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Impact of *Pestarella tyrrhena* on benthic metabolism in sediment microcosms enriched with seagrass and macroalgal detritus

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ABSTRACT: The impact of *Pestarella* (= *Callianasa*) *tyrrhena* (Decapoda: Thalassinidea), a common burrowing shrimp in the Mediterranean Sea on sediment–water fluxes (O_2, TCO_2, NH_4^+ and NO_3^- + NO_2^-), sediment characteristics (organic matter, chlorophyll *a*) and porewater solutes (TCO_2, NH_4^+ and NO_3^- + NO_2^-) was investigated in laboratory microcosms over a period of 42 d. Microcosms containing homogenised fine sandy sediment were amended with either dead *Posidonia oceanica* leaves or fresh *Ulva lactuca* thalli. Reworking activity by the animal resulted in a rapid burial of surface deposited organic matter into the sediment. Porewater profiles of both TCO_2 and NH_4^+ indicated that *P. tyrrhena* activities result in a significant flushing of porewater solutes. Total sediment metabolism and carbon mineralisation were enhanced in the presence of *P. tyrrhena.* Metabolism of *P. tyrrhena* individuals was approximately 3 times higher in *Ulva*-amended sediment, probably due to a high activity level when nutritious food sources are in excess. Accordingly, animal respiration explained approximately half of the total enhancement in *Ulva*-amended sediment, while microbial decomposition of refractory seagrass detritus contributed about 4 times more to the stimulated carbon mineralisation than animal respiration. Despite the higher initial addition of carbon in *Posidonia*-amended sediment compared to *Ulva*-amended sediment, the amount of excess carbon mineralised was 4.7 times higher in the latter, indicating that mineralisation processes depend on the degradability rather than the quantity of the organic pool. Although *P. tyrrhena* excretion constituted only a minor part of the total nitrogen mineralised, macrofaunal activities were the major factor affecting total nitrogen mineralisation, and not the enrichment with organic matter.

KEY WORDS: Bioturbation · *Pestarella tyrrhena* · *Posidonia oceanica* · *Ulva lactuca* · Benthic fluxes · Nutrient change

INTRODUCTION

The role of benthic macrofauna in modifying coastal sediment properties, metabolism and nutrient exchange has been well documented (Aller et al. 1983, van Duyl et al. 1992, Pelegri & Blackburn 1995, Kristensen 2000). Macroinfaunal structures and activities create a variety of physico-chemical and biological microenvironments with potential impact on the distribution and composition of microbial communities, as well as rates of sediment processes. Sediment particles and organic matter are redistributed by faunal feeding and burrowing activities, whereas mucous secretions and faecal pellet deposition introduce new reactive substrates for microbial decomposition (Aller et al. 1983, Branch & Pringle 1987, Christensen et al. 2000). The presence of deep and complex tubes and burrows, on the other hand, increases the sediment–water surface available for solute exchange (Koike & Mukai 1983, Ziebis et al. 1996). Combined with macrofaunal irrigation effects, such as porewater flushing and introduction of oxygen deeper in the sediment, these structures affect the vertical distribution of diagenetic reactions (Aller 1994, Banta et al. 1999). Various

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burrow-dwelling infauna have been shown to stimulate the total microbial respiration and enhance solute exchange in sediments by 25 to 271% (Kristensen 2000). The stimulatory effect depends on a number of key factors, e.g. faunal density, mobility, size and feeding type, as well as quantity and quality of organic matter (van Duyl et al. 1992, Forster & Graf 1995, Hansen & Kristensen 1998, Banta et al. 1999, Bartoli et al. 2000).

Thalassinidean shrimps represent an important component of the marine benthos in many intertidal and subtidal areas. They have been recognized for their importance as bioturbators with a significant impact on the environment. This includes enhanced sediment turnover, organic matter subduction and nutrient cycling (Waslenschuk et al. 1983, Branch & Pringle 1987, Ziebis et al. 1996, Webb & Eyre 2004), altered structure of benthic bacterial and faunal communities (Berkenbusch et al. 2000, Dworschak 2001) and redistribution of metals and contaminants (Suchanek et al. 1986, Abu-Hilal et al. 1988). *Pestarella* (= *Callianassa*) *tyrrhena* (Petagna, 1972) is the most common thalassinidean shrimp inhabiting sandy and muddy substrates in the lower intertidal and shallow subtidal zones along Mediterranean coasts. *P. tyrrhena* burrows consist of a more or less symmetrical upper U-shaped section and a vertical shaft in the form of a spiral reaching a maximum depth of at least 62 cm (Dworschak 2001). The shaft is characterised by segments of constant diameter linked to wider chambers (turning chambers) and to short side branches. The burrow shape changes over time due to the constant reworking activity by the animal. *P. tyrrhena*, a deposit feeder, takes up sediment from one part of the burrow, feeds for several seconds, and then transports the remaining material into existing branches of the burrow or out to the sediment surface creating characteristic mounds (Dworschak 1987, Kapareliotis 1996). Although comprehensive knowledge exists on *P. tyrrhena* biology, such as burrow structures, population dynamics, reproduction and physiology (Ott et al. 1976, Dworschak 1987, 2001, Thessalou-Legaki et al. 1997, 1999), the effect of this important bioturbator on sediment–water fluxes and porewater solute distribution is almost unknown.

Seagrasses and macroalgae are common sources of organic matter in coastal areas inhabited by thalassinidean shrimps. Burrow chambers of *Pestarella tyrrhena* are often loaded with seagrass detritus that originates either from *in situ* seagrass meadows or material transported from adjacent areas. This detritus is probably used directly or indirectly (by 'gardening') as food (Ott et al. 1976, Dworschak 1987, 2001). *P. tyrrhena* may therefore have an important effect on the food web dynamics in such ecosystems by enhancing decomposition and recycling of the most important source of organic matter (Cebrian & Duarte 2001). Mass occurrence and subsequent collapse of drifting macroalgae, on the other hand, can be a serious problem in eutrophic coastal bays, causing mass mortality of the indigenous flora and fauna (Morand & Briand 1996, Herbert 1999). This serious environmental impact may be alleviated when burrowing infauna is capable of accelerating decomposition processes and, thus, the removal of macroalgal carbon and nitrogen (Hansen & Kristensen 1997, Bartoli et al. 2000).

The aim of the present study was to quantify the impact of the thalassinidean shrimp *Pestarella tyrrhena* on decomposition of organic matter and nutrient exchange in sediments amended with 2 types of commonly encountered plant detritus in coastal areas of the Mediterranean Sea. Mineralisation of fresh, easily degradable, green macroalga *Ulva lactuca* and of dead, more refractory, seagrass *Posidonia oceanica* was followed by monitoring the fluxes of TCO_2, O_2 and dissolved inorganic nitrogen (DIN) species across the sediment–water interface for a period of 42 d. Moreover, the vertical distribution of sediment characteristics and porewater solutes was measured at the end of the experimental period. Our results not only provide information on the effect of *P. tyrrhena* bioturbation on solute fluxes, but also on carbon and nitrogen mineralisation stoichiometry of seagrass and macroalgal detritus in Mediterranean coastal sediments.

MATERIALS AND METHODS

Sediment and animal collection. Sediment, animals and plant material were collected from an intertidal-shallow subtidal sand flat at Vravrona Bay (southern Evoikos Gulf, Aegean Sea) in May 2001. The sediment consisted of moderately organic-rich fine sand (2.2% organic content as loss-on-ignition, LOI), with a medium particle size of 0.2 mm. The mud shrimp *Pestarella tyrrhena* occurs at a mean yearly population density of 63 ± 9 ind. m^{-2}, reaching 144 ind. m^{-2} in some cases (Thessalou-Legaki 1987). Other common, but low in abundance, macrofaunal species found in the area include other thalassinids (*Upogebia pusilla*, *Calliax punica*), polychaetes (*Notomastus latericeus*, *Phylo foetida*, *Microspio mecznikowianus*, *Neanthes caudata*) and amphipods (*Urothoe pulchella*, *Erichthonius brasiliensis*) (Nicolaidou & M. T.-L. unpubl. data). The macrophyte vegetation consists of scattered occurrence of the seagrass *Cymodocea nodosa*, mainly in the outer part of the sand flat (Thessalou-Legaki 1987). Benthic microalgae, on the other hand, are most abundant in the inner part of the sand flat, but contribute only a small part to the sediment organic pool (S. P. et

al. unpubl. data). Dead leaves of another seagrass species, *Posidonia oceanica*, are continuously transported to the area from deeper waters and accumulate on the sand flat, representing the most important carbon source (S. P. et al. unpubl. data). The area is usually characterised by extensive spring blooms of the macroalgae *Ulva lactuca*, covering the largest part of the area. At the sampling time, salinity was 38‰ and the temperature 19°C.

