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Impacts of mussel (*Mytilus galloprovincialis*) farming on oxygen consumption and nutrient recycling in a eutrophic coastal lagoon

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Abstract

Fluxes of oxygen, nitrogen and phosphorus were determined in two areas of the Sacca di Goro lagoon, at a site influenced by the farming of the mussel *Mytilus galloprovincialis* and a control site. Mussel farming induced intense biodeposition of organic matter to the underlying sediments, which stimulated sediment oxygen demand, and inorganic nitrogen and phosphorus regeneration rates compared to the nearby control station. Overall benthic fluxes (–11.4 ± 6.5 mmol O_2 m^{-2} h^{-1}; 1.59 ± 0.47 mmol NH_4^+ m^{-2} h^{-1} and 94 ± 42 μmol PO_4^{3-} m^{-2} h^{-1}) at the mussel farm are amongst the highest ever recorded for an aquaculture impacted area and question the belief that farming of filter-feeding bivalves has inherently lower impacts than finfish farming. *In situ* incubations of intact mussel ropes demonstrated that the mussel rope community was an enormous sink for oxygen and particulate organic matter, and an equally large source of dissolved inorganic nitrogen and phosphate to the water column. Overall, a one meter square area of mussel farm (mussel ropes and underlying sediment) was estimated to have an oxygen demand of 46.8 mmol m^2 h^{-1} and to regenerate inorganic nitrogen and phosphorus at rates of 8.5 and 0.3 mmol m^2 h^{-1}, with the mussel ropes accounting for between 70 and more than 90% of the overall oxygen and nutrient fluxes. Even taking into account that within the farmed area of the Sacca di Goro lagoon, there are 15–20 m^{-2} of open water for each one covered with mussel ropes, the mussel ropes would account for a large and often dominant part of overall oxygen and nutrient fluxes. These results demonstrate that it is essential to take into account the activity of the cultivated organisms and their epiphytic community when assessing the impacts of shellfish farming. Overall, whilst grazing by the mussel rope community could act as a top-down control on the phytoplankton, most of the ingested organic matter is rapidly recycled to the water column as inorganic nutrients, which would be expected to stimulate phytoplankton growth. Consequently, the net effect of the mussel farming on phytoplankton dynamics, may be to increase phytoplankton turnover and overall production, rather than to limit phytoplankton biomass.

Introduction

Coastal lagoons and nearshore environments are characterised by elevated inputs of nutrients of continental origin, which can sustain high rates of primary productivity (Castel et al., 1996). The high availability of particulate nutrients in lagoon environments, in conjunction with generally shallow water depths and easy access to land based facilities makes them prime locations for the cultivation of filter-feeding molluscs. Shellfish farming, in common with other types of aquaculture has undergone a rapid expansion over recent decades (Kaiser et al., 1998; Naylor et al., 2000;

FAO, 2003). According to the FAO, in 2002 total aquaculture production attained 10.7 million tonnes, with mollusc farming representing 23.5% of total production and mussel cultivation approximately 14% of total shellfish production (FAO, 2003). In Italy, mussel cultivation is both a socially and economically important industry. For example, in 1997 the estimated yield of mussels was over 100,000 tonnes and accounted for ~30% of total mussel production in the Mediterranean basin, which itself represents 70% of Worldwide production (MacAlister, 1999).

The impressive growth of the aquaculture industry and the fact that activities are mostly concentrated in shallow, often sensitive coastal areas has stimulated research to assess the potential impacts on the exploited environments (Rana, 1998). Generally, the extensive cultivation of filter-feeding bivalves is considered to have low impacts compared to fish farming, as it does not require any inputs of feeds, as the shellfish production is dependent upon *in situ* phytoplankton productivity (Naylor et al., 2000). Indeed, it has been suggested that filter feeders can act as a buffer against eutrophication processes, as they impose a top down control on the phytoplankton biomasses and sequester nutrients, which would subsequently be removed from the system if the shellfish were harvested (Officer et al., 1982; Kaspar et al., 1985; Soto & Mena, 1999; Nakamura & Kerciku, 2000; Cloern, 2001). Conversely, intense filtration, coupled with the production and the subsequent deposition of faeces and pseudofaeces (biodeposition) increases inputs of labile organic matter to the superficial sediment by up to orders of magnitude (Dahlbäck & Gunnaersson, 1981; Jaramillo et al., 1982; Graf & Rosenberg, 1997). These high organic matter loads fuel mineralisation processes, stimulating both aerobic and anaerobic metabolism, and nutrient recycling back to the water column (Kaspar et al., 1985; Baudinet et al., 1990). Since oxygen transfer to marine sediments is limited due to the low solubility of oxygen in seawater and the inherent slowness of diffusion over distances of even a few millimetres, increased organic matter loads resulting from mussel farming may preferentially favour anaerobic metabolism and particularly sulphate reduction, leading to deterioration in sediment redox status and the accumulation of toxic free sulphides in the porewater (Dahlbäck & Gunnaersson, 1981; Sorokin et al., 1999; Christensen et al., 2003). Thus, mussel cultivation may result in the formation of "hot spots" of eutrophication and nutrient recycling, and patches of organic rich, highly reduced sediments below the farming installations.

Studies on the impacts of biodeposition from suspended shellfish farming have reported low to moderate stimulations of benthic metabolism and medium to high increases in the rates of nutrient recycling to the water column (Dahlback & Gunnarsson, 1981; Kaspar et al., 1985; Hatcher et al., 1994; Kaiser et al., 1998; Christensen et al., 2003). For example, in Beatrix Bay, New Zealand, Christensen et al. (2003) measured a 2-fold increase in oxygen consumption beneath mussel long lines, compared to the reference site, associated with a ~14-fold increase in ammonium efflux. Similarly, Kaspar et al. (1985) a 2- to 4-fold increase in nitrogen mineralisation rates in an area of Kenepuru Sound, New Zealand, exploited for long line cultivation of the mussel *Perna canaliculus*. However, most of these studies on the effects of shellfish farming on the biogeochemistry of the underlying sediment have focussed on temperate, deep waters with relatively high water flushing and impacts may be significantly greater in Mediterranean lagoons, where shallow water depths and low tidal exchanges would favour local deposition of the mussel faeces and high summer temperatures would be expected to stimulate microbial mineralisation processes.

