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DOC dynamics in a Mediterranean seagrass system

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ABSTRACT: In a study on energy flow in a *Posidonia oceanica* system, an attempt was made to explain the marked seasonal variations in DOC, POM and bacteria concentrations in the water above and within a seagrass meadow at the Island of Ischia (Lacco Ameno) off the Gulf of Naples (Italy). There was no correlation between seasonal variations of the 3 parameters within and between stations from shallow to deep. DOC concentrations showed distinct peaks for nearly every sampling period and ranged from 0.4 to 31.4 mg l^{-1}. Although similar variations could be recorded for bacteria over the year, densities remained below 1.2×10^5 cells ml^{-1}. Variations in the concentration of POM over the seasons were less obvious than for DOC and bacteria; concentrations ranged from 3.5 to 30 mg AFDW l^{-1}. Weighted average concentrations of DOC, bacteria and POM in 1 m^3 water representative for the water body above the *P. oceanica* bed showed that bacterial contribution to the overall POM standing stock is insignificant. Daily variations of the same parameters reveal peaks of DOC appearing first within the meadow, later in the water above the meadow, and a slow increase and decrease of bacteria and POM, following the DOC variations with a time lag. Deviations from this pattern could be recorded as conditions of water movement changed, due to the mixing effect of wind-induced wave action. Bell-jar experiments with enclosed *P. oceanica* shoots within the meadow and control jars enclosing bare sediment showed high DOC pulses up to 25 mg l^{-1}, indicating that most of the DOC in the water column may be generated by the *P. oceanica* system, and that allochthonous influx of carbon need not take place to explain the monitored seasonal and daily variations. Leaching from healthy *P. oceanica* leaves, determined in laboratory experiments, amounts to 1.9% of the photosynthetic carbon fixation and contributes only 0.61% of the system's DOC release, amounting to 571.9 mg C h^{-1} m^{-2}. The organic carbon pool in the sediment, expressed as particulate and dissolved fraction, shows that for temperature conditions between April and September the release rates, as determined by the *in situ* experiments, could be maintained for 157 d, assuming that no new carbon influx takes place. The fate of the released DOC is discussed, and since high DOC decrease rates could not be correlated to high respiration rates indicating heterotrophic consumption, nor to biomass increase of bacteria, physico-chemical processes must take place which result in a phase shift from DOM to POM.

INTRODUCTION

Studies of food resources and energy partitioning during the past decade revealed that the major fraction of macrophyte production undergoes transformation before entering the food web (Mann 1969). This transformation, in which a variety of physical and biological processes are involved, alters not only the chemical composition of POM, but also its availability to the consumers (Newell 1965, Fenchel 1970, Tenore & Rice 1980, Velimirov et al. 1981).

Leaching of dissolved organic compounds is one of these processes and loss of readily soluble organic components is not restricted to POM degradation, but is also observed in metabolizing, healthy autotrophs. Although a good deal is known of the release of dissolved organic matter from both macroalgae (Khailov & Burlakova 1969, Sieburth 1969, Moebus & Johnson 1974, Harlin & Craigie 1975, Brylinski 1977) and from seagrasses (Brylinski 1977, Penhale & Smith 1977, Wetzel & Penhale 1979), we know very little of either DOC release or the contribution of such material by the seagrass *Posidonia oceanica* which dominates many Mediterranean coastal systems (Bay 1978, 1984, Ott 1980).

On the average, seagrasses release less than 10% of the total carbon fixed (Bryslinski 1977, Penhale & Smith 1977, Wetzel & Penhale 1979) and part of this DOC is incorporated by epiphytic microheterotrophs on the seagrass leaves (Smith & Penhale 1980, Kirch-

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man et al. 1984). Whole shoots, including dying leaves, release as much as 48 % of the annual primary production into the water (Kirkman & Reid 1979). Despite the fact that a number of marine invertebrates are able to utilize dissolved organic nutrients (e.g. Southward & Southward 1972, Stewart 1979) the main DOC pool in the seawater, representing globally 2×10^{17} g (Cauwet 1978), remains unavailable to consumers other than bacteria. Mechanisms and processes which derive POC from DOC are, therefore, of major interest to biological oceanographers since this transfer of phases represents an additional possibility of tapping energy within the DOC pool.

Laboratory simulations (Robertson et al. 1982) showed that microbial processing of DOC from seagrass leads to a build-up of particles reaching a size that could be fed on by consumers. These findings were supported recently by laboratory experiments from Biddanda (1985) which indicate that the presence of bacteria is necessary for synthesis of macroparticulate matter in DOC enriched seawater. A clear boundary between dissolved and particulate matter is difficult to set; a dissolved organic molecule in an aqueous medium is defined as one in which minimum free energy is attained by hydration of all potentially hydrophilic sites on the molecule (Sharp 1973). Consequently any association of molecules allowing for water loss by hydration and formation of a less hydrophilic species tends to remove the resulting molecular associate from solution. Therefore, a functional size boundary of 0.2 µm is accepted in most ecological studies.

In an attempt to quantify the amount of DOC released by the *Posidonia oceanica* system and to relate it to the POM available in the water column, a holistic approach, combining parameter measurements in the water and *in situ* experiments was adopted. Although *in situ* experimentation was restricted by water movement and could only be performed in spring and summer, evidence is presented that DOC release from both living and dead leaves on the shoots is masked by the DOC release from the sediment, and indirect evidence that a phase shift from dissolved to particulate takes place in the system.

MATERIAL AND METHODS

Collection of material. The study area (Lacco Ameno) is located on the north coast of the Island of Ischia, off the Gulf of Naples in southern Italy (Fig. 1). Seagrass beds, extending from 0.5 to 33 m depth, dominate the benthos along the north coast. Water samples of 1 l were taken with a PVC syringe (outlet diameter 9 mm) by SCUBA from stations along a line transect through a *Posidonia oceanica* meadow from 1 to 30 m depth. Stations 1 to 4 covered the depth range from 1 to 20 m in 5 m depth intervals; Station 5 was situated at 30 m (Fig. 2). At all stations samples were collected from the water surface, as well as within and above the meadow near the leaf tips. At Stations 2 to 5 additional samples were taken from the water column (Fig. 2), leading to a total of 21 samples. Sampling took place over all 4 seasons, always between 11.00 and 13.00 h and within a period of 50 min. At the same time wind direction, wave height and dominant current direction were recorded. A permanent station for daily samples was situated in 12 m depth.

The water samples were transferred immediately to light-proof cooling bags (8 to 10 °C) on the boat, brought to the laboratory and processed as follows. All samples were inspected for living faunal components, which were removed by filtering through a 250 µm mesh-size sieve. The remaining particulate matter, separated from living components, was kept for ash-free dry weight determination. Additionally, subsamples of 150 ml were filtered through a 0.2 µm Nucleopore polycarbonate filter for SEM observations.

Bacterial counts. Twenty ml were subsampled from each sample and preserved with 200 µl of 35 % formaldehyde for determination of total bacterial density using epifluorescence microscopy according to Hobbie

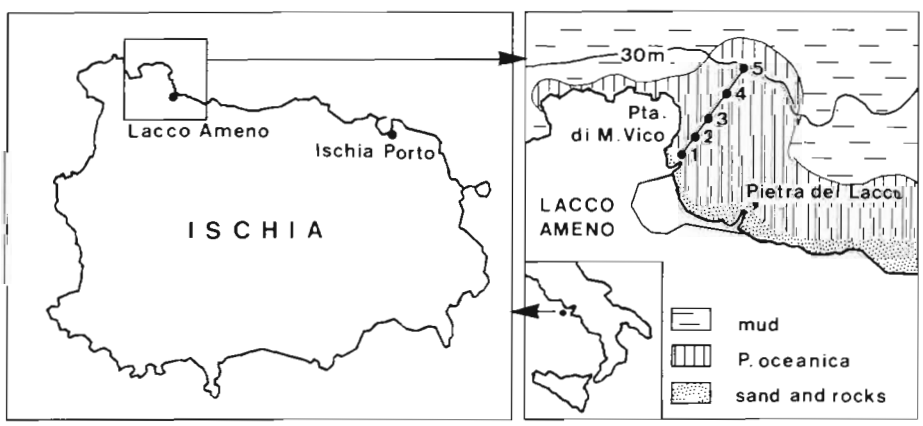


Fig. 1. Sampling site, Lacco Ameno on the northern coast of the island of Ischia (southern Italy) with a schematic representation of the seagrass cover in the study site

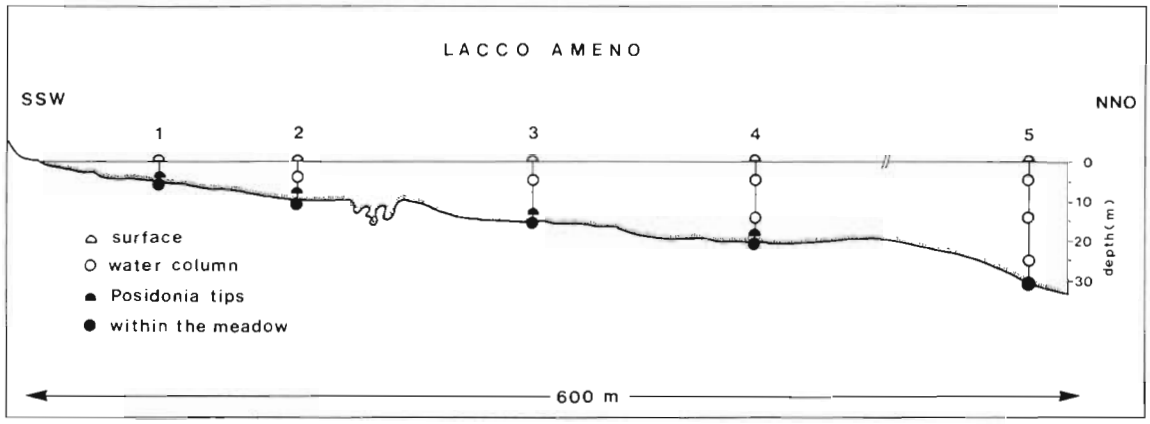


Fig. 2. Semi-schematic representation of the bottom profile at Lacco Ameno with sampling stations and substations along a line transect from shallow to deep

et al. (1977). Mean volume of rods and cocci was obtained from 60 to 100 random measurements on rods and cocci each. Although biometric measurements on bacteria are more easily obtained from SEM photos, only epifluorescence microscopy was used for this purpose. This eliminated errors due to shrinking of the cells when preparing samples for SEM (critical point drying). Conversion from total bacterial number to dry mass, carbon, and nitrogen were calculated according to Luria (1960), Troitsky & Sorokin (1967) and Ferguson & Rublee (1976).

Particulate organic matter. In order to estimate the POM load, the remaining water (800 ml) from the sample was filtered through a pre-ashed (480 °C) Whatman GF/F filter (nominal pore size 0.7 µm) and then through a 0.2 µm Sartorius filter. Prior to filtration, the Sartorius filter had been kept in double distilled water for 48 h, the water being changed at 15 h intervals before drying and constant weight determination. After drying the filters plus residue, ash-free dry weight (AFDW) was obtained *via* combustion at 480 °C for 6 h. The larger particles from the sieve fraction were processed in the same way.

Dissolved organic carbon. Twenty ml of the 0.2 µm filtered water was acidified with 2% HCl and sparged with synthetic CO_2-free air for 15 min. Subsequently, 100 µl of the acidified sample were injected into a total organic carbon analyser (Beckmann Tocamaster, Model 915-B) operating at an oxidation temperature of 950 °C and fitted with an IR detector. The standard self-draining condensate traps were replaced by larger self-made units minimizing transport of the condensate by the gas flow into the IR detector. The instrument was calibrated with anhydrous potassium biphthalate dissolved in carbon-free (oxidation with $KMnO_4$) double-distilled water. Each 20 ml was subsampled 5 times to obtain an average.

