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Effects of suspended mussel culture on benthic–pelagic coupling in a coastal upwelling system (Ría de Vigo, NW Iberian Peninsula)

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ABSTRACT

The influence of suspended mussel culture on the benthic–pelagic coupling was evaluated in the Ría de Vigo, in the coastal upwelling system of the NW Iberian Peninsula, during the month of July 2004. Measurements of water column properties were carried out at three stations in the Ría de Vigo: under a mussel raft (1), and at two reference sites in the main channel (2) and in the inner part (3) of the Ría. Dissolved nutrients, dissolved oxygen and inorganic carbon benthic fluxes were measured by means of a benthic chamber at stations 1 and 3. Sediment traps were deployed at 6 locations to estimate vertical fluxes. The water column structure at the three study stations was very similar, characterized by upwelling conditions during the second week of July and a posterior stratification showing a strong thermocline, with a depth fluctuation mainly modulated by the shelf wind regime. Vertical POC fluxes underneath the mussel raft (3 g C m^{-2} d^{-1}) were 3 times higher than those obtained between rafts and 10 times higher than in the main channel reference site. Dissolved oxygen, ammonium, silicate and phosphate benthic fluxes were significantly higher under the raft than at the inner Ría reference site. A 1D carbon budget showed the importance of benthic metabolism under the raft (2.3 ± 0.8 g C m^{-2} d^{-1}), being higher than the organic carbon produced at the photic layer (0.7 ± 0.3 g C m^{-2} d^{-1}), as a result of higher organic loading compared to the inner Ría reference site. The results show for the first time the important role that suspended mussel cultures play in the benthic–pelagic coupling in this coastal upwelling ecosystem.

1. Introduction

Intensive studies of shallow coastal ecosystems have in recent decades shown the complexity of the couplings between biogeochemical processes in the benthos and water column (Giordani et al., 2002; Trimmer et al., 2003; Lund-Hansen et al., 2004). Pelagic production in these systems may be stimulated by continental inputs (Kemp and Boynton, 1984), nutrient regeneration at the sediment–water interface (Nixon, 1981; Herbert, 1999; Gibbs et al., 2005) and in coastal upwelling systems by nutrient enrichment from upwelled offshore waters (Wooster et al., 1976; Fraga, 1981). The coupling between the benthic and pelagic realms works in both directions: sediment nutrient fluxes fuel primary production into the water column (Nixon et al., 1976) and cycles of production in the water column provide pulsed inputs of labile organic substrate for regeneration in the sediments (Hatcher et al., 1994). Thus, benthic–pelagic coupling appears to be a key feature in coastal ecosystems (Grenz et al., 2000) where the benthic system generally plays an important role in coastal nutrient regeneration (Balzer et al., 1983).

The appearance of an intensive bivalve culture, which introduces a large biomass of filter feeders, may alter the biogeochemistry on the system. Dense bivalve populations may exert a strong “top-down” control on suspended particulate matter (including phytoplankton, detritus, auto- and heterotrophic picoplankton and microzooplankton) in coastal systems through their huge capacity to clear particles from the surrounding waters (Dame, 1996). Contemporary studies to the present one in the Ría de Vigo, working on a single mussel raft scale, observed that depletion of phytoplankton (Petersen et al., 2008) and zooplankton (Maar et al., 2008) resulted from the feeding activity of cultured mussels and associated epifaunal community. This feeding activity results in the packing of organic and inorganic material in their faeces and pseudofaeces (biodeposits) that rapidly settle to the seabed (Kautsky and Evans, 1987).

Bivalve faeces and pseudofaeces are characterized by large bioavailability to microbial assemblages and by rapid degradation rates (Grenz et al., 1990). Biodeposition leads to an increase in microbial activity and an enhancement of nutrient regeneration at the sediment–water interface under the mussel rafts. Benthic mineralization processes will vary depending on suspension filter feeder

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population and the rate of mixing of oxygenated water down to the sediment surface. As a result, different chemical processes like denitrification (Kaspar et al., 1985) or sulphate reduction (Hatcher et al., 1994) may occur at the sediment–water interface under mussel cultures. In short, suspended mussel culture activities divert primary production and energy flow from planktonic food webs by producing faeces and pseudofaeces, and cause strong changes in the physical and chemical characteristics of the sediments, playing a key role in the benthic–pelagic coupling of the ecosystem.

Studies on the effects of mussel culture within the water system have been mainly focused on its capability for increasing organic matter deposition to the sediment (Dahlback and Gunnarsson, 1981; Hatcher et al., 1994; Hartstein and Stevens, 2005) and enhancing the rate of nutrient recycling at the sediment–water interface (Dahlback and Gunnarsson, 1981; Nizzoli et al., 2005). Few investigations exist reporting its influence on the water column inorganic and organic suspended matter (Souchu et al., 2001; La Rosa et al., 2002; Nizzoli et al., 2005) and the number of studies targeting the three processes simultaneously is even less. In the present work, we have performed direct measurements in order to examine the impacts of suspended mussel cultures on the biogeochemistry of the water column, water–sediment interface, and vertical fluxes of biogenic particles and finally, evaluate their effect on the benthic–pelagic coupling. Furthermore, most of the studies on the effects of mussel farming have been carried out in low energy tide-dominated areas (Hatcher et al., 1994; Christensen et al., 2003; Giles et al., 2006; Nizzoli et al., 2006). The present work represents the first study on the effects of mussel culture in a highly dynamic coastal upwelling system.

The NW Iberian coast is characterized by upwelling northerly winds from March to September. For the rest of the year the winds are predominantly from the south and southwest, favouring the predominance of downwelling conditions. The extension and intensity of the seasonal upwelling and downwelling favourable periods varies strongly from year to year. One of the main features of this region is the Galician Rías Baixas, four large (>2.5 km^3) and V-shaped coastal inlets. They are openly connected with the adjacent shelf and the interaction between coastal upwelling and the circulation patterns in the Rías Baixas promotes a massive response of phytoplankton productivity inside the Rías (~1.4 g C m^{-2} d^{-1} during upwelling season; Figueiras et al., 2002). This high primary production enables the culture of *Mytilus galloprovincialis* Lamark in the Rías, supporting the highest mussel production in Europe. Mussels are the major herbivore harvesting bursts of pelagic primary production associated with intermittent upwelling (Tenore et al., 1982). Nowadays, the number of suspended mussel rafts in the Rías Baixas is 3237, with an estimated annual mussel production per raft of 75×10^3 kg raft^{-1} y^{-1}, rendering a total estimated production 243×10^6 kg y^{-1} of edible mussels, which represents enough biomass to have clear impact on the Rías as an entire ecosystem (Figueiras et al., 2002). Mussel production gives employment to 9000 people directly and 20,000 indirectly, and hence it is an activity of great socio-economic importance for the region (Labarta et al., 2000).

Several studies of the Rías Baixas have reported that the organic load under the rafts area seems to be high enough to cause important effects on the sedimentary environment (Tenore et al., 1982; Macias et al., 1991; García-Gil, 2003; Otero et al., 2006) and over the benthic community structure (López-Jamar, 1978; Tenore et al., 1982; Ysebaert et al., 2009). However, very few studies report rates of biogenic vertical fluxes (Cabanas et al., 1980; Tenore et al., 1982) and none of them investigate the role played by the mussel culture on the benthic–pelagic coupling of the ecosystem.

In this context, the aim of this work was to study the impact of suspended mussel culture on the benthic–pelagic coupling in the Ría de Vigo by means of direct measurements of water column properties, biogenic sinking material and benthic fluxes. Even though the Galician Rías Baixas are the most important mussel farming producer of Europe, no study of these characteristics has been carried out for this system. This study was carried out in July 2004, in the framework of the EU-funded MaBenE project, which aimed to develop fully coupled ecological models for ecosystems dominated by filter feeders to optimise shellfish production in terms of yield as well as nature conservation.

2. Materials and methods

2.1. Study site

The study site is located in the Ría de Vigo, one of the four Rías Baixas of the NW Iberian Peninsula (Fig. 1). The circulation in the Ría de Vigo follows a two-layered residual circulation pattern, positive under upwelling (Prego and Fraga, 1992) and negative under downwelling conditions (Piedracoba et al., 2005). Under upwelling conditions, nutrient-rich subsurface Eastern North Atlantic Central Waters (ENACW) enter the Rías by positive estuarine circulation. Conversely, downwelling conditions cause the slowdown or even reversal of the positive circulation pattern, with the inflow of nutrient-poor surface oceanic waters. A total of 478 mussel rafts are located inside the Ría de Vigo, occupying ~5% of its surface. Nowadays, rafts are 500 m^2 with an average of 500 hanging ropes at 12 m long each. In the Ría de Vigo rafts are organized in several polygons differing in size. Most of the rafts occur in the inner part of the Ría, but three polygons are located in its outer part (Fig. 1). The experimental raft for this study was situated in the outer part, located at the southeastern part of a polygon with a total of 68 rafts that were arranged in five parallel rows (100 m apart).