An additional problem with most previous studies is that only the sediment system has been considered and very few studies have addressed the direct role of the suspended shellfish cultures. Mussels are generally farmed as rope cultures with biomasses in the order of several to 10's of kg m^{-2}. These ropes form a complex environment, which is rapidly colonised by a diverse faunal community of attached filter-feeding epifauna and free living fauna which inhabit the interstitial spaces, and feed on the organic detritus which covers the mussels and accumulates within the mussel rope structure (Mazouni et al., 2001). Therefore, due to the high biomass and metabolic activity of the mussels and colonising fauna, and microbial mineralisation of accumulated organic detritus, the mussel ropes themselves can represent a significant sink for oxygen and source of inorganic nutrients (Kaspar et al., 1985; Mazouni et al., 2001), which must be taken

into account to assess the true environmental impacts of mussel farming.

In this study we have quantified the effects of suspended mussel (*Mytilus galloprovincialis*) farming on sediment characteristics, sediment oxygen consumption and sediment-water column nutrient fluxes, in a shallow, Mediterranean lagoon by comparing a farmed and a control area. In addition at the mussel-farmed site the role of the mussel ropes as a sink for oxygen, and particulate organic matter and a source/sink for inorganic N and P was directly determined during *in situ* incubations of entire, intact mussel ropes, to allow estimation of the global effects of mussel farming on oxygen and nutrient dynamics, and the quantitative contribution of the mussel ropes.

Study site and sampling stations

The study was carried out in the Sacca di Goro (44° 82′ N, 12° 27′ E) a shallow, micro-tidal, coastal lagoon located in the southernmost part of the Po River Delta (Northern Italy). The lagoon has a total surface area of ~26 km^2, a mean depth of 1.5 m and receives freshwater inputs from the Po di Volano and Po di Goro deltaic branches. At present approx. 8 km^2 of the lagoon surface (approx. 30%), are licensed for the farming of clams (*Ruditapes philippinarum)* and 0.4 km^2 for mussel farming (Fig. 1). The mussel-farmed area consists of 5 parallel 1 km lines of trellis, separated by approximately 50 m of clear water. The mussels are cultivated as 1–1.5 m long ropes, suspended from the trellis at a mean density of 5 ropes m^{-2}. At maturity the ropes attain a biomass comprised between 9 and 12 kg fresh weight. Annual production is maximally 1500–2000 tons, but in recent years part of this activity has been transferred to areas outside of the lagoon because of mussel deaths due to high summer water temperatures and episodic anoxia, and mussel production within the lagoon has declined to less than 1000 tons y^{-1}.

In this study two sampling sites were considered, stations C and M (Fig. 1), station M was located within the mussel-farmed area and station C, which served as a control site was located approx. 500 m outside of this area in a zone with similar water depth and hydrodynamics.

Materials and methods

Sample collection and maintenance

All samples were collected on the 5th September 2000. At each sampling station, 10 sediment cores were collected using plexiglass core tubes (30 × 5 i.d. cm) for determination of sediment density, porosity, organic matter content, AVS (S^{2-} + FeS)

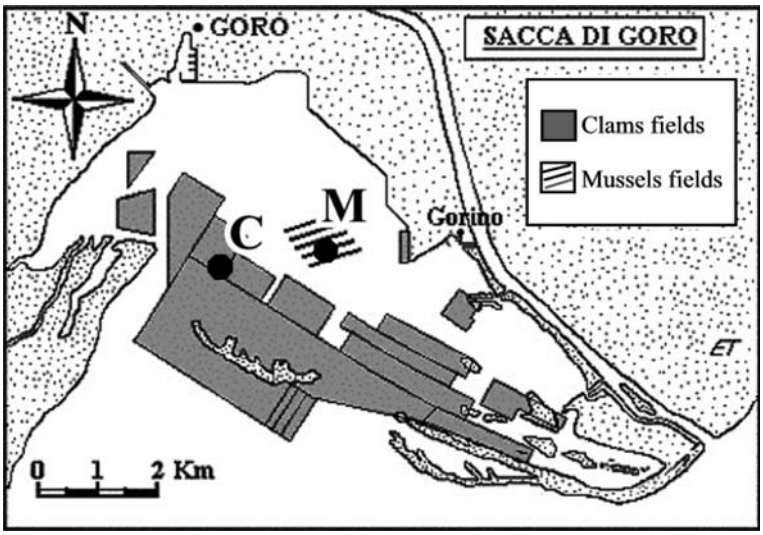

Figure 1. Map of the Sacca di Goro lagoon indicating the distribution of areas licensed for clam (*Ruditapes philippinarum*) and mussel (*Mytilus galloprovincialis*) farming and the locations of sampling stations C (control) and M (mussel) (●).

concentrations and nutrient content, and 5 using 30 × 8 i.d. cm plexiglass core tubes for determination of sediment-water column oxygen and nutrient fluxes. In addition at each site water samples were collected for NH_4^+, NO_2^-, NO_3^-, phosphate, particulate nitrogen and phosphorous, and salinity determinations. An additional 75 l of water was collected from each site for core maintenance. All samples were returned to the laboratory within 1 h of collection. Water samples were immediately processed and the samples frozen for later analysis. Sediment cores were transferred to 30 l incubation tanks containing water from the same sampling station and maintained at *in situ* temperature in the dark with constant aeration. In cores for flux determinations mixing of the water within the cores was assured by suspended magnets fitted inside the cores and driven by a central electric motor as previously described (Welsh et al., 2001). All cores were maintained overnight prior to the initiation of experiments.

Sediment characterisation

A set of five cores were sliced into 4 depth horizons (0–1; 1–2; 2–5; 5–10 cm), each sediment slice was immediately homogenised and samples collected using cut-off 10 or 2 ml syringes for determination of sediment density, porosity, organic matter content and bio-available ammonium and phosphate contents.

Sediment density was determined by transferring 5 cm^3 of homogenised sediment to preweighed aluminium dishes and immediately reweighing them. The samples were then dried at 70 °C for 24 h and reweighed to determine sediment porosity (ml H_2O ml sed^{-1}) as loss of wet weight. Weighed sub-samples of the dried sediment were subsequently combusted at 550 °C for 3 h and reweighed to determine organic matter content (LOI) as loss of dry weight.