Bell jar experiments. In order to determine the contribution of DOC released from *Posidonia oceanica* to the total DOC pool in the water column, and to express this release as percentage of the plant's primary production, an *in situ* oxygen monitoring system (Svoboda & Ott 1983) was adapted. The bell jars consisted of clear acrylic glass tubes of 142 mm inner diameter, covering $^1/_{64}$ m^2. To seal the bell jars against the sediment with the rhizome system, thick, short polypropylene tubes with a serrated metal cutting edge on the lower rim and reinforced upper rim were used. The polypropylene tube was driven into the bottom by turning movements and the bell jar fitted gently into the tubes sealed with an O-ring. The top of the bell jar was also closed with an O-ring-sealed lid. Self-sealing silicon rubber fittings allowed penetration with a syringe needle (0.5 mm diameter) to withdraw water samples of 20 ml for determination of DOC and bacterial density. This water was replaced via a minute glass tube (0.6 mm diameter) fitted on the O-ring-sealed lid.

The jars were connected to a small glass chamber containing a magnetic stirring bar; this acted as a centrifugal pump which constantly stirred the water in the bell jar. Complete mixing was achieved within 10 min (Ott 1980). Total water volume in the experimental system was 15.80 l. A polarographic oxygen electrode was inserted into the stirring chamber. Electronics, batteries and strip chart were placed nearby in watertight housings; the unit could monitor 48 h *in situ* or be used in the laboratory (Stazione Zoologica, Laboratorio del Benthos) with small incubation chambers for individual seagrass leaves. In the laboratory, light received by the plants was measured with a Lambda quantum meter (Model LI-185). *In situ*, polypropylene tubes were left undisturbed for a minimum of 24 h after having been driven into the bottom. After this time bell jar and related system were fitted to the tubes. Maximum depth of penetration for the tubes was 15 cm. Each run, lasting between 6 and 27 h, required 2 bell

jars; 1 was placed over *P. oceanica* shoots, the other over bare sediment within 2 m of the first. Parallel to the bell jar experiments, 1 l water samples were taken with the PVC syringe above and within the meadow from a station nearby. Effort was made to take the samples at the same time as for the bell jars; they were stored in cooling bags as described above, and DOC and bacterial density was determined as described above.

Pore water content and organic content of sediment. Pore water content of the sediment was estimated from the sediment wet weight/dry weight relation. PVC cores (5 cm diameter, 20 cm length) were taken between 5 and 20 m depth. The dried samples (80 °C) were then combusted at 450 °C for 7 h to minimize interference from $CaCO_3$ sediments. To characterize the dissolved organic content of the pore water, a pore-water sampler (Giere 1982) was used for stratified collection between 1 and 15 cm sediment depth. After filtration, dissolved monosaccharides (MCHO) were determined according to the method of Johnson & Sieburth (1977) as modified by Dawson & Liebezeit (1983). Reactions entail reduction of the monosaccharides to the respective sugar alcohols, periodate oxidation to formaldehyde, and detection of this compound with MBTH (3 methyl-2-benzothiazohmone hydrazon) as a coloured complex at 635 nm. Results are expressed in glucose equivalents. Dissolved free amino acids (DFAA) were determined by HPLC according to Dawson & Liebezeit (1983). In brief, the DFAA method is based on the reaction of primary amines with O-phthalaldehyde/mercaptanol to form highly fluorescent isoindole derivatives. The class of detected compounds is expressed in glycine equivalents.

RESULTS

Study area

Sampling for parameter measurements and *in situ* experimentation were performed in the area between Punta di M. Vico and Pietro del Lacco (Fig. 1) where the lower limit of the *Posidonia oceanica* meadow is at 33 m. The total surface area between these 2 points and from the shore to the lower *P. oceanica* limit amounts to 0.192 km^2 (see Discussion) of which 85.9 % (0.165 km^2) are covered by the seagrass (calculated after Colantoni et al. 1982). This corresponds to 5.3 % of the total *P. oceanica* cover of the northern sector of Ischia, which is 3.08 km^2 between Punta di M. Vico and Ischia Porto (Colantoni et al. 1982). Rocks and stones with scattered plants and sporadic patches of *Cymodocea nodosa* form the upper limit of the prairie. The dense *P. oceanica* stand is characterized by a well defined mat between 9 and 11 m depth; at the lower limit where plant density gradually decreases, showing trailing rhizomes arranged in parallel rows, the prairie ends evenly on muddy sand without features of erosion. The main direction of the water movement as indicated by ripple marks in this area (Colantoni et al. 1982) is from NW to SE.

Seasonal variations of bacterial density, DOC and POM

Fig. 3A to G show the variations of the 3 parameters in the water column for each of the 5 stations along the transect. A general trend is the presence of great variations in bacterial density and DOC and POM concentrations within and between stations for each month. The exception is May 1984, where the concentrations of the 3 variables remain low and uniform over all stations. At Stations 1 to 4, which cover the depth range from 5 to 20 m, the variations are most pronounced; above the deepest part of the meadow, at Station 5, a more homogenous distribution of the various parameters is apparent in the water column. An exception is July 1983, where a relatively high DOC concentration (13 mg l^{-1}) at 25 m and a peak density of bacteria (3.2 $\times$ 10^4 cells ml^{-1}) occurs, as compared to the other samples from this station.

Similarly, DOC peaks at 15 m depth with a value of 4.8 mg l^{-1} in April 1984 at the same station. Bacterial densities in the water body over the *Posidonia oceanica* meadow vary by 1 order of magnitude (1.1 $\times$ 10^4 to 1.2 $\times$ 10^5 cells ml^{-1}) between samples within the same station and month, as in April, May and July 1983; for samples from November 1983 and those from 1984, the variations are less pronounced (0.2 $\times$ 10^4 to 4 $\times$ 10^4 cells ml^{-1}) and densities in general lower than in 1983.

DOC concentrations are also characterized by highly differing values, with the difference that these fluctuations were recorded over the sampling periods of both years. Concentrations ranged from 0.8 to 31.5 mg l^{-1} in 1983 and from 0.4 to 30.3 mg l^{-1} in 1984. Variations in concentrations of the organic fraction of the particle load in the water body ranged from 3.5 to 30 mg l^{-1} in both years. Although these variations were less pronounced than for DOC and bacteria, as demonstrated for the 1984 samples, POM peaks could be recorded in May and July 1983.

The 3 parameters vary independently from each other in the water body and no correlation between any 2 pairs of parameters was found. Similarly, no consistent increase or decrease of the variables was found when comparing water samples above and within the meadow. Although values in the water

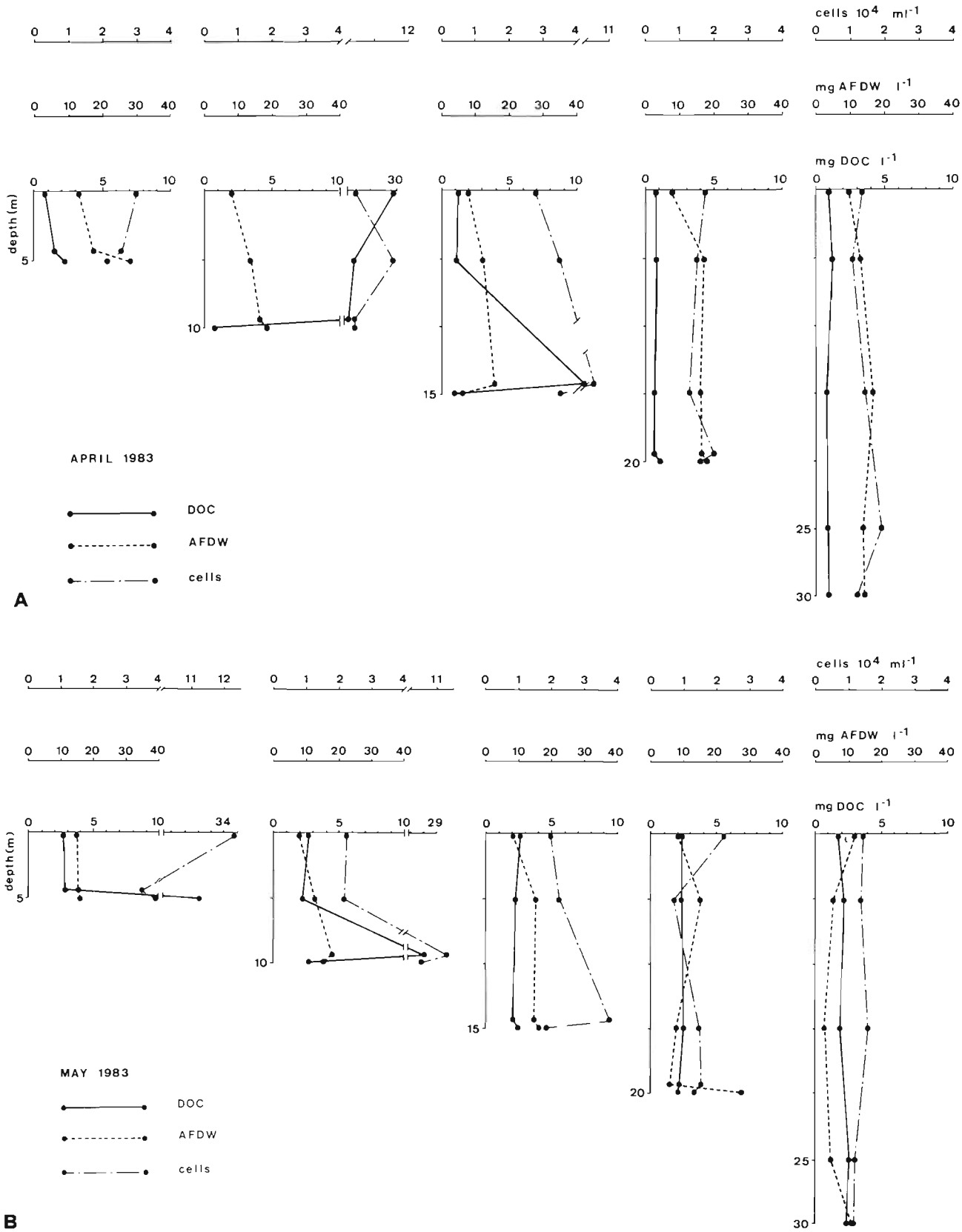
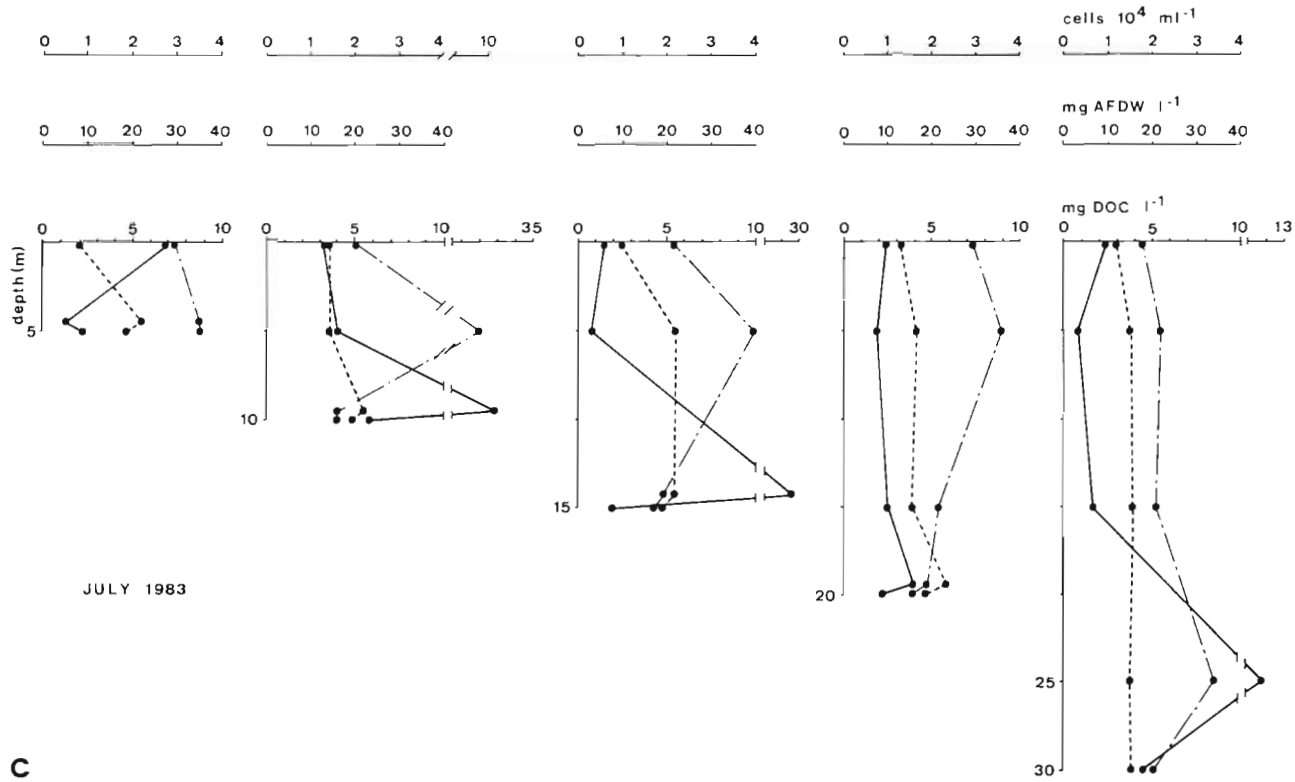


