

# Dynamics of Millenary Organic Deposits Resulting from the Growth of the Mediterranean Seagrass *Posidonia oceanica*

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The Mediterranean seagrass *Posidonia oceanica* accumulates large quantities of organic debris as roots, rhizomes and leaf sheaths are progressively buried forming a bioconstruction called 'matte'. The organic material remains with little morphological alteration for millennia. Several strata from these accumulations in various *P. oceanica* meadows were sampled. Radiocarbon dating of samples yielded a range of 0–3370 years before present. From these data, accretion rates averaging 0.175 cm year<sup>-1</sup> (range: 0.061–0.414) were inferred. Significant differences between sites were found. Accretion rates showed significant differences between matte strata (i.e. with time), but no defined patterns were appreciated. Such differences were not coherent across sites. It is concluded that accretion rates are mainly controlled by local factors.

Analysis of carbon, nitrogen and phosphorous in the organic debris showed that there was not a net release during the process of matte construction; in some sites, nitrogen and phosphorus concentration remained constant throughout the matte profile, while in the other sites, their concentration increased significantly with age. This confirms the role of *P. oceanica* meadows as sinks for biogenic elements.

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## Introduction

The *in situ* accumulation of large quantities of biogenic materials over millennia is of ecological relevance (e.g. paleoclimatic records, sinks for biogenic elements, organic reservoirs etc.), and occurs only in a limited number of ecosystems. Peat is probably the best-known example among terrestrial ecosystems (Gorham, 1991; Clymo, 1992), and coral reefs (Clausen & Roth, 1975; Barnes & Chalker, 1990) among marine ecosystems. *In situ* organic accumulations in the marine environment are rare, having been described for mangroves (Macintyre *et al.*, 1995) and seagrass species (*Thalassodendron ciliatum*: Lipkin, 1979; *Posidonia australis*: Shepherd & Sprigg, 1976; *Posidonia oceanica*: Boudouresque & Meinesz, 1982) for which belowground organs (roots and rhizomes) are preserved within the sediment. Quantitative data on these accumulations and their accretion dynamics are very scarce (Aloisi *et al.*, 1975; Belperio *et al.*, 1984; Boudouresque *et al.*, 1980). In the Mediterranean seagrass *P. oceanica* (L.) Delile, the slow upward growth of the bed results in the pro-

gressive burial of roots, rhizomes and the attached leaf sheaths, which are preserved in the sediment forming a coarse-fibred structure called 'matte' (Boudouresque & Meinesz, 1982).

In a previous paper (Romero *et al.*, 1994), the large accumulation of carbon, nitrogen and phosphorous resulting from this bioconstruction was investigated. The present paper investigates its organic accretion rates and the rate at which carbon, nitrogen and phosphorous are accumulated by dating (using standard <sup>14</sup>C methods) different strata of organic detritus in several sites in the North-western Mediterranean.

## Methodology

Samples were obtained from seven sites heavily vegetated with *P. oceanica* meadows (Figure 1). Sampling strategy differed according to local conditions. In most sites, samples were taken from vertical peat walls created by partial erosion of the matte. At one site (Medes islands), a 60° slope was excavated to achieve a vertical profile. At another site (Culip), advantage was made of an excavation in the seagrass deposits performed by archaeologists working on a fourteenth century shipwreck.

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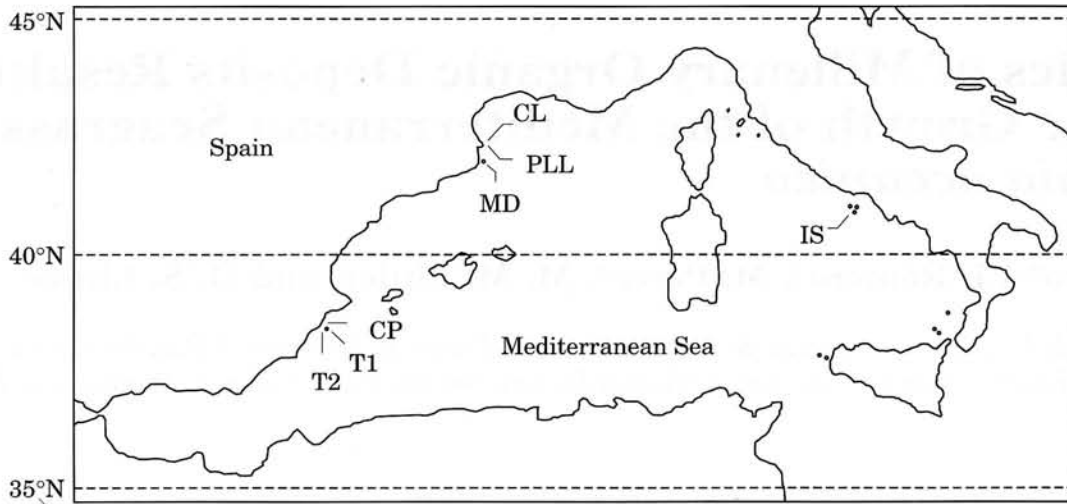


FIGURE 1. Geographical location of the different study sites: Culip (CL), Port Lligat (PLL), Medes (MD), Campello (CP), Tabarca (T1 and T2) and Ischia (IS).