2.2. Water column characterization

During the MaBenE cruise (19th July to 29th July), daily water column observations were carried out on board R/V Mytilus at three stations in the Ría de Vigo: (1) the Raft station (RF), with the vessel attached to the experimental raft, (2) the Channel station (CH), in the main channel away from the mussel rafts and (3) the Inner Ría station (IR), situated in the inner part of the Ría de Vigo (Fig. 1).

At each station, vertical profiles of temperature, salinity, photosynthetic active radiation (PAR), transmittance (Sea Tech, 25 cm wavelength) and fluorescence were obtained with a Seabird CTD probe with a Seatech fluorometer. Besides, at the IR station, in order to have a continuous recording of water temperature profile, an array with 8 thermistors, at 0.5, 2, 5, 8, 11, 14, 17.5 and 20 m of water depth, was deployed from July 6th till July 30th.

Bottle casts (rosette sampler with 10-L PVC Niskin bottles) were made to obtain water samples for dissolved oxygen, dissolved nutrients, chlorophyll *a* (chl *a*) and phaeopigments (phaeo), suspended particulate matter concentrations (SPM), particulate organic carbon and nitrogen concentrations (POC and PON, respectively). Dissolved oxygen was determined by Winkler potentiometric titration. The estimated analytical error was ±1 µM. Nutrient samples were determined by segmented flow analysis with Alpkem autoanalyzers following Hansen and Grassoff (1983) with some improvements (Mouriño and Fraga, 1985). The analytical errors were ±0.02 µM for nitrite, ±0.05 µM for nitrate, ammonium and silicate and ±0.01 µM for phosphate. Total dissolved inorganic nitrogen (TIN) is the sum of NO_3–N, NO_2–N and NH_4^+–N. The concentrations of chl *a* and phaeopigments were measured by fluorometry, using acetone extracts after filtration through Whatman GF/F filters. Fluorescence values from the CTD closely followed the chl *a* measurements from the Niskin bottles, obtaining a regression line: Fluorescence = 0.245 (±0.009) Chl *a* + 0.26 (±0.06) (r^2 = 0.83, 135 points). This relationship was used to represent the chl *a* profiles in the Results section.

For analysis of SPM, POC and PON, between 2.5 and 5 L were filtered on pre-weighted, pre-combusted (6 h, 550 °C) Whatman GF/F filters. After being rinsed with Milli-Q water to remove the salts, filters

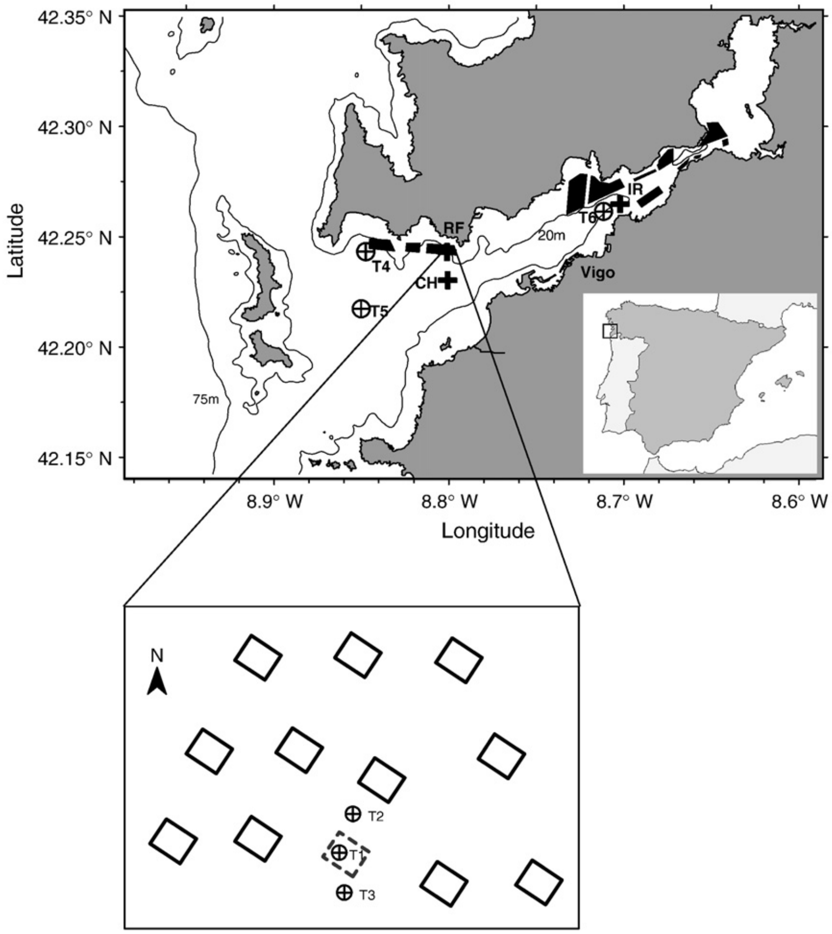

Fig. 1. Map of the Ría de Vigo showing the location of raft polygons, the three sampling stations (RF: Raft, CH: Channel and IR: Inner Ría), and the positions used for trap deployments (T4 downstream the polygon, T5 the reference station in the main channel and T6 the reference station in the inner Ría). Below, zoom in nearby the experimental raft (dotted square) showing the locations (T1 underneath the raft, T2 50 m north from the experimental raft, inside the polygon, and T3 50 m south from the experimental raft, outside the polygon) used for trap deployments.

were dried at 70 °C and stored until analysis. SPM was determined gravimetrically. POC and PON were determined using a Carlo Erba Element Analyzer after Cr_2O_3 and $AgCo_3O_4$ catalysed oxidation and segregation on a Haysep-Q-column.

2.3. Sediment traps

Five Technicap PPS 4/3 sediment traps with 12 collecting cups (250 mL) were positioned at different places in the Ría during three different periods (Fig. 1). These sediment traps have a collecting area of 500 cm^2 and an aspect ratio of 6.25. The first deployment started on July 20th at 23:00 h with a synchronized interval of 3 h at stations T1, T2, T3 and T4. All traps were placed at a depth of 18 m, which is below the thermocline. The second deployment started on July 25th at 04:00 h with an interval of 2 h. Traps were deployed at T1 (18 m depth), T2 (8 and 18 m) and T5 (8 and 18 m). The third deployment started on July 28th at 13:45 h with an interval of 1 h. Similar positions were used as for the second deployment, but at T1 no trap was placed at 8 m depth. No preservation was used in any sediment trap since the deployment duration was very short.

All samples were inspected for swimmers and, when present, were hand-picked and removed (observed in only a few occasions). Samples were manually split into two for pigment and particulate matter analyses respectively. The residue for pigment analysis was filtered onto glass fiber filters (Schleicher & Schuell, No 6) and stored at −80 °C. Pigments were extracted in 90% acetone and analyzed using reversed phase HPLC according to Wiltshire et al. (1998). The residue for particulate matter analysis was filtered onto pre-weighted, pre-combusted Whatman GF/F filters, rinsed with milli-Q water to remove salts, and dried at 70 °C. The carbon and nitrogen isotopic composition of the particulate material was measured using a Carlo Erba Elemental analyzer coupled on line to a Finnigan Delta S isotope ratio mass spectrometer (IRMS). The carbon and nitrogen isotope ratios are expressed in the delta notation $\delta^{13}C$ and $\delta^{15}N$.

Additional vertical particle fluxes were estimated, using a homemade multitrap collector (MC) system. It was composed of 4 PVC trap baffled cylinders of 28 cm^2 collecting area and an aspect ratio of 10.76. Sediment traps were deployed at two sites, one situated approx. 15 m from the raft, close to position T2, and within the raft polygon, the other at the inner Ría station (T6, Fig. 1). They were deployed at 18 m depth for a 24 hour period on the 19th, 22nd, 26th and 29th of July.

The material collected in the cylinders was filtered under low-vacuum on pre-weighed and pre-combusted (450 °C, 4 h) 47 mm GF/F filters (0.7 µm pore size) for analysis of SPM, POC and PON. Filters were dried and frozen (−20 °C) before analysis. A Perkin Elmer 2400 CHN analyzer was used for the measurements of POC and PON, using an acetanilide standard daily. The precision of the method is $\pm 0.3\,\mu mol\,C\,L^{-1}$ and $\pm 0.1\,\mu mol\,N\,L^{-1}$.