Fig. 3. Seasonal variations of DOC (mg l^{-1}) bacteria (cells ml^{-1})and POM (mg AFDW l^{-1}) at different sampling stations and substations at Lacco Ameno. (Continued on following pages)



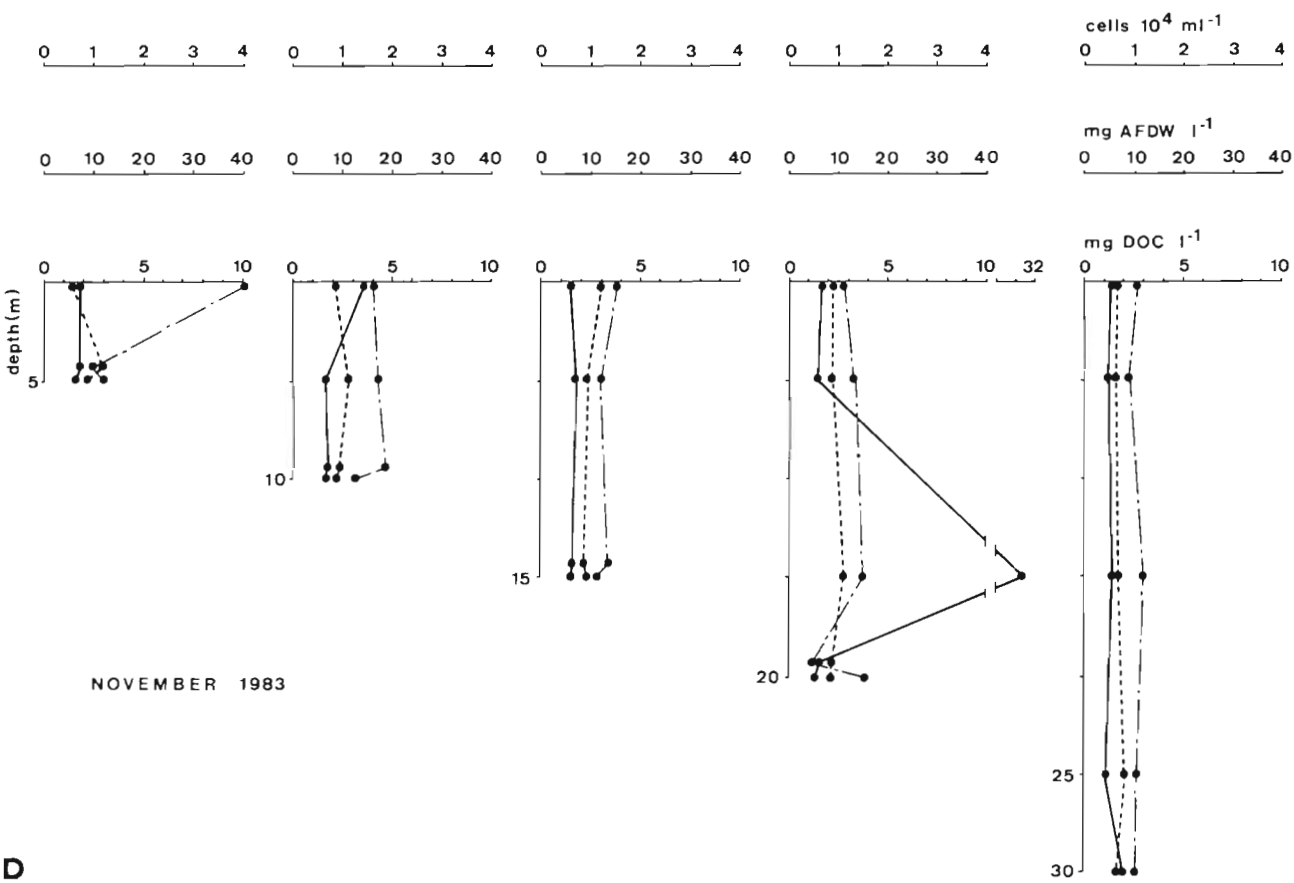
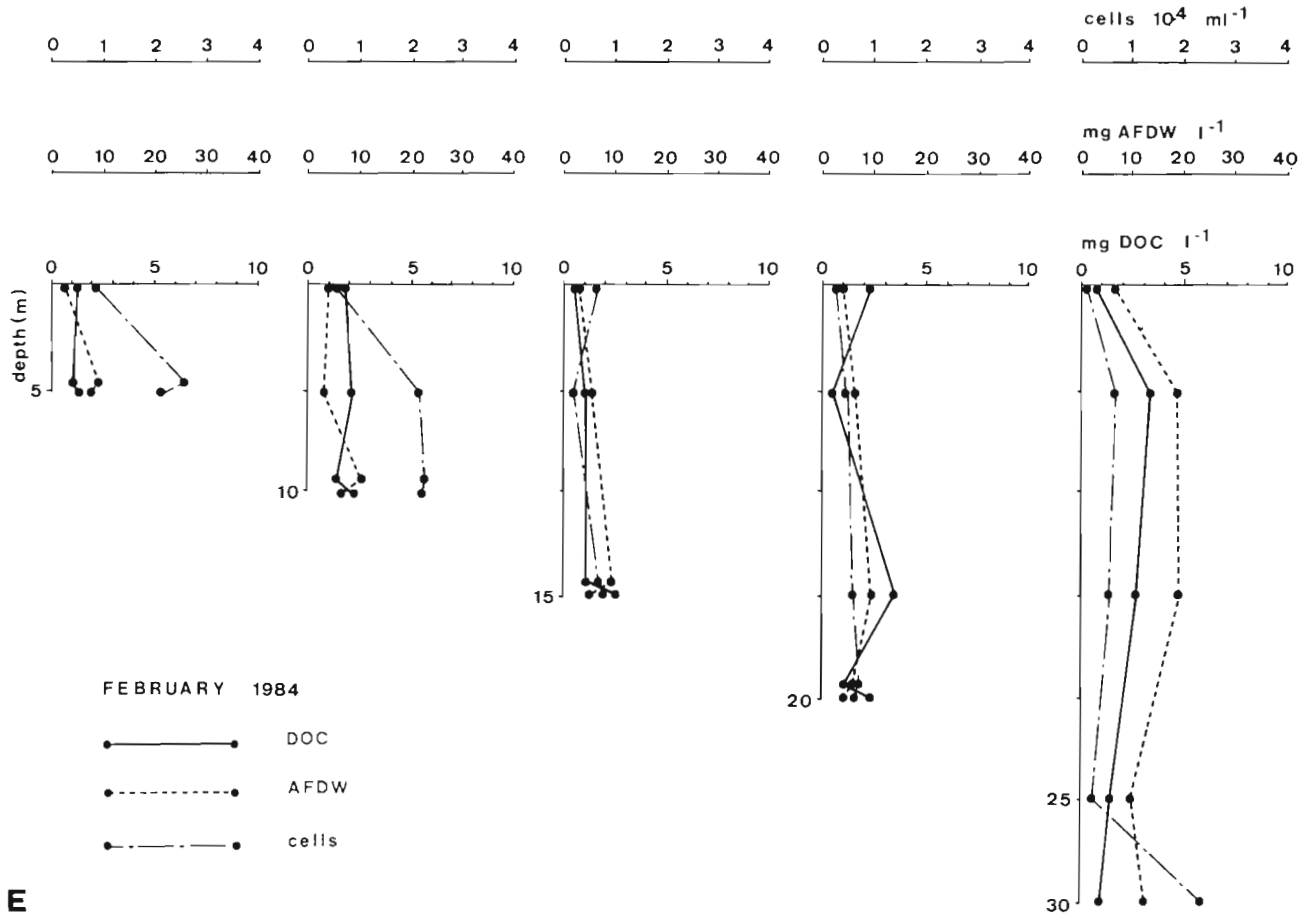