The uppermost 5 to 10 cm of the sediment was gently sieved through a 1.0 mm mesh on location, to remove larger macrofauna species and sediment particles (shell debris and pebbles). Intact specimens of *Pestarella tyrrhena* were captured by use of a 'yabby pump' (Manning 1975). Macrophyte material (dead old leaves of *Posidonia oceanica* and fresh thalli of *Ulva lactuca*, hereafter referred to as *Posidonia* and *Ulva*, respectively) was also collected from the site 3 d later and kept at 4°C. The molar C:N ratio of the plant material was 18.3 and 88.6 for *Ulva* and *Posidonia*, respectively.

Experimental set-up. Before being introduced to the cores, the animals were kept separately in 100 ml plastic containers filled with sediment to acclimatise at the experimental conditions (19°C, 38‰) for 1 wk. The sediment was homogenised 3 d after collection and transferred to 33 cm long and 8 cm i.d. Plexiglas core liners, closed at the bottom with a rubber stopper, to a height of about 20 cm (Day 0). The cores were submerged into a darkened 350 l tank filled with *in situ* seawater. Water in the tank was continuously recirculated by 2 submersible pumps (400 l h^{-1}) and aerated. All cores were supplied with internal magnetic stirrers placed about 8 cm above the sediment, driven by an external rotating magnet at 40 rpm to assure continuous exchange of water between core tubes and the surrounding tank. Pre-amended fluxes were measured in duplicates on Days 2 and 4. Two cores were used for determination of sediment and porewater conditions (IN) before the addition of animals. Subsequently, 1 small *Pestarella tyrrhena* specimen (0.4 to 0.9 g wet wt) was added to each of half of the cores, corresponding to a density of 200 ind. m^{-2}. This density is higher than the maximum reported for natural populations (160 ind. m^{-2}, Dworschak 2001), but cores of larger diameter were impractical for the purposes of this study. However, the small-sized individuals used may have compensated for the high experimental density. The animals immediately dug into the sediment and were allowed to establish burrows for 3 d, an adequate period for completing a burrow with 2 openings (Kapareliotis 1996). The remaining cores were kept as defaunated controls.

Fluxes of bioturbated and non-bioturbated sediment were measured in duplicates on Day 7. Two cores from each treatment were also sacrificed to determine any changes in sediment and porewater conditions after the addition of animals (data not shown). Subsequently, the plant materials were coarsely blended (size range 0.1 to 1 cm) and washed in seawater to remove excess dissolved organic carbon released during blending. Then, 6 cores with and 6 cores without animals were removed from the tank, and 5 g wet wt of blended *Ulva* or 10 g of *Posidonia* detritus (corresponding to 1.0 and 2.0 kg wet wt m^{-2} or 3.7 and 9.3 mol C m^{-2}, respectively) was carefully added to the surface of each core. *Posidonia* detritus added corresponded to the amount of seagrass debris found in the sediment at Vravrona Bay (1.9 kg wet wt m^{-2}) (S. P. et al. unpubl. data). Data on *Ulva* biomass at Vravrona Bay are not available; however, the amount added was at the lower level of *Ulva* spp. biomass reported from macroalgal blooms in many south European coastal areas (Morand & Briand 1996). The above set-up resulted in an experimental scheme with 3 replicates for each of the 6 combinations: control sediment (C), *Ulva*-enriched (CU), *Posidonia*-enriched (CP), bioturbated sediment (B), bioturbated *Ulva*-enriched (BU) and bioturbated *Posidonia*-enriched microcosms (BP). The cores were returned to the tank after settling of the plant material. Thereafter, fluxes were measured at 3 to 5 d intervals until O_2 fluxes returned back to initial pre-amendment levels (Day 42).

Flux measurements. In order to measure fluxes of O_2, TCO_2 and DIN (NO_3^- + NO_2^- and NH_4^+) across the sediment–water interface, cores were sealed and water samples were taken before and after a 3 to 5 h incubation period under continuous stirring. Concentration changes in the overlying water during incubations were assumed linear, since O_2 did not decrease below 60% of air saturation. Water samples for oxygen determination were analysed immediately by the standard Winkler method. TCO_2 samples were transferred to gas-tight Exetainers (Labco, High Wycombe, UK) with no headspace, preserved with a few drops of saturated $HgCl_2$ and kept at 5°C until analysed within 3 mo by the flow injection/diffusion cell technique (Hall & Aller 1992). Water samples for nutrient analysis were filtered through combusted GF/F filters (520°C, 5 h) into 20 ml polyethylene vials, frozen and analysed within 1 to 3 mo. NH_4^+ was determined manually using the salicylate method (Bower & Holm-Hansen 1980), while NO_3^- + NO_2^- (hereafter referred to as NO_3^-) were analysed by the standard autoanalyser method of Armstrong et al. (1967).

Core sectioning. Plant material remaining on the sediment surface at the end of the experimental period was carefully removed with a wide bore pipette, dried and weighed. Subsequently (Days 42 to 45), sediment cores were sliced into 8 depth intervals: 0–1, 1–2, 2–3,

3–4, 6–8, 10–12, 14–16 and 18–20 cm using a piston and a steel plate. A drawback of the chosen sectioning technique in bioturbated sediment was the mixing of the burrow water with the surrounding porewater as burrows collapsed during slicing. Based on burrow volume measurements (data not shown), burrow water accounted for 9 to 30% of the water below the sediment surface. However, since the solute concentrations in each compartment (burrow water and porewater) and at each depth interval are unknown, any estimate of the dilution effect would be unwarranted. Porewater results therefore represent an unknown mixture of burrow water and porewater.

Subsamples of the sediment sections were analysed for porewater and solid phase characteristics: wet sediment density, water content (weight loss after drying at 105°C for 6 h) and organic content as loss-on-ignition (LOI) (combustion at 520°C for 6 h). The concentration of chlorophyll *a* (chl *a*) in the sediment was determined by extracting 2 to 3 g of wet sediment in 5 ml of 90% acetone overnight at 5°C. The extract was centrifuged at 3000 rpm for 10 min, and the supernatant was analysed spectrophotometrically at 665 and 750 nm before and after addition of 2 drops of 2 M HCl (Parsons et al. 1984).

Porewater for TCO_2 and DIN was isolated by centrifuging the remaining sediment at 1500 rpm for 10 min in double centrifuge tubes containing GF/C filters. Samples for TCO_2 were stored in gas-tight vials and analysed as described above, while samples for DIN were additionally filtered through a pre-washed 0.45 µm Millipore HA filter and stored frozen for later analysis. Unfortunately, some of the porewater TCO_2 samples were lost due to storage failure.

Pestarella tyrrhena individuals retrieved unharmed during slicing were used on the same day for respiration and ammonium excretion assays. Animals were washed with seawater and placed individually in 300 ml BOD (biological oxygen demand) bottles containing GF/F-filtered seawater (Thessalou-Legaki et al. 1997). Blank bottles containing only filtered seawater represented water processes. Initial and final O_2 and NH_4^+ concentrations after a 2 h incubation period were analysed as described above. Animals were left to defecate, and released faecal pellets were collected and analysed for particulate organic carbon and nitrogen (POC and PON, respectively) content on a Carlo Erba EA1108 CHN Elemental Analyser (Kristensen & Andersen 1987). The oxygen consumption of faecal pellets released during the incubation was tested in BOD bottles and found to be non-detectable.