Regarding the catchment efficiency for both types of trap, data from current meters mounted at the trap mouth registered water current velocities of $<12\ cm\ s^{-1}$ for 90% (de la Granda, pers. comm.) and 100% (Wiles, pers. comm.) of the deployment time at the IR and RF sites respectively. Baker et al. (1988) concluded that for speeds $<12\ cm\ s^{-1}$, mass flux collected from moored sediment traps was indistinguishable from that collected in drifting traps, which are considered to be free of hydrodynamic biases. Therefore, although some hydrodynamic bias could have influenced the trap catchment efficiency, its influence is negligible for the results presented.

2.4. Benthic fluxes

Fluxes of nutrients (nitrate, nitrite, ammonium, phosphate and silicate), total alkalinity, oxygen and pH at the sediment–water interface were measured *in situ* by means of a benthic chamber (Ferrón et al., 2008), placed by a diver directly on the sediment surface. Four samplings were conducted during the field survey (19th, 22nd, 26th and 29th of July), just close to the experimental raft (26 m depth). Also at the IR station (Fig. 1) similar measurements were performed during the first half of July (6th, 8th, 12th and 15th). These data are used to analyze the spatial variation in benthic fluxes.

Discrete samples were withdrawn from the chamber at prefixed times with a multiple water sampler provided with 12 syringes of 50 mL (KC Denmark). Samples were split for analysis of nutrients, total alkalinity and pH. Total alkalinity was determined by potentiometric titration with HCl to a final pH of 4.4 (Pérez and Fraga, 1987) and adapted for small sampling volume of 5 mL. The analytical error was ±4 μM. The measurements of pH were analyzed spectrophotometrically following Clayton and Byrne (1993). Nutrient samples were determined in the same way as described for the water column measurements.

Total CO_2 (TCO_2) was estimated from pH and total alkalinity using the carbonic system equations with the carbonic and boric acid dissociation constants of Lueker et al. (2000). Benthic fluxes were calculated by empirical linear fitting of concentration against time.

2.5. Offshore Ekman transport

As previously described in the Introduction, northerly winds provoke the upwelling of subsurface ENACW (Eastern North Atlantic Central Water) in the Rías Baixas and thus regulate the oceanographic conditions in this region. Thus in order to understand the oceanographic conditions, we analyze the intensity of this upwelling based on the upwelling index. The upwelling index (Iw) was estimated using the component $-Q_x$ of the Ekman transport following Bakun's (1973):

$$Iw = -Q_x = -\frac{\rho_{\mathrm{air}} \cdot C_{\mathrm{D}} \cdot |V| \cdot V_{\mathrm{y}}}{\rho_{\mathrm{sw}} \cdot f}$$

where ρ_{air} is the density of air (1.22 kg m^{-3} at 15 °C), C_D is an empirical dimensionless drag coefficient (1.4×10^{-3} according to Hidy (1972)), f is the Coriolis parameter (9.946×10^{-5} at 43°N), ρ_{sw} is the density of seawater (1025 kg m^{-3}) and $|V|$ and V_y, are the average daily module and northerly component of the geostrophic winds centred at 43°N and 11°W. Average daily geostrophic winds were estimated from atmospheric pressure charts. Positive values of Iw indicate upwelling and correspond to predominance of northerly winds.

3. Results

3.1. Hydrographic conditions and suspended particulate matter characteristics

The first two weeks of July were mainly characterized by strong northerly winds (avg $-Q_x = 476 \pm 449$ m^3 $(s\,km)^{-1}$; Fig. 2a), that provoked the entry of cold (<13.5 °C) ENACW from the shelf through the bottom ingoing layer based on the thermistor array data at the IR station (Fig. 2b). During the second half of July, winds reversed and they were mainly blowing from the southwest, with an average $-Q_x$ of 31 ± 217 m^3 $(s\,km)^{-1}$. These conditions favoured the surface intrusion of warm water (~19 °C) and the development of a strong stratification, deepening the thermocline from 10 m to 20 m depth. However, the weak upwelling event between July 25th and 27th resulted in a re-entry of subsurface ENACW, displacing the thermocline lower limit back to ~10 m depth. Finally, reversal of northerly winds on the adjacent shelf on July 28th had a clear impact on the water column structure, pushing again the thermocline downwards. This temporal evolution of the water column hydrographic conditions was also observed at the RF and CH stations according to the daily CTD profiles (Fig. 3, first row).

The nutrient distributions observed at the RF station were clearly controlled by these hydrographic conditions (Fig. 4). Nutrient levels were low above the thermocline except for nutrient injection to the photic zone during the weak upwelling events (July 19th and 26th). Below the main thermocline, nutrient concentrations were high due to the presence of nutrient-rich subsurface ENACW and remineralization processes. In fact, for similar TS properties of ENACW on July 19th and 26th, we observed higher nutrient levels, except for ammonium, at the beginning of the cruise due to oxidation of organic matter as the lower oxygen levels on July 19th indicated (distribution not shown). The other two stations (IR and CH stations) responded to a similar pattern based on the nutrient relationships (Table 1). The correlation of nitrate *vs* phosphate for water samples with temperature <14 °C was not significantly different ($p>0.05$) for the 3 stations with slopes lower than the Redfield ratio. The N:P slope increases to the Redfield value when we consider total inorganic nitrogen (TIN) *vs* phosphate for the RF and CH stations. However for the IR station, we have obtained a lower N:P ratio pointing to a faster remineralization of phosphorus *vs* nitrogen. The N:Si slope was similar at the raft and channel stations, considering only TIN and we did not observe any correlation at the IR location.

The temporal distributions of chl *a* (Fig. 3, second row) for the RF and CH stations were very similar. The highest values were observed at the beginning and end of the survey (>10 mg m^{-3}), during the periods of spin-down from previous upwelling events. These high values were located from the thermocline to the bottom, with maximum values just below the thermocline. For the IR station, the chl *a* distribution was similar to other stations, but chl *a* maximum at the end of the survey was less pronounced. The surface chl *a* concentration was usually below 2 mg m^{-3} at the RF station; except for July 26th and 27th with chl *a* concentrations >2 mg m^{-3}, and these surface values were lower than at the CH and IR stations.

The temporal distributions of transmittance percentage (Fig. 3, last row) mirrored the chl *a* distributions with low values associated with the chl *a* maxima and with higher percentage during the middle of the survey for the three stations.

Total suspended particulate matter concentrations (SPM) were lowest near the surface (1.03 ± 0.26 mg L^{-1}, above the main thermocline) and generally increased with depth in all stations (1.95 ± 0.52 mg L^{-1}, below the main thermocline; Table 2). POC concentrations did not exceed 0.3 mg L^{-1} most of the time and did not show strong gradients with depth. However, we did observe an increasing trend with depth of algal C in relation to non-algal C for the three stations associated with higher chl *a* concentrations below the thermocline. Algal C was calculated as the concentration of chl *a* times 25.2 ± 15.6, which was the average C:Chl *a* ratio (g/g) during the campaign period. PON concentrations were significantly correlated with POC concentrations ($r^2 = 0.93$) with an average C:N ratio of 6.8 (close to the Redfield ratio). Based on these data, we did not observe significant differences in the quantity and quality of suspended particulate matter among the three study stations though the quality of the suspended matter was different above and below of the thermocline.

3.2. Vertical fluxes

The rates of sedimentation of particulate matter differed substantially between stations (Table 3). The highest values were observed