Fig. 3 (continued). Seasonal variations of DOC, bacteria and POM



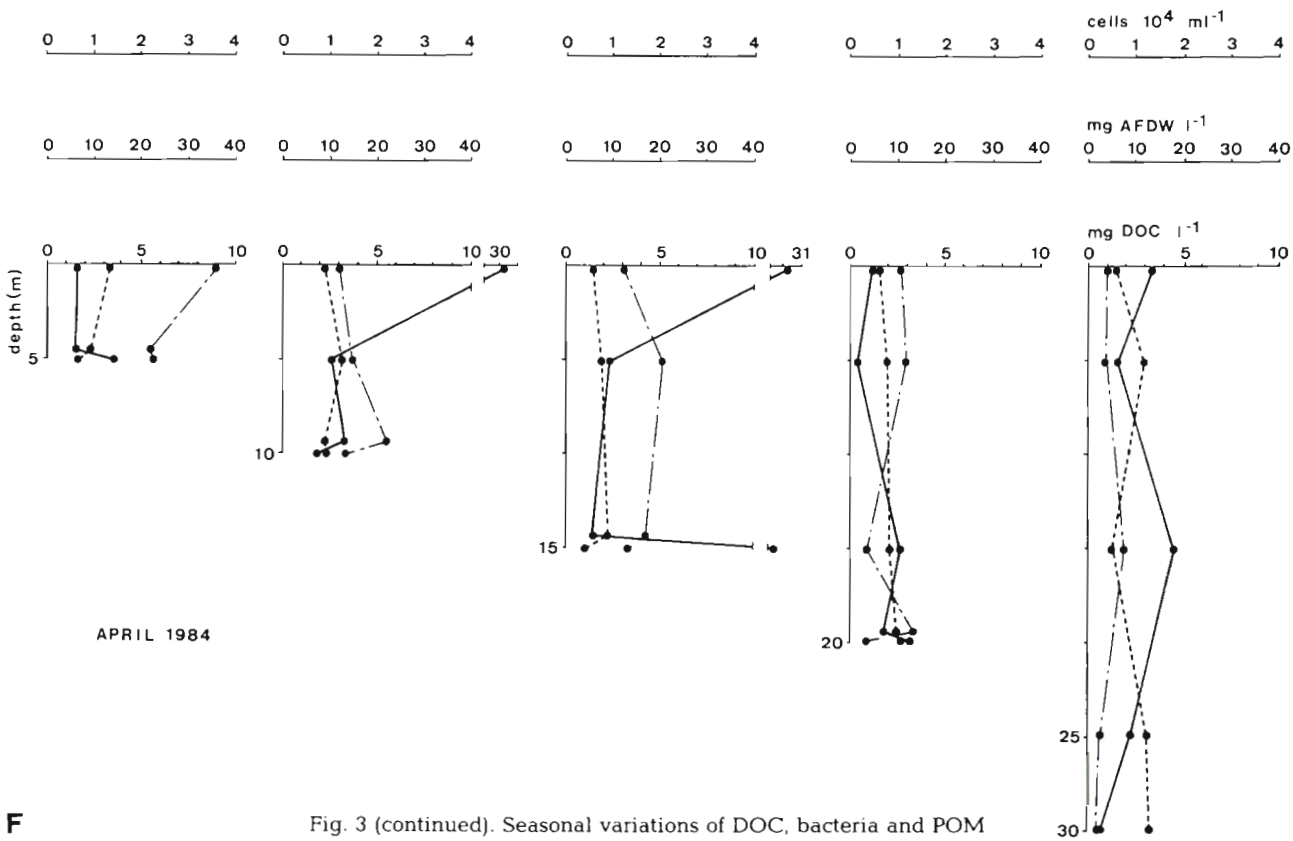
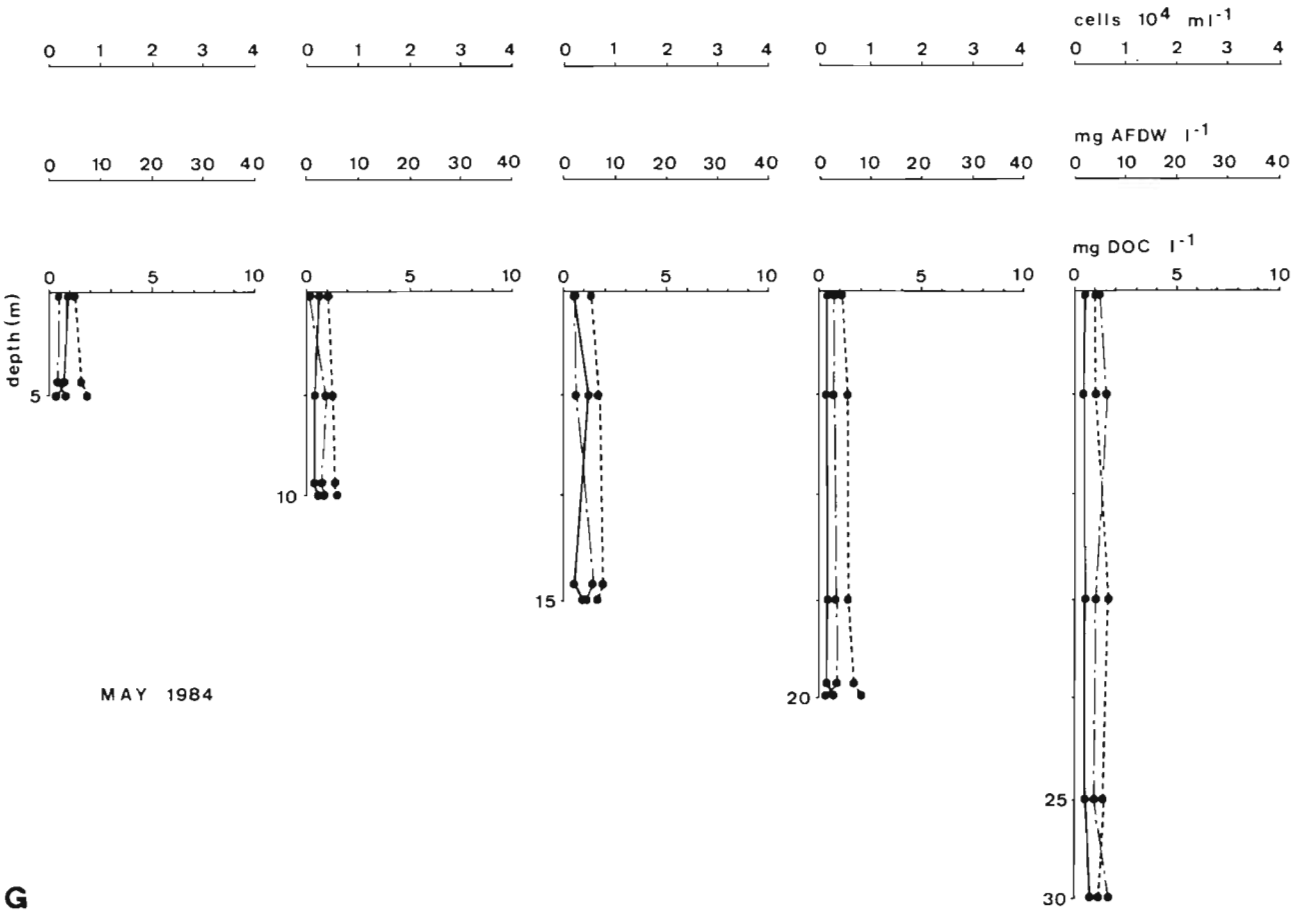


Fig. 3 (continued). Seasonal variations of DOC, bacteria and POM



G

Fig. 3 (continued). Seasonal variations of DOC, bacteria and POM

column and the meadow differ (Fig. 3A to G), the null hypothesis, i.e. that there is no predictable increase or decrease of the measured parameter from the water column down to the meadow, was accepted by the sign test ($p < 98.5\%$, Dixon & Mood 1946).

For a better understanding of the process leading to the observed peaks in the parameters under consideration in the water column, the same parameters were followed in one station over the day and bell jar experiments were set up in the meadow.

Daily variations of bacterial density, DOC and POM

The variations of the 3 parameters in the water above and within the meadow, recorded in April 1983 over 2 d at 12 m depth on the transect line, showed that all parameters had higher values on the first day than on the second day (Fig. 4A, B). On April 26, DOC peaked at 12.00 h within the meadow (6.5 mg l^{-1}); at 14.00 h a peak was noticed above the meadow (9.7 mg l^{-1}), while bacteria showed a steady increase from 9.30 until 14.00 h, reaching a density of 9.8×10^4 and 12.2×10^4 cells ml^{-1} within and above the meadow,

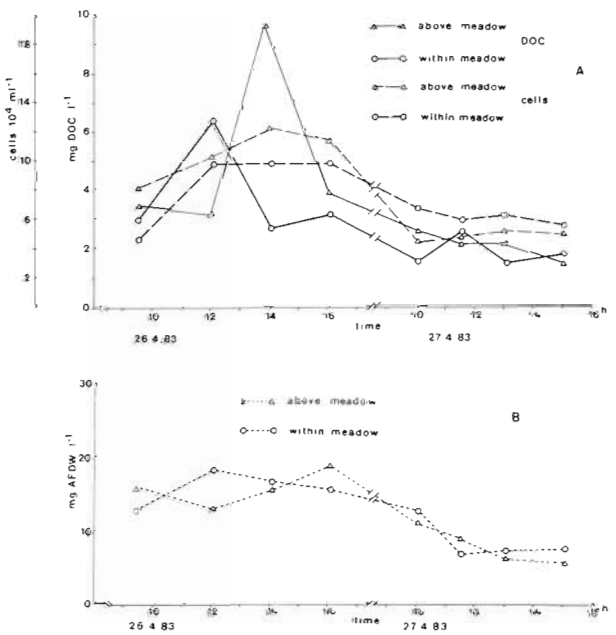


Fig. 4. (A) Daily variations of DOC and bacteria in water within and above the meadow at a 12 m station in April 1983. (B) Variations of POM in water within and above the meadow at the same station and same time

respectively. Within the same period an increase was also noticed for POM within the meadow. Above the meadow POM showed a minimum at 12.00 h and increased until 16.00 h to reach 20 mg AFDW l^{-1}.

DOC, bacteria and POM decreased overnight and maintained lower concentration levels during the following day. Only DOC within the meadow showed a small peak (2.9 mg l^{-1}) between 11.00 and 12.00 h. The decrease in concentration of the 3 parameters is correlated with the build up of wind from Northeast in the evening of April 26. Also, currents parallel to the coast were recorded above the meadow in the morning of April 27; this was combined with an increasing wave height.

In contrast to April, sea conditions in September 1983 were calm, with less obvious current directions and water movement in the Lacco Ameno area. This is also reflected by the fluctuation pattern of the measured parameters which peak at both days in September (Fig. 5A, B). Again, DOC within the meadow attained the daily maximum earlier than above the meadow. On September 9, DOC within the meadow reached a maximum concentration of 9.0 mg l^{-1}, while a peak of 20.4 mg l^{-1} was measured above the meadow at 12.30 h. This increase in DOC above the meadow was followed by an increase of bacteria (18 × 10^4 cells ml^{-1}) at 16.00 h, while the cell number within the meadow dropped from 14.2 × 10^4 to 11.0 × 10^4 cells ml^{-1}.

POM in the water decreased within and above the meadow until 14.00 h (Sep 9) to 5.0 and 7.0 mg AFDW l^{-1} respectively and increased again in the afternoon to 8.0 and 15.0 mg AFDW l^{-1}. For September 10, the same rhythm in DOC fluctuations was noted. An increase in DOC took place within the meadow at 12.30 h, followed by an increase above the meadow at 14.00 h. Again, an increase in bacterial number was measured within the meadow (17.1 × 10^4 cells ml^{-1}), taking place 2 h after the DOC peak. POM also increased within and above the meadow until 12.00 h (11.5 and 20.2 mg AFDW l^{-1} respectively) but dropped in the early afternoon.

The same station was sampled on 6 d over a period from 16 to 23 November (Fig. 6A, B). Between November 18 and 21, wind-induced waves and rain led to 2 d interruption of the sampling program; in addition, fewer samples were taken per day during this period due to rough weather.

Fluctuations of DOC concentrations were similar within and above the meadow for the 6 d, with peaks on November 17 and 21, the only days with calm water. Bacterial densities were lower than in the other seasons, ranging from 0.7 × 10^4 to 1.4 × 10^4 cells ml^{-1} within the meadow and from 0.9 × 10^4 to 2 × 10^4 cells

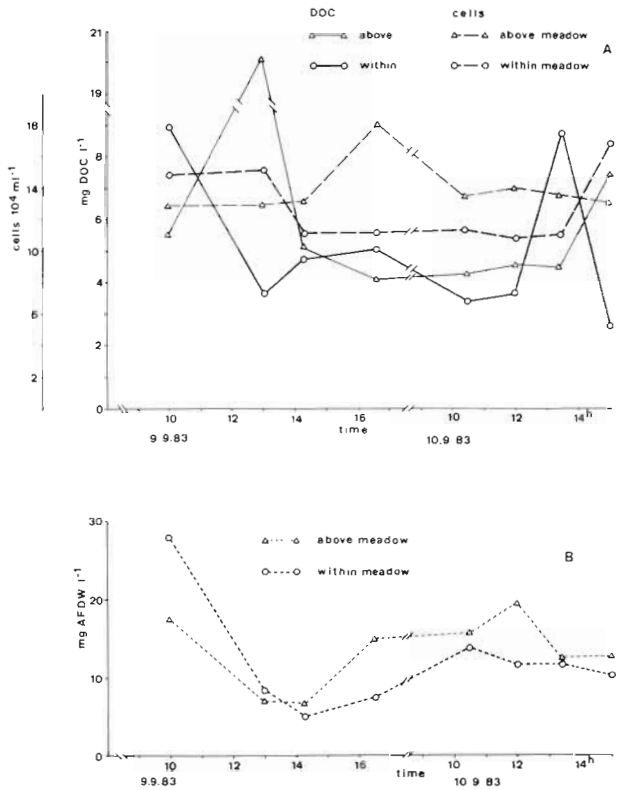


Fig. 5. (A) Daily variations of DOC and bacteria within and above the meadow at the 12 m station in September 1983. (B) Variations of POM in water within and above the meadow at the same station and same time

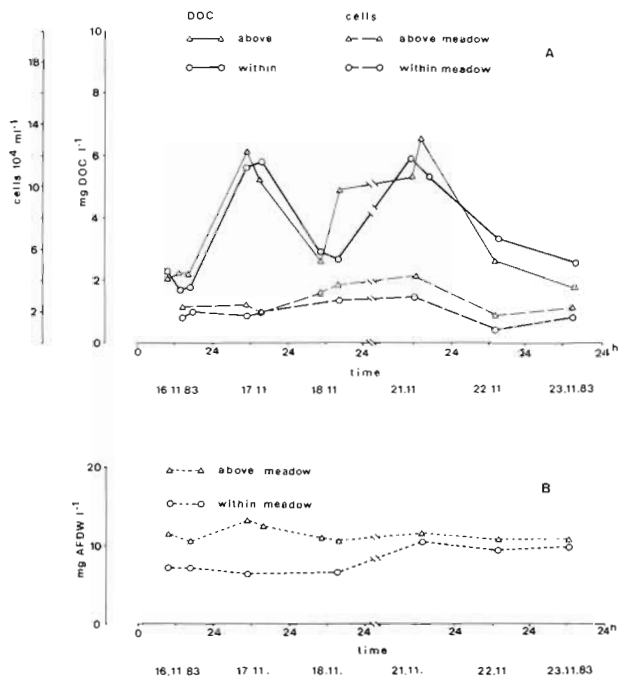


Fig. 6. (A) Daily variations of DOC and bacteria in water within and above the meadow at the 12 m station in November 1983. (B) Variations of POM in water within and above the meadow at the same station and at the same time