Statistical analysis. To test the effects of animal presence (control and *Pestarella tyrrhena* sediment) and addition of organic matter (unamended, *Ulva*, *Posidonia*) on the measured parameters, analysis of variance (ANOVA) was performed. Data were log $(1 + x)$-transformed where necessary to correct for lack of homogeneity of variances. Significant effects were subsequently analysed by performing a Tukey post hoc test (Zar 1984).

RESULTS

General observations

The control sediment (C) maintained a smooth surface throughout the experiment. A visible oxidised zone was present in the upper 2 mm, while the rest of the sediment showed a homogenous, grey-blackish colour. In the detritus-amended and non-bioturbated sediments (CU and CP), plant material present on the sediment surface at the end of the experiment constituted about 25 and 60% of the initial addition of *Ulva* and *Posidonia*, respectively. In the *Ulva*-enriched cores (CU), a black sulphidic layer could be observed between the sediment surface and the remaining plant material.

All *Pestarella tyrrhena* individuals constructed a complete burrow with mound and funnel, and reached the bottom of the sediment cores within a week. During the rest of the experimental period, the animals continued reworking the sediment within the burrow, digging new branches and filling up existing ones for feeding purposes. The mounds were characterised by distinctive layers of displaced brownish and oxidised sediment. An oxidised zone was also evident along the burrow walls, even down to 20 cm depth. In the bioturbated cores, most of the plant material disappeared from the surface after a few days, either buried under the mounds or subducted into the burrows, thus resulting in a mosaic of grey and black sediment from the decomposing detritus. No *Ulva* detritus was macroscopically observed within the sediment of the *Ulva*-enriched cores (BU) during slicing, whereas patches of buried *Posidonia* detritus were clearly visible in distinct chambers or in burrow walls of the *Posidonia*-enriched cores (BP).

Sediment characteristics

LOI was unaffected by the presence of *Pestarella tyrrhena* when no detritus was added to the sediment (Fig. 1). In the *Ulva*-amended sediment, *P. tyrrhena* caused a slight (3 to 16%) decrease in LOI from 3 to 16 cm depth, while an increase of similar magnitude (4 to 15%) was observed in the *Posidonia* treatment.

Sediment chl *a* content at the end of the experiment was lower than initial values in all treatments (Fig. 1). As

for LOI, chl *a* showed no significant difference between bioturbated and non-bioturbated unamended treatments. In amended sediment, *Pestarella tyrrhena* caused generally a decrease in chl *a* (5 to 40%). An increase (18%) in both LOI and chl *a* was observed around 2.5 cm depth in *Ulva*-amended bioturbated sediment.

Porewater profiles

TCO_2 increased with depth in all 3 types of non-bioturbated sediment (C, CU, CP) at the end of the experiment (Fig. 2), from about 3 mM in the water column to a more or less steady level of 10 to 13 mM below 7 to 10 cm depth in the sediment. The presence of *Pestarella tyrrhena* caused a dramatic reduction in porewater TCO_2 compared with both initial and final non-bioturbated sediments. TCO_2 concentrations increased only slightly with depth (most conspicuous in the upper 1 to 2 cm) in all 3 bioturbated treatments (B, BU, BP), reaching 4 to 6 mM at 18 to 20 cm depth.

Porewater ammonium showed almost the same profiles as TCO_2 (Fig. 2). All non-bioturbated sediments exhibited a prominent NH_4^+ increase with depth from about 0.1 mM at the sediment surface to a level of 1.3 to 1.5 mM below 7 to 10 cm depth, whereas in the bioturbated sediments NH_4^+ increased rapidly only in the upper 1 to 2 cm and reached levels of 0.2 to 0.5 mM in deeper layers.

Nitrate concentration in the overlying water column increased after Day 21 from 0.5 to 14 µM by the end of the experiment (data not shown). NO_3^- concentrations in porewater, on the other hand, were rather low at the end of the experimental period, showing a significant reduction from the overlying water level to just a few micromolar below the sediment surface in all treatments (Fig. 2). The steepness of this reduction was most pronounced in the detritus-amended cores.

Sediment–water fluxes

The introduction of *Pestarella tyrrhena* to the unamended microcosms led to a dramatic and immediate increase in both O_2 uptake and TCO_2 release as depicted by a 3- and 4-fold difference, respectively, between bioturbated and non-bioturbated treatments on Day 7 ($p < 0.001$) (Fig. 3). Subsequently, fluxes remained relatively constant throughout the experimental period. Bioturbated microcosms (B) showed a mean O_2 uptake after Day 21 of 52 mmol m^{-2} d^{-1} and a TCO_2 efflux of 92 mmol m^{-2} d^{-1} as compared to 32 mmol m^{-2} d^{-1} and 52 mmol m^{-2} d^{-1}, respectively, in the non-bioturbated microcosms (C) (Table 1).

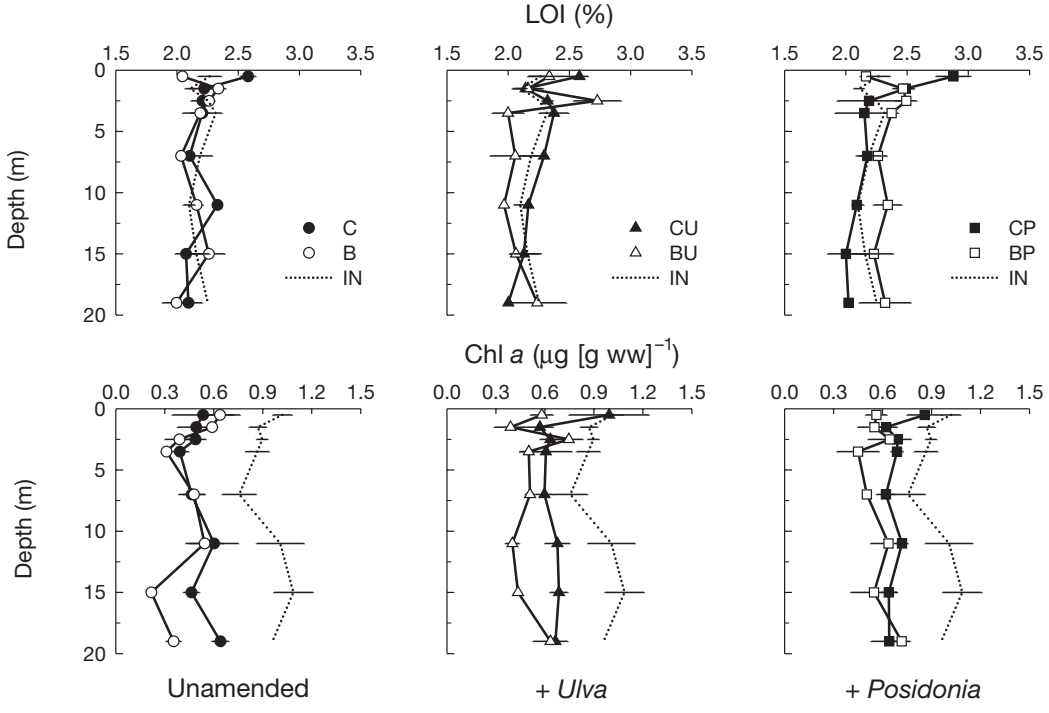

Fig. 1. Vertical profiles of organic matter (LOI, loss-on-ignition) and chl *a* in initial treatment (IN) and unamended (C, B), *Ulva lactuca* (CU, BU) and *Posidonia oceanica* detritus treatments (CP, BP) with (open symbols) and without (solid symbols) *Pestarella tyrrhena* after 42 d. Values represent mean ± SE (n = 2 to 3)