TABLE 1. Main features of the sampling programme

Site	Site	Depth (m)	Replicates	Material	Thickness sampled (cm)	Number of samples
IS	Ischia	10	1	Rhizomes + roots	320	5
CL	Culip	4	1	Rhizomes + roots	160	9
PLL	Port-Lligat	3	3	Rhizomes	135	3
CP	Campello	3	3	Rhizomes	200	5
T1	Tabarca 1	5	3	Rhizomes	170	4
T2	Tabarca 2	1.5	1	Rhizomes	100	3
MD	Medes	14	1	Rhizomes + roots	200	10

Samples were taken at regular intervals along the matte profile; the number of samples per site depended on the total height of the exposed matte (Table 1).

Except for one site, each sample consisted of a horizontal core taken from the wall, with a volume of 3500 cm<sup>3</sup>. Only the distal third of the core was retained and processed to avoid effects derived from the exposure of the front of the wall to the open water. In the Culip site, a complete section (160 × 20 × 20 cm) of the matte was extracted, and then divided into subsections.

In three sites, replicate profiles (n=3) were obtained, separated by about 50 cm, to assess within-site variability.

After collection, samples were washed in seawater until sediments were eliminated. Whenever possible, the rhizomes and attached leaf sheaths were separated from the roots and a fine undifferentiated organic debris fraction, and kept for subsequent analysis. Such fractionation was done to avoid dating errors derived from downward growth of roots, which do not reflect

the ages of the strata where they were found. A certain error associated to plagiotrophic (horizontal) growth of rhizomes cannot be avoided as it is not possible to determine precisely their original growing direction in most of the samples. However, given the rates of horizontal growth and the size of the samples, the errors eventually derived from this circumstance may remain largely below the intrinsic errors of the dating methods.

The part of the sample retained was desiccated (70 °C until constant weight) and then finely ground. Subsamples were used for radiocarbon dating and carbon, nitrogen and phosphorus analysis.

The current ages are reported as radiocarbon dendrocalibrated years before present (reference year for present: 1950 AD) using the National Bureau of Standards oxalic acid as reference sample and following standard procedures (Talma & Vogel, 1993; Vogel *et al.*, 1993). Intrinsic error of the method was ± 50–80 years including the counting of the modern standard, background and the sample being analysed.