Sediment bio-available ammonium ($NH_{4\,bio}^+$; pore water + exchangeable NH_4^+) content was determined by extracting a 1 cm^3 aliquot of the homogenised sediment with 20 ml of 1 M KCl for 1 h under constant shaking. Following extraction the samples were centrifuged and the supernatant decanted and frozen for later analysis. Similarly, pore water and sediment exchangeable phosphate pools ($PO_{4\,bio}^{3-}$) were determined by transferring 1 cm^3 aliquots of sediment to tubes containing 20 ml of deoxygenated (N_2-sparged) 1 M $MgCl_2$ pH 7.5. The tubes were sealed, flushed for 5 min with N_2 and the phosphate pools extracted for 2 h with constant shaking. Following extraction, the samples were centrifuged, the supernatant were decanted to a second tube, the sediment resuspended in a further 20 of 1 M $MgCl_2$ pH 7.5 and the extraction procedure repeated. The pooled supernatants of the two extractions were then frozen for later analysis.

A second set of five cores were sectioned as described previously, each sediment slice was rapidly homogenised and a 2 cm^3 aliquot of sediment immediately collected and transferred to tubes containing 5 ml 10% (w/v) zinc acetate to fix the sediment reduced sulphur compounds. Pools of acid volatile sulphides (AVS; free sulphides + FeS) were extracted by distillation for 40 min at room temperature with 1 M HCl under a constant stream of N_2 as previously described (Fossing & Jorgensen (1989)). The evolved H_2S in the N_2 stream was trapped and fixed as ZnS by bubbling through 10 ml 10% (w/v) zinc acetate and stored for later analysis.

Determination of sediment-water column oxygen and nutrient fluxes, and sediment buffering capacity against sulphide release

Oxygen, DIN (dissolved inorganic nitrogen: $NO_3^- + NO_2^- + NH_4^+$) and phosphate fluxes were determined during dark incubations of 30 × 8 cm i.d. cores. Immediately prior to incubations the water in the incubation tank was replaced with fresh water from the same sampling site and the water within each core exchanged with the tank water by repeatedly withdrawing water from within the core tube using a 100 ml syringe. To initiate the incubations, the level of the water in the tank was lowered to below the tops of the core tubes, initial samples for determination of oxygen, and inorganic nitrogen and phosphorous concentrations were collected from each core and the cores sealed with floating plexiglass lids. Cores were then incubated in the dark for 2 h. After 1 h and at the end of the incubation the floating lids were removed, and water samples were collected for oxygen and inorganic nutrient determinations. Flux rates were calculated from the change in

water column concentration of the individual solutes according to the following formula:

$$F_x = (\beta * V/At) \quad (1)$$

where F_x is the flux of solute x (μmol x m^{-2} h^{-1}), β the slope of the regression line between the concentration of x compound and time, V the volume of water (l), A the surface area of the core (m^2), t the incubation time (h). Thereafter, the cores were resealed and incubated for a further 78 h to assess the residual sediment buffering against sulphide release. Samples of water from each core were collected after 3.5, 6, 8, 17, 27, 29, 33, 41, 46, 56, and 78 h in order to follow changes in oxygen and sulphide concentrations in the water column.

Determination of oxygen, particulate organic and dissolved inorganic nitrogen and phosphorus fluxes between the mussel ropes and water column

Fluxes of oxygen, particulate organic and dissolved inorganic nutrients between the water column and the mussel rope community where determined during *in situ* dark incubations of three intact mussel ropes on 5th September 2000. Three PVC tubes (25 cm i.d. × 2 m) were inserted into the sediment and an intact mussel rope was suspended within each tube and left to stabilise for 2 h before incubations were initiated. During this stabilisation period the water within each tube was continuously exchanged with the lagoon water using two high capacity water pumps, which respectively added water to or removed water from the tube.

To initiate incubations, the external water supply was interrupted and the tubes sealed with floating polystyrene lids. At time zero and at 10 min intervals during the 1 h incubations, water samples were collected via a sampling tube (see Fig. 2) for determination of oxygen, DIN, inorganic phosphorous and particulate nitrogen, and phosphorous concentrations. Samples for oxygen determinations were immediately fixed with Winkler reagents (APHA, 1975), samples for particulate nutrients were filtered on to 47 mm Whatman GF/F filters and the filters retained, and subsamples of the filtered water were retained for inorganic nutrient determinations. Samples were kept on ice until return to the laboratory, where the oxygen samples were analysed immediately, and the other samples frozen for later analysis. During the incubations, the water within the tubes was continually mixed via two submerged water pumps fixed within the tubes (Fig. 2), so that they created a circular current flow. Flux rates of particulate nutrients and dissolved solutes between the water column and the mussel ropes were calculated using the best fit linear regressions of the individual species concentrations. At the end of the

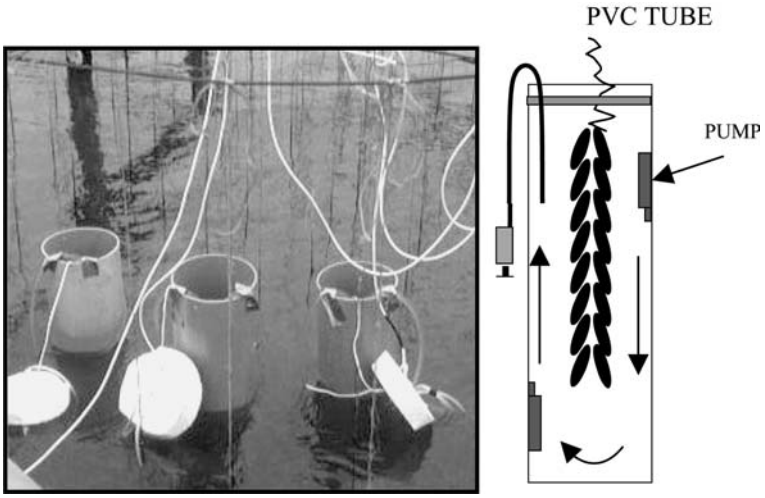

Figure 2. Schematic representation of the *in situ* incubation system used for the determination of oxygen and nitrogen fluxes due to the activity of the mussel ropes (more detail in the text) and photograph showing deployment of the incubation tubes in the field.

incubations the mussel ropes were removed and weighed to allow calculation of weight standardised flux rates.