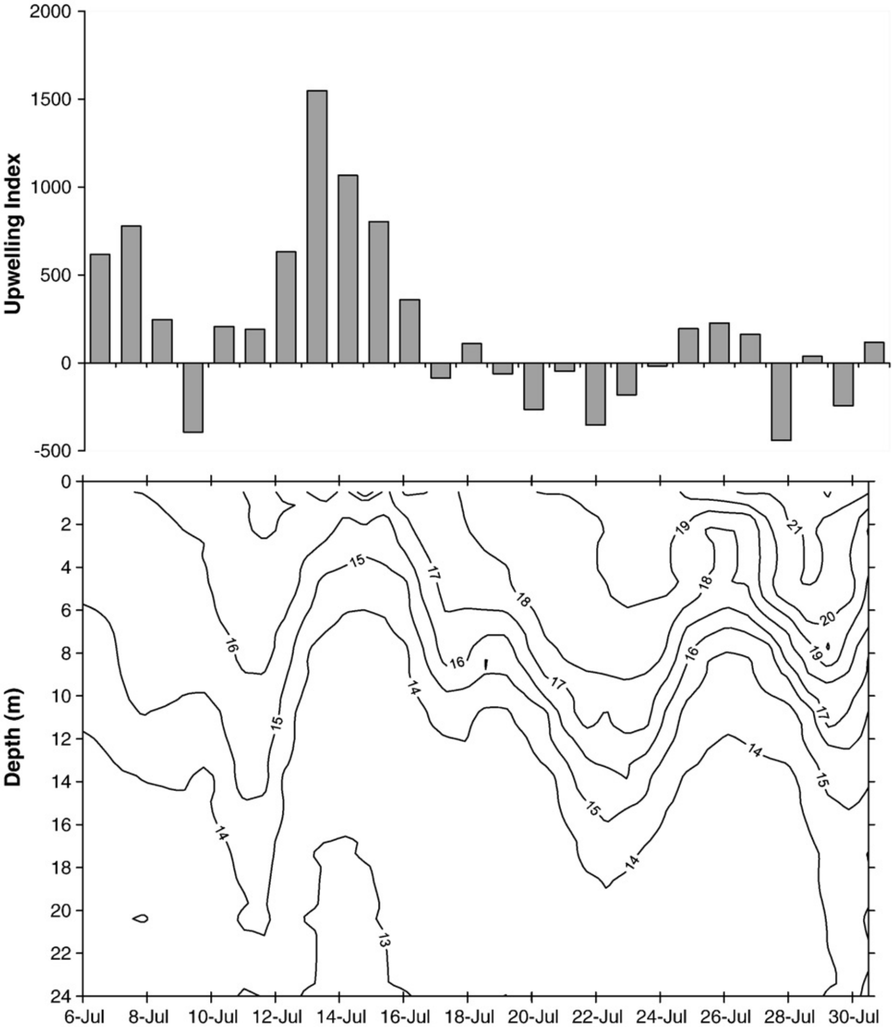

Fig. 2. a) Offshore Ekman transport presented as upwelling index ($-Q_x$: $m^3 s^{-1} km^{-1}$). b) Time evolution of temperature (°C) derived from thermistor mooring at the inner Ría station.

directly under the raft (T1), with average values ranging from 25 to 37 g DW $m^{-2} d^{-1}$, and the multitrap collector value (31 g $m^{-2} d^{-1}$) within this range. The high-resolution temporal variability observed underneath the raft with the Technicap sediment traps showed a large variation. This was probably partly caused by the fact that visual inspection of the filters showed, besides mussel faecal pellets, sometimes drop-off material from the raft, such as small mussel shell fragments and fragments of green macroalgae. In between and in the vicinity of the rafts, the collected DW was 5–11 g $m^{-2} d^{-1}$, being a factor 3 to 5 smaller than directly underneath the raft. The CH station, (see Fig. 1, T5) showed much lower values, in the order of 2 g DW $m^{-2} d^{-1}$. A large difference was observed between the traps deployed at 18 m and 8 m, with much lower values in the traps at 8 m, especially at T5. POC concentrations were on average highly correlated with total DW (r^2: 0.91), representing about 10% of the total DW (Table 3). Underneath the raft average POC rates varied between 2.2 and 3.9 g C $m^{-2} d^{-1}$. At T2 and T3 trap stations POC was trapped at a rate of 0.9 ± 0.2 g C $m^{-2} d^{-1}$. Much lower POC fluxes were observed in the CH station, especially at 8 m. Similar trends were observed for PON, showing significant correlation with POC ($r^2 = 0.99$). Also chl *a* was correlated with POC ($r^2 = 0.58$). At T5, chl *a* was very low or even zero at two occasions (Table 3). The average C:N ratio for the settled material under the raft was 7.6:7.7 for the traps located between rafts and 7.0 at T5.

The values of $\delta^{13}C$ of the settled material under the raft and in the vicinity of the rafts were similar (Table 3), whereas the $\delta^{13}C$ values at T5 were more negative during the two occasions. This variation in isotopic values for $\delta^{13}C$ was related to the variation in the algal proportion of the POC in relation to non-algal POC. Higher non-algal proportions in the POC resulted in significantly more negative isotopic values for $\delta^{13}C$ ($r^2 = 0.92$ for the sediment traps at 18 m).

3.3. Benthic fluxes

Fig. 5 displays a comparison on the magnitude of the benthic fluxes of oxygen, total CO_2 (TCO_2) and nutrients between the RF station and the IR station. It clearly shows that sediment–water fluxes were significantly higher ($p < 0.01$) under the raft than at the IR station. For benthic fluxes at the RF station, rates obtained for July 14th were significantly higher than for the rest of the sampling days; but even if we do not consider this day, fluxes under the RF station are still significantly higher. Besides, benthic fluxes under the raft showed much more variability than at the IR station, based on the corresponded standard deviations (Table 4).

Dissolved oxygen uptake by the sediments was on average 7 times higher under the raft, obtaining its maximum on July 14th (-428 mmol O_2 $m^{-2} d^{-1}$). Regarding nitrate benthic fluxes, it seems that there is a net release of nitrate from the sediment to the water column under the raft, though with a high daily variability; whereas, nitrate benthic fluxes at the IR station were consistently negative in all cases and showed much less variability, which may be the result of denitrification processes. Ammonium was the main N-containing

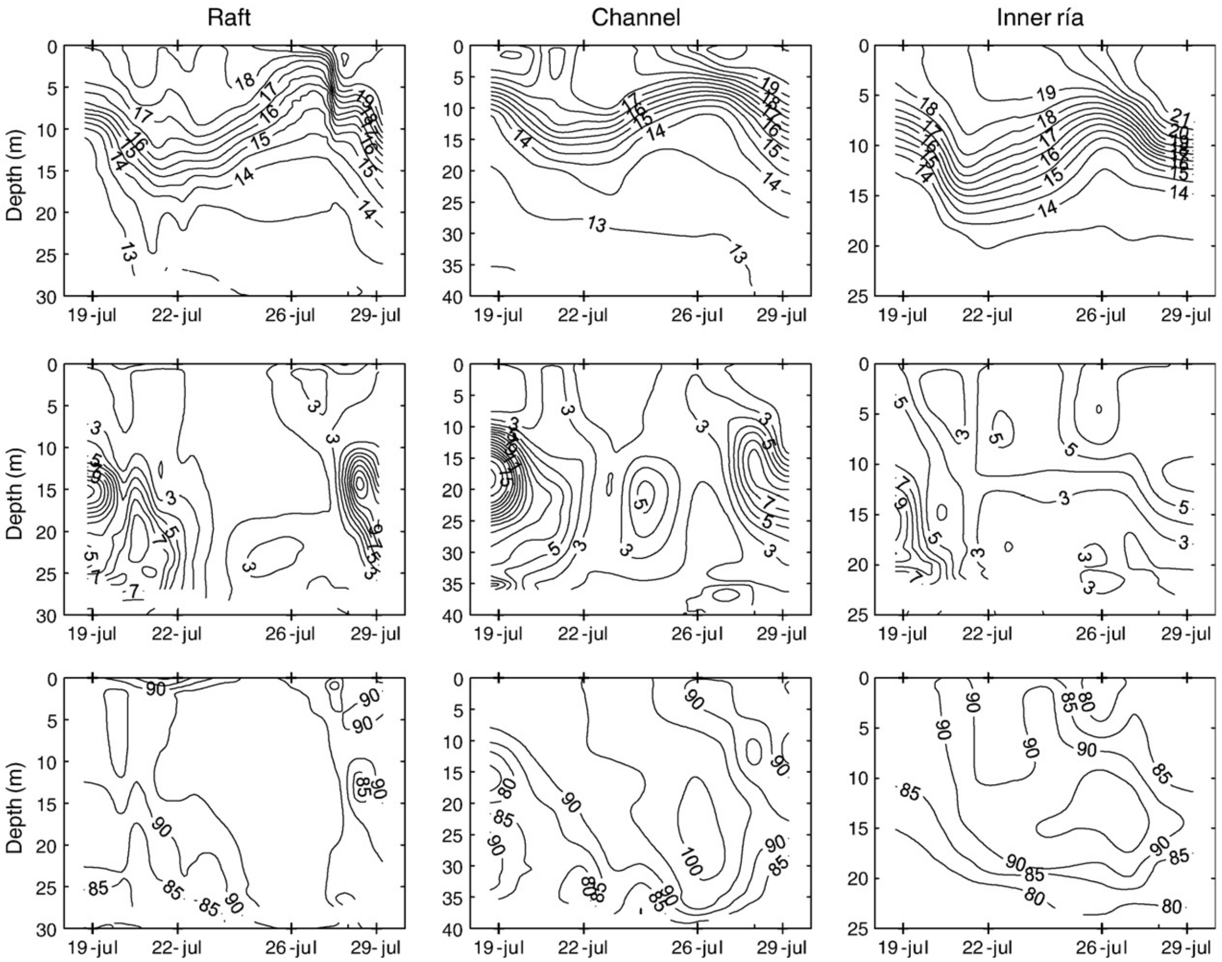

Fig. 3. Time evolution of temperature (°C), chlorophyll *a* (mg m^{-3}) and transmittance (%) at the raft, channel and inner Ría stations during the MaBenE campaign. Note the different depth scale.

nutrient released from the sediment. Benthic NH_4^+ fluxes were on average 40 mmol m^{-2} d^{-1} under the raft, being 17 times higher than at the IR station. Phosphate fluxes showed a proportional difference between sites similar to the ammonium fluxes ratio (17-fold increase under the raft), obtaining average fluxes of 3.6 ± 1.6 mmol m^{-2} d^{-1} and 0.21 ± 0.1 mmol m^{-2} d^{-1} for the RF and IR stations, respectively.