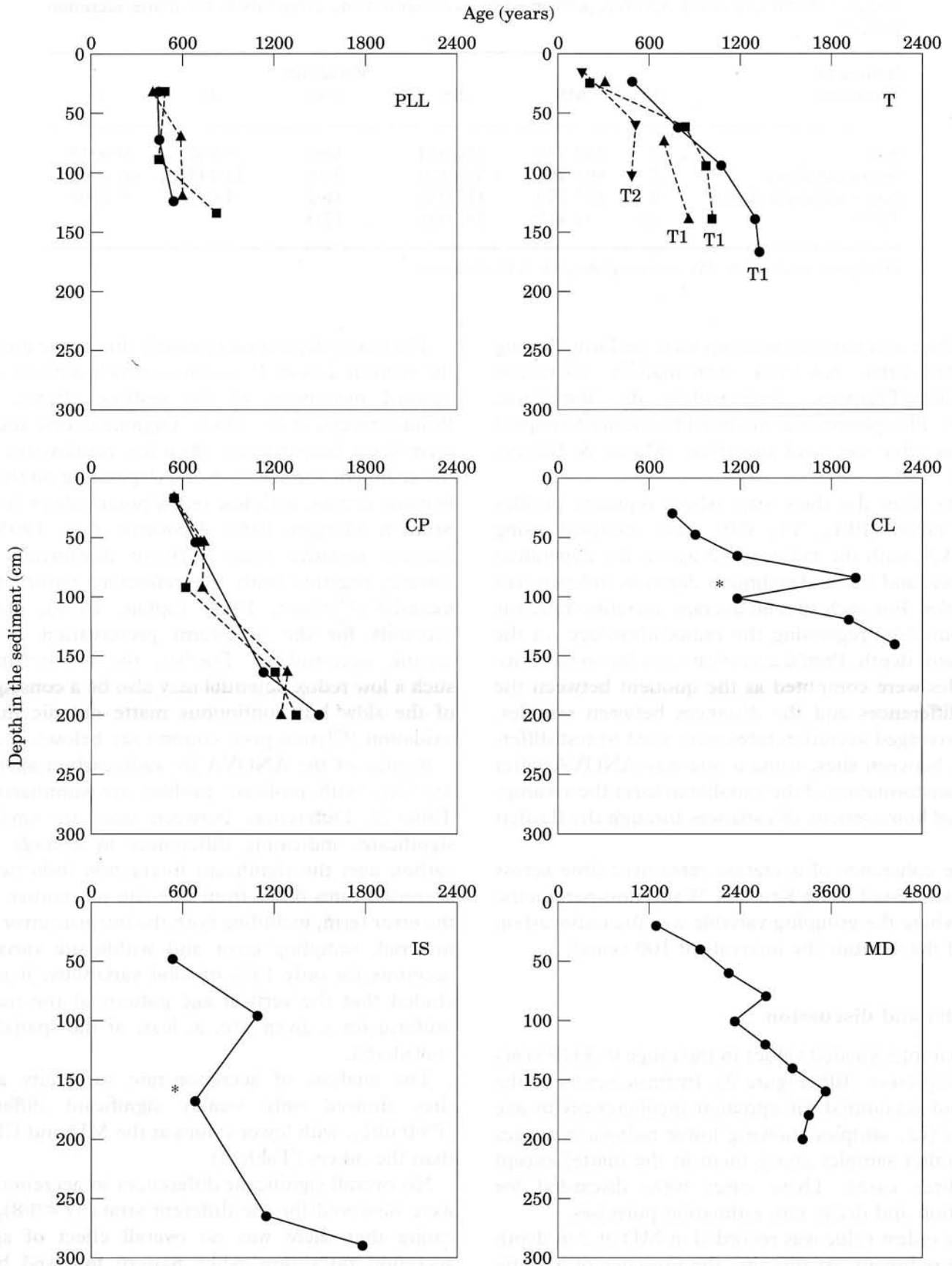


FIGURE 2. Standard radiocarbon ages (years before present) as a function of depth in the matte for the seven sites sampled. Notice that the range of the Age axis for MD is twice the range of the others. \*Samples showing age values significantly lower than the ones above them. These values have been excluded for accretion rates estimation purposes and for statistical analysis (abbreviations as in Figure 1).

TABLE 2. Summary of the ANOVA performed to assess within-site variability in the matte accretion process

Source of variability	df	MS	SS	Variability (%)	F	P
Site	2	212 337	424 674	16.6	9.961	0.0015
Sediment depth	2	691 585	1 383 170	53.9	32.445	<0.0001
Site × sediment depth	4	103 759	415 038	16.2	4.867	0.0092
Error	16	21 315	341 041	13.3		

df, degrees of freedom; MS, mean squares; SS, sum of squares.

Carbon and nitrogen analyses were performed using a Carlo-Erba NA 1500 Autoanalyser (Servicios Científico-Técnicos, Universidad de Barcelona, Spain). Phosphorus was analysed by induced coupled plasma after wet acid digestion (Mateo & Sabaté, 1993).

Data from the three sites where replicate profiles were taken (PLL, T1, CP) were analysed using ANOVA, with the radiocarbon age as the dependent variable, and site and sediment depth as independent variables. For each site, an average accretion rate was computed by regressing the radiocarbon age on the sediment depth. Partial accretion rates for consecutive samples were computed as the quotient between the age differences and the distances between samples. The averaged accretion rates were used to test differences between sites, using a one-way ANOVA (after log transformation of the variable to meet the assumptions of homogeneity of variances through the Bartlett test).

The coherence of accretion rates over time across sites was tested using Kruskal–Wallis non-parametric test, where the grouping variable was the radiocarbon age of the stratum (by intervals of 100 years).

## Results and discussion

The samples yielded values in the range 0–3370 years before present (BP; Figure 2). Intrinsic errors of the method accounted for apparent incoherences in age values (i.e. samples showing lower radiocarbon ages than other samples above them in the matte) except for three cases. These cases were discarded for accretion and decay rate estimation purposes.

The oldest value was recorded at MD at 2 m depth in the sediment. At this site, the presence of a matte formation extending to 4 m depth in the sediment was verified. This was not sampled due to technical problems in the excavation process; thus, it is likely that the age of this accumulation is at least in the range of 6000–7000 years BP.

The matte deposition is mostly due to the growth of the vertical axis of *P. oceanica*, which induces a slow upward movement of the seafloor (Pérès, 1982; Boudouresque *et al.*, 1984). Organic debris and sediment form this structure. At a few centimetres below the sediment surface (2–6 cm, depending on the site), hypoxia occurs, with low redox potentials (<165 mV; Stum & Morgan, 1981; Alcoverro *et al.*, 1995) that become negative from 8–10 cm downwards. This feature, together with the refractory nature of the material (Crouzet, 1984; Lipkin, 1979), probably accounts for the long-term preservation of these organic accumulates. Further, the maintenance of such a low redox potential may also be a consequence of the slow but continuous matte organic material oxidation (Clymo, pers. comm.; see below).

