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Bacterial activity in NW Mediterranean seagrass (*Posidonia oceanica*) sediments

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Abstract

We examine here the hypothesis that benthic bacterial activity in seagrass [*Posidonia oceanica* (L.) Delile] meadows is dependent on seagrass growth and availability of inorganic nutrients in the sediments. This was achieved by measuring bacterial activity (ammonification rates, and exoproteolytic and exoglucosidase activities) during an annual cycle in five *P. oceanica* meadows in the NW Mediterranean. Benthic bacterial activity was high, and tended to increase with increasing seagrass production. This trend is likely to involve a direct effect derived from the greater supply of organic carbon in productive meadows, and an indirect effect derived from the fact that productive meadows develop over nutrient-rich sediments and yield nutrient-rich detritus. Phosphorus availability to bacteria was low, for plant detritus was deficient in phosphorus relative to bacterial requirements, and bacterial activity was reduced after seagrasses depleted inorganic phosphorus from the sediments at the onset of exponential plant growth. These results indicate that, on local and annual time scales, benthic bacterial activity is directly related to seagrass production in the NW Mediterranean, because of enhanced inputs of organic matter by the seagrasses, while on seasonal scales, bacteria and seagrass metabolism are inversely related, apparently because of competition for inorganic nutrients.

Keywords: Ammonification rate; Carbon supply; Exoenzymatic activity; Nutrient availability; Seasonality

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1. Introduction

The activity of benthic bacteria is closely controlled by the flux of organic matter to the sediments, which, in turn reflects the availability of nutrients in the water column (Meyer-Reil, 1984; Richards 1984). Thus, nutrient-poor systems are often characterised by low bacterial activity in their sediments (e.g. Capone & Kiene 1988; Seitzinger 1988). However, shallow coastal areas of oligotrophic oceans often support highly productive benthic macrophytic communities (Mann, 1982) and high benthic bacterial activities (Caffrey & Kemp, 1990). Benthic bacteria are particularly active in seagrass-dominated systems, for seagrasses provide, in addition to organic nutrients and carbon derived from plant detritus, labile organic compounds excreted by their roots and rhizomes (Jørgensen et al., 1981; Moriarty & Boon, 1989; Moriarty et al., 1990; Chin-Leo & Benner, 1991). Thus, the activity of benthic bacteria in seagrass ecosystems is believed to be closely controlled by the production of the overlying plants (e.g. Smith et al., 1984; Moriarty & Boon, 1989, Chin-Leo & Benner, 1991). Seagrass tissues are often depleted in nitrogen and, specially, phosphorus, relative to carbon (Duarte, 1990, 1992) compared to the nutritional requirements of bacteria (cf. Thingstad, 1987). As a consequence, the growth efficiency of bacteria dependent on seagrass-derived material must be low, unless bacteria use additional sources of nutrients to balance their growth. Bacterial activity in seagrass sediments is expected, therefore, to be influenced both by the production of the overlying macrophytes and the availability of additional nitrogen and phosphorus in the sediments to meet their nutritional requirements.

We thus hypothesise that the regulation of bacterial activity in seagrass sediments must involve a relationship with macrophyte growth and the availability of inorganic nutrients in the pore waters (e.g. Smith et al., 1984). We examine this hypothesis by examining the activity of benthic bacteria in sediments under *Posidonia oceanica (*L.) Delile, the dominant seagrass in the Mediterranean (den Hartog, 1970), and its relationship to plant growth and nutrient concentrations in sediment pore waters. The processing of organic matter by benthic bacteria is represented here by their exoenzymatic capacity (Hoppe, 1983; King, 1986; Meyer-Reil, 1987; Boon 1989), and the potential ammonification activity, as an index of nutrient recycling (Boon et al., 1986; Smith et al., 1984).

Temperature is known to have a strong influence on bacterial activity, adequately described by Arrhenius equations with Q_{10}'s about 2–3 (e.g. Jørgensen, 1977; Hobbie & Cole, 1984; Jørgensen & Sørensen, 1985; Joint & Pomeroy, 1987; Hall et al., 1989), which we will not attempt to describe here. In addition to the seasonality in bacterial activity imposed by temperature, seasonality in seagrass production is also expected to result in seasonality in bacterial activity. Similarly, differences in bacterial activity among sites may reflect differences in seagrass productivity. Thus, differences in seagrass production should help to explain both seasonal changes in bacterial activity and differences among locations with different seagrass cover. To examine both these roles, we focused our study on the seasonal activity of benthic bacteria in five different *P. oceanica* meadows in the NE coast of Spain (Mediterranean Sea; Fig. 1) spanning a range of plant cover.