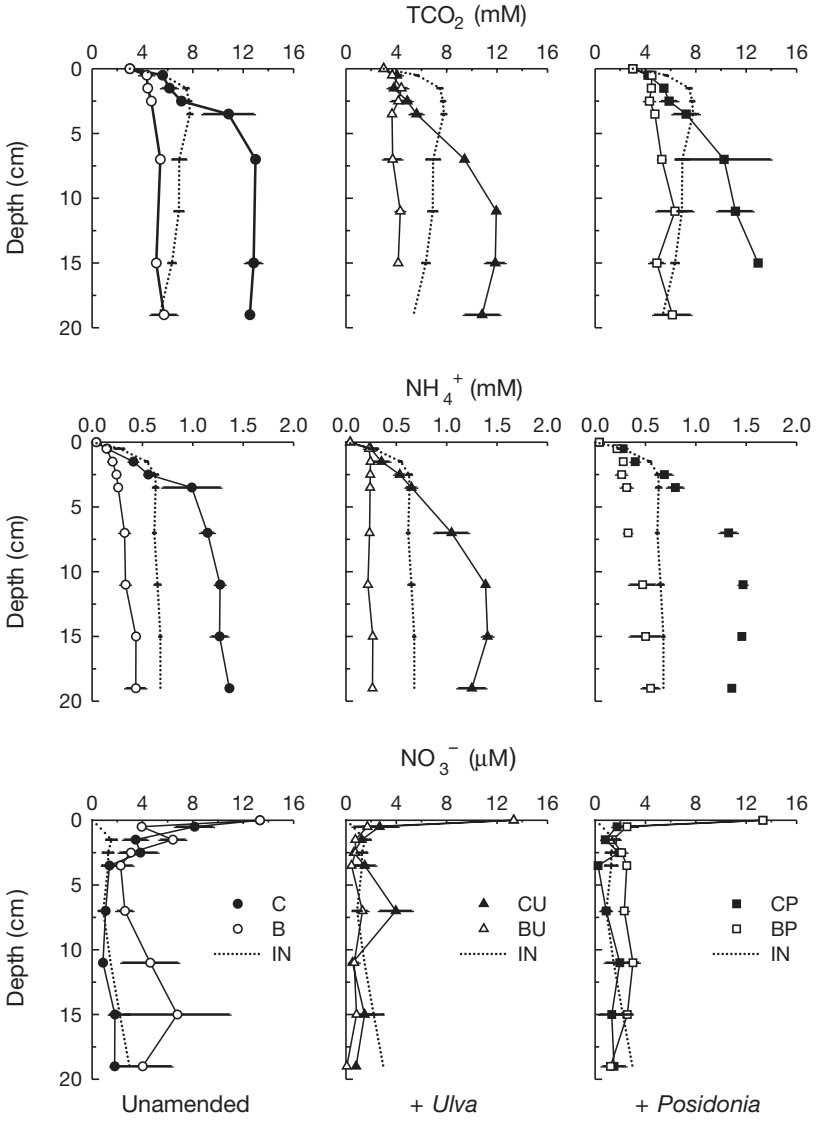

Fig. 2. Vertical profiles of porewater TCO_2, NH_4^+ and NO_3^- in initial treatment (IN) and unamended (C, B), *Ulva lactuca* (CU, BU) and *Posidonia oceanica* detritus treatments (CP, BP) with (open symbols) and without (solid symbols) *Pestarella tyrrhena* after 42 d. Values represent mean ± SE (n = 2 to 3)

The addition of *Posidonia* detritus to the bioturbated sediment (BP) resulted in an immediate, but slight increase (factor of 1.2) of O_2 uptake with only limited changes for most of the remaining experimental period. In the non-bioturbated microcosms (CP), on the other hand, the detritus caused an instant doubling of O_2 uptake, which subsequently decreased gradually to the initial level. TCO_2 efflux remained initially unaffected by the addition of *P. oceanica* detritus, irrespective of the presence or absence of *P. tyrrhena*, showing an increasing trend with time in the non-bioturbated sediment.

The community respiratory quotient (CRQ: CO_2 production/O_2 consumption) was calculated from the ratio of the average fluxes of CO_2 and O_2 after the establishment of relative steady-state conditions from Day 21 onwards (Hansen & Kristensen 1997, Banta et al. 1999). The CRQ values were always >1 (Table 1). Addition of *Posidonia* resulted in a 45% increase of CRQ, while no such effect was evident in *Ulva*-amended sediment. The presence of *Pestarella tyrrhena* increased CRQ in the unamended and *Ulva*-enriched treatments by 10 to 20%, whereas in the *Posidonia* treatment CRQ exhibited a 20% reduction.

Ammonium fluxes showed a similar pattern in all bioturbated sediments: a 4-fold increase immediately after the addition of animals, followed by a rapid decrease during the next 3 to 6 d (Fig. 4). Subsequently, the release of NH_4^+ ceased more gradually, reaching rates near or below the initial level (2 to 3 mmol m^{-2} d^{-1}). In the control sediment (C), on the other hand, NH_4^+ fluxes turned negative after Day 14 and remained with some fluctuation around a mean net uptake of 3.6 mmol m^{-2} d^{-1} during the rest of the experimental period. Both *Ulva*- and *Posidonia*-enriched and non-bioturbated microcosms (CU, CP) generally showed a low but steady release of ammonium from the sediment, with a mean rate of 1.7 and 1.4 mmol m^{-2} d^{-1}, respectively.

The addition of *Ulva* detritus caused an instant (within 4 d) 5- and 2.4-fold increase in O_2 and TCO_2 fluxes, respectively, in the non-bioturbated cores (CU), and a 2-fold increase within 10 d for both solutes in the bioturbated cores (BU). Subsequently, the O_2 uptake decreased gradually in both bioturbated and non-bioturbated microcosms, reaching about half of its maximum value at the end. TCO_2 release from the bioturbated sediment decreased rapidly after the peak, whereas the non-bioturbated, *Ulva*-amended sediment exhibited a rather constant TCO_2 flux over time.

After an initial lag phase, where no net exchange occurred, a steadily increasing NO_3^- efflux was observed in unamended sediment, both with and without *Pestarella tyrrhena* (C, B) (Fig. 4), showing a maximum of 6 and 4 mmol m^{-2} d^{-1}, respectively, at the end. The *Ulva*-enriched and non-bioturbated treatment

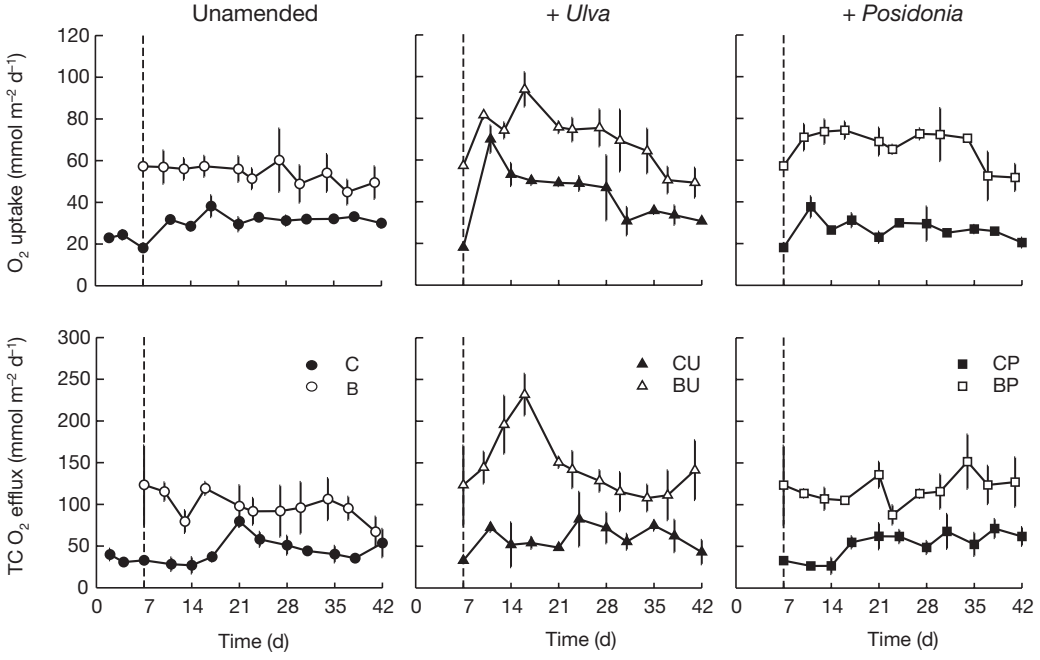

Fig. 3. Oxygen uptake and TCO_2 release during the experimental period, in the unamended (C, B), *Ulva lactuca* (CU, BU) and *Posidonia oceanica* detritus treatments (CP, BP) with (open symbols) and without (solid symbols) *Pestarella tyrrhena*. Values represent mean ± SE (n = 2 to 3). Animals were added on Day 4. Dashed line corresponds to the day of detritus addition (Day 7)

(CU), on the other hand, rarely exhibited any net exchange, while bioturbation caused a slightly increasing influx towards the end of the experimental period (–1 mmol m^{-2} d^{-1}). Also, both bioturbated and non-bioturbated microcosms enriched with *Posidonia oceanica* detritus showed a low and progressively increasing flux directed into the sediment.