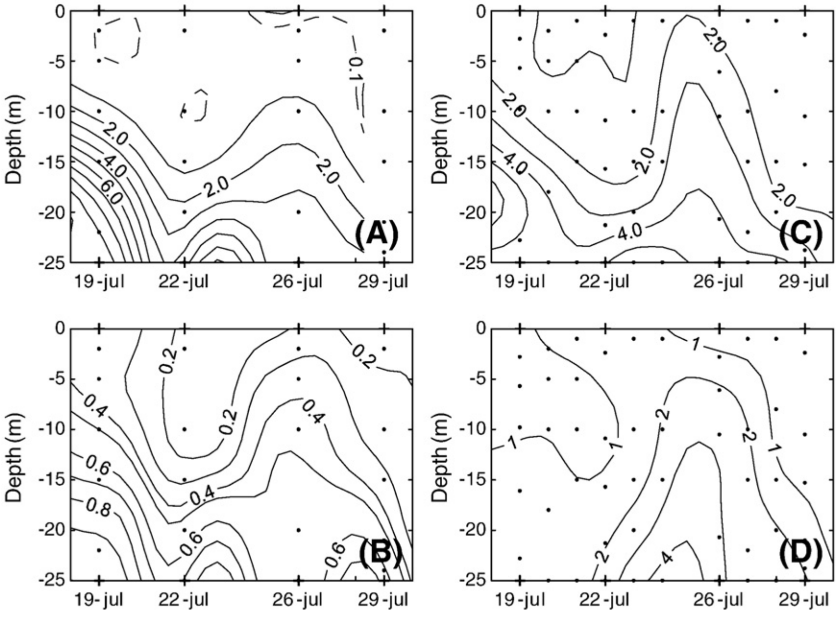

Fig. 4. Time evolution of nitrate (A); phosphate (B); silicate (C) and ammonium (D) at the raft station during the MaBenE campaign. Unit is μM.

Table 1

Slope, standard error, and determination coefficient of the correlations between nutrients at the three study locations. Nutrients are in µM.

		Raft	Channel	Inner Ría
NO_3^- *vs* HPO_4^{2-}	Slope	14.7 ± 2.2	13.3 ± 1.9	12.1 ± 1.7
	$r^2(n)$	0.81 (17)	0.86 (14)	0.95 (7)
TIN *vs* HPO_4^{2-}	Slope	16.2 ± 2.9	16.1 ± 2.4	13.5 ± 3.2
	$r^2(n)$	0.73 (17)	0.87 (13)	0.84 (7)
NO_3^- *vs* SiO_2	Slope	1.78 ± 1.5	1.53 ± 1.4	n.s.[a]
	$r^2(n)$	0.82 (17)	0.72 (14)	
TIN *vs* SiO_2	Slope	1.95 ± 1.7	1.94 ± 1.7	n.s.
	$r^2(n)$	0.86 (17)	0.90 (13)	

[a] Not significant.

Silicate was released to the water column in a higher amount under the raft (5 times higher), but the difference between sites was not as high as for ammonium and phosphate.

Alkalinity fluxes (Alk Corr) were corrected for the influence of ammonium and nitrate fluxes by adding the fluxes of NO_3^- and subtracting the NH_4^+ fluxes (Table 4). Assuming that calculated TCO_2 fluxes account for organic carbon remineralization and net dissolution of $CaCO_3$, we can establish an upper limit of the amount of carbon oxidized (Max Cox) as the calculated TCO_2. As Ca^{+2} fluxes were not measured, an estimate of the maximum dissolution of $CaCO_3$ was calculated as ½ Alk Corr fluxes following Berelson et al. (1998). Consequently, the lower limit of the carbon oxidation (Min Cox) was obtained subtracting maximum $CaCO_3$ dissolution rates from measured TCO_2 fluxes. Based on these assumptions, averaged carbon oxidation rates are significantly higher ($p > 0.01$) under the raft than at the IR station. The benthic respiration quotient (BRQ), calculated as the ratio between the averaged Cox and the oxygen flux, was higher (1.2 ± 0.2) under the raft than at the IR station (0.6 ± 0.3).

4. Discussion and conclusions

4.1. Water column

Studies of the role of suspension filter feeders on the nutrient cycling of coastal systems have been principally focused on benthic regeneration of the biodeposits (Dahlback and Gunnarsson, 1981; Hatcher et al., 1994; Nizzoli et al., 2005). However, direct release of nutrients in the water column from filter feeders and their epibiota can also be an important pathway of nutrient cycling (Souchu et al., 2001; Nizzoli et al., 2006; Richard et al., 2007). In fact, these last two studies have reported a contribution of mussel lines (*vs* benthic fluxes) to the total oxygen and nutrient fluxes greater than 30% in semi-enclosed lagoons.

In our case, we did not observe significant differences in dissolved inorganic nutrients and suspended particulate matter quality and quantity between the raft site and the other two study sites. We only detect a lower N:P ratio at the IR station, probably due to a faster remineralization of phosphorous over nitrogen at this location as the low N:P ratios of the benthic fluxes also suggest (Table 1). The fact that we did not detect any significant alteration of the water column biogeochemistry associated to mussel farming can result from the system dynamics. The previously reported shellfish culture areas were semi-enclosed lagoons, physically forced by tides. In contrast, the Ría de Vigo is an upwelling driven system characterized by shorter water residence time, between 14 and 7 days for the upwelling season (Álvarez-Salgado et al., 2000). Consequently, the rapid water renewal inside the Ría seems to dilute the possible effect of nutrient release from the mussel ropes.

4.2. Vertical fluxes

In this study we have observed significant spatial variations between vertical fluxes of POC, with the highest values under the raft (average 3.1 g C m^{-2} d^{-1}). Rates of sedimented POC were 3 times higher than the vertical fluxes obtained between the rafts (0.9 g C m^{-2} d^{-1}) and 10 times higher than in the reference site (0.3 g C m^{-2} d^{-1}), supporting the hypothesis that suspended mussel farming increases sedimentation rates of SPM and organic matter (Hatcher et al., 1994; Stenton-Dozey et al., 1999; Hartstein and Rowden, 2004; Callier et al., 2006). For the Rías Baixas, Cabanas et al. (1980) presented organic carbon fluxes under a mussel raft (up to 24.6 g C m^{-2} d^{-1}), much higher than our results and the values reported by Tenore et al. (1982) (up to 2.4 g C m^{-2} d^{-1}). The large difference between the vertical fluxes measured in this work and data from Cabanas et al. (1980) might be related with a different mussel growth state when the measurements were carried out. Organic carbon fluxes at the CH station are at the low range of values obtained in the Ría de Pontevedra (0.5–1.8 g C m^{-2} d^{-1}; Varela et al., 2004) and a coastal site off A Coruña (0.3–1.2 g C m^{-2} d^{-1}; Bode et al., 1998).

Sediment traps may have been influenced by re-suspension processes as they were deployed 5 m above sea-bottom at the RF and IR stations which would provoke overestimation on the results obtained. However, from the transmittance profile (Fig. 3, third row) it can be observed that this variable does not decrease abruptly near the sea-bottom as expected when re-suspension occurs. On the contrary, transmittance is well correlated with chl *a* ($r^2 = 0.5$) which may indicate that lower values of transmittance are the result of higher phytoplankton biomass – just below the thermocline – and not due to the presence of material resuspended from the seabed. Furthermore, on a year sediment trap sampling at IR site, (Zuñiga et al., in preparation) found that only during the winter period we observe the presence of some benthic phytoplankton species (*Paralia sulcata*). Therefore, although re-suspension may occur, based on these results we believe that this process was not significantly important during the sampling period.

Regarding the quality of the sinking material, results showed no significant differences between the RF site and the CH reference site in

Table 2

Averaged values (± S.D.) of the quality and quantity of particulate matter above and below the main thermocline. SPM: suspended particulate matter; POC: particulate organic carbon; PON: particulate organic nitrogen; Chl *a*: Chlorophyll *a*.