Analytical methods

Dissolved oxygen concentrations were determined by the Winkler method (APHA, 1975), ammonium was determined by the indophenol blue method according Bower & Holm Hansen, (1986) and phosphate was determined spectrophotometrically according to Valderrama (1977). Nitrite concentrations were determined by diazotation (APHA, 1975) and nitrate was determined by the same method following reduction to nitrite over cadmium columns (APHA, 1975) and correction for the nitrite concentration. Particulate phosphorus and nitrogen were determined as phosphate and nitrate respectively, following persulphate oxidation and extraction of the glass fibre filters. Sulphide concentrations were determined spectrophotometrically according to Cline (1969).

Statistical methods

Normality of data was assumed, and homoscedasticity was confirmed using the Cochrane test. Differences between the two stations were tested using a one-way ANOVA (Sokal & Rohlf, 1995).

Results

Characteristics of water column, sediments and mussel ropes

The two sampling stations were located in the central part of the Sacca di Goro, approx. 500 m apart and were subject to similar hydrodynamics, as is reflected by the identical water temperature (22 °C) and salinity (20%), at both stations. However, inorganic nutrient concentrations were higher at station M than station C (Table 1), with DIN concentrations being 3.8-fold higher and soluble reactive phosphorous (SPR) concentrations 2-fold higher at the mussel-farmed site. Conversely, particulate nitrogen and phosphorous concentrations were slightly higher at station C.

The period of the present study coincided with the beginning of the mussel farming cycle in the Sacca di Goro, where most mussels are sown in late summer or autumn and are harvested in spring or early summer. Therefore the biomass of the individual ropes was relatively low and comprised between 2.5 and 3.5 kg, equivalent to 12.5 to 17.5 kg m^{-2} at the cultivated density of 5 ropes m^{-2}. The ropes were covered with detritus, settled both on the shell surfaces and trapped in the spaces between the shells. The ropes were also colonised by a macrofaunal community composed mainly of small crustaceans (*Gammarus* spp.), barnacles (*Balanus* spp.), polychaete worms (*Neanthes succinea*), other mussel species (*Musculista senhousia*), oysters (*Crassostrea* spp.) and crabs (*Carcinus* spp.). On average mussel biomass represented only 60–70% of the mussel rope fresh weight with accumulated detritus and epifaunal organisms accounting for the remainder.

Table 1. In situ water column temperature, salinity and NH_4^+, NO_2^-, NO_3^-, DIN ($NH_4^+ + NO_2^- + NO_3^-$), SRP, particulate nitrogen (TPN) and particulate phosphorus (TPP) concentration at stations C (control) and M (mussel) on 5th September 2000

	Station M	Station C
Temperature (°C)	22	22
Salinity (%)	20	20
NH_4^+ (μM)	18.8	5.5
NO_2^- (μM)	1.9	0.1
NO_3^- (μM)	18.0	4.4
DIN (μM)	38.7	10.0
SRP (μM)	0.6	0.3
DIN/SRP	64.5	38.7
TPN (μM)	19.0	22.0
TPP (μM)	2.0	2.5
TPN/TPP	9.5	8.8

The sediments below the mussel ropes were almost completely devoid of macrofauna and only a few large *Nereis succinea* individuals, which had probably fallen from the overhanging mussel ropes where present. Macrobenthic organisms were also generally sparse at station C, where the benthic community was composed of low densities of *Nereis succinea* and small sized crustaceans (data not shown).

At station M the sediments directly below the mussel ropes were composed mostly of fine textured muds and silts (mussel biodeposits)

trapped within a matrix of mussel shell fragments. The sediment was poorly compacted and had a very high water content throughout the 0–10 cm depth profile, with a mean porosity of 0.83 ml ml^{-1}. Sediments at control site were sandier, with a low silt content. Whilst the porosity was similar to station M in the surface 0–1 cm layer, it decreased rapidly with depth to 0.63 ml ml^{-1} in the deepest layer (Table 2). At both sites reduced sulphur compounds (AVS) concentrations increased with depth, but at station M concentrations in the first 10 cm of sediment were very much higher (Table 2), especially in surficial sediments, with the concentration of 3.2 μmol ml sed^{-1} in the 0–1 cm depth horizon at station M being more than 32-fold higher than that in the same layer and more than 2-fold higher than that in the deepest, 5–10 cm depth horizon at station C. This difference in AVS pools was also evident from the colour of the sediment at station M, which was jet black to almost the sediment surface.

The sediment organic matter content, measured as loss on ignition (LOI), was significantly higher at station M (ANOVA $p < 0.01$) compared to the control station. At station M the profile of sediment organic matter content was quite homogenous, with values comprised between 10.9 and 8.1% dry weight (Table 2). Whereas, at station C the sediment organic matter content decreased sharply with depth from 8.1 to 3.6% dry weight over the 0–10 cm depth profile.

Bioavailable ammonium ($NH^+_{4\,bio}$), which comprises the porewater and sediment exchangeable ammonium pools was significantly more abundant (ANOVA $p < 0.01$) at station M (Table 2). At this site $NH^+_{4\,bio}$ concentrations increased markedly with depth from 4.1 to 10.2 μmol ml sed^{-1} in the 5–10 cm depth horizon (Table 2). Whereas, at the control station $NH^+_{4\,bio}$ concentrations were 2- to 3-fold lower, with concentrations of 1.8 μmol ml sed^{-1} in the 0–1 cm sediment horizon and approx. 3.0 μmol ml sed^{-1} at all depths below this layer. Conversely, although low at both stations (range 0.02–0.14 μmol ml sed^{-1}), bioavailable phosporous ($PO^{3-}_{4\,bio}$; combined porewater and sediment exchangeable pools), was generally more abundant in the sediments of station C than those of station M (Table 2).

Sediment oxygen demand, inorganic nitrogen and phosphorus fluxes and short-term sulphide retention capacity

Sediment oxygen consumption rates (SOD) were spatially variable at both stations and especially so at station M, with individual core rates comprised between 4.3–16.8 and 6.2–10.6 mmol m^{-2} h^{-1} at stations M and C respectively. This elevated variability masked differences due to mussel farming even though mean SOD was approximately 3 mmol m^{-2} h^{-1} higher at the mussel-farmed station than at station C.