Animal metabolism

The respiration of *Pestarella tyrrhena* individuals after 38 d in the non-enriched and in the *Posidonia*-enriched microcosms was similar (3.1 ± 0.3 and 3.9 ± 0.4 µmol O_2 g wet wt^{-1} h^{-1}, respectively). A much higher value of 12.1 ± 2.2 µmol O_2 g wet wt^{-1} h^{-1} was recorded for the animals from the *Ulva*-enriched treatment ($p < 0.01$). Ammonium excretion rates, on the other hand, did not show any significant differences between the 3 treatments (0.36 ± 0.12, 0.38 ± 0.19 and 0.12 ± 0.08 µmol NH_4^+ g wet wt^{-1} h^{-1} in B, BU and BP, respectively) ($p > 0.05$), although the latter (BP) tended to be lowest. The C:N ratio of faecal pellets tended to be lowest for the animals from the *Ulva*-enriched sediment (24.0 ± 1.7), compared with non-exposed and *Posidonia*-exposed animals (27.3 ± 0.4 and 28.6 ± 1.7). However, these differences were not statistically significant ($p > 0.05$).

Total mineralisation and stoichiometry of reactions

Total carbon and nitrogen mineralisation was calculated as the sum of time-integrated fluxes from Day 4 to the end of the experimental period and the simultaneous accumulation of porewater solutes. NO_3^- accumulation in the sediment was insignificant and is ignored.

Bioturbation significantly affected carbon mineralisation (bioturbated vs non-bioturbated, $p \ll 0.001$), as indicated by a 1.8 to 2.2 times higher TCO_2 generation

Table 1. Benthic fluxes (O_2 and TCO_2) and community respiratory quotient (CRQ) for the benthic community from Day 21 to the end of the experimental period (mean ± SE, n = 3). Values in parentheses represent the change (%) relative to the corresponding control (CU, CP and B vs C, BU vs CU, BP vs CP). Statistically significant differences are noted with asterisks ($^*p < 0.05$, $^{**}p < 0.01$)

Treatment	O_2 uptake (mmol m^{-2} d^{-1})		TCO_2 efflux (mmol m^{-2} d^{-1})		CRQ
C	31.5 ± 1.2		51.8 ± 3.6		1.64
CU	39.3 ± 1.5	(+25)*	62.6 ± 5.0	(+21)	1.60
CP	25.6 ± 1.0	(–19)*	60.8 ± 3.1	(+18)	2.38
B	52.1 ± 7.6	(+65)	92.3 ± 7.6	(+78)**	1.82
BU	65.6 ± 6.7	(+67)*	128.1 ± 8.0	(+105)**	2.00
BP	64.8 ± 4.6	(+153)**	122.1 ± 3.7	(+101)**	1.90

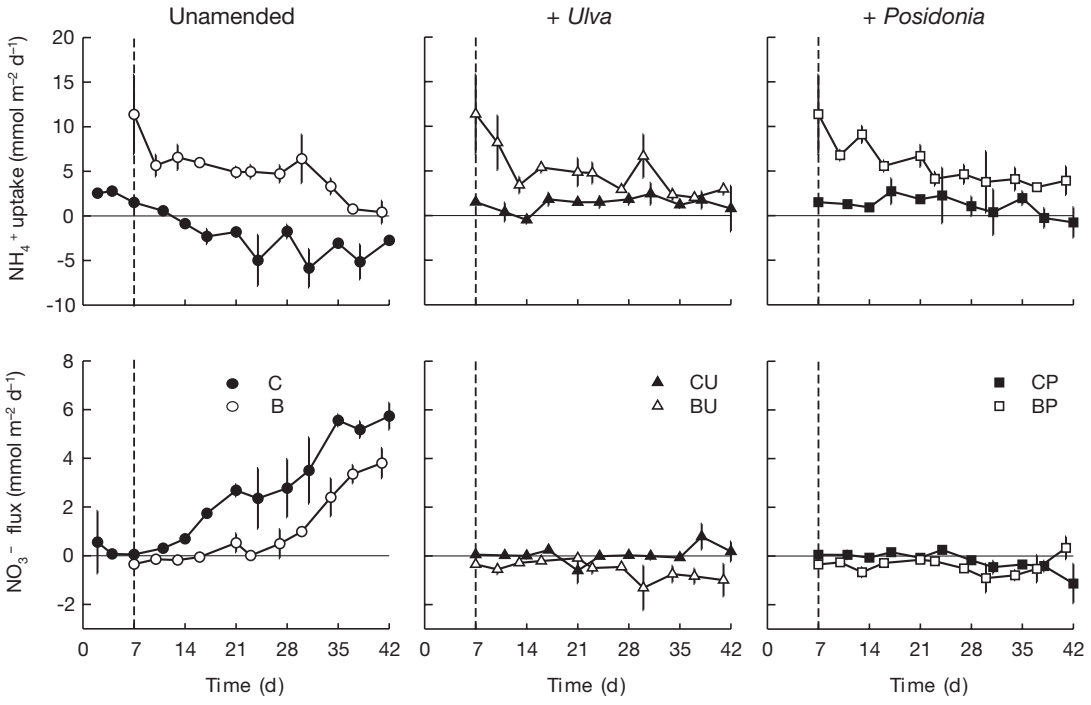

Fig. 4. Ammonium and NO_3^- flux during the experimental period, in the unamended (C, B), *Ulva lactuca* (CU, BU) and *Posidonia oceanica* detritus treatments (CP, BP) with (open symbols) and without (solid symbols) *Pestarella tyrrhena*. Values represent mean ± SE (n = 2 to 3). Animals were added on Day 4. Dashed line corresponds to the day of detritus addition (Day 7)

in the presence of *Pestarella tyrrhena* (Fig. 5). Among the defaunated sediment treatments, mean carbon mineralisation was similar ($p > 0.05$), irrespective of the addition or type of the organic matter, whereas in the presence of *P. tyrrhena* significantly higher TCO_2 generation ($p < 0.001$) was observed in the amended microcosms compared to unamended ones.

Total nitrogen mineralisation was also highest (1.8 to 4.8 times) in the presence of *Pestarella tyrrhena* (bioturbated vs non-bioturbated, $p \ll 0.001$) (Fig. 5). No statistically significant difference was evident between defaunated microcosms ($p > 0.05$), while *Ulva*-enriched bioturbated sediment (BU) exhibited significantly lower DIN generation ($p < 0.05$) than unamended bioturbated (B) sediment.