Results of the ANOVA for radiocarbon ages from the sites with replicate profiles are summarized in Table 2. Differences between sites are small but significant, indicating differences in average radiocarbon age; the significant interaction indicates that accretion rates differ from one site to another. Since the error term, including both the intrinsic error of the material, sampling error and within-site variability, accounts for only 13% of total variability, it is concluded that the vertical age pattern of the matte is uniform for a given site, at least at the spatial scale considered.

The analysis of accretion-rate variability among sites showed only weakly significant differences ( $P=0.091$ ), with lower values at the MD and CL sites than the others (Table 3).

No overall significant differences in accretion rates were observed for the different strata ( $P=0.8$ ), indicating that there was no overall effect of age on accretion rates (linear-like pattern followed by age with depth in the sediment; Figure 1). This lack of consistency between sites in accretion rates suggests that the accretion process is not controlled by large-scale factors [e.g. changes in temperature or  $\text{CO}_2$  (aq) concentration] in the time period considered.



TABLE 3. Average estimated carbon, nitrogen and phosphorus accumulation rates in the matte

	cm year <sup>-1</sup>	g m <sup>-2</sup> year <sup>-1</sup>			
		Dry weight	C	N	P
Ischia	0.165	84.2	30.0	0.32	0.011
Culip	0.061	26.8	9.0	0.22	0.006
Port Lligat	0.414	178.0	75.0	0.86	0.046
Campello	0.203	255.8	112.1	1.03	0.051
Tabarca 1	0.114	143.6	61.7	0.66	0.042
Tabarca 2	0.188	236.9	104.2	0.85	0.050
Medas	0.079	30.8	12.6	0.16	0.010
Mean	0.175	136.6	57.8	0.59	0.031

Elementary composition of the material studied ranked from 35.0–44.0% C, 0.35–0.84% N and 0.020–0.037% P relative to dry weight. These values are relatively high compared to the composition of living rhizomes at 37.8–38.4% C, 0.65–0.86% N and 0.028–0.045% P (Pirc, 1983; Romero *et al.*, 1992, Mateo, 1995). Net nutrient release along the vertical profiles was not observed; element concentration remained more or less constant with time or increased significantly. Carbon accumulated significantly with age in some sites (CP:  $r=0.663$ ,  $P<0.00001$ ,  $n=13$ ; MD:  $r=0.550$ ,  $P<0.00001$ ,  $n=10$ ) or remained constant in some others (CL, PLL and IS). Nitrogen accumulated significantly in CL ( $r=0.743$ ,  $P<0.0032$ ,  $n=8$ ) and T1 ( $r=0.594$ ,  $P<0.00001$ ,  $n=13$ ), while phosphorus did so in MD ( $r=0.681$ ,  $P<0.0029$ ,  $n=9$ ) and T1 ( $r=0.901$ ,  $P<0.00001$ ,  $n=13$ ). Figure 3 shows the cases where elemental accumulations occur.

Assuming a matte thickness of 1–4 m, and around 100 mg dry weight cm<sup>-3</sup> of bulk density (Romero *et al.*, 1992 and unpubl. data), the amount of necromass accumulated under *P. oceanica* seagrass beds can be estimated as around 4–16 × 10<sup>4</sup> gC m<sup>-2</sup>, of the same order as accumulated by peat (12 × 10<sup>4</sup> gC m<sup>-2</sup>; Warner *et al.*, 1993) or coral reefs (15–60 × 10<sup>4</sup> gC m<sup>-2</sup>; Stoddart, 1969, Kinsey, 1983). However, in global terms and assuming that the species covers 2% of the Mediterranean sea-floor (Béthoux & Copin-Montégut, 1986), the total carbon storage below *P. oceanica* is relatively modest (2.0–8.1 × 10<sup>15</sup> gC, 34.8–139.2 × 10<sup>15</sup> gN and 3.5–13.9 × 10<sup>12</sup> gP), and much lower than for peat (450 × 10<sup>15</sup> gC; Warner *et al.*, 1993) or coral reefs [100–400 × 10<sup>15</sup> gC, for the upper 1–4 m of reefs; data combined from Stoddart (1969), Smith (1978) and Kinsey (1983)].

The rates of carbon, nitrogen and phosphorus accretion in the matte appear in Table 3. There are strong disparities, due both to differences in the