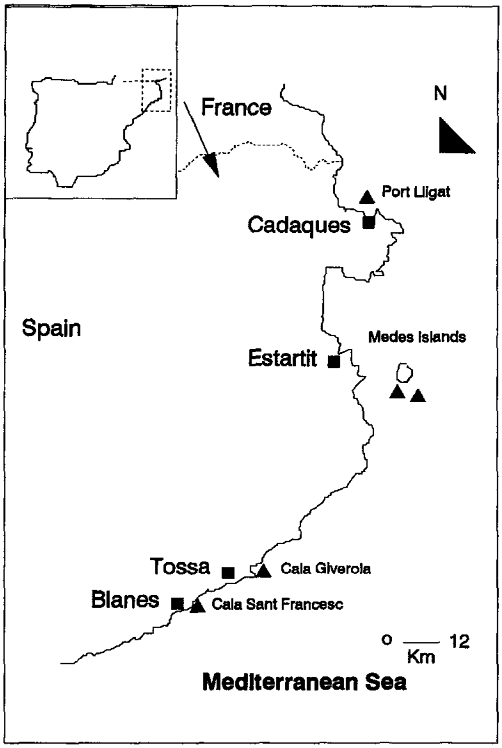

Fig. 1. Map of the study area showing location of the five seagrass meadows studied (▲).

2. Study area

The study was conducted in five littoral (−4 to −13 m) sites along the NE coast of Spain (Fig. 1) vegetated with *P. oceanica*, which areal production varies considerably depending both on season and plant cover (e.g. Romero, 1989; Alcoverro et al., 1995). This area is characterised by steep slopes, coarse sandy sediments, and oligotrophic, unproductive waters supporting sparse phytoplankton populations (Masó & Duarte, 1989). The five meadows selected, which were representative of a range of plant covers (78–627 shoots m^{-2}), were studied over an annual cycle, encompassing water temperatures from 11.2 to 23.3 °C. The activity of benthic bacteria in these littoral sites was examined, along with measurements of sediment characteristics, parallel to studies of plant growth and production (cf. Alcoverro et al., 1995).

3. Methods

Sediment samples were collected at each sampling station from October 1990 to November 1991 at intervals of about 40–50 days, representing a total of nine sampling events for each station. Each sample consisted of three replicated corers (5 cm internal diameter) pushed to a depth of about 5 cm into the sediments and kept refrigerated until processed (within 24 h). At the laboratory, we extruded the core and sliced off the upper 2 cm of sediment. We collected subsamples of this sediment fraction to measure nutrient (ammonium, nitrite, nitrate, and phosphate) concentrations in the pore waters, organic matter and water contents, and to estimate bacterial activity. Nutrient concentrations were measured in the supernatant of centrifuged subsamples (3000 *g*, 10 min), which was kept frozen until analysed. Exchangeable ammonium was extracted by adding 20 ml of KCl (2 M) to the pore water (Alef & Kleiner, 1986). All nutrient analyses were performed on an autoanalyzer following standard methods (Grashoff et al., 1983). Sediment water content and organic content were measured by mass loss after desiccation (24 h) and ignition (2 h) at 105 °C and 450 °C of fresh and dried sediment subsamples, respectively. Previous examinations of the potential interference of carbonates (about 30% of DW in the area, Vidal, 1988) on organic content estimates indicate this to be minimal at the combustion temperature used (Vidal, 1988). Sediment samples in sandy, unvegetated sediments were collected, from the same depths as the vegetated sediment samples, for measurements of organic content at two of the sites (i.e. those with patchy vegetation).

Exoenzymatic bacterial activity was represented by the exoproteolytic (EPA) and exoglucosidase (EGA) activities, which were assayed following techniques modified after Mayer (1989) and King (1986), respectively. Slurries, prepared suspending a 2–3 g sediment subsample in 50 ml of filtered (0.2 μm Nuclepore filter) seawater collected from the core, were stirred at 30 °C for 1 h prior to addition of the appropriate substrates. These were L-leucil-β-napthylamide (2 mM, Sigma N-8381) and 4-methylumbelliferyl-α-D-glucoside (20 μM, Sigma M-9766), which are surrogates of the aminopeptidase and α-glucosidase activities, respectively. Aliquots (5 ml) of the slurry were sampled at various intervals and centrifuged (700 *g*, 5 min). Fluorescence in the supernatant was measured with a Shimazdu RF-540 spectrofluorometer (excitation and emission wavelengths, 340 and 410, and 365 and 440 nm, for EGA and EPA, respectively).