Station	SPM	POC	PON	C:N	Chl *a*	$\delta^{13}C$	$\delta^{15}N$	Non-algal C/algal C
Unit	mg L^{-1}	mg L^{-1}	mg L^{-1}		mg m^{-3}	‰	‰	
RF_Above	1.01 ± 0.25	0.19 ± 0.05	0.03 ± 0.01	6.68	2.16 ± 2.43	− 19.87 ± 0.66	6.34 ± 0.99	5.02 ± 3.18
RF_Below	1.87 ± 0.60	0.28 ± 0.15	0.05 ± 0.01	7.02	5.00 ± 3.76	− 18.75 ± 0.69	5.17 ± 0.95	2.21 ± 2.80
RF_Total	1.24 ± 0.53	0.22 ± 0.10	0.04 ± 0.01	6.77	2.92 ± 3.05	− 19.60 ± 0.82	6.06 ± 1.09	4.25 ± 3.29
CH_Above	1.04 ± 0.30	0.25 ± 0.07	0.04 ± 0.01	6.81	2.98 ± 2.95	− 20.12 ± 0.67	6.28 ± 0.61	4.03 ± 2.47
CH_Below	1.88 ± 0.48	0.28 ± 0.15	0.05 ± 0.03	6.84	5.73 ± 5.94	− 19.35 ± 1.08	5.70 ± 1.80	1.78 ± 1.30
CH_Total	1.44 ± 0.58	0.26 ± 0.11	0.04 ± 0.02	6.82	4.29 ± 4.71	− 19.75 ± 0.95	6.01 ± 1.31	2.96 ± 2.26
IR_Above	1.12 ± 0.20	0.26 ± 0.07	0.04 ± 0.01	6.95	4.20 ± 1.49	− 20.09 ± 0.51	7.61 ± 1.29	1.84 ± 1.62
IR_Below	2.16 ± 0.49	0.27 ± 0.06	0.05 ± 0.01	6.47	4.90 ± 2.80	− 19.24 ± 0.58	5.46 ± 0.47	1.82 ± 1.33
IR_Total	1.69 ± 0.66	0.27 ± 0.05	0.05 ± 0.01	6.71	4.55 ± 2.17	− 19.67 ± 0.69	6.54 ± 1.47	1.83 ± 1.41
Above_Total	1.03 ± 0.26	0.21 ± 0.06	0.04 ± 0.01	6.72	2.71 ± 2.56	− 19.97 ± 0.65	6.43 ± 0.87	4.22 ± 3.00
Below_Total	1.95 ± 0.52	0.28 ± 0.13	0.05 ± 0.02	6.81	5.28 ± 4.47	− 19.14 ± 0.87	5.48 ± 1.29	1.93 ± 1.86

Table 3
Integrated values of daily flux rates of settling particles for each station and each measuring period. SPM: total suspended matter; POC: particulate organic carbon; PON: particulate organic nitrogen; chl *a*: chlorophyll *a*. See Fig. 1 for station locations.

Station	Depth	Date	SPM	POC	PON	C:N	$\delta^{13}C$	$\delta^{15}N$	Chl *a*
Unit	m		$g\ m^{-2}\ d^{-1}$	$g\ m^{-2}\ d^{-1}$	$g\ m^{-2}\ d^{-1}$		‰	‰	$mg\ m^{-2}\ d^{-1}$
Raft T1 (MC[a])	18	14-Jul-04	31.4 ± 0.3	3.76 ± 0.2	0.50 ± 0.1	8.77			29.38 ± 7.03
Raft T1	18	22-Jul-04	25.5 ± 2.1	2.18 ± 0.24	0.36 ± 0.04	7.06	−19.59 ± 0.25	5.86 ± 0.23	5.22 ± 1.52
Raft T1	18	26-Jul-04	25.2 ± 4.1	2.92 ± 0.46	0.41 ± 0.07	8.31	−19.36 ± 0.19	5.29 ± 0.17	12.27 ± 2.57
Raft T1	18	28-Jul-04	37.2 ± 4.3	3.58 ± 0.62	0.54 ± 0.07	7.73	−19.47 ± 0.32	6.44 ± 0.16	6.81 ± 2.30
Between rafts (MC)	18	19-Jul-04	16.5 ± 4.1	1.52 ± 0.58	0.22 ± 0.07	8.23			13.55 ± 4.54
Between rafts (MC)	18	22-Jul-04	9.2 ± 1.3	1.11 ± 0.17	0.18 ± 0.02	7.33			2.67 ± 0.81
Between rafts (MC)	18	26-Jul-04	14.5 ± 6.5	0.85 ± 0.07	0.13 ± 0.01	7.37			4.94 ± 0.54
Between rafts (MC)	18	29-Jul-04	17.8 ± 0.1	1.10 ± 0.05	0.17 ± 0.02	7.65			10.28 ± 0.48
Between rafts T4	18	22-Jul-04	11.0 ± 3.0	1.05 ± 0.22	0.18 ± 0.03	6.81	−19.67 ± 0.12	5.94 ± 0.21	3.78 ± 0.90
Between rafts T3	18	22-Jul-04	5.3 ± 0.3	0.81 ± 0.05	0.12 ± 0.02	7.88	−19.87 ± 0.07	6.50 ± 0.39	1.98 ± 0.35
Between rafts T2	18	22-Jul-04	7.4 ± 13.4	0.99 ± 0.15	0.15 ± 0.02	7.70	−19.73 ± 0.06	6.15 ± 0.15	2.17 ± 0.40
Between rafts T2	18	26-Jul-04	5.8 ± 1.1	0.91 ± 0.17	0.15 ± 0.03	7.08	−19.05 ± 0.09	5.39 ± 0.08	4.34 ± 0.55
Between rafts T2	18	28-Jul-04	6.2 ± 0.7	0.70 ± 0.07	0.11 ± 0.01	7.42	−19.52 ± 0.26	5.58 ± 0.20	1.76 ± 0.36
Between rafts T2	8	26-Jul-04	1.7 ± 0.1	0.29 ± 0.03	0.055 ± 0.008	6.15	−19.47 ± 0.19	6.71 ± 0.24	0.15 ± 0.02
Between rafts T2	8	28-Jul-04	3.1 ± 0.1	0.31 ± 0.04	0.068 ± 0.007	5.32	−20.52 ± 0.13	5.95 ± 0.16	0.48 ± 0.10
Channel T5	18	26-Jul-04	1.8 ± 0.1	0.38 ± 0.05	0.064 ± 0.01	6.93	−19.03 ± 0.21	5.79 ± 0.14	0
Channel T5	18	28-Jul-04	2.3 ± 0.2	0.17 ± 0.01	0.028 ± 0.004	7.08	−21.79 ± 0.36	4.83 ± 0.22	0.13 ± 0.01
Channel T5	8	26-Jul-04	1.0 ± 0.07	0.05 ± 0.002	0.002 ± 0.0008	29.17	−24.55 ± 0.13	3.14 ± 0.45	0

[a] MC: Multitrap collector.

terms of C:N ratio and isotope $\delta^{13}C$ (−19.7‰ and −20.4‰, respectively) and $\delta^{15}N$ (6.0‰ and 5.3‰, respectively). Also, non-algal C:algal C ratio appeared to be significantly lower (9.83 ± 4.55) at the RF site than

in the CH station (50.9) which points to a major vertical flux of material derived from phytoplankton under the raft. These data are supported by findings from Zuñiga et al. (in preparation), where the phaeo/chla ratio