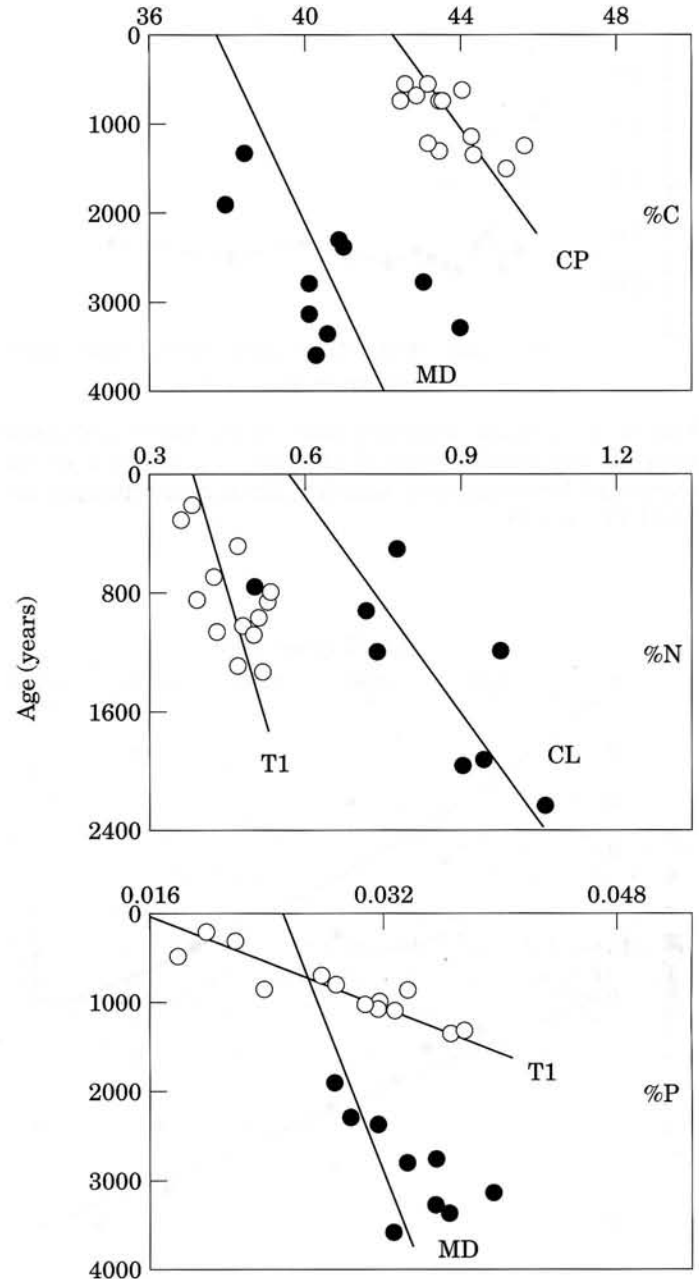


FIGURE 3. Carbon, nitrogen and phosphorus concentration in the organic debris plotted against depth in the matte for the sites where a significant accumulation of these elements was observed (abbreviations as in Figure 1).

accretion rates and in the presence or absence of nutrient concentration increase with time (see Figure 3), but the ranges given here do not differ substantially from the tentative values estimated previously, and thus confirm that the role of these seagrass beds as sinks for biogenic elements can be relevant at a local scale (e.g. neritic waters: Romero *et al.*, 1994).

Values of matte accretion reported in Table 3 are substantially lower than those from the literature (accretion rates: 0.34–1.5 cm year<sup>-1</sup>; Bay, 1978; Boudouresque *et al.*, 1983; Pirc, 1983; Bay, 1984; Thelin & Boudouresque, 1985; Romero, 1985;

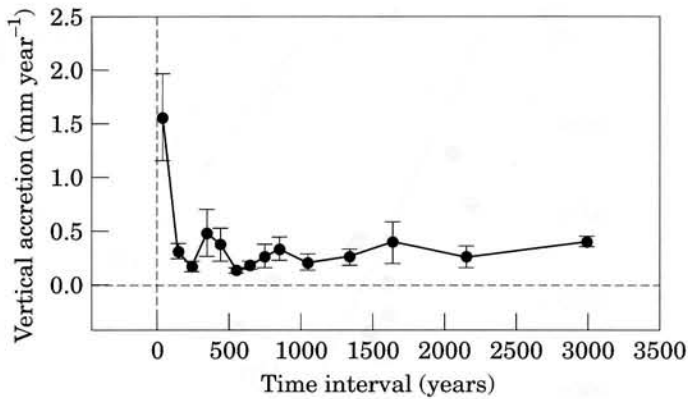


FIGURE 4. Vertical accretion rates of the matte computed between any possible pair of samples as a function of age increment between those samples. Error bars represent the SEM ( $5 \leq n \leq 15$ ).