Potential ammonification rates were measured by following the conversion of arginine to ammonium (Alef & Kleiner, 1986). We prepared, for each replicate core, two replicate slurries consisting of 1–1.5 g wet weight of sediment, 1 ml of seawater, and 0.5 ml of an arginine solution (0.2% in sterile distilled water). One of them was frozen at −20 °C and subsequently analysed for ammonium concentration (see above), to be used as a blank, and the other was analysed for ammonium concentration after dark incubation at 30 °C overnight in a shake water bath to measure ammonium formation. The standard error of measurements of bacterial activity was calculated using boot-strap techniques (Efron & Tibshirani, 1986) on the triplicate series of initial and incubated samples. All rates measured were expressed as per cm^3 of sediment to avoid spurious correlations between them (Bird & Duarte, 1989), except for dissolved nutrient concentrations, which were expressed per unit volume of interstitial water to allow comparisons with published values.

The variance in the variables measured was partitioned into that attributable to seasonal changes, differences among meadows, the interaction between seasonal and among-meadow differences, and measurement error (as that between the triplicate measurements), using Nested-ANOVA analysis (Sokal & Rohlf, 1969). The overall seasonality of the variables measured in the area studied was described by compositing the measurements in all five meadows for each sampling event into an average value. The degree of association between the variables measured was quantified using Pearson correlation analysis.

4. Results

The sediments studied were mostly coarse sands, with concentrations of organic matter substantially higher, on the average (Table 1), than the values measured in neighbour, unvegetated sediments (average for two sites = 7.4 mg cm^{-3}). Yet, sediments were reduced at only one (Port Lligat) of the sites, with the remaining having positive redox potentials within the top 10 cm (Alcoverro et al., 1995). Nutrient concentrations in interstitial waters (Table 1) were comparable to those measured in other seagrass sediments (Moriarty & Boon, 1989), but highly variable, with dissolved inorganic nitrogen (DIN) pools dominated by ammonium (90% of DIN on the average). Exoproteolytic activities were high, whereas exoglucosidase activities tended to be low (Table 1), compared to those observed in Atlantic sediments (King, 1986; Meyer Reil, 1986,1987; Mayer, 1989). Arginine ammonification rates were also high, similar to those found in other seagrass sediments (Boon et al., 1986; Caffrey & Kemp, 1990), consistent with the high exoproteolytic activity measured. Differences in bacterial activity among meadows were considerable (2–30-fold), and partially associated to differences in the concentration of sediment organic matter (Fig. 2), particularly for exoenzymatic activities. Exoenzymatic activities also tended to increase with increasing inorganic phosphate concentration in the sediments (Fig. 2), whereas the ammonification rate tended to increase with increasing sediment nitrate concentration (Fig. 2). We also observed a tendency for the sediment exoenzymatic activities to increase with increasing plant production (Fig. 2).

Nutrient concentrations in sediment pore waters showed strong seasonal changes (Fig. 3). DIN maxima were observed in early spring and late summer, with minimum values observed in June, coinciding with peak growth, and October to December

Table 1
Average and range for the sediment characteristics, and bacterial activity measured in this study

Variable	Mean (range)
Organic matter content ($mg \cdot cm^{-3}$)	42.6 (14.7–116.2)
Water content (% ww)	28.0 (16.8–51.0)
Pore-water dissolved inorganic nitrogen (μM)	456.8 (219–862)
Pore-water phosphate (M)	21 (0.77–60.4)
Exoglucosidase activity ($nmol \cdot cm^{-3} \cdot min^{-1}$)	0.096 (0.018–0.272)
Exoproteolytic activity ($nmol \cdot cm^{-3} \cdot min^{-1}$)	6.76 (1.29–37.27)
Ammonification rate ($\mu g\ NH_4^+ \cdot cm^{-3} \cdot h^{-1}$)	0.31 (0.01–1.57)