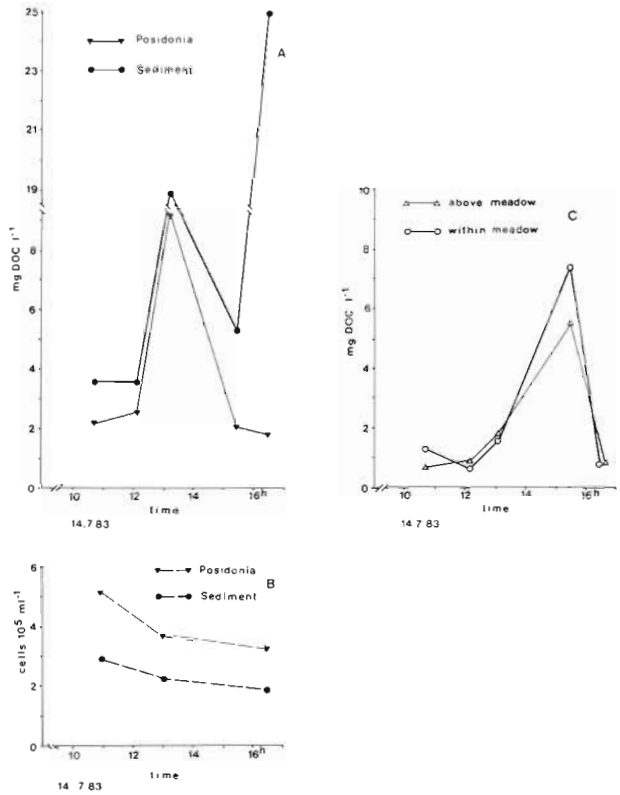


Fig. 7. (A) Time course of DOC in water of *Posidonia oceanica* and sediment jars during a 6 h *in situ* experiment, July 1983. (B) Changes in bacterial density in water of the same jars. (C) Daily variations of DOC in water within and above the *Posidonia oceanica* meadow at a station within 6 m of the bell jars

ml^{-1} above the meadow. No bacterial peaks were detected over the sampling period. The same lack of pronounced fluctuations was evident for POM over this period; values ranged from 8 to 10 mg AFDW l^{-1} within the meadow and from 9.2 to 14.0 mg AFDW l^{-1} above the meadow.

Bell jar experiments

The strong seasonal variations of DOC (Fig. 3A to G) between and within stations on the one hand, and the daily variations (Fig. 4 to 6) within a single station on the other, which are characterized by rhythmic appearance of DOC peaks, led to the following hypothesis: DOC is generated in high concentrations by the *Posidonia oceanica* meadow. The appearance of the DOC peak above the meadow 1 to 2 h after the peak within the meadow provides strong evidence for an important DOC transfer from the meadow into the water column. To test this hypothesis bell jar experiments were carried out; graphs of representative time courses of DOC increase and decrease in summer 1983 and spring 1983/84 are shown in Fig 7 to 10.

Again, distinct peaks could be seen in the DOC time course in the enclosed water body. These DOC pulses were recorded in all bell jar experiments, undertaken in May and July. Contrary to expectation, DOC pulses were not only observed in the bell jars enclosing *Posidonia oceanica* shoots, but also in the control bell jars, enclosing the adjacent bare sediment surface.

July 1983 experiments (depth 8 m, duration 6 h, Fig. 7A, B) revealed peaks of DOC at 13.00 h in both the *Posidonia oceanica* and sediment jar, amounting to 9.2 mg l^{-1} and 19.0 mg l^{-1} respectively. After a drop at 15.00 h, DOC peaked again to 25.0 mg l^{-1} at 16.30 h in the sediment jar, while a further decrease to 1.8 mg l^{-1} was measured in the *P. oceanica* jar.

Although most of the DOC disappeared from the experimental system within 1.5 h after being recorded (Fig. 7A) no corresponding increase in bacteria, considered to be the main consumers of DOM, was noticed in the jars. Bacteria decreased from 5.2×10^5 to 1.9×10^5 cells in the *Posidonia oceanica* jar and from 2.9×10^5 to 1.9×10^5 cells in the sediment jar over the 6 h (Fig. 7b).

Concurrent water samples taken 5 times a day within and above the meadow at a station within 6 m of the bell jars showed peaks of 5.2 and 7.9 mg l^{-1} DOC (Fig. 7C). A similar sequence of events was observed for the time course of DOC in bell jars in May 1984 (19 m depth; Fig. 8A, B) with the difference that DOC appearance in the sediment jar took place at 14.00 h, amounting to 24.8 mg l^{-1}; DOC in the *Posidonia oceanica* jar began to increase after 14.00 h, reaching only 2.8 mg l^{-1} at 17.00 h. A decrease of bacteria was observed similar to that in summer (Fig. 7B) and peaks of DOC could again be seen within and above the meadow in the early afternoon at the adjacent station (Fig. 8C).

The rhythmic appearance of DOC peaks was even more conspicuous in summer experiments (15 m depth) lasting 25 and 27 h. From July 20 to July 21, 3 peaks were recorded in the sediment jar (Fig. 9A, B). Two peaks were at equal height (5.8 mg l^{-1}), at 12.00 h on July 20 and at 11.00 h on July 21. In the *Posidonia oceanica* jar the initially high DOC concentration decreased during the entire day (Jul 20), increased again overnight and showed a small peak at 14.00 h on July 21 (Fig. 9A). None of the DOC peaks was followed by a bacteria increase. Bacterial density varied insignificantly in the *P. oceanica* jar, ranging from 1.9 to 2.8 $\times 10^5$ cells ml^{-1}; in the sediment jar the fluctuations were more pronounced on the second day (Fig. 9B) where density dropped from 3.0×10^5 to 1.3×10^5 cells ml^{-1} Water samples from the adjacent station (again within 6 m of the bell jars) taken at longer time intervals than from the jars, showed high DOC peaks of 35.3 mg l^{-1} within the meadow on July 21 (Fig. 9C).

DOC variation pattern in the bell jars from July 25 to July 26 (Fig. 10A) was similar to variations in the jars on July 20, with the difference that *Posidonia oceanica* jars had DOC peaks with 11.8 mg l^{-1} and 11.3 mg l^{-1}; these were higher than those in the sediment jars, which ranged from 5.5 to 9.5 mg l^{-1}. While little change was seen in bacterial numbers in the sediment jar (Fig. 10B), bacteria increased overnight in the *P. oceanica* jar to 9.2 × 10^4 cells ml^{-1} as DOC peaked to 11.3 mg l^{-1}.

At the adjacent station DOC variations were less pronounced; within the meadow, DOC increased dramatically at 13.00 h on July 26 after a linear time course on the previous day; above the meadow only a smaller peak was registered in the afternoon of July 25 (Fig. 10C).

Detailed data on DOC budget from all bell jar experiments, as well as photosynthetic carbon fixation and respiration within the experimental system, are presented in Table 1. In most of the experiments the concentration of DOC released into the water above the enclosed *Posidonia oceanica* is much higher than the carbon fixation by the macrophytes over the experimentation time. The only exceptions were the experiments of 11 and 13 May 1983 where total DOC released represented 15.3 and 59.2% of the photosynthetic carbon fixation. In all other experiments the total DOC released in the *P. oceanica* jars was 2 to 5 times higher than carbon fixation by macrophytes.

Assuming a mean carbon content of 29% for intermediate and adult leaves of dry *Posidonia oceanica* shoots from April to August (Velimirov unpubl.) ca 0.48 g dry weight of seagrass would have to change from the particulate into the dissolved phase within 6 h in order to account for the 138.1 mg DOC increment in the jar of the 14 July 1983. This corresponds to a leaf length of 80.0 cm (Pirc 1984). Similarly, the dissolution of 0.61 g dry weight of seagrass, corresponding to

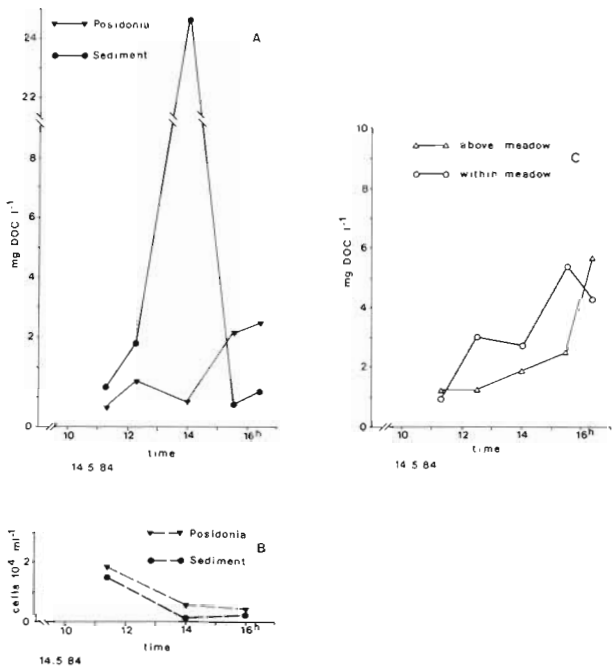


Fig. 8. (A) Time course of DOC in water of *Posidonia oceanica* and sediment jars during a 6 h *in situ* experiment, May 1984. (B) Changes in bacterial density in water of the same jars. (C) Daily variations of DOC in water within and above the *P. oceanica* meadow at a station within 6 m of the bell jars

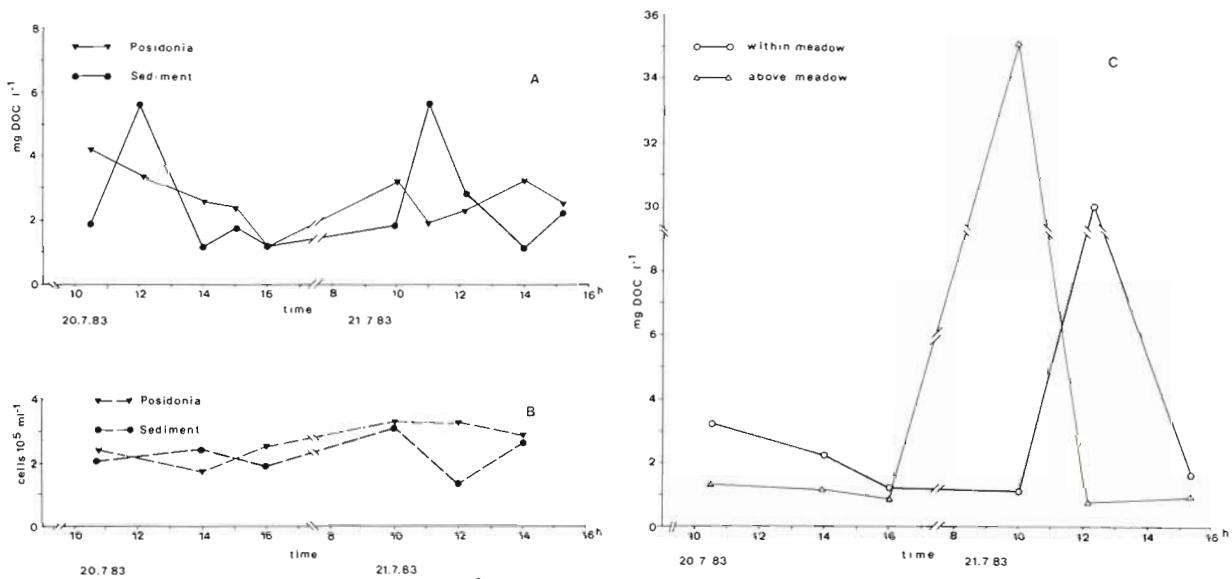


Fig. 9. (A) Time course of DOC in water of *Posidonia oceanica* and sediment jars during a 25 h *in situ* experiment, July 1983. (B) Changes in bacterial density in water of the same jars. (C) Daily variations of DOC in water within and above the *P. oceanica* meadow at a station within 6 m of the bell jars