CO_2 production by *Pestarella tyrrhena* was estimated from the measured oxygen consumption. Benthic macrofauna respiratory quotient (RQ) theoretically ranges from 0.7 to 1.0, depending on the metabolic fuel used. Assuming an RQ of 1.0 (Hatcher 1989), animals accounted for 21 to 28% of the enhanced CO_2 production in the non-enriched (B) and *Posidonia*-enriched treatments (BP), while the animal contribution was much higher (47%) in the *Ulva*-enriched (BU) sediment (Table 2). The microbial contribution, derived as the difference between total community CO_2 produc-

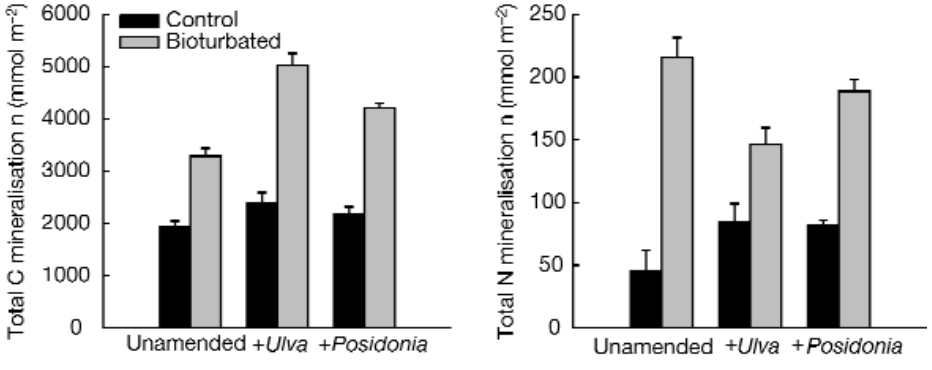

Fig. 5. Total integrated carbon and nitrogen mineralisation over the whole experimental period in the unamended treatment, *Ulva lactuca* and *Posidonia oceanica* detritus-amended treatments, with and without *Pestarella tyrrhena*. Values represent mean ± SE (n = 3)

tion and *P. tyrrhena* respiration, was highest in the *Posidonia*-enriched (79%) and lowest in the *Ulva*-enriched sediment (53%).

The C:N ratio of mineralised organic matter in the sediment was estimated from the slope of CO_2 versus NH_4^+ porewater profile plots ($\Delta CO_2/\Delta NH_4^+$), taking into consideration that the transport coefficients of the 2 solutes (D_C/D_N) relate to production rates (R) according to Kristensen & Hansen (1999): $R_c/R_n = (\Delta CO_2/\Delta NH_4^+) \times (D_c/D_n)$. The basic assumptions are: (1) decomposition must follow first-order kinetics, (2) there must be no accumulation of dissolved organic carbon, (3) microbial reaction rates must be constant with depth below 1 cm, (4) transport conditions are depth-independent in bioturbated sediment. Any potential effect of denitrification is ignored. The ratio D_c/D_n ranges from 0.6 when molecular diffusion dominates to 1.0 when advective transport dominates. The mineralisation C:N ratios derived in the non-bioturbated sediment, assuming no porewater advection, ranged from 3.4 (CP) to 4.6 (C) (Table 3). The C:N ratios in bioturbated sediment range from 2.9 (BU) to 4.9 (BP), when it is assumed that advective transport dominates (Kristensen & Hansen 1999). The sediment–water fluxes, on the other hand, revealed C:N ratios ranging from 14.7 (B) to 30.9 (BU) in the *Pestarella tyrrhena* treatments and from 44.4 (CP) to 78.3 (C) in the non-bioturbated treatments (Table 3).

Table 2. Average daily total community CO_2 production, *Pestarella tyrrhena* respiration and estimated microbial metabolism (mean ± SE, n = 3). Total community CO_2 production was calculated from the total carbon mineralisation from Day 4 to the end of the experimental period. Microbial respiration was estimated as the difference between total community and *P. tyrrhena* CO_2 production. *P. tyrrhena* and microbial contribution to the total enhancement represents the increase (%) of total CO_2 production due to animal and microbial respiration, respectively, compared to the control treatments (B vs C, BU vs CU and BP vs CP)

Treatment	CO_2 production (mmol m^{-2} d^{-1})			Contribution to enhancement (%)	
	Total	*P. tyrrhena*	Microbial	*P. tyrrhena*	Microbial
C	49.0 ± 2.6		49.0 ± 2.6		
CU	60.7 ± 5.5		60.7 ± 5.5		
CP	55.4 ± 3.5		55.4 ± 3.5		
B	88.9 ± 4.1	10.4 ± 2.1	78.4 ± 6.0	+28	+72
BU	135.9 ± 6.0	34.9 ± 3.6	101.1 ± 7.7	+47	+53
BP	114.0 ± 2.3	12.0 ± 1.8	102.0 ± 3.4	+21	+79

DISCUSSION

Experimental considerations

Macrofaunal activities can have a significant effect on solute exchange across the sediment–water interface and porewater distribution within sediments (Aller et al. 1983, Ziebis et al. 1996, Webb & Eyre 2004). The consequences of bioturbation are often difficult to assess by field studies, due to heterogeneity with respect to abundance and composition of macrofauna as well as sediment structure and organisation. Moreover, the lack of adequate control areas without macrofaunal involvement hampers the direct evaluation of bioturbation. Manipulated sediment microcosms, on the other hand, allow the establishment of homogeneous experimental environments with controlled abundances of macrofauna (van Duyl et al. 1992). However, handling of sediment, such as sieving and homogenising, will temporarily destroy its natural chemical and biological stratification (Lanzegaal et al. 2003). In the present experiment *Pestarella tyrrhena* was kept within the limited space of a (8 × 20 cm) sediment core, which must have affected the natural burrow construction activities of the animals. As these animals construct complex, multi-chambered burrows reaching deep into the sediment (Dworschak 2001), the obtained results cannot be directly extrapolated to *in situ* conditions. Despite these limitations, the present experimental set-up can provide important information on the impact of this burrowing organism and demonstrate how it affects benthic metabolism and nutrient exchange across the sediment–water interface.

Faunal impact on sediment properties and transport conditions

Pestarella tyrrhena is an active bioturbator that excavates new and fills up existing branches of the burrow by selectively transporting sediment material within

Table 3. Stoichiometry of dissolved inorganic carbon and nitrogen in the porewater pool and the fluxes, and estimated denitrification rates. Calculations to obtain denitrification rates are explained in 'Discussion'

Treatment	Porewater C:N (R_c/R_n)	C:N flux ratio (TCO_2/DIN)	Denitrification rates (mmol N m^{-2} d^{-1})
C	4.6	78.3	8.8
CU	4.5	54.1	11.1
CP	3.4	44.4	13.0
B	3.9	14.7	16.6
BU	2.9	30.9	38.7
BP	4.9	21.0	16.4

the burrow tunnels or out to the sediment surface (Dworschak 1987, Kapareliotis 1996). At the same time, the funnel-shaped burrow opening acts as a trap for drifting macroalgal debris and seagrass detritus, which either passively fall into the burrow or are actively subducted from the opening by *P. tyrrhena* and transported deep into the burrow (Dworschak 1987, 2001). Such translocation and incorporation of surface-deposited organic matter into the sediment was probably evident from the increase in subsurface LOI (Fig. 1) and the observed presence of seagrass detritus in burrow chambers of the *Posidonia*-amended sediment. In the *Ulva*-amended treatment, on the other hand, subsurface LOI and chl *a* were low and may indicate a priming effect (Aller 1994, Kuzyakov et al. 2000), i.e. introduction of easily degradable *Ulva* detritus not only resulted in a rapid decomposition of the detritus itself, but also of the bulk sediment organic matter.

The elevated LOI and chl *a* around 2.5 cm depth in the *Ulva*-amended treatment corresponded to the initial sediment surface. Surface detritus was buried by the continuous ejection of sediment through the mound opening during burrow construction and sediment reworking, which means that an average of 3.2 cm^3 $ind.^{-1}$ d^{-1} sediment was ejected. This rough estimate is lower than the 7 and 25 cm^3 $ind.^{-1}$ d^{-1} previously reported for burrow maintenance by *P. tyrrhena* (Ott et al. 1976, Kapareliotis 1996), but slightly higher than the 1.1 to 1.7 cm^3 $ind.^{-1}$ d^{-1} found for *Callianassa subterranea* (Witbaard & Duineveld 1989, Stamhuis et al. 1997). However, straightforward comparisons are difficult due to differences in the experimental set-up, data collection, calculation and expression methods of sediment turnover estimates (Rowden & Jones 1993).