The sediments at both stations represented a net source of dissolved inorganic nitrogen (DIN = NH^+_4 + NO^{2-} + NO^{3-}) to the water column, with the mean DIN efflux of 1245 ± 315 μmol m^{-2} h^{-1} at Station M being significantly greater ($p < 0.01$) than that of 132 ± 76 μmol m^{-2} h^{-1} measured at station C. Ammonium was the dominant component of the net DIN flux at both stations, with its efflux more than compensating for the consumption of oxidised forms of nitrogen by the sediments at

Table 2. Depth profiles of sediment porosity, organic matter content, bio-available ammonium and phosphate pools, and AVS content in the sediment of stations M (mussel) and C (control). All data are presented as means ± one standard deviation ($n = 5$)

Sediment layer	Porosity		Organic matter (%)		$NH^+_{4\,bio}$ (μmol ml sed^{-1})		$PO^{3-}_{4\,bio}$ (μmol ml sed^{-1})		AVS (μmol ml sed^{-1})	
	M	C	M	C	M	C	M	C	M	C
0–1	0.85	0.84	10.2 ± 0.1	8.14 ± 0.6	4.1 ± 0.5	1.8 ± 0.1	0.03 ± 0.01	0.09 ± 0.03	3.2 ± 2.0	0.1 ± 0.1
1–2	0.85	0.81	10.9 ± 0.6	6.35 ± 0.5	5.6 ± 0.4	2.9 ± 0.2	0.02 ± 0.01	0.05 ± 0.01	4.6 ± 2.7	0.2 ± 0.2
2–5	0.83	0.68	9.6 ± 1.1	4.70 ± 0.7	7.1 ± 0.6	3.2 ± 0.3	0.04 ± 0.02	0.04 ± 0.01	9.5 ± 3.1	1.0 ± 1.2
5–10	0.80	0.63	8.1 ± 0.9	3.65 ± 0.5	10.2 ± 0.7	2.9 ± 0.4	0.06 ± 0.01	0.14 ± 0.09	7.3 ± 3.6	1.5 ± 0.4

both stations. Ammonium effluxes were significantly different between the stations, with the ammonium efflux at station M of almost 1.6 mmol m^{-2} h^{-1} being approx. 4-fold higher than that at station C. Whereas, mean sediment nitrate consumption rates were similar for both sites (Fig. 3) with all the individual core fluxes comprised between −180 and −522 μmol m^{-2} h^{-1}. The mean nitrite fluxes of −28.1 ± 9.8 and −8.5 ± 2.3 μmol m^{-2} h^{-1} at stations M and C respectively, were significantly different ($p < 0.05$), but of little importance due to their very low values compared to ammonium and nitrate fluxes.

SRP fluxes were also markedly influenced by mussel farming and differed significantly between the two stations (Fig. 3). At station M there was a consistent release of SRP from the sediment with a mean efflux of 94 ± 42 μmol m^{-2} h^{-1}. Whereas at the station C, SRP fluxes were low and variable between replicates, with the mean value indicating a small SRP uptake of −4.6 ± 20.6 μmol m^{-2} h^{-1} by the sediment.

The sediments of the two stations also differed greatly in their capacity to retain sulphides under anaerobic conditions (Fig. 4). At station M, immediately after oxygen was depleted in the water column and therefore no longer available for sulphide oxidation, free sulphides were released from the sediment and accumulated in the overlying water (Fig. 4). The sulphide accumulation rates corresponded to a mean sulphide efflux rate from the sediment of 648 ± 300 μmol S m^{-2} h^{-1}, with the highest single fluxes of up to of 1500 μmol S m^{-2} h^{-1}. In contrast, in sediment cores from the control station, no sulphide was detectable in water column of any of the five replicate cores even after almost 40 h of anoxia, indicating that this sediment maintained a high capacity to trap and retain the sulphides generated during bacterial sulphate reduction.

Oxygen, DIN, SRP and particulate nitrogen and phosphorous fluxes across the mussel ropes

The biological activity of the whole mussel rope community as a source/sink for oxygen, dissolved inorganic and particulate organic nutrients was assessed during *in situ* incubations of three intact mussel ropes and standardised per kg to eliminate effects of differences in the weight of the individual ropes. The results of these incubations (Table 3) demonstrate that due to the filtration activity of the mussels and their epiphytes, the mussel ropes were a large sink for particulate nutrients in the water column, with uptake rates of particulate organic nitrogen and phosphorus being −565 μmol N kg^{-1} h^{-1} and 42 μmol P kg^{-1} h^{-1} respectively. This organic matter fuelled high metabolic activity and the mussel ropes consumed 2.4 mmol kg^{-1} h^{-1} of oxygen and regenerated

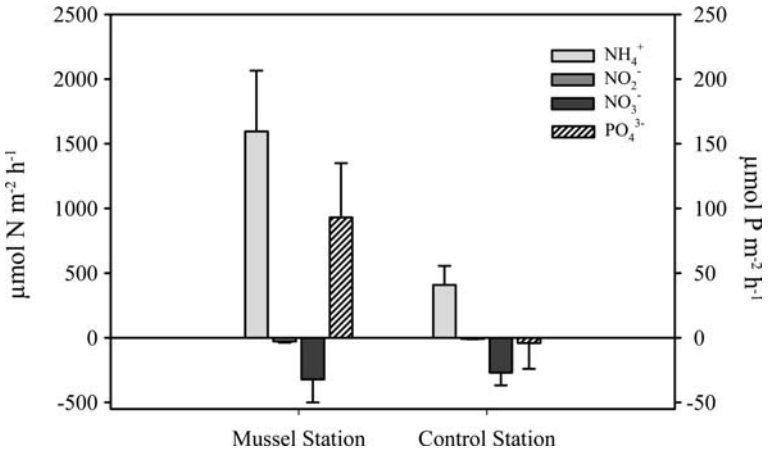

Figure 3. Sediment-water column fluxes of ammonium, nitrite, nitrate and phosphate at control and mussel-farmed stations. Data are the means from five replicate incubations and error bars indicate one standard deviation. Please note difference in scale for phosphate compared to the DIN fluxes.