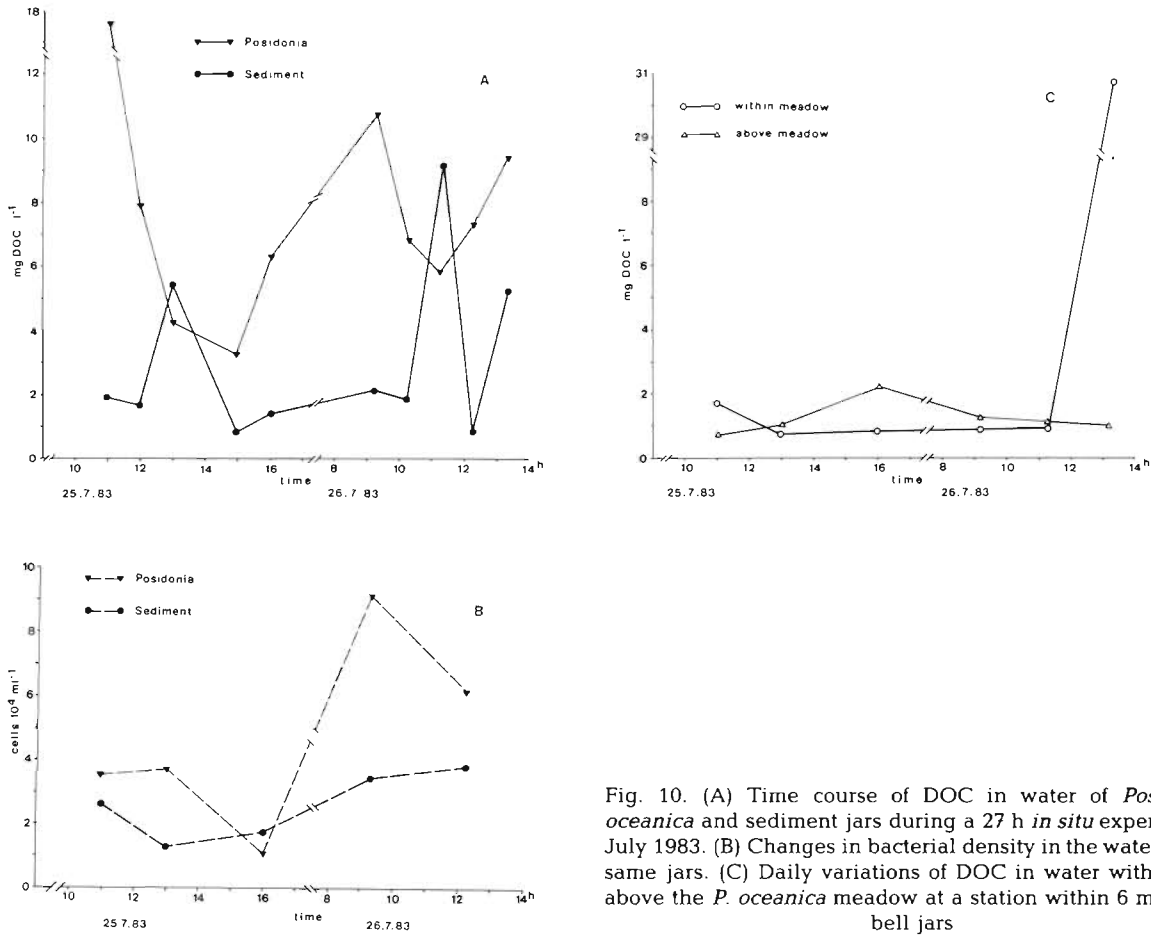


Fig. 10. (A) Time course of DOC in water of *Posidonia oceanica* and sediment jars during a 27 h *in situ* experiment, July 1983. (B) Changes in bacterial density in the water of the same jars. (C) Daily variations of DOC in water within and above the *P. oceanica* meadow at a station within 6 m of the bell jars

101.6 cm leaflength, would be required in the experiment of 25/26 July 1983.

Within the sediment jars, where primary production is small (diatoms and other microalgae) or not measurable, high DOC release, as already shown in Fig. 7A to 10A, was detected in all experiments. With the exception of the experiment of 18 May 1984, DOC values were 1.5 to 30 times higher than the DOC released in the *Posidonia oceanica* jars.

These results indicate that the main source of released DOC is not the photosynthetically fixed carbon from live seagrass and epiphytes, but rather sediment with the rhizome system, containing an extensive carbon pool and including an important dissolved-matter compartment.

In experiments lasting 6 h and over 24 h part, but not all, of the DOC decrease can be explained by consumption of the microbial community (see Discussion); a corresponding increase in bacterial numbers in both *Posidonia oceanica* and sediment jars, as noted during daily DOC and bacteria variations within and above the meadow (Fig. 9B, 10B), was noticed only in experiments lasting 25 and 27 h (Table 1). Virtually all other experiments were characterized by a net decrease of the bacterial population (a small increase was recorded only on 11 May 1983 in the *P. oceanica* jar and on 14 May 1984 in the sediment jar). In the 25 and 27 h experiments, the major bacterial increase was recorded during the night; the density decrease over the day may indicate grazing pressure by a protozoan community and by meiofauna, both on the *P. oceanica* leaves and in the water/sediment compartment; thus bacterial density in the water never passed 2.6×10^6 cells ml^{-1} and remained far below this value in most experiments.

To obtain information on the magnitude of the DOC contribution of the different compartments it was necessary to perform incubation experiments in the laboratory on old and senescent leaves as well as on green healthy leaves. Additionally a quantification of the amount of organic matter within the sediment was desirable.

Graphs on time course of DOC for all experiments can be obtained from the author.

Table 1. Parameter values of bell-jar experiments enclosing *Posidonia oceanica* shoots or sediment. Total carbon fixation, respiration and DOC concentrations expressed in mg per total jar volume (15.82 l) over the experimentation time, bacteria in cells ml^{-1}

	11 May 83		13 May 83		14 Jul 83		20/21 Jul 83		25/26 Jul 83		14 May 84		18 May 84	
	Posidonia	Sediment	*Posidonia*	Sediment	*Posidonia*	Sediment	*Posidonia*	Sediment	*Posidonia*	Sediment	*Posidonia*	Sediment	*Posidonia*	Sediment
Duration (h)	6		6		6		27		25		6		6	
Depth (m)	12		12		8		15		15		19		11	
Posidonia green (g)	10.10	–	10.40	–	10.20	–	6.80	–	8.40	–	9.75	–	3.70	–
Posidonia brown (g)	0.02	–	0.02	–	0.80	–	0.02	–	0.02	–	0.01	–	–	–
Epiphytes (g)	1.38	–	1.42	–	1.70	–	0.02	–	0.04	–	0.50	–	0.62	–
Photosynth. carbon fixation	20.21	1.20	25.30	0	26.11	2.37	39.16	5.63	34.65	0	27.65	1.96	12.45	0
Carbon respiration	–	–	–	2.60	–	1.18	17.79	2.60	20.40	7.70	–	–	–	0.59
Carbon (fixation–respiration)	20.21	1.20	25.30	−2.60	26.11	1.19	21.36	3.03	14.25	−7.70	27.65	1.96	12.45	−0.59
Initial DOC conc.	49.04	308.50	105.99	15.82	31.96	58.53	66.76	31.32	278.43	66.76	53.80	44.45	664.44	103.94
Total DOC increase	3.10	105.20	15.00	294.20	138.10	559.20	51.10	156.4	177.30	269.20	53.3	399.7	57.70	43.10
Total DOC decrease	30.00	389.90	103.60	292.60	141.20	215.90	74.50	150.7	305.4	217.80	10.6	377.1	700.00	47.30
DOC (increase – decrease)	−26.80	−284.70	−88.50	1.5	−3.10	343.20	−23.40	5.68	−128.10	51.40	42.7	22.6	−642.20	−4.11
Initial bact. density	2.4×10^4	2.94×10^4	5.2×10^4	2.26×10^4	5.2×10^5	3.0×10^5	2.3×10^5	2.05×10^5	3.08×10^4	2.7×10^4	1.9×10^4	1.6×10^4	–	–
Total bact. increase	0.6×10^4	–	–	–	–	–	1.6×10^5	2.55×10^5	8.4×10^4	2.5×10^4	–	0.2×10^4	–	–
Total bact. decrease	2.1×10^4	1.8×10^4	4.1×10^4	1.6×10^4	2.05×10^5	1.1×10^5	1.1×10^5	2.12×10^5	5.71×10^4	1.3×10^4	1.4×10^4	1.3×10^4	1.12×10^4	1.05×10^4

Laboratory experiments

Enclosure of single seagrass leaves in specially adapted cylinders with 0.2 µm filtered seawater receiving 200 µEin m^{-2} s^{-1} resulted in a DOC increase in the jars with adult brown and senescent leaves which were eroded (Table 2); these were the remains of the oldest leaf on a shoot. Single green, photosynthesizing leaves which belonged to the intermediate and intact adult leaf classes did not release measurable amounts of DOC. Yet, photosynthetic carbon fixation could be confirmed by O_2 evoluton in the container. In some of the experiments using heavily epiphytized leaves, the DOC concentration decreased within 3 h.

Table 2. *Posidonia oceanica*. Rates of soluble carbon release by brown and senescent adult leaves

Time (h)	Weight (mg)	C release (mg h^{-1} g^{-1})	% $\frac{\text{Release}\times100}{\text{weight}}$
10.00–13.00	75.9	4.78	0.47
11.00–14.30	230.5	2.86	0.28
11.00–14.30	84.1	8.29	0.82
13.00–16.50	97.7	3.35	0.33
13.00–16.50	102.2	1.60	0.16
19.40–23.20	126.3	0.42	0.04
19.40–23.20	94.0	2.51	0.25
20.30–24.30	1320.0	1.07	0.10

Only by increasing the number of leaves to obtain a higher biomass in the containers (Table 3) could a concentration increase of DOC be detected, due to cumulative leaching. For brown senescent leaves plus epiphytes the carbon fixation was negligible; respiration by the bacterial community and other microorganisms on these leaves balanced the O_2 release and in some of the experiments net respiration was observed. The overall rate of carbon release by these leaves

Table 3. Rates of carbon fixation and soluble release in intermediate and adult *Posidonia oceanica* leaves. Proportion of adult to intermediate leaves was 1 to 1, based on length/width measurements (nd = not detected)

Time (h)	Weight (mg)	C fixation (mg h^{-1} g^{-1})	C release (mg h^{-1} g^{-1})	%
10.00–13.00	960	0.291	0.0090	3.09
10.30–14.30	870	0.218	0.0065	2.84
10.30–14.30	1165	0.152	0.0049	3.20
10.30–14.30	745	0.254	0.0065	2.55
12.00–15.00	790	0.334	nd	0
12.00–15.00	685	0.297	nd	0
19.20–22.20	930	−0.150	0.0058	–
20.00–23.00	840	−0.145	0.0052	–
20.00–23.00	690	−0.109	nd	–

amounted to 3.11 mg DOC h^{-1} g^{-1} (SD=2.5) and is considered to be the result of a bacterial decomposition process in addition to the release of dissolved compounds by the leaf, ranging from 0.42 mg h^{-1} g^{-1} to 4.78 mg h^{-1} g^{-1}

Although some of these leaves were already dead when collected, all of them were still part of the shoot, being loosely connected to the base, and would have fallen off during the following storm; others, however, still had traces of green pigmentation in parts of the leaf or underneath the epigrowth layer. All leaves showed strong erosion marks and their length ranged from 11 to 24 cm, being no different from the leaves in the wrack beds within the meadow.

For photosynthetically active leaves which form the main bulk of the biomass in the shoot (adult and long intermediate leaves) the release rate of carbon ranged from not detectable to 9 µg DOC h^{-1} g^{-1} with an overall average of 4.2 µg DOC h^{-1} g^{-1} (SD=3.4) (Table 3). This represents 1.95 % of the photosynthetic carbon fixation which appears in the water after being 'reworked' (Kirchman et al. 1984) by the epibacteria on the leaves.

Organic content in sediments of the *Posidonia oceanica* bed

Particle-size analysis from a separate study (Hertweck unpubl.) was used to characterize the mobile substrate. The weight percent distribution of sediment size classes from the study area, taken at 4 different depth stations (Table 4) reveals an increase of the fine

Table 4. Weight percent of sediment size classes from 4 stations of *Posidonia oceanica* meadow

Sediment size (mm)	Depth (m)			
	5	10	12	30
Gravel (20–6.3)	0.48	0.74	–	–
Fine gravel (6.3–2)	5.38	16.51	0.09	1.79
Coarse sand (2–0.63)	37.40	45.32	0.51	9.86
Medium sand (0.63–0.2)	55.17	30.11	53.62	32.57
Fine sand (0.2–0.063)	1.32	6.44	45.63	53.61
Silt + clay (< 0.063)	0.25	0.89	0.14	2.17

sand fraction towards deeper stations; gravel, fine gravel and coarse sand dominate the shallower 5 and 10 m stations.