Burrowing organisms irrigate their burrows to maintain an oxic environment for respiration purposes. Thalassinidean shrimps typically show intermittent irrigation (Foster & Graf 1995, Stamhuis et al. 1996). Since thalassinid burrows are enriched in nutrients compared to overlying water, it has been argued that the frequency and intensity of irrigation events are not sufficient to keep walls of the entire burrow in contact with oxygenated water (Koike & Mukai 1983, Waslenchuk et al. 1983, Forster & Graf 1995). Although the method we used for porewater extraction could not distinguish between burrow water and porewater, the almost vertical porewater profiles (Fig. 2) indicate that *Pestarella tyrrhena* activities result in a significant flushing of porewater solutes. Ziebis et al. (1996) found a comparable decrease in porewater ammonium concentrations near *Callianassa truncata* burrows *in situ*, when compared to adjacent non-bioturbated sediment, suggesting that *C. truncata* irrigation may affect a sediment column with a radius of at least 5 cm around each burrow.

Christensen et al. (2000) argued that the usually linear relationship between porewater solute (TCO_2 or NH_4^+) profiles in defaunated and bioturbated sediment provides a measure of the excess transport caused by bioirrigation. When the basic assumptions (i.e. depth-independent and constant reaction rates; depth-independent transport conditions in the bioturbated sediment) are accepted, slopes <1 indicate faster removal of solutes due to animal irrigation than by molecular diffusion. The slopes derived from relationships between non-bioturbated and *Pestarella tyrrhena* bioturbated sediment using TCO_2 and NH_4^+ porewater profiles (Fig. 6) were all considerably <1, indicating that irrigation significantly affected transport conditions in *P. tyrrhena* treatments. The irrigation-derived transport appears to be higher in sediment amended with *Ulva* detritus than in unamended and *Posidonia*-amended sediment. When the relationship between irrigation rate and porewater slopes provided by

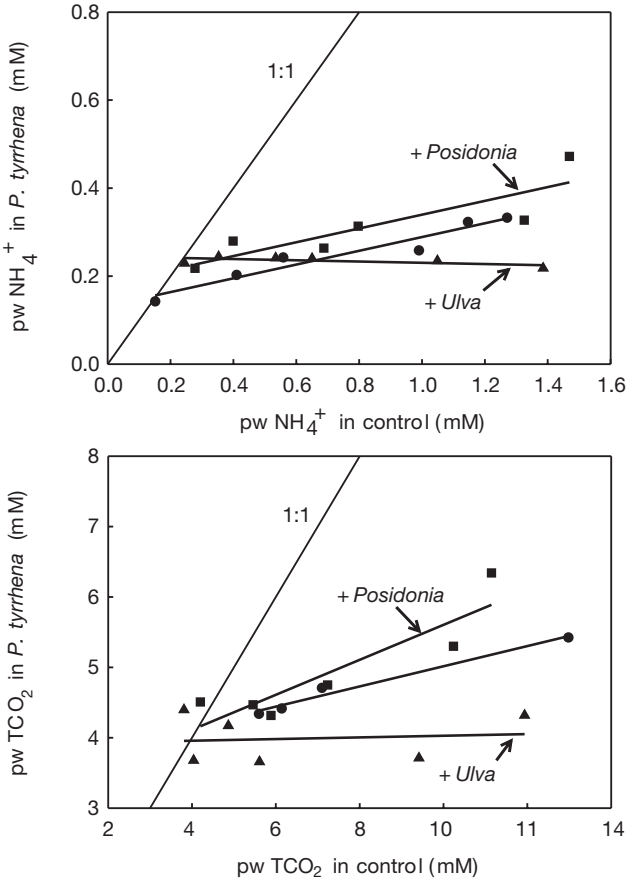

Fig. 6. Porewater concentration plots of TCO_2 and NH_4^+ in the control sediments versus the *Pestarella tyrrhena*-inhabited sediment in the unamended treatment (●), *Ulva lactuca* (▲) and *Posidonia oceanica* (■) detritus amended treatments. Solid line corresponds to a 1:1 relation. Least-squares regression lines are shown

Christensen et al. (2000) for 2 species of *Nereis* in sandy sediment is applied to *P. tyrrhena*, a crude estimate of its irrigation can be deduced. It appears that irrigation by *P. tyrrhena* in *Ulva*-amended sediment is 4 to 6 times more intense (3000 to 6300 l m^{-2} d^{-1}) than in *Posidonia*-amended (400 to 1300 l m^{-2} d^{-1}) and unamended (1000 to 1300 l m^{-2} d^{-1}) sediment. The irrigation estimates for *P. tyrrhena* in *Posidonia*-amended and unamended sediment are comparable to those of other mud shrimps, when differences in abundance are considered (Dworschak 1981, Gust & Harrison 1981, Koike & Mukai 1983, Webb & Eyre 2004).

Faunal impact on carbon mineralisation

The presence of *Pestarella tyrrhena* enhanced total sediment metabolism and carbon mineralisation, as indicated by the increased CO_2 efflux and O_2 uptake. Enhanced sediment oxygen uptake of similar magnitude has been reported previously for other thalassinidean shrimps, such as *Callianassa subterranea*, *Callianassa truncata*, *Nihonotrypaea* (= *Callianassa*) *japonica* and *Trypaea australiensis* (Koike & Mukai 1983, Forster & Graf 1995, Ziebis et al. 1996, Webb & Eyre 2004). The enhancement is usually the combined effect of animal metabolism, irrigation activities and stimulation of respiration by the resident microbial community (Kristensen 2000).

The irrigation effect on CO_2 flux was clearly evident during initial burrow construction, and resulted from an immediate efflux due to porewater flushing of accumulated CO_2. Thus, summed CO_2 release in the unamended bioturbated treatment was increased by 231 mmol m^{-2} from Day 4 to Day 7, while the porewater lost 174 mmol CO_2 m^{-2} during the same period. However, only a fraction of the excess 57 mmol m^{-2} of CO_2 production in the non-enriched microcosms can be attributed directly to animal respiration (28%). The enhanced CO_2 production was instead largely devoted to the stimulated microbial respiration caused by macrofaunal activities. Microbial metabolism is known to be affected by translocation of particles, secretion of mucous substances, removal of inhibitory metabolites and introduction of oxygen into the burrows (Aller 1994, Pelegri & Blackburn 1995, Banta et al. 1999, Kristensen 2001).

Carbon mineralisation was affected most by *Pestarella tyrrhena* in the presence of *Ulva* detritus. The enhancement was primarily due to increased animal respiration, which constituted about 47% of the total stimulation. The high metabolic rate of *Pestarella tyrrhena* in *Ulva*-amended sediment corresponds well with the very high irrigation rates, as estimated above for this treatment, and is probably due to a high overall activity level when nutritious food sources are in excess. The microbial decomposition of old and refractory seagrass detritus, on the other hand, contributed about 4 times more to the stimulated carbon mineralisation than animal respiration (Table 2). These results indicate a differential interaction between *P. tyrrhena* and sediment microorganisms when they are offered detritus of different lability. As shown for other detritivores, fresh and labile detritus is assimilated more easily than refractory detritus, leading to a relative increase in faunal metabolism (Tenore et al. 1982, Kristensen et al. 1992). *P. tyrrhena* is a deposit feeder that ingests and assimilates both detritus and microbes from the sediment environment (Dworschak 1987). In the presence of *Ulva*, *P. tyrrhena* probably competes with sediment microbes for this labile detritus. In fact, large pieces of macroalgal detritus have been found in the stomach of thalassinidean shrimps (Dworschak 1987, Boon et al. 1997). On the other hand, microbial degradation of old and refractory detritus, such as *Posidonia* detritus, is stimulated more profoundly by macrofaunal activities (Kristensen 2001), in which case microorganisms may constitute a large proportion of its food source. Accordingly, it has been suggested that *P. tyrrhena* is actively 'gardening' bacteria for feeding purposes in burrow chambers filled with seagrass detritus (Ott et al. 1976, Dworschak 1987, 2001).