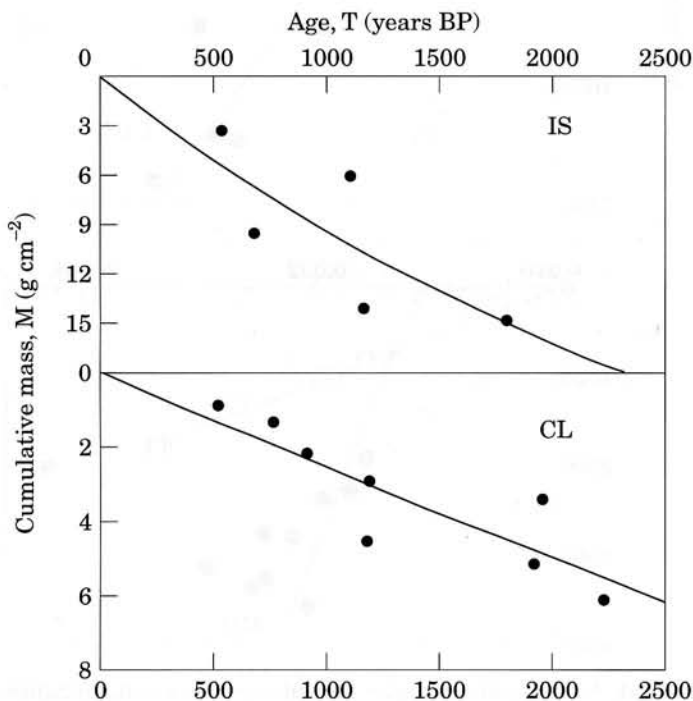


FIGURE 5. Curves resulting from fitting the equation  $M = (p/a) * (1 - \exp[-aT])$  to the observed data (Clymo, 1984).  $M$ , cumulative dry weight;  $T$ , dendrochronological calibrated radiocarbon age of the material;  $P$  and  $a$  are the parameters to be estimated, the accretion and decay rates, respectively (abbreviations as in Figure 1).

Pergent, 1987; Pergent *et al.*, 1989; Semroud *et al.*, 1990; Romero *et al.*, 1992; Sánchez-Lizaso, 1993; Romero *et al.*, 1994; Marbà, 1995), and are due to differences in the time scale considered. While most of the data from the literature were obtained on a short-term basis (a maximum of 30 years), the present data represent net accretion values integrated over centuries or millennia, and thus include mortality and erosional events. This is supported by a strong negative effect of the time elapsed between consecutive measurements and resulting accretion rates, with strong differences (significance level  $P < 0.0001$ : *post-hoc* Tukey test) between 'short-term' (i.e. less than 100 years) and 'long-term' estimates (Figure 4).

Decay rates for belowground organs of this species have been estimated in  $0.086\text{--}0.216 \text{ year}^{-1}$  (Romero *et al.*, 1992 and unpubl. data), but these data are only for parts exposed to the open water or within the few upper aerated centimetres of the sediments. Obviously, they are not maintained throughout the matte: observation of the oldest materials indicate that the most refractory organs are the leaf sheaths (which external morphology remains almost intact after more than 3000 years), and the roots, which are usually found fragmented; the rhizomes seem to be less refractory, and no identifiable remains are found in the oldest ( $>1000$  year) samples.

To estimate a long-term decay rate for these debris, the model proposed by Clymo (1984) was used:

$$M = (p/a) * (1 - \exp[-aT]) \quad (1)$$

where production ( $p$ ) and decay rate ( $a$ ) are the parameters to be estimated in the function relating the observed cumulative mass ( $M$ ) to the age of the material ( $T$ ).

Data of  $M$  vs.  $T$  were plotted (Figure 5), and Equation (1) was fitted to the data from CL and IS sites (where data of density of the matte were available), using the Quasi-Newton method. The estimates of  $a$  and  $p$  appear in Table 4. The decay rates obtained, given the reduced number of points to fit

TABLE 4. Fitted parameter values for Equation (1) (see text)

Species	Site	$P$		$a$		Var. exp. (%)	$r$	$n$
		$\text{g m}^{-2} \text{ year}^{-1}$	SEM	$\text{year}^{-1}$	SEM			
<i>Posidonia</i>	Ischia	113	66.3	0.00036	0.00092	58.5	0.765	6
<i>Posidonia</i>	Culip	27	11.4	0.00008	0.00047	76.6	0.875	9
Peat	New Brunswick	190	5.5	0.00011	0.00001	—	—	16

The parameters  $P$  and  $a$  are the accretion and the decay rates, respectively. Data for the peat formation at New Brunswick are from Warner *et al.* (1993).

the curves, must be considered only as a rough approximation. Despite the multiple and obvious differences between peat and matte formations, the results obtained evidence the concurrence of analogous processes (e.g. the rapid isolation relatively refractory material from the oxidizing atmosphere) resulting in a similar balance between accretion and decay (Table 4; Warner *et al.*, 1993).

Seagrass ecosystems are, in general, subjected to decline, mostly due to human activities (e.g. Larkum & West, 1983). *Posidonia oceanica* beds have declined or regressed over the last decades (Blanc & Jeudy de Grissac, 1984; Porcher, 1984; Zavodnik & Jaklin, 1990), and this may change the role of the matte from a carbon sink to a carbon source. Using the same assumptions as above (1–4 m thickness of matte, dry bulk density of 100 mg dry weight cm<sup>-3</sup>) and the decay rates derived from Table 4, this potential carbon source is estimated to be in the range 3–55 gC m<sup>-2</sup> year<sup>-1</sup>.