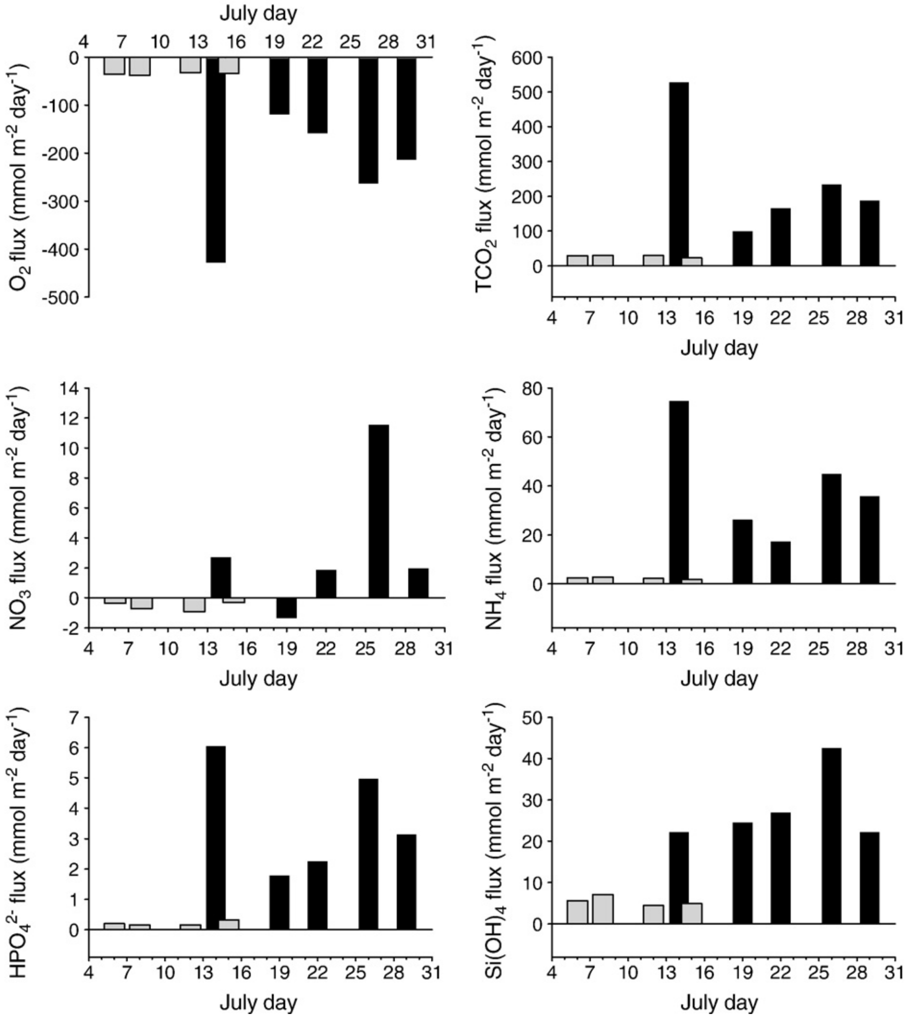

Fig. 5. Bar plots reflecting a comparison of the oxygen, TCO_2 and nutrients benthic fluxes between the raft station (dark bars) and the inner Ría station (light bars) during the sampling period.

Table 4
Summary of benthic fluxes at the RF station and IR stations. BRQ: Benthic respiration quotient. Units are in mmol m^{-2} d^{-1}. S.D.: standard deviation.

	Oxygen	Nitrate	Ammonium	Phosphate	Silicate	Alk Corr[a]	Max Ca Dis[a]	Min Cox[a]	TCO$_2$ max Cox	Cox (avge)	BRQ
Raft stn											
14-Jul-04	−428 ± 7.2	2.7 ± 2.1	75 ± 6	6.0 ± 0.8	22 ± 6	650 ± 62	325 ± 31	535 ± 69	859 ± 61	697	1.6
19-Jul-04	−119 ± 0.6	−1.3 ± 0.2	26 ± 2	1.8 ± 0.1	25 ± 1	120 ± 9	60 ± 5	108 ± 9	168 ± 8	138	1.2
22-Jul-04	−158 ± 0.5	1.9 ± 0.7	17 ± 2	2.3 ± 0.3	27 ± 1	238 ± 34	119 ± 17	169 ± 35	288 ± 31	229	1.4
26-Jul-04	−263 ± 0.5	11.5 ± 1.4	45 ± 5	5.0 ± 0.8	43 ± 3	203 ± 31	101 ± 16	235 ± 39	337 ± 36	286	1.1
29-Jul-04	−213 ± 0.9	2.0 ± 0.4	36 ± 1	3.1 ± 0.3	22 ± 2	158 ± 23	79 ± 12	189 ± 32	268 ± 30	229	1.1
Average	−236	3.3	39.7	3.6	27.6	180	90	175	384	316	1.2
S.D.	107	4.3	19.8	1.6	7.6	52	26	53	273	220	0.2
Inner Ría stn											
6-Jul-04	−36.0 ± 0.0	−0.4 ± 0.1	2.5 ± 0.5	0.20 ± 0.03	5.6 ± 0.4	43 ± 10	21 ± 5	7 ± 13	29 ± 12	18	0.5
8-Jul-04	−37.8 ± 0.1	−0.7 ± 0.1	2.7 ± 0.1	0.16 ± 0.03	7.1 ± 0.6	23 ± 10	12 ± 5	19 ± 8	30 ± 6	25	0.6
12-Jul-04	−32.4 ± 0.0	−0.9 ± 0.1	2.3 ± 0.2	0.16 ± 0.01	4.5 ± 0.4	−2 ± 3	−1 ± 2	31 ± 12	30 ± 12	31	1.0
15-Jul-04	−34.2 ± 0.0	−0.3 ± 0.1	1.8 ± 0.5	0.32 ± 0.03	5.0 ± 0.2	44 ± 16	22 ± 8	1 ± 10	23 ± 7	12	0.3
Average	−35	−0.6	2.3	0.21	5.5	27	13	15	28	21	0.6
S.D.	2.0	0.3	0.3	0.1	1.0	22	11	13	3	8	0.3

[a] Uncertainties are based on the propagation of random errors from measured benthic fluxes.

in sediment traps appeared to be higher, though not statistically significant (P: 0.13), under the raft (4.6 ± 3.2 S.D.) than at the IR station (1.4 ± 0.6 S.D.). The high phaeo/chl *a* ratio obtained under the raft may be the result of mussel grazing on the phytoplankton, a process on which chlorophyll is degraded to phaeopigments (Dahlback and Gunnarsson, 1981), promoting a high sedimentation of algal decay products (Kautsky and Evans, 1987). Jordan and Valiela (1982) proposed that half of the particulate nitrogen and carbon consumed by mussels is expelled as faeces; therefore it seems that mussel grazing does not alter significantly the C:N over the material processed but it may degrade chlorophyll to phaeopigments. This fact may indicate that chlorophyll collected under the raft was more degraded than at the IR station, as low values of phaeo/chla reflect phytoplankton not highly degraded (Varela et al., 2004). Jordan and Valiela (1982) obtained 10 times higher deposition of phaeo than chla under mussel culture. The lower C:N molar ratio at the IR station (6.9) than under the raft (8.1) also reflects a higher degraded phytoplankton sinking under the raft.

Comparison of the quality of suspended particulate matter and sediment trap material showed no difference on the C:N ratio between these two partitions for the RF and CH stations. However, the contribution of non-algal carbon was higher on the trap material than on suspended particulate matter as it could be expected taking into account that the algal carbon is more labile and thus easier to degrade.

4.3. Benthic fluxes

Even though the Rías Baixas are the most important shellfish farming area of Europe, the present study shows for the first time its impact on the benthic fluxes and consequently on the sediment biogeochemistry. The high sedimentation under the suspended mussel raft provoked an intense accumulation of organic carbon and consequently intense benthic recycling processes.

Several authors observed a positive correlation between sea-bottom temperature and benthic oxygen fluxes (Klump and Martens, 1989; Hatcher et al., 1994; Nicholson and Longmore, 1999). In our case, we observed benthic oxygen fluxes ranged from −119 to −428 mmol m^{-2}day^{-1} and from −32.4 to −37.8 mmol m^{-2} day^{-1} for the RF and IR stations respectively and however sea-bottom temperatures were very similar at both stations (RF and IR, 13.16 ± 0.21 °C) in July 2004. For the raft area, unexpected maximum benthic fluxes were registered during the peak of upwelling event (oxygen flux: −428 mmol m^{-2} day^{-1}), when sea-bottom temperature was at the minimum (12.91 °C). We suggest that the entrance of cold subsurface ENACW water through the Ría bottom layer probably favoured intense re-suspension processes at the benthic boundary layer on July 14th, causing significantly higher benthic fluxes for all the variables compared to the following days. As it was expected from previous studies on the effects of mussel suspended culture on benthic oxygen fluxes (Baudinet et al., 1990; Hatcher et al., 1994; Christensen et al., 2003), oxygen uptake from the raft sediments was higher than on the reference site (IR). Benthic oxygen fluxes obtained under the raft were higher than most studies on mussel culture (Hatcher et al., 1994; Stenton-Dozey et al., 2001; and Giles and Pilditch, 2006) and of the same order of magnitude than those obtained by Nizzoli et al. (2005) and by Richard et al. (2007) in semi-enclosed lagoons of the Mediterranean Sea and Gulf of St Lawrence (Canada) respectively.