Organic content and pore-water volume of cores taken along a depth gradient in the vicinity of the transect line (Table 5) show that the water content of the sediment, ranging from 601 to 722 ml dm^{-3} tends to increase with depth; organic matter, however, reveals no such tendency. A relatively high standard deviation

Table 5. Percent weight loss at combustion, organic content in g and water in ml of sediment from the *Posidonia oceanica* meadow, taken between 5 and 20 m depth (sampled in May/Jul 1983 and May 1984). Standard deviation in parenthesis

Depth (m)	% weight loss at 450 °C	Org. content of sediment (g dm^{-3})	Water content of sediment (ml dm^{-3})
5	5.12	45.20	601
5	6.94	28.10	616
10	12.36	95.28	630
10	7.23	44.10	642
10	5.22	23.60	702
12	8.30	72.0	651
15	4.23	19.87	710
15	8.30	41.0	719
15	6.80	25.48	680
20	8.76	61.49	700
20	14.80	119.01	722
$\bar{X}$	8.00 (3.15)	52.28 (31.93)	670.17 (43.76)

for the average organic content per dm^3 sediment (Table 5) indicates the heterogeneous organic content in the substrate. It consisted mainly of *Posidonia oceanica* leaves (wrack) on and in the upper few centimeters, followed by a bulk of dead rhizomes and roots, fractionated leaves, fibers and small unidentifiable POM.

Concentrations of dissolved monomeric carbohydrates in the sediment porewater (Table 6) were 200 to 1000 times higher than dissolved free amino acids; in some cases (15 m depth, Station 3) the concentrations of the latter were beyond the HPLC detection limit. Calculated DOC equivalents for average dissolved components per core, as sum of MCHO and DFAA, ranged from 94.6 to 412.6 mg dm^{-3} (Table 6). In contrast, concentrations of MCHO and DFAA in the seawater above and within the meadow (Table 7) were much lower Values for MCHO ranged from not detectable to 0.6 mg l^{-1}. Calculated DOC equivalents for those easily metabolizable components in the sea water represented only a small fraction of the measured DOC in the water, amounting on average to 2.32 % (SD=2.14) but being sometimes as low as 0.4 % of the total DOC.

DISCUSSION

DOC pulses recorded in bell jar experiments indicate that most of the seasonal and daily variations in DOC concentrations in seawater can be produced by the *Posidonia oceanica* system. An input of phytoplankton, boosting the DOC pool via exudates (Hellebust 1965, Anderson & Zeutschel 1970) may take place, but is expected to be negligible most of the year,

Table 6. Concentration of monomeric carbohydrates (MCHO) and dissolved free aminoacids (DFAA) in pore water of the *Posidonia oceanica* meadow sediment. All values in mg dm^{-3} sediment; DOC equivalent for MCHO and DFAA was calculated assuming 41.16 and 38.98 % carbon content respectively. Values in parenthesis are standard deviations (sampled in May 1982)

Sediment depth (cm)	Water depth 5 m MCHO	5 m DFAA	10 m MCHO	10 m DFAA	15 m MCHO	15 m DFAA	20 m MCHO	20 m DFAA
1	277	0.246	565	0.951	58.3	1.565	973	0.861
5	286	0.250	298	0.947	105	–	1441	3.861
9	376	0.204	360	0.833	459	–	736	1.880
13	308	0.140	1020	0.633	297	0.628	853	1.465
$\bar{X}$	299	0.210	560	0.841	229	1.097	1000.7	1.804
	(60)	(0.051)	(326)	(0.149)	(184)	(–)	(309)	(1.408)
DOC calculated	123.15		230.82		94.68		412.60	

Table 7. Concentration of monomeric carbohydrate (MCHO) and dissolved amino acids (DFAA) in seawater above and within the *Posidonia oceanica* meadow. All values mg l^{-1}. DOC equivalent calculated as for pore water and expressed as % of total DOC in the seawater above and within the meadow. tr: traces (sampled in May 1982)

	Water depth 5 m Above	5 m Within	10 m Above	10 m Within	15 m Above	15 m Within	20 m Above	20 m Within
MCHO	tr	0.605	0.216	0.128	0.073	0.110	0.060	tr
DFAA	0.116	0.070	0.085	0.221	0.076	0.056	0.053	0.050
DOC calculated	0.045	0.276	0.122	0.139	0.075	0.052	0.045	0.019
% $\frac{100 \times \text{DOC calc.}}{\text{DOC measured}}$	1.73	0.85	0.43	6.95	3.75	2.080	1.957	0.826

except for April, according to Carrada et al. (1980). Over the seasons, small peaks of chlorophyll *a*, amounting to 1 mg m^{-3}, were recorded only in late spring (Jun) and early autumn (Oct) for an offshore station west of Ischia. SEM observations of filtered water samples from May repeatedly showed skeletons and fragments of *Chaetoceros* sp. and pennate diatoms (*Nitzschia* sp.) among the particulate matter. For the rest of the year chlorophyll *a* concentrations were well below the above value averaging 0.53 mg m^{-3} (calculated from Carrada et al. 1980). Similarly, zooplankton biomass values at the same station, expressed as dry weight, show 3 peaks over the year, but were generally below 4 mg m^{-3}. The peaks were mostly due to an increase of doliolids and appendicularians in March, and copepods and cladocerans in June and October. The main water transport in the area, as indicated by Düing (1965) and Colantoni et al. (1982) is from NW to SE and transports offshore water past the study site. Deviations of surface water by local winds (Düing 1965) can take place, but are expected to be negligible as main transport agents bringing about an important input of zooplankton. The only faunal component repeatedly found in the samples was a juvenile stage of the isopod *Gnathia phallonajopsis* known as a fish parasite which is common in water within and above *P. oceanica* stands (Lorenti pers. comm.). Calculated concentrations of total DOC, POM and bacteria per m^3 water above an idealized *P. oceanica* bed are shown in Table 8. Defining the study area as a surface area of 600 m (extension of the meadow from 0 to 33 m depth) by 320 m (from Punta Vico to Pietro del Lacco), one obtains a water wedge of 33 m height (Fig. 1 & 2) with a volume of 31.68×10^5 m^3. Considering both surface water and water in the immediate vicinity of the meadow as distinct water bodies of 1 m thickness, one

Table 8. Average concentration of DOC, bacterial carbon and POM (expressed as ash-free dry weight) in an idealised m^3 of seawater from the *Posidonia oceanica* system

	Apr 1983	May 1983	Jul 1983	Nov 1983	Feb 1984	Apr 1984	May 1984
DOC (g m^{-3})	4.11	2.53	2.41	4.82	2.15	3.06	0.53
Bacteria (mgC m^{-3})	0.450	0.250	0.480	0.248	0.223	0.128	0.036
POM (g m^{-3})	14.54	9.94	16.21	8.27	10.54	8.94	5.24

obtains a surface layer and a bottom layer of nearly equal volume and a large midwater body in between. In order to estimate the variables' concentrations per m^3, the data per station and substation from Fig. 3A to G were averaged and weighted according to the volume of the water body thus obtaining an overall mean per unit. According to Table 8 the standing stock of bacterial carbon represents only a minute fraction of the overall POM standing stock. This is in agreement with data from pilot studies in 1981 and 1982 (Velimirov et al. 1984).

Mass balance calculation

Since allochthonous inputs are considered negligible, an attempt is made in the following to allocate release rates of DOC to the different carbon pools in a hypothetical m^2 of a representative *Posidonia oceanica* bed. For simplicity of calculation, DOC release rates were averaged over all experiments. A release rate of 7.65 mg C h^{-1} (SD=7.66) per *P. oceanica* bell jar with an enclosed substrate surface of 158.29 cm^2 was calculated from Table 1. This corresponds to 483.2 mg C h^{-1} m^{-2}. Similarly, the release rate for the sediment jar was calculated to be 2257.3 mg C h^{-1} m^{-2}.

Since the total sediment surface over the Lacco Ameno study area was estimated to amount to 5% (unpubl. own data) the weighted DOC release rate per average m^2 *P. oceanica* is 571.9 mg C h^{-1} m^{-2} and assumed to be representative of the temperature range 16 to 25 °C of the period March to September.

Leaching from *Posidonia oceanica* shoots, amounting to 1.9% of the primary production, covers 3.52 mg C h^{-1} m^{-2}, based on the average carbon net fixation (calculated from Table 1) of 180.4 mg C h^{-1} m^{-2}; carbon release from *P. oceanica*, therefore, represents only 0.61% of the total system release. Brown, dead or senescent leaves still connected to the shoot are considered functional debris and therefore classified as part of the sediment/wrack compartment. Within the sediment, under a surface of 1 m^2 and 20 cm depth (depth extent of sediment cores; Table 5) the average organic content amounts to 10456.0 g ash-free dry weight. Assuming that the source of most of this material is *P. oceanica*, an organic carbon content of 30% is appropriate for conversion (Velimirov unpubl.) based on a carbon analysis of all leaf types for spring and summer. After addition of the calculated 8.03 g senescent brown leaves per m^2 – still part of the shoots (Table 9) – the 10464.0 g organic matter correspond to 3139.2 g carbon (Table 9) which is a slight underestimation, as the meiofauna plus bacteria of the sediment have a higher carbon content than the seagrass. Table 6 shows that at least 43.03 g C of this organic carbon are present in dissolved form, represented by DFAA and MCHO. With the calculated release rate of 568.5 mg C h^{-1} m^{-2} from the sediment/rhizome substrate (Table 9), the easily metabolizable fraction of the total carbon pool would be depleted in 3.15 d.

If DFAA plus MCHO in the sediment represent only up to 2% of the total DOC, which is the proportion of these compounds in the DOC of the seawater (Table 7), the total soluble fraction of the sediment carbon pool would amount to 2151.5 g and be released in 157 d, assuming that during this time no boosting of the DOC pool occurs, i.e. degradation processes in the sediment are reduced to a minimum.

So far, only little information is available on the quantitative contribution of dissolved free compounds to total DOC in both pore water and water column. Mopper et al. (1980) indicate that DFAA and MCHO represent only 1 to 2% of the DOC pool in the water, which is in agreement with our own findings concerning the water column. In contrast, Bölter (1981) found that mono- and disaccharides alone represent 1 to 2% of the DOC and up to 30% of the free dissolved carbohydrates in the inner Kiel Fjord. Since accurate stratified *in situ* sampling of pore water yields generally too small sample volumes, even if the total water content of the sediment is high as in the present study, most workers have concentrated on the quantification of the soluble compounds (Meyer-Reil et al. 1978, 1980, Giere et al. 1982, Liebezeit & Velimirov 1984). Only Lyons et al. (1979) found a mean contribution of 10% MCHO to the total DOC in the pore water of Bermuda, ranging from 3 to 51% and indicating a much higher percentage of easily metabolizable compounds compared to DOC in the water column.

There is growing evidence that recycling of elements in sediments plays a quantitatively important role in coastal environments (Hargrave 1973, Thorstenson & MacKenzie 1974). Most recent recycling studies have concentrated on inorganic nutrient fluxes (Nixon et al. 1976, Billen 1978, Balzer 1984) while studies on

Table 9. Average carbon concentrations in organic pools and carbon production/release rates of different compartments. All values based on data from Table 1

Standing stock of carbon	g m^{-2}
Posidonia oceanica + epiphytes	160.7
Sediment content	3139.2
Rates	mg C h^{-1} m^{-2}
Primary production	180.4
DOC release *Posidonia* + epiphytes	3.5
DOC release sediment	568.4
Total release	571.9

organic nutrient fluxes, especially in seagrass systems, are rare.

Jørgensen et al. (1981) determined release rates of organic nutrients in the *Posidonia oceanica* sediments of the Bay of Calvi (Corsica) but the study was restricted to DFAA. Measurements in the water layer above sediment cores incubated in the laboratory led to net transfer rates of amino acids amounting to 1 nmol cm^{-2} h^{-1}. This corresponds to 0.44 mg C m^{-3} h^{-1} (calculated after Jørgensen et al. 1981, assuming a mean molecular weight of 110 for the amino acid spectrum of the Calvi area and an average carbon proportion of 40 %) and would account only for 0.08 % of the measured DOC release from seagrass sediments at Lacco Ameno.