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### References

- Alcoverro, T., Duarte, C. M. & Romero, J. 1995 Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. *Marine Ecology Progress Series* **120**, 203–210.
- Aloisi, C., Monaco, A., Thommeret, J. & Thommeret, Y. 1975 Evolution paléogéographique du plateau continental languedocien dans le cadre du golfe du Lion. Analyse comparée des données sismiques, sédimentologiques et radiométriques concernant le quaternaire récent. *Revue de Géographie Physique et de Géologie Dynamique* **27**, 13–22.
- Barnes, D. J. & Chalker, B. E. 1990 Calcification and photosynthesis in reef-building corals and algae. In *Coral Reefs* (Dubinsky, Z., ed.). Elsevier, Amsterdam, p. 550.
- Bay, D. 1978 *Etude in Situ de la Production Primaire d'un Herbiere de Posidonies (Posidonia oceanica (L.) Delile) de la Baie de Calvi-Corse*. Ph.D. Thesis, Faculté des Sciences, Université de Liège, Belgium.
- Bay, D. 1984 A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) Delile in Calvi bay, Corsica. *Aquatic Botany* **20**, 43–64.
- Belperio, A. P., Smith, B. W., Polach, H. A. *et al.* 1984 Chronological studies of the quaternary marine sediments of Northern Spencer Gulf, South Australia. In *The Spencer Gulf Region* (Hails, J. R. & Gostin, V. A., eds). *Marine Geology* **61**, 265–296.
- Béthoux, J. P. & Copin-Montégut, G. 1986 Biological fixation of atmospheric nitrogen in the Mediterranean Sea. *Limnology and Oceanography* **31**, 1353–1358.
- Blanc, J. J. & Grissac, A. J. D. 1984 Erosions sous-marines des herbiers à *Posidonia oceanica* (Méditerranée). In *International Workshop on Posidonia oceanica Beds, France Vol. 1* (Boudouresque, C. F., Grissac, A. J. D. & Olivier, J., eds), pp. 23–28.
- Boudouresque, C. F., Crouzet, A. & Pergent, G. 1983 Un nouvel outil au service de l'étude des herbiers à *Posidonia oceanica*: la lépidochronologie. *Rapports et Procès Verbaux de la Réunion de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée, Monaco* **28**, 111–112.
- Boudouresque, C. F., Giraud, G., Thommeret, J. & Thommeret, Y. 1980 First attempt at dating by <sup>14</sup>C the undersea beds of dead *Posidonia oceanica* in the bay of Port-Man (Port-Cros, Var, France). *Travaux Scientifiques du Parc National de Port-Cros, France* **6**, 239–242.
- Boudouresque, C. F. & Meinesz, A. 1982 *Découverte de l'Herbier de Posidonie*, Vol. 4, Hyères, Cahier Parc National de Port-Cros, 79 pp.
- Boudouresque, C. F., Jeudy de Grissac, A. & Meinesz, A. 1984 Relations entre la sédimentation et l'allongement des rhizomes orthotropes de *Posidonia oceanica* dans la baie d'Elbu (Corse). In *International Workshop on Posidonia oceanica Beds, Vol. 1* (Boudouresque, C. F., Grissac, A. J. D. & Olivier, J., eds). Gis Posidonie, Marseille, pp. 185–191.
- Clausen, C. C. & Roth, A. A. 1975 Estimation of coral growth rates from laboratory <sup>45</sup>Ca-incorporation rates. *Marine Biology* **33**, 85–91.
- Clymo, R. S. 1992 Productivity and decomposition of peatland ecosystems. In *Peatland Ecosystems and Man: An Impact Assessment* (Bragg, O. M., Hulme, P. D., Ingram, H. A. P. & Robertson, R. A., eds). Department of Biological Sciences, Dundee, U.K., pp. 3–16.
- Clymo, R. S. 1984 The limits to peat bog growth. *Phil. Trans. R. Soc. Lond.* **303**, 605–604.
- Crouzet, A. 1984 Contribution à l'étude anatomique des feuilles de *Posidonia oceanica* (Potamogetonaceae). Variations de la structure le long d'une écaille épaisse. In *International Workshop on Posidonia oceanica Beds, Vol. 1* (Boudouresque, C. F., Grissac, A. J. D. & Olivier, J., eds). Gis Posidonie, Marseille, pp. 109–117.
- Gorham, E. 1991 Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* **1**, 182–195.
- Kinsey, D. W. 1983 Standards of performance in coral reef primary production and carbon turnover. In *Perspective on Coral Reefs* (Barnes, J. D., ed.). Australian Institute of Marine Science, pp. 209–218.
- Larkum, A. W. D. & West, R. J. 1983 Stability, depletion and restoration of seagrass beds. *Proceedings of the Linnean Society N.S.W.* **106**, 201–212.
- Lipkin, Y. 1979 Quantitative aspects of seagrass communities, particularly of those dominated by *Halophila stipulacea*, in Sinai (Northern Red Sea). *Aquatic Botany* **7**, 119–128.
- Marbá, N. 1995 *Biología Clonal dels Herbeis d'Angiospermes Marines*. Ph.D. Thesis, University of Barcelona, Spain, 178 pp.
- Mateo, M. A. & Sabaté, S. 1993 Wet digestion of vegetal tissue using a domestic microwave oven. *Analytica Chimica Acta* **279**, 273–279.
- Mateo, M. A. 1995 *El Compartimento Detrítico en Ecosistemas de Fanerógamas Marinas Mediterráneas*. Ph.D. Thesis, University of Barcelona, Spain, 214 pp.
- Macintyre, I. G., Littler, M. M. & Littler, D. S. 1995 Holocene history of Tobacco Range, Belice. *Atoll Research Bulletin* **430**, 1–18.
- Péres, J. M. 1982 Specific benthic assemblages. In *Marine Ecology Vol. 5* (Kinne, O., ed.). Wiley, Chichester, pp. 523–582.
- Pergent, G. 1987 *Recherches Lépidochronologiques chez Posidonia oceanica (Potamogetonaceae)*. *Fluctuations des Paramètres*