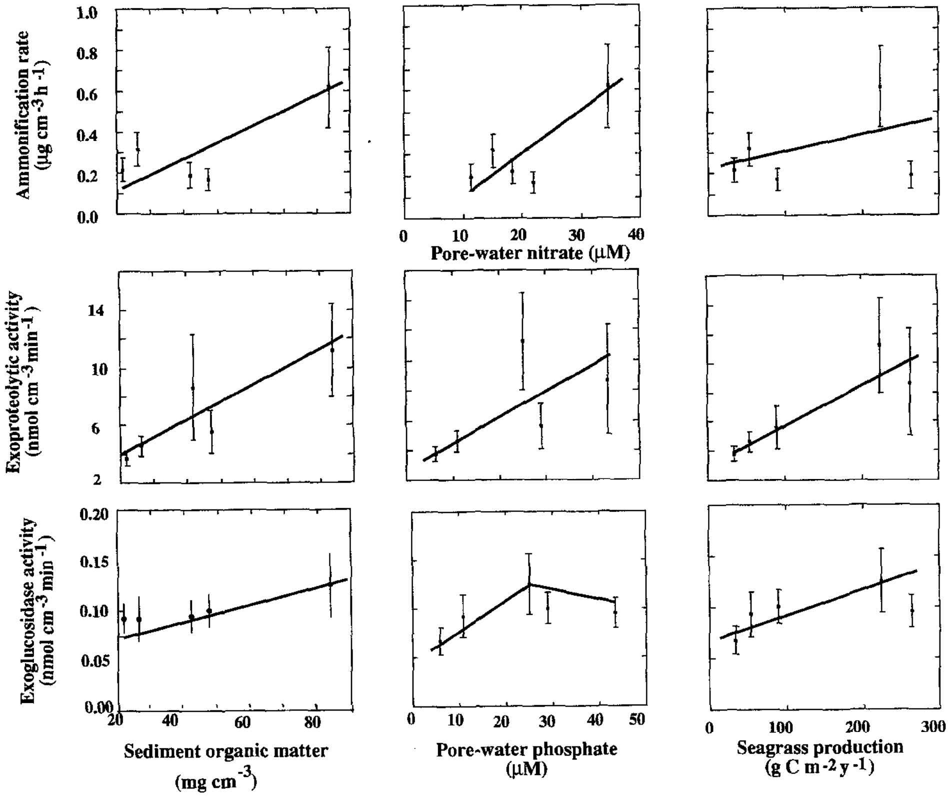

Fig. 2. The relationship between the average (±SE) activity of benthic bacteria in the five meadows examined and sediment organic matter and pore water nutrient concentrations, and seagrass growth. Seagrass growth from Alcoverro et al. (1995).

(Fig. 3). Sediment phosphate concentrations were highest in winter and decreased in early spring to remain at values close to analytical detection limits until summer (Fig. 3). The depletion of sediment phosphorus occurred simultaneously to the onset of exponential seagrass growth (Fig. 3), suggesting that it may reflect uptake by the plant's roots. As a result, the seasonal changes in sediment DIN and phosphate resulted in a highly unbalanced inorganic nitrogen to phosphorus ratio (727 by atoms, Fig. 3) at the onset of exponential seagrass growth.

Bacterial activity also showed considerable seasonal variation (Table 2), being low in March (Fig. 4), the time when phosphate was depleted from the sediment and inorganic N:P ratios were highest (Fig. 3). Average exoglucosidase activity followed a seasonal course (Fig. 4) parallel to that of average sea temperature ($r = 0.83$, $p < 0.05$). Maximum exoproteolytic activity was observed in June (Fig. 4), coincident with the mid-summer minimum DIN concentration in sediment pore waters. Ammonification rates declined from winter to March (Fig. 4), parallel to the decline in phosphate concentration in the porewater ($r = 0.71$, $p < 0.05$) and the increase in plant growth