The TCO$_2$ fluxes were calculated from direct measurements of pH and alkalinity. Unfortunately we do not have direct CaCO$_3$ measurements and hence the exact source of alkalinity is unknown. Therefore, the amount of oxidized carbon was estimated as an average value of the upper and lower limits of benthic TCO$_2$ fluxes, assuming that part of the alkalinity flux was due to carbonate dissolution and part was due to sulphate reduction (Berelson et al., 1998). As expected, carbon oxidation rates were higher at the RF site (316 ± 220 mmol m^{-2} day^{-1}; Table 4) than at the IR site (21 ± 8 mmol m^{-2} day^{-1}) due to a larger availability of organic matter derived from the higher vertical carbon fluxes under the raft. Although carbon oxidation rates are not commonly reported on studies regarding mussel culture, our results are similar to those obtained by Nizzoli et al. (2006) for Goro Lagoon, where TCO$_2$ effluxes varied between 415 and 96 mmol m^{-2} day^{-1}. In any case, these benthic carbon oxidation rates under mussel farming are much higher than the average respiration rate (34 mmol m^{-2} day^{-1}) from 48 estuarine systems around the world compiled by Hopkinson and Smith (2005).

Based on these oxygen benthic fluxes and the estimated average carbon oxidized, we obtained the benthic respiration quotient (BRQ), that indicates to what extent the aerobic respiration and re-oxidation of reduced compounds from anaerobic respiration occur simultaneously in the sediment. Under balanced conditions, where all organic matter is either aerobically metabolized and/or all the anaerobic products reoxidized, the BRQ would be in the range of 0.7 to 1.1 (Anderson et al., 1986; Glud, 2008). According to this, the higher BRQ obtained at the RF site (1.2 ± 0.2) indicates that some of the reduced compounds from anaerobic respiration are not completely oxidized. By contrast, the lower BRQ (0.6 ± 0.3) at the IR site may reflect that aerobic respiration is the main mineralization process at this site.

On the other hand, ammonium fluxes also support these two different benthic metabolism pathways at the RF and IR stations.

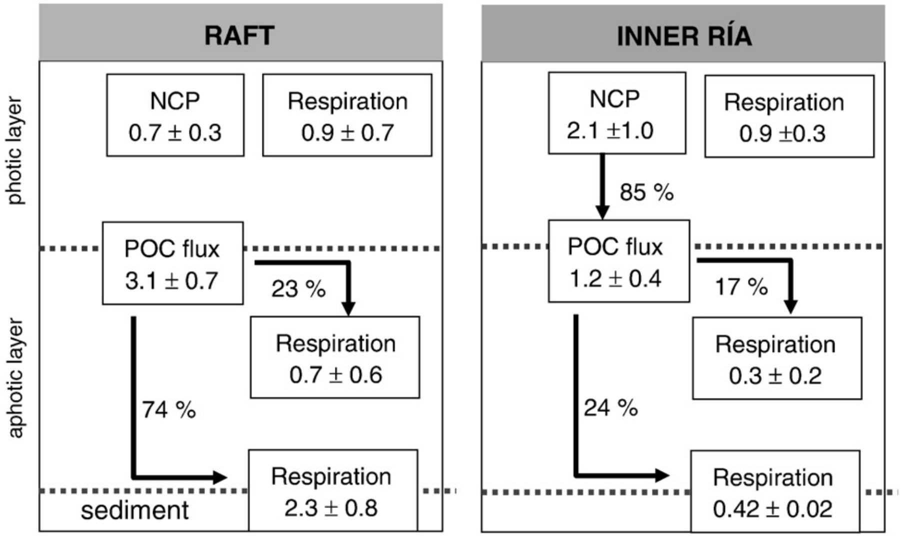

Fig. 6. 1D carbon budgets for the raft (RF) and inner Ría (IR) stations. Unit is g C m^{-2} d^{-1}. NCP: net community production. NCP and respiration data are from Arbones et al. (2008). POC: particulate organic carbon.

The NH_4^+ effluxes under the raft were 17 times higher (39.7 ± 19.8 mmol m^{-2} d^{-1}) than at the IR site (2.3 ± 0.3 mmol m^{-2} d^{-1}), pointing to a dominance of anaerobic processes under the raft. Oxidation of organic matter loading to the raft sediments generates higher benthic dissolved nitrogen fluxes, mainly in the form of NH_4^+ (Hatcher et al., 1994). The flux of ammonium under the raft was in accordance to Nizzoli et al. (2005, 2006) but much higher than most of other reported benthic fluxes (3–20 mmol m^{-2} d^{-1}) associated to mussel culture (Baudinet et al., 1990; Hatcher et al., 1994; Stenton-Dozey et al., 2001; Christensen et al., 2003; Giles et al., 2006) and also than other undisturbed coastal sediments (Nixon, 1981; Devol and Christensen, 1993; Berelson et al., 2003). As described by Nizzoli et al. (2006), this situation might be the result of the predominance of sulphate reduction and subsequently oxidation of sulphide, generating more reducing conditions under the raft. In fact, Otero et al. (2006) described the formation of reducing conditions that favour the processes of sulphate reduction and methanogenesis in sediments under a mussel raft in the Rías Baixas. Following Christensen et al. (2003), under these environments characterized by high sulphide levels, nitrification is inhibited and consequently denitrification processes avoided, and the prevailing nitrogen route is dissimilative reduction of nitrate to ammonium (DNRA). Our nitrogen benthic fluxes, dominated by high NH_4^+ effluxes and very low nitrate fluxes, respond to this pattern. In contrast, nitrogen fluxes at the IR station were completely different from the RF station with much lower NH_4^+ fluxes and recurrent negative nitrate fluxes. These fluxes and the observed BRQs seem to point out the prevalence of nitrification–denitrification metabolism route in this site, though further studies are needed to explore this via.

In contrast to the observations obtained by Hatcher et al. (1994) under mussel culture, sediments in the Ría de Vigo act as a source of phosphate to the overlying water, and remineralization of organic phosphorous was much more intense under the mussel raft (3.6 ± 1.6 mmol m^{-2} d^{-1}) than at the IR site (0.21 ± 0.1 mmol m^{-2} d^{-1}). Benthic phosphate fluxes under the raft were higher than those obtained by Giles et al. (2006) and Richard et al. (2007) (max. 0.6 mmol m^{-2} d^{-1} and 1.2 mmol m^{-2} d^{-1}, respectively) and comparable to the highest fluxes (2.7 mmol m^{-2} d^{-1}) obtained in a one year study under mussel culture (Baudinet et al., 1990).

The higher release of silicate to the water column from the sediment at the RF site was probably related to a high content of diatom frustules in the mussel faeces exported from the water column to the sediment. This observation is supported by data from Zuñiga et al. (in preparation) that obtained much higher vertical fluxes of biogenic silica under the raft (95 mol m^{-2} d^{-1}) than at the IR site (15 mol m^{-2} d^{-1}).

4.4. 1D budget: benthic–pelagic coupling

Based on the benthic and pelagic fluxes presented here, and considering the primary production and pelagic respiration rates obtained by Arbones et al. (2008) from *in situ* 24 h incubations of ^{14}C and oxygen collected simultaneously to our data set for the two sites, we have built up a 1D budget for the RF and the IR locations (Fig. 6). Net community production (NCP) at the IR station during the first two weeks of July was 2.1 g C m^{-2} d^{-1}, much higher than at the raft station (0.7 g C m^{-2} d^{-1}). The organic carbon collected on the sediment trap at this IR station, represented ~85% of the NCP, a value which is higher than the 75% obtained by Varela et al. (2004) in the Ría de Pontevedra and the value of 25–30% presented as the overall range for coastal areas (Berger et al., 1989). Part of this falling material is respired in the water column ~17% (0.3 ± 0.2 g C m^{-2} d^{-1}) (Arbones et al., 2008), and ~24% is oxidized at the water–sediment interface. Thus, at this location, the benthic fluxes represented 20% of the net community production in the upper photic zone. However, the situation is completely different for the RF station. At this position, both the organic carbon settled on the traps (3.1 ± 0.7 g C m^{-2} d^{-1}) and the material oxidized at the sediment–water interface (2.3 ± 0.8 g C m^{-2} d^{-1}) were much higher than the organic carbon produced at the photic zone. Carbon oxidation at the sediment–water interface represented ~74% of the settling material and ~23% is respired in the water column. Considering these 1D budgets, the importance of the benthic metabolism is enhanced at the mussel raft site, in response to the higher organic loading at this site. However, it has to be mentioned that vertical and benthic fluxes may be affected by horizontal advection within this area and therefore limit the results shown in the 1D budget.

In summary, our study demonstrates the importance of benthic nutrient regeneration in coastal upwelling systems like the Rías Baixas and shows that mussel cultures can lead to a redistribution of organic material and nutrients. However, seasonal variability of net primary production will have an effect on the mussel harvest and consequently over the vertical and benthic fluxes. The quality and quantity of the mussels' (pseudo) faecal pellets are also dependent on the mussel growth state. Therefore, these aspects must be considered and studied before extrapolating our results to evaluate the impact of mussel farming on ecosystem nutrient dynamics.

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