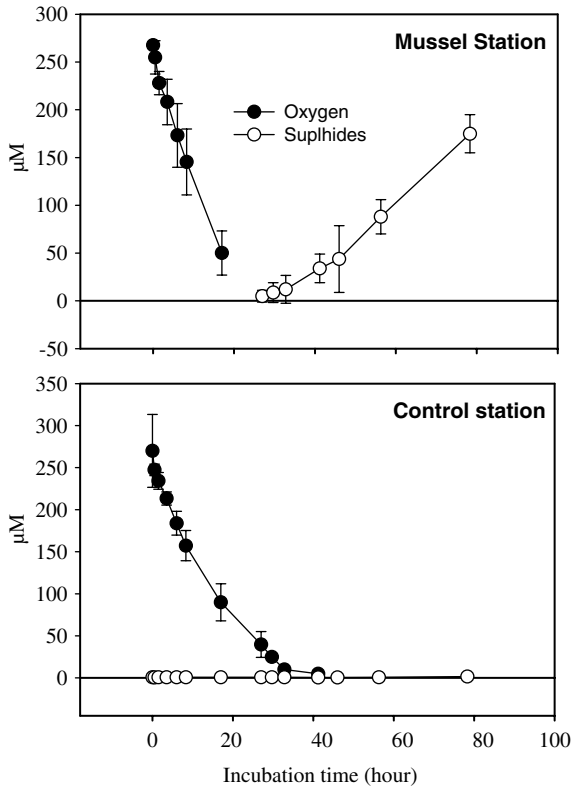

Figure 4. Time course of water column oxygen and sulphide concentrations during incubations of closed cores from station M (upper panel) and C (lower panel) to assess the sediment capacity to retain sulphides under anaerobic conditions. Data points are the means for five replicate incubations and error bars indicate one standard deviation.

ammonium and inorganic phosphate at rates of 580 and almost 15 μmol kg^{-1} h^{-1} (Table 3). Additionally, the mussel ropes were a significant sink for water column nitrate (−113 μmol kg^{-1} h^{-1}) and a small source of nitrite (18 μmol kg^{-1} h^{-1}) (Table 3).

Discussion

Sediment characteristics, redox status and metabolic activity

The comparison of the two studied stations indicates that mussel farming greatly influenced the physicochemical features and biogeochemistry of the underlying sediments. The mussel farm sediment had a finer texture, higher porosity and a 3-fold higher organic matter content than that of the control station. These differences can be directly related to the intense filtration activity of the mussels and other filter feeders colonising the mussel ropes. Fine organic and inorganic particles are actively removed from the water column and the resulting biodeposits (faeces and pseudofaeces) then accumulate within the sediments under the mussel ropes and are stabilised by the matrix of shells and shell fragments. Similar accumulations of organic rich sediments have previously been reported in other environments exploited for this kind of aquaculture (Grant et al., 1995; Christensen et al., 2003). Rates of organic matter biodeposition associated with dense natural or farmed bivalve populations can attain 70 g C m^{-2} d^{-1} (See Graf & Rosenberg, 1997 for review) and Grenz (1989) suggested that total biodeposition associated with suspended bivalve culture could reach quantities of 100's kg dry weight m^{-2} $year^{-1}$. Thus, it is unsurprising that mussel farming was a major determinant of sediment characteristics, especially in a micro-tidal, shallow water system such as the Sacca di Goro, where one would expect that most of the faeces and pseudofaeces would be rapidly deposited near to their site of production.

Such high organic matter inputs to the mussel-farmed sediments would be expected to fuel benthic metabolism. At our mussel-farmed site, the

Table 3. Mussel rope biomass for a stocking density of five ropes m^{-2} and specific flux rates of oxygen, inorganic N and P species, and particulate nitrogen (TPN) and phosphorus (TPP) between the water column and the mussel ropes

Biomass (kg m^{-2})	O_2 (mmol kg^{-1} h^{-1})	NH_4^+ (μmol kg^{-1} h^{-1})	NO_2^- (μmol kg^{-1} h^{-1})	NO_3^- (μmol kg^{-1} h^{-1})	PO_4^{3-} (μmol kg^{-1} h^{-1})	TPN (μmol kg^{-1} h^{-1})	TPP (μmol kg^{-1} h^{-1})
15.3 ± 1.4	−2.4 ± 1.2	579.7 ± 100.8	18.0 ± 11.5	−112.6 ± 28.0	15.2 ± 6.3	−564.5 ± 128.1	−41.9 ± 9.6

All values were determined during three replicate *in situ* incubations of individual mussel ropes and have been standardised per kg wet weight, to remove effects due to differences in the individual ropes weights. Negative fluxes indicate consumption and positive fluxes production of the organic or inorganic species by the mussel rope community. Mean values ± one standard deviation are presented.

SOD of almost 11 mmol m^{-2} h^{-1} is amongst the highest values ever measured at any aquaculture site, including intensive fin-fish farmed sites (Baudinet et al., 1990; Hargrave et al., 1993; Barranquet et al., 1994; Christensen et al., 2000; Holmer et al., 2002) and is much higher than values determined below mussel long-lines in temperate, deep water, macro-tidal systems (Kaspar et al., 1985; Hatcher et al., 1994; Christensen et al., 2003). However, despite this extremely high mean SOD at the mussel-farmed station, the SOD at this station was not significantly different from that at station C. This lack of difference can be attributed to three principal factors. First, the high variability in the replicate SOD determinations at station M may have masked differences between the sites. Similarly high variability in SOD has previously been described for mussel-farmed areas and was proposed to arise from non-homogenous deposition of faeces and pseudofaeces (Hargrave et al., 1993). But at our site, may also reflect the heterogeneous nature of the sediments below the mussel ropes and especially the distribution of shell and shell fragments at the sediment surface, which would have reduced the actual sediment surface area available for oxygen exchange. Secondly, the fact that the SOD at station C was also very high, due to the hypereutrophic nature of the Sacca di Goro lagoon in general (Viaroli et al., 2001) and possible resuspension and lateral transport of biodeposits from the nearby mussel and clam farms (Fig. 1) to this station C during stormy or windy weather. Finally, in marine sediments, SOD may not be a very sensitive indicator of overall sediment metabolism, as a large proportion of organic matter mineralisation proceeds via anaerobic pathways and this proportion increases with increasing organic matter loads (Jørgensen, 1977; Holmer & Kristensen, 1992; Blackburn & Blackburn, 1993). If all or part of the reduced products generated via anaerobic metabolism are sequestered in the sediment rather than reoxidised, then SOD will underestimate sediment metabolism. Our data support the hypothesis that SOD underestimated overall benthic metabolism at station M to a greater extent than at Station C, as sediment AVS pools at station M were up to 30 times higher than those at station C. AVS is composed of free sulphide and iron mono-sulphide which forms when sulphide precipitates with porewater Fe^{2+} and can be considered to represent the initial products of sulphate reduction, the dominant anaerobic respiration process in marine sediments (Jørgensen, 1982; Thode Andersen & Jørgensen, 1989). Therefore, the much greater pools of AVS in the sediments below the mussel ropes directly demonstrates that a larger part of the products of anaerobic metabolism are sequestered at station M than at station C and consequently, that SOD underestimates the difference in benthic metabolism between the two stations.