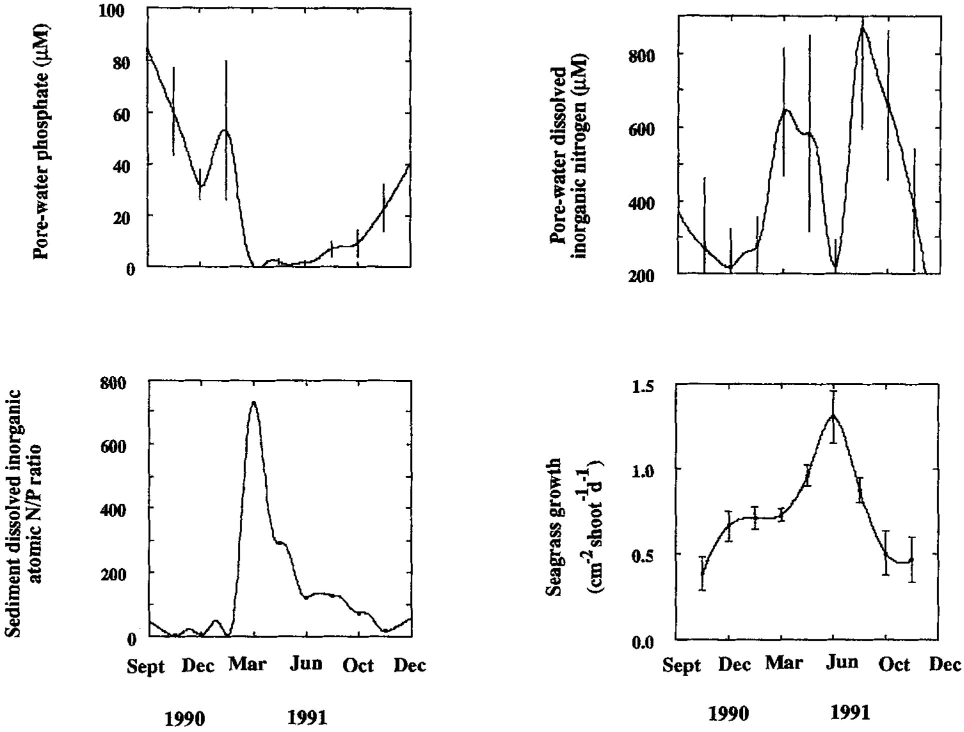

Fig. 3. The average seasonal time course of sediment pore water nutrient (phosphate and dissolved inorganic nitrogen) concentrations, and the corresponding N:P ratio, and seagrass growth. Values represent mean (± SE) of observations for all five meadows.

(Fig. 3), as observed in the past for sediments under other seagrass species (Smith et al., 1984). However, most (45–52%) of the variance in bacterial activity observed was attributable to temporal changes peculiar to the different meadows (i.e. the interaction

Table 2

Partition of variance (as % of the variance observed) in bacterial activity into its different components

Variance component	Exoglucosidase activity (nmol · cm^{-3} · min^{-1})	Exoproteolytic activity (nmol · cm^{3} · min^{-1})	Ammonification rate (μg NH$_4^+$ · cm^{-3} · h^{-1})
Meadow	4.40**	27.41**	30.60**
Seasonality	40.22**	18.16**	14.06**
Meadow* seasonality	49.31**	52.76**	45.79**
Error among replicates	6.06	1.68	9.54

Asterisks indicate results of F-test; * = $p < 0.05$, ** = $p < 0.001$.