Despite the higher microbial stimulation and the 2.5 times higher initial availability of carbon in the seagrass-amended microcosms, total carbon mineralisation was highest in the *Ulva*-enriched sediment (Fig. 5). Approximately 47% of the excess carbon added initially was mineralised in the *Ulva*-enriched microcosms, while only 10% was degraded in *Posidonia*-enriched microcosms. This difference clearly suggests that mineralisation processes depend on the degradability rather than the quantity of the organic pool (Westrich & Berner 1984, Hansen & Kristensen 1998). The relatively high content of cellulose and lignin in seagrass detritus apparently hampers microbial degradation compared with macroalgae low in structural carbohydrates (Enriquez et al. 1993). Microbial communities in the sediment therefore need a longer time to colonise and effectively degrade seagrass detritus. This is supported by the relatively low, but stable CO_2 fluxes in the *Posidonia*-enriched microcosms throughout the experiment.

The community respiratory quotient is an indicator of the coupling between anaerobic carbon mineralisation (e.g. sulphate reduction) and reoxidation of reduced metabolites (e.g. sulphide). Values >1, as those found in the present study (Table 1), indicate a non-steady-state system, in which reduced metabolites accumulate (e.g. iron sulphides) within the sediment (Canfield et al. 1993). In the non-bioturbated

sediment added organic matter was decomposed at the sediment surface, but only the upper part of the detritus layer was in direct contact with oxygen. Most of the detritus was probably degraded anaerobically, as evident from the development of a black sulphidic layer at the bottom of the *Ulva* detritus layer (Nedergaard et al. 2002). Similarly, the decreased influx of oxygen to the *Posidonia*-enriched sediment suggests that the detritus layer acted as a diffusion barrier leading to anoxia and accumulation of metabolites. The high CRQ in bioturbated sediment is probably a consequence of detritus translocation deep into the sediment by the macrofauna, where anaerobic decomposition predominates and accumulation of metabolites occurs.

Faunal impact on nitrogen transformations

Macrofaunal activities (e.g. irrigation and translocation of material) have a significant impact on reactions affecting nitrogen in sediments, such as ammonification, nitrification and denitrification (Kristensen 1988, Pelegri & Blackburn 1995, Hansen & Kristensen 1997). As found here for *Pestarella tyrrhena*, the efflux of ammonium usually increases instantly from sediments after the introduction of macrofauna due to porewater flushing. Subsequently, the efflux decreases to a lower, but a stable level. Although *P. tyrrhena* excretion constituted only a minor part of the total nitrogen mineralised in the present experiment, it appears that the macrofaunal activities are the major factor affecting nitrogen transformations, and not the enrichment with organic matter.

When the carbon and nitrogen stoichiometry of the organic matter actually being mineralised in the sediment is derived from porewater profiles of TCO_2 and NH_4^+, the results are usually different from those of the bulk organic pool in the sediment (Aller et al. 1983, Kristensen & Hansen 1999). A similar pattern was obtained from both the defaunated and the *Pestarella tyrrhena*-inhabited sediment, and indicates a preferential microbial mineralisation of organic nitrogen (Hansen & Kristensen 1997, Christensen et al. 2000). A labile source of nitrogen was probably microalgae mixed into the sediment (diatoms C:N ≈ 7, Enriquez et al. 1993) during the initial sediment handling (Sloth et al. 1995, Bartoli et al. 2000, Christensen et al. 2000), since the C:N ratios of both types of plant detritus added were significantly higher. C:N ratios determined from effluxes across the sediment–water interface were considerably higher than those derived from the porewater pools, indicating nitrogen incorporation into bacterial biomass utilising high C:N substrates (Pedersen et al. 1999) or loss of nitrogen via denitrification (Pelegri & Blackburn 1995).

Nitrate fluxes in the unamended treatments, which were negatively related to those of ammonium, are affected by sources such as nitrification, and sinks such as assimilation, denitrification and dissimilatory NO_3^- reduction to ammonium. The net influx of ammonium in the defaunated control of the same magnitude as the NO_3^- efflux shows that the internal supply of ammonium was insufficient to support nitrification. However, the net release of NO_3^- from the unamended treatments shows that nitrification within the sediment actually exceeded denitrification. The initial time lag in NO_3^- efflux must be attributed to the generally slow growth rate of nitrifying bacteria (Henriksen & Kemp 1988). The much longer time-lag in the *Pestarella tyrrhena* sediment compared with the defaunated treatment was probably due to the disturbance caused by the construction of the burrow; nitrifying bacteria were not allowed sufficient time to grow at oxic interfaces before new interfaces were created. Furthermore, denitrification is known to be stimulated more than nitrification by the presence of macrofauna, which results in a lower NO_3^- efflux (Kristensen 1988, Pelegri & Blackburn 1995, Bartoli et al. 2000, Webb & Eyre 2004). Addition of detritus to the sediment resulted in no or slightly negative net fluxes of NO_3^-, as a result of stimulated denitrification and/or lowered nitrification (Sloth et al. 1995, Hansen & Kristensen 1998). Nitrifying bacteria were probably limited by oxygen availability or inhibited by the presence of sulphide (Henriksen & Kemp 1988, Sloth et al. 1995).

A crude estimate of denitrification can be obtained from the difference between the theoretical DIN fluxes, based on measured carbon release and porewater C:N ratio, and measured DIN fluxes (Hansen & Kristensen 1997) according to: $D = [C_{flux}/(R_c/R_n)] - N_{flux}$, where D is the denitrification rate, while C_{flux} and N_{flux} are the measured TCO_2 and DIN fluxes, respectively (mmol m^{-2} d^{-1}). The estimated denitrification rates ranged from 8.8 to 13.0 mmol N m^{-2} d^{-1} in the non-bioturbated sediment, while rates in the treatments with *Pestarella tyrrhena* were slightly higher for the unamended and *Posidonia*-enriched treatments (16.6 and 16.4 mmol N m^{-2} d^{-1}, respectively) and 2.5 times higher for the *Ulva*-enriched sediment (38.7 mmol N m^{-2} d^{-1}), suggesting a significant effect of the macrofauna (Kristensen 1988, Pelegri & Blackburn 1995, Bartoli et al. 2000, Webb & Eyre 2004), in particular, for the sediment enriched with labile detritus. These rates are in the upper range of values reported for coastal and estuarine sediments (Table 7 in Herbert 1999), and characterise shallow nearshore waters, where the supplies of organic carbon and NO_3^- runoff are high.

Conclusions — ecological importance

Pestarella tyrrhena has significant influences on benthic metabolism and nutrient exchange across the sediment–water interface. Total carbon and nitrogen mineralisation are increased about 2-fold. The enhancement is due to activities such as sediment reworking, irrigation and animal metabolism. Organic matter deposited at the surface was buried under the ejected sediment from the burrow or subducted and incorporated into burrow chambers. Animal irrigation introduces oxygen deeper into the sediment and removes porewater solutes, resulting in a stimulation of the sediment microbial community respiration. Total carbon mineralisation was enhanced more in sediment amended with *Ulva* detritus than *Posidonia* detritus. The stimulation in the former case was to a large extent due to increased animal respiration, whereas in the latter case the stimulation was caused by increased microbial decomposition. These results indicate that the different nutritious values of the 2 types of detritus affect their availability to animals and microorganisms and cause a differential utilisation by these organisms. Organic matter enrichment irrespective of quality and quantity, however, did not affect total nitrogen mineralisation as pronounced as did the presence of macrofauna.

Accumulations of seagrass debris often occur in coastal areas where *Pestarella tyrrhena* is abundant (Dworschak 1987, 2001). Vravrona Bay is characterised by large accumulations of seagrass litter imported from meadows offshore, creating occasionally large wrack beds. Seagrass debris is abundant within the sediment, and its distribution is related to the abundance of the thalassinidean shrimps (S. P. et al. unpubl. data). Macroalgal blooms, on the other hand, show a seasonal pattern and, depending on the conditions, can be significant. Decomposition of the easily degradable macroalgal material and the recovery of the system can proceed quite efficiently both aerobically and anaerobically in the absence of animals. However, when the loading of refractory seagrass detritus is considered, the presence of the animals is crucial for accelerating decomposition. Taking into account the constant loading of seagrass material in the area, the observed faunal effect suggests that *P. tyrrhena* is important for the recycling of carbon in Vravrona Bay and other coastal areas. However, evaluation of *P. tyrrhena* bioturbation on organic matter turnover and nutrient cycling at the ecosystem level need further *in situ* studies.

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