Although SOD was not significantly different between the two stations, N and P fluxes did differ significantly and ammonium efflux rates were $\sim$4 times higher at station M than station C. Similar large increases in ammonium effluxes have been reported in many studies of the effects of suspended shellfish cultivation on the underlying sediments (Kaspar et al., 1985; Baudinet et al., 1990; Hatcher et al., 1994; Kaiser et al., 1998; Christensen et al., 2003). In contrast to ammonium fluxes, nitrate fluxes at both stations were of similar magnitude and were directed towards the sediment, demonstrating that nitrate reduction processes dominated over nitrification (nitrate production). This observation supports the data from model and manipulative microcosm studies, that despite high ammonium availability, nitrification rates are limited in organic matter rich, highly metabolic sediments due to competition for oxygen (Blackburn & Blackburn, 1993; Sloth et al., 1995). Additionally, even though nitrate fluxes to the sediments were high at both stations, it cannot be concluded that these fluxes supported high rates of denitrification, as the high temperature and high organic matter content, especially at station M, may favour dissimilatory nitrate reduction to ammonium (DNRA) over denitrification as a sink for nitrate (Tiedj, 1987; Christensen et al., 2000). Thus, particularly at station M, a large proportion of the nitrate diffusing to the sediment, may have been reduced to ammonium and recycled to the water column via DNRA, rather than been eliminated as gaseous products via denitrification.

Considering overall DIN fluxes, which represent the net product of all the individual inorganic nitrogen species fluxes, the net efflux of DIN from the sediments at stations M of 1.25 mmol N

m^{-2} h^{-1} was almost 10 times higher than that at the control site.

Phosphate fluxes also differed markedly between the two sampling stations, with the sediments at station C being a small sink for phosphate, whereas the sediments below the mussel ropes were a moderate source of phosphate to the water column. However, it is difficult to relate these differences in phosphate directly to the increased organic matter inputs to the sediments at station M from the mussel biodeposits, as phosphate fluxes depend not only upon phosphate regeneration rates during organic matter mineralisation, but also on the sediments capacity to bind and retain inorganic phosphate. This sediment binding capacity for phosphate depends on the availability of oxidised metal complexes such as iron III oxyhydroxides which can complex with and sequester inorganic phosphate (Slomp et al., 1996) and is redox sensitive as reduction of ferric iron to ferrous iron causes release of the bound phosphate (Golterman, 1995; Hejis et al., 2000). The high sediment AVS pools at station M and the fact that this sediment had no capacity to retain sulphides under anoxic conditions (See following discussion) strongly indicates that in this sediment, most of the iron was already reduced and precipitated with sulphur. Therefore, the sediment has a low phosphate binding capacity and phosphate regenerated during organic matter mineralisation would accumulate in the porewater and drive fluxes to the water column. In contrast the sediment at control station had much lower AVS pools and retained sulphide during anoxic conditions, indicating that free iron was present and consequently, this sediment could sequester phosphate regenerated within the sediment or diffusing to the sediment from the water column.

Overall, the flux data demonstrate that organic matter biodeposition by the mussels stimulated the metabolism of the underlying sediments, enhancing nutrient regeneration and driving high fluxes of nutrients back to the water column. These data also refute the claim that farming of filter-feeding bivalves has intrinsically lower environmental impacts than intensive finfish farming. Since, on an areal basis the SOD and nutrient effluxes we measured are equivalent to or higher than those determined in studies of the impacts of finfish farming on the underlying sediments (e.g., Blackburn et al., 1988; Hargrave et al., 1993; Christensen et al., 2000; Holmer et al., 2002). These, high impacts probably also reflect the generally high eutrophication status in the Sacca di Goro lagoon (Viaroli et al., 2001), and the shallow water depth and low hydrodynamics of this water body, which favours the deposition of faeces and pseudofaeces close to their site of production, resulting in intense organic matter inputs to the sediments in the immediate vicinity of the mussel farming installations.

Sediment buffering against sulphide release

Throughout the 1980's and 90's the Sacca di Goro lagoon has been afflicted by dystrophic crises, which occur in late spring or early summer, when periods of warm, calm weather in concert with minimum neap tides, result in anoxia and the accumulation of free sulphides in the water column for periods of a few days (Viaroli et al., 2001). Whilst, these crises mainly occurred in the confined Eastern part of the lagoon, which was subject to mass blooms of the green alga *Ulva rigida* (Viaroli et al., 2001), they have been implicated in shellfish mortalities in other parts of the lagoon. Since mussels, like most bivalves are relatively resistant to anoxia, it is probably the accumulation of sulphides in the water, which is the critical step in determining mussel mortality (de Zwaan et al., 2002). Therefore, we tested the capacity of the sediments to retain sulphides when the water column was anoxic and sulphide oxidation was not possible.

Sediment capacity to immobilise sulphides is related to the availability of reactive ferric iron, and manganese III and IV, which can chemically oxidise sulphide. Moreover, ferrous iron can directly precipitate sulphide as FeS and this can further react with elemental sulphur or polysulphides to generate pyrite (Jørgensen, 1977; Berner, 1984; Luther, 1991). However, as sediment iron and manganese pools are finite, this mechanism represents only a temporary sink for sulphides and the maintenance of this buffering capacity is ultimately dependent upon the reoxidation of the accumulated sulphur compounds and reoxidation of Fe^{2+} and Mn^{2+} to Fe^{3+}, and Mn^{3+} and Mn^{4+}.