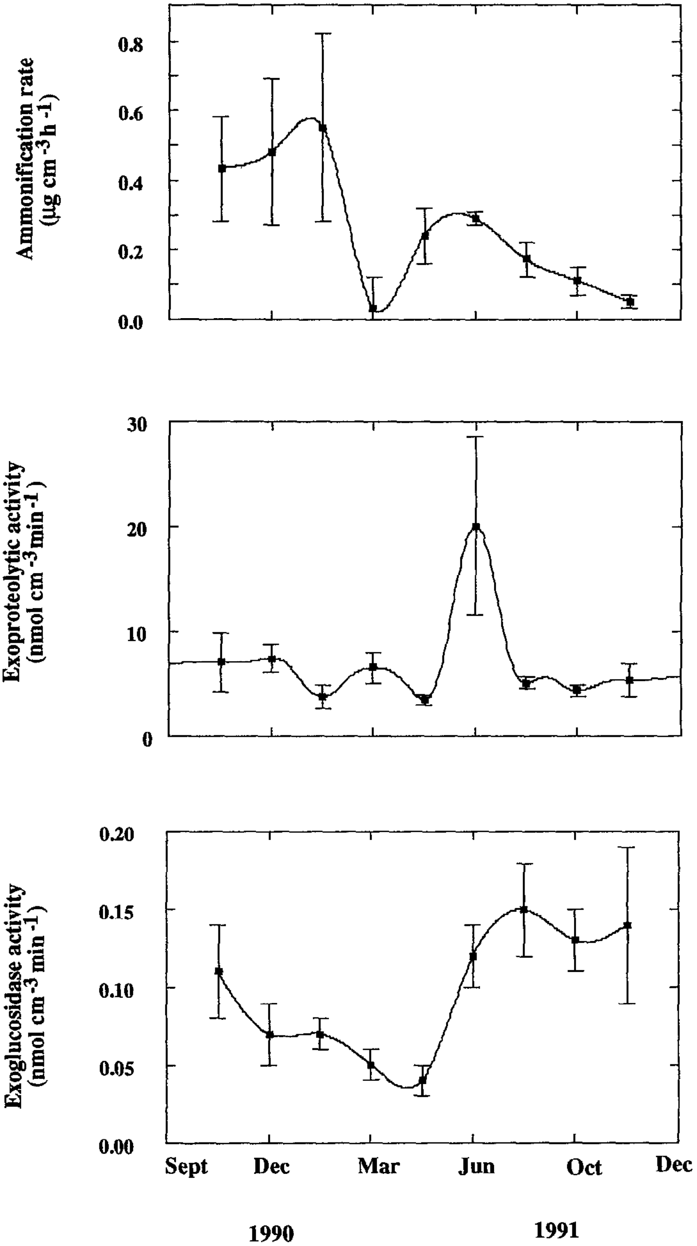

Fig. 4. The average seasonal time course of bacterial activity in the seagrass sediments studied. Values represent mean (± SE) of observations for all five meadows.

between meadow and seasonality, Table 2), which reflects an important local forcing on the seasonal response of bacterial activity.

5. Discussion

The results obtained indicate high bacterial activity in the sediments under *P. oceanica* meadows, attributable to their high supply of organic matter to the sediments, which are enriched in organic matter relative to unvegetated sediments, as observed in other seagrass meadows (Moriarty & Boon, 1989). Accordingly, differences in seagrass production and the associated differences in sediment organic matter were related to the differences in bacterial activity, particularly their exoenzymatic activity, among the meadows examined. These findings support previous demonstrations of the importance of the concentration of sediment organic matter in regulating bacterial activity (e.g. Meyer-Reil, 1986,1987; Chróst, 1990).

The high exoproteolytic activity relative to the exoglucosidase activity in these sediments indicates a faster degradation of proteins, and that amino acids were probably an important substrate for bacterial growth. Seagrass detritus is enriched in carbon relative to nitrogen (average atomic C:N ratio = 21.2 , Alcoverro et al., 1994) compared to the bacterial C:N quota (C:N of about 9; Thingstad, 1987), and is rich in cellulose, which is difficult to lyse by bacterial exoenzymes (Valiela, 1984). The quality of seagrass detritus as a substrate for bacterial growth was even poorer for phosphorus (N:P atomic ratio in old leaves = 35.6 , compared to about 16 required by bacteria, Thingstad, 1987). Yet, sediment bacteria could still achieve a balanced growth on seagrass detritus if they were able to draw nutrients, particularly phosphorus, from an external source.

The depletion of sediment phosphate resulted in a highly unbalanced inorganic nitrogen to phosphorus ratio (727 by atoms) at the onset of exponential seagrass growth, suggesting seagrasses to be largely responsible for the observed depletion of the phosphorus pool. Bacterial activity declined at that time, perhaps because the very low availability of phosphorus in the sediments did not allow them to compensate for the low phosphorus supply in the seagrass detritus. This results suggest that the interaction between seagrasses and bacteria may also involve a competition for sediment phosphorus. Yet, the vastly larger storage capacity of seagrasses compared to that of bacteria should allow them to sequester the available phosphorus and be, therefore, unaffected by bacterial requirements.

Our results suggest a strong relationship between plant production and sediment bacterial activity in these *P. oceanica* meadows, productive meadows supporting more active bacterial communities. This relationship may involve a direct effect attributable to estimulation of bacterial activity by the organic enrichment of the sediments under highly productive meadows, and a possible indirect effect, resulting from the tendency for highly productive meadows to develop over nutrient-rich sediments (Alcoverro et al., 1994). Seagrass growing over nutrient-rich sediments also develop nutrient-rich detritus, suitable to support efficient bacterial growth. The net result of these direct and indirect effects is that bacterial activity increases with increasing *P. oceanica* production. We, therefore, conclude that, on local and annual time scales, benthic bacterial activity is directly related to seagrass production in the NW Mediterranean, because of enhanced inputs of organic matter by the seagrasses, while on seasonal scales, bacteria and seagrass metabolism are inversely related, apparently because of competition for inorganic nutrients.

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