- Anatomiques et Morphologiques des écailles des Rhizomes*. Ph.D. Thesis, Université of Aix-Marseille II, France, 240 pp.
- Pergent, G., Boudouresque, C.-F., Crouzet, A. & Meinesz, A. 1989 Cyclic changes along *Posidonia oceanica* rhizomes (lepidochronology): present state and perspectives. *PSZNI: Marine Ecology* **10**, 221–230.
- Pirc, H. 1983 Belowground biomass of *Posidonia oceanica* (L.) Delile and its importance to the growth dynamics. *Proceedings International Symposium on Aquatic Macrophytes*, Nijmegen, pp. 77–78.
- Porcher, M. 1984 Impact des mouillages forains sur les herbiers à *Posidonia oceanica*. In *International Workshop on Posidonia oceanica Beds, France*, Vol. 1 (Boudouresque, C. F., Grissac, A. J. D. & Olivier, J., eds). pp. 145–148.
- Romero, J. 1985 *Estudio Ecológico de las Fanerógamas Marinas de la Costa Catalana: Producción primaria de Posidonia oceanica (L.) Delile en las Islas Medes*. Ph.D. Thesis, Facultad de Biología, Universidad de Barcelona, Spain, pp. 261.
- Romero, J., Gérard, P., Pergent-Martini, C., Mateo, M. A. & Regnier, C. 1992 The detritic compartment in a *Posidonia oceanica* meadow: litter features, decomposition rates and mineral stocks. *P.S.Z.N.I.: Marine Ecology* **13**, 69–83.
- Romero, J., Pérez, M., Mateo, M. A. & Sala, E. 1994 The belowground organs of the Mediterranean seagrass *Posidonia oceanica* as a biogeochemical sink. *Aquatic Botany* **47**, 13–19.
- Sánchez-Lizaso, J. L. 1993 *Estudio de la Pradera de Posidonia oceanica (L.) Delile de la Reserva Marina de Tabarca (Alicante): Fenología y Producción Primaria*. Ph.D. Thesis, Universidad de Alicante, Spain, 121 pp.
- Semroud, R., Mezegrane, S. & Soltane, L. 1990 Etude lépido-chronologique de *Posidonia oceanica* dans la région d'Alger (Algérie): données préliminaires. *Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* **32** B-I 15: 10.
- Shepherd, S. A. & Sprigg, R. C. (1976) Substrate, sediments and subtidal ecology of Gulf St. Vincent and Investigator strait. In *Natural History of the Adelaide Region* Twidale, C. R., Tyler, M. J. & Webb, B. P., eds). Royal Society of South Australia, Adelaide, pp. 161–174.
- Smith, S. V. 1978 Coral-reef area and the contribution of reefs to processes and resources of the world's oceans. *Nature* **273**, 225–226.
- Stoddart, D. R. 1969 Ecology and morphology of recent coral reefs. *Biological Review* **44**, 433–497.
- Stum, W. & Morgan, J. J. 1981 *Aquatic Chemistry*. John Wiley & Sons, New York, p. 780.
- Talma, A. S. & Vogel, J. C. 1993 A simplified approach to calibrating C14 dates. *Radiocarbon* **35**, 317–322.
- Thélin, I. & Boudouresque, C. F. 1985 *Posidonia oceanica* flowering and fruiting: recent data from an international inquiry. *Posidonia Newsletter* **1**, 5–14.
- Vogel, J. C., Fuls, A., Visser, E., & Becker, B. 1993 Pretoria calibration curve for short lived samples. *Radiocarbon* **35**, 73–86.
- Warner, B. G., Clymo, R. S. & Tolonen, K. 1993 Implications of peat accumulation at Point Escuminac, New Brunswick. *Quaternary Research* **39**, 245–248.
- Zavodnik, N. & Jaklin, A. 1990 Long-term changes in the Northern Adriatic marine phanerogam beds. *Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* **32**, 15.