Comparing both the Lacco Ameno and Calvi study sites, it is noteworthy that the sediments of the latter site are composed of coarse sand, while the former site is characterized by an important fraction of medium and fine sand (Table 4), especially in the part of the meadow below 10 m depth. Also the water content in the sediment of the Calvi *Posidonia oceanica* bed (48 %) is lower than at Lacco Ameno (67 %). Although this water content is not corrected for the amount of buried leaves and faunal components, the wet weight/dry weight relation of dead wrack leaves and rhizomes (Velimirov unpubl.) showed that this would account for at most 1 % of the total water content per dm^3 sediment.

Leaching rates by marine vascular plants

Most of the information on leaching from seagrasses is based on ^{14}C labelling (Brylinsky 1977, Penhale & Smith 1977, Wetzel & Penhale 1979, Kirchman et al. 1984) which is more precise for obtaining release rates from isolated leaves than the direct measurement of DOC in water. Nonetheless the average DOC release rates determined in the present study, ranging from not detectable to 3 % (Table 3), are within the range of those determined by radio isotopes. Brylinsky (1977) reported an average release rate of 1.2 % from carbon fixation in *Thalassia testudinum*; Penhale & Smith (1977) found that heavily colonized *Zostera marina* plants release 0.9 %, while *Z. marina* alone releases 1.5 %. In a later study (Wetzel & Penhale 1979), the whole *Z. marina* plant, including roots and rhizomes, released between 5.2 and 9.5 %, depending on the site where the labelled carbon was administered. *Halodule wrightii* (including root and rhizomes) excreted between 1.2 and 1.8 %, while for *T. testudinum* a release was only reported when the labelled carbon was administered to the root-rhizome system; it amounted to 8.3 % of the total carbon fixation. Kirchman et al. (1984) report DOC excretion rates of 2 %.

From senescent or dead leaves high losses of organic matter have been reported for vascular plants. Harrison & Mann (1975a, b) report that in *Zostera marina* total and soluble organic matter dropped to 70 and 28 % respectively over a 24 d incubation period. For *Spartina alterniflora* (Gallagher et al. 1976), a study on DOC release from standing dead plants indicated that the DOC contribution per m^2 was 1.6 times higher than from green plants. Also most of the DOC release by shoots of *Posidonia australis* (Kirkman & Reid 1979), as much as 48 % of the annual primary production, is assumed to result from the dead plant fraction.

Obviously the high release rates of carbon recorded in Table 2 are expected to decrease. With increasing depletion of dissolved organic matter in the leaf, ranging from 5 to 20 % of the dry weight (Velimirov & Pirc 1983) and the easily degradable leaf fraction, the slower processes of cellulose breakdown will determine the magnitude of the DOC release. Klumpp & van der Valk (1984) found that after 240 d, bagged and bundled material of *Posidonia australis* had lost only 30 and 39 % of its dry weight, and own observations (Velimirov unpubl.) of isolated *P. oceanica* leaves kept in aquaria with minimum water movement showed that they were brown and brittle but without major visible degradation marks after 19 mo.

DOC release by meadow substrate is partly supported by the rhizome-root system. Data from 2 preliminary *in situ* experiments, using partitioned chambers to separate the leaves from the rhizomes showed an increase in DOC in the water of the rhizome chamber of 0.80 mg l^{-1} within 3 h (mean of 2 experiments), while a net DOC decrease was monitored in the leaf chamber.

In view of the higher content of live and dead rhizomes in the sediments of the shallow meadow at 4 m depth (Pirc 1983) compared to the deeper meadow, this carbon pool may contribute significantly to the DOC release rates in the shallow meadows or in mat areas of the *Posidonia oceanica* stands.

Fate of DOC released by *Posidonia oceanica*

A characteristic feature of all *in situ* incubation experiments is the high rate of DOC decrease. Of 14 experiments, 6 (1 *Posidonia oceanica* jar and 5 sediment jars) had a positive DOC balance at the end of incubation (Table 1). In all other experiments total DOC decrease was higher than total DOC release. Considering the proportion of 5 % bare sediment surface per m^2 *P. oceanica* bed, the average amount of DOC which disappears per m^2 (and overlying water-volume proportional to the volume of the bell jar) and hour (calculated from Table 1) amounts to 1641.8 mg.

This is 2.8 times more than the amount of carbon released during the same time. However, DOC concentrations at the end of experiments were always within the range of DOC concentrations measured in the water column; consequently initial DOC concentrations at the start of experiments plus the amount released during the experiment was always well above total DOC decrease.

A cumulative effect of several processes is responsible for the recorded decrease rates and various parameters need to be discussed in order to explain DOC disappearance: (1) adsorption of dissolved material at jar surfaces and macrophyte leaves; (2) uptake by macrofauna; (3) uptake by bacteria and protozoans; (4) phase shift from dissolved to particulate matter.

Adsorption is considered to be a negligible process in contributing to the observed DOC decrease for the following reasons: although the jars containing seagrass plus epiphytes have a much larger potential adsorption surface for dissolved compounds than sediment jars, the average DOC decrease rate was lower for the *Posidonia oceanica* jars (25.59 mg h^{-1}) than for the sediment jars (33.53 mg h^{-1}). Moreover, adsorption effects on jar walls are minimized by constant water circulation in the experimental system; rinsing of laboratory incubation containers (250 ml volume) after 24 h experiments with double distilled water indicated an insignificant increase of DOC in the water (less than 2 %) compared to its initial concentration.

Similarly, an important macrofaunal component responsible for DOC uptake was excluded; all sediment surfaces were carefully inspected for burrows of crustaceans, irregular urchins or bivalves before setting up the jars. In addition, the sediment within the jars was sampled and sieved for control after termination of the experiment. Therefore most of the DOC decrease must be due to uptake by the microheterotrophic community and the formation of DOC-derived POM.

In the following, the data on changes of bacterial density and the magnitude of O_2 evolution in the bell jar experiments will be used to assess the importance of each of the 2 processes for controlling DOC levels in the system. In all day experiments (6 h duration) a net decrease in bacterial density was observed (Table 1). Only the day/night experiments (25 and 27 h duration) showed a low net increase in bacterial numbers over the experimentation time. Fig. 7B and Fig. 8B show that for *in situ* experiments the effect of predation pressure, exerted by flagellates and ciliates – repeatedly found while AODC counting – can already be noticed after 3 h of incubation. To which extent bacterial settling on the walls of the jar contributes to the observed decrease in cell number cannot be quantified at present, but Hagström et al. (1984) who submerged glass coverslips in marine bacteria cultures showed that cell density on the glass surface gave only a slight increase after 4 d of exposure and that frequency of dividing cells was not significantly different from the cells in suspension. A further possibility to explain the decrease in bacteria could be increasing bacteria settling on particulate matter Due to the size-limiting diameter of the syringe needle used for bell-jar sampling, all bacteria counted in aggregates and on particles were restricted to a size of 0.5 mm. However, the majority of the particles in seawater of the study area were well below this size (Velimirov unpubl.) and variation in bacterial numbers during AODC count experiments is considered to be representative for attached and free suspended bacteria.

In most bell-jar experiments, variations in O_2 levels seem to be mainly controlled by the autotrophs. In day incubation experiments, O_2 evolution from seagrass and epiphyte primary production masks all bacterial oxygen consumption, and during the night, respiration of bacteria is never expected to be as high as that of macrophytes, despite the bacterial community on the seagrass leaves (Velimirov et al. 1981, Novak 1984). In sediment jars the enclosure of microalgae, mostly diatoms (Mazella pers. comm.) resulted also in net community production; only experiments of 13 May 1983, 25/26 July 1983 and 18 May 1984 showed net community respiration.

Assuming that this respiration is mainly due to bacteria and that zooplankton plus protozoans are negligible in the system, a rough estimation of the carbon requirements necessary to support this oxygen consumption can be obtained. Although the calculated values (using a RQ of 0.75 for bacteria according to Bauerfeind 1985) of 0.73, 2.16 and 0.16 mg C for the 3 experiments entail an error, it can be seen that bacterial metabolism plus biomass increase can never account for the disappearance of 292.6, 217.8 and 47.3 mg DOC from the experimental system at the same time.

In none of the experiments is the DOC decrease correlated to equivalent respiration values. Therefore heterotrophic utilization is not an explanation for the observed disappearance of DOC. Consequently one may speculate that an important fraction of the DOC is transferred to the particulate fraction in the sytem. Findings by Robertson et al. (1982) and Biddanda (1985) support the above phase-shift hypothesis.

CONCLUSIONS

One of the most striking features of the described seagrass system is the low number of bacteria in the water body despite the relative high variations in DOC concentrations. From other macrophyte systems, such

as kelp beds (Linley & Field 1982) and the Australian seagrass beds (Moriarty & Pollard 1982), bacterial densities between 10^6 and 10^8 cells ml^{-1} were reported.

An earlier study on the hydrolytic capabilities of the bacterial community in the water of the seagrass system, investigated on 2 occasions (Velimirov et al. 1984), indicated that most of the colony forming units (CFU) could hydrolyse a large spectrum of mono- and disaccharides; more complex sugars like cellobiose or starch were hydrolysed only by a small percentage of the CFU. None of the CFU could hydrolyse cellulose. Information which complements the findings on the limited hydrolytic capabilities of the suspended bacterial community is seen in Table 7; the amount of total free sugars comprises only a small proportion of the total DOC, being sometimes below detection limit or present as trace concentrations.

This indicates that the main fraction of the DOC in water consists of polymerized compounds which are difficult to degrade and that the low-molecular-weight fraction is depleted shortly after being released from the sediment or taken up by microorganisms in the sediment layer. Consequently, number and activity of bacteria in the water body are regulated to a large extent by the amount of low-molecular-weight compounds released from the meadow. Since the suspended bacterial community is unable to hydrolyse structural carbohydrates, most of the breakdown processes of the macrophyte material must take place in the sediments. However, in contrast to other sediments, such as the sediment of *Spartina* systems (Andersen & Hargrave 1984, Kepkay & Andersen 1985) where the breakdown of buried leaves results in small DOC release rates (2.8 % of 67 % carbon mineralization), DOC release rates of the *Posidonia oceanica* system are high. Therefore a significant amount of dissolved organic matter, which most of the CFU are unable to utilize, is available for various types of interactions leading to particle formation.

According to Robertson et al. (1982) and Biddanda (1985) high concentrations of DOC and the presence of bacteria are necessary for POM formation, but in contrast to our own measurements, bacteria densities in the experiments of the above mentioned studies were high, ranging from 10^5 to 10^8. Also, bacterial aggregate formation as shown by Biddanda (1985) was observed only occasionally in bell-jar water samples, and most of the particles inspected after acridine orange staining or by SEM were only sporadically colonized by bacteria. For this reason the abiotic physico/chemical processes (Baylor & Sutcliff 1963, Sheldon & Parsons 1967, Riley 1970, Kranck & Milligan 1980, Velimirov 1980) are favoured to explain particle formation in the water column of the *Posidonia oceanica* system.

Recent studies, based on gas chromatography, mass spectrometry and ^{13}C-nuclear resonance spectroscopy (Ittekkot & Degens 1984) reveal that marine DOC is, to a large proportion, of essentially aliphatic nature (Hatcher 1983). Aliphatic molecules are known to display lipid characteristics, and aliphatic fatty acids – also when combined with carbohydrates or amino acids – can behave like surface active agents (Velimirov 1985). Depending on the concentration of the surfactants, these amphiphilic organic compounds with distinct hydrophobic and hydrophilic regions can form association colloids or micelles, and micelle aggregation can form particles from 1 µm to 0.5 mm in size. Also, *in situ* conditions favour organic-inorganic interactions which may be the major controlling factors in the formation of organic-rich aggregates.

Despite a number of studies which have shown that synthesis of macroparticulate matter from DOM functions via interaction of bacteria, the above information, as well as own microscopic observations and the discrepancy between high DOC decrease versus low O_2 consumption in the experimental system, provide evidence for the fact that physical/chemical processes are more important in the *Posidonia oceanica* system in contributing to POM formation than are bacteria.

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