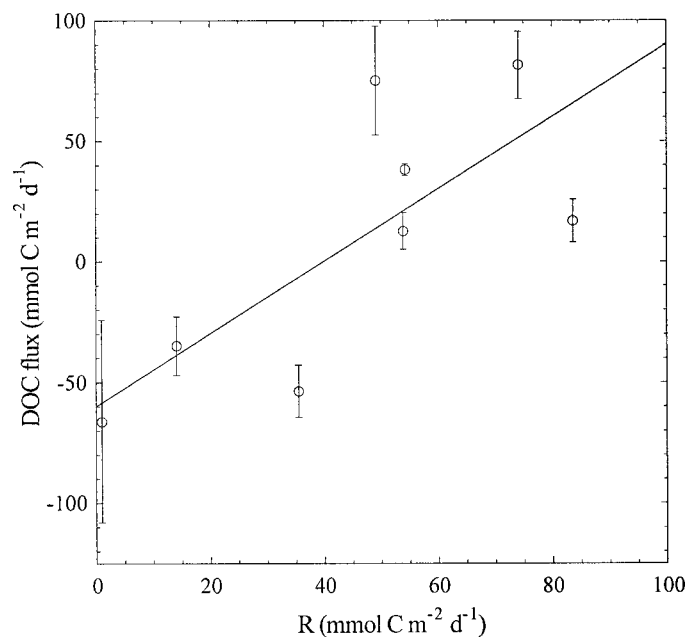
chambers and design; therefore, the extrapolation of the re-sults to the whole ecosystem should be considered with cau-tion. However, the direction of the changes in metabolism and associated processes along colonization should be robust ones and suggest what the processes involved should be. The finding of an input of allochthonous organic material along the development of *C. nodosa* meadows implies the trapping of materials along the colonization process, which could not

Fig. 6. Relationship between the time since seagrass coloniza-tion (years) and the net DOC flux from the benthic incubations (mmol C m⁻² d⁻¹). Negative values represent net DOC consump-tion. Solid line shows the fitted linear regression.

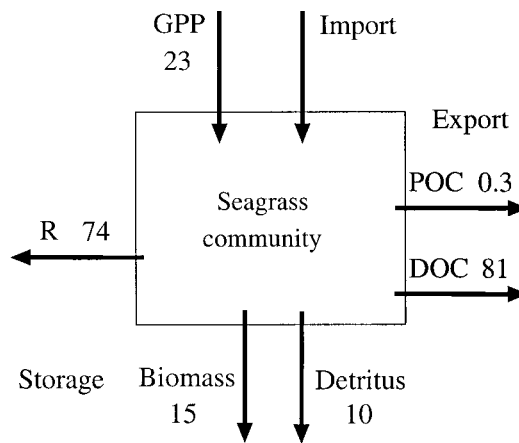Import > R + Export + Storage - GPP > 157 mmol C m⁻² d⁻¹

Fig. 8. Organic carbon mass balance for a developed *C. nodosa* community (6.1 yr old). All fluxes in mmol C m⁻² d⁻¹. POC export from Cebrián et al. (2000).

be demonstrated directly in this study and must be confirmed.

This study was made possible because of the peculiar conditions of the study area, where disturbances by the transit of sand waves maintain the seagrass arrested in a permanent state of recolonization (Marbà and Duarte 1995). Hence, the conclusions reached may not be extrapolated to other seagrass ecosystems. Yet seagrass recolonization is expected to result from efforts worldwide to protect and recover seagrass ecosystems (Duarte 2002). Hence, assessing the generality of the results obtained in this study may help us understand how the ecosystems will respond to the recovery of these meadows.

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