In our experiments, no sulphide was released from the sediments of station C even after almost 40 h of anoxia, indicating that despite the meta-

bolically active nature of this sediment, there remained a considerable residual iron and manganese buffering capacity. Conversely, at the mussel-farmed station, sulphide fluxed to water column immediately after the imposition of anoxia. This would correspond to a situation where oxidised forms of iron and manganese where absent and the ferrous iron present was already combined in iron–sulphur compounds i.e., the ferrous iron buffering capacity was saturated. This interpretation is in accordance with our data on AVS pools in the two sediments, which clearly demonstrated that there were much higher concentrations of sulphides and FeS in the sediments of station M compared to station C, especially in the surficial sediment layers. Thus, the mussel farming activity, by augmenting organic matter loads to the sediment, which preferentially stimulate anaerobic metabolisms such as sulphate reduction, depletes the sediments buffering capacity against sulphides, thereby increasing system vulnerability to the dystrophic crises, which can cause mass mortality amongst the farmed mussels.

The contribution of the mussel ropes to overall oxygen and nutrient fluxes

The mussel rope community represented a large sink for oxygen and particulate nutrients and an equally large source of DIN and phosphorus to the water column. However, whilst the generated ammonium and phosphate may largely be excretion products of the mussels and their faunal epiphytes, the consumption of nitrate and production of nitrite by the rope community, demonstrates that the ropes were also the site of microbial activities such as nitrification, denitrification and DNRA. A previous study of the mussels in the Sacca di Goro has demonstrated that the mussel's shells and internal tissues are colonised by nitrifying bacteria (Welsh & Castadelli, 2004). Therefore, it cannot be concluded that the measured oxygen consumption, and ammonium and phosphate effluxes result solely from animal's metabolism, as microbial processes may also contribute significantly, through the mineralisation of organic matter deposited on the mussel shells or trapped in the interstices between the shells.

Considering, the fluxes of particulate nitrogen and phosphorus, and DIN and phosphate shown in Table 3, it is possible to construct simple nitrogen and phosphorus budgets for the mussel ropes, assuming that our *in situ* incubations represent a steady state situation. Using this approach the ratios between particulate nutrient consumption and net dissolved nutrient regeneration rates were 1.1 for nitrogen and 2.5 for phosphorous or that 86 and 36% respectively of the particulate nutrients taken up by the ropes were returned to the water column as DIN and phosphate. The remaining 14 and 64% respectively of the organic N and P being either assimilated by the mussel rope organisms, released as faeces or pseudofaeces or in the case of N, denitrified and lost from the system as gaseous products, which were not measured during this study.

These estimates demonstrate that the mussel rope community plays an important role in the recycling of particulate nutrients and that there was a preferential remineralisation of organic nitrogen compared to phosphorous. Whilst the N:P ratio of the organic matter consumed by the mussel ropes was 13.5 and close to the Redfield ratio for phytoplankton of 16 (Redfield et al., 1963), the N:P ratio of the inorganic nutrients released was 31.5 and closer to the macroalgal ratio of 35 (Atkinson & Smith, 1983). Similar preferential recycling of N compared to P has previously been observed in other systems dominated by high densities of filter-feeding bivalves, such as oyster reefs (Sornin et al., 1986; Dame et al., 1989) or sediments farmed with clams (Bartoli et al., 2001). This shift in N:P ratio has been attributed to the preferential mineralisation of organic N compared to P rather than a difference in the N and P assimilation dynamics of the bivalves themselves, thus much of the consumed phosphorus remains in the animal's faeces and pseudofaeces (Dame et al., 1989). For example, Sornin et al. (1986) calculated that the oyster, *Crassostrea gigas* assimilated only 3% of the phosphorus it consumed and the remainder was lost as inorganic phosphate or deposited to the sediment as faeces and pseudofaeces. However, our data on sediment-water column nutrient fluxes in the mussel-farmed area do not support this hypothesis, as the ratio's of the ammonium to phosphate and net DIN to phosphate fluxes were

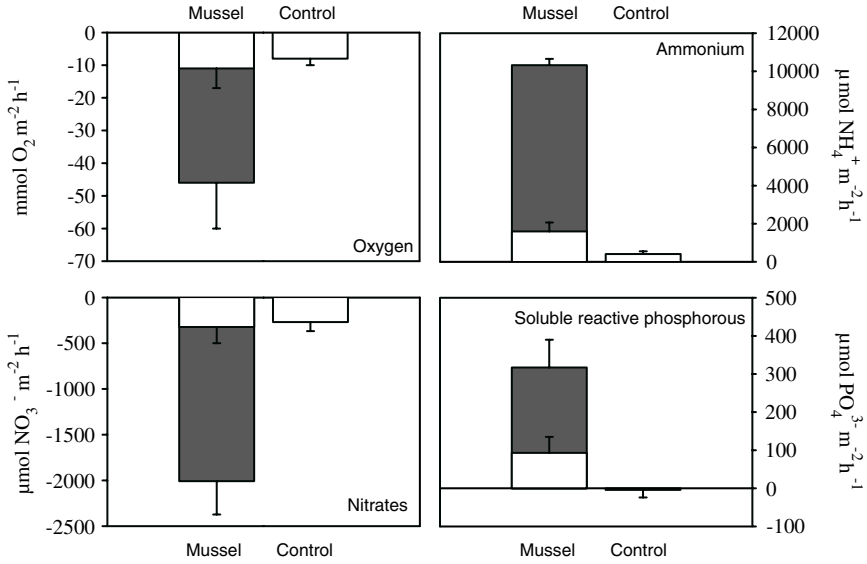

Figure 5. Estimated oxygen and inorganic nutrient fluxes for a hypothetical one square meter area of mussel farm with a stocking density of five mussel ropes per square meter. Total bar height indicates the overall net flux, the white areas of the bars correspond to the flux between the sediment and the water column and the grey areas of the bars correspond to the flux between the mussel ropes and the water column. Sediment-water column fluxes at station C are shown for comparison. Negative fluxes indicate consumption and positive fluxes production of the solute by sediment and mussel ropes. Mussel rope and sediment data are mean values for three and five replicate incubations respectively, and in both cases error bars indicate one standard deviation. Please note differences in scale for the individual solutes.

16.5 and 13.2 respectively. These ratio's are similar to the N:P ratio of the organic matter consumed by the mussel ropes, indicating that the biodeposited faecal material was not preferentially enriched in phosphorus. Therefore, alternative mechanisms are required to account for the apparently missing phosphorus. One potentially important phosphorus sink is the surface of the mussel ropes, which are rich in biogenic carbonates, which could immobilise phosphate via adsorption or co-precipitation processes (Golterman, 1995).

It has been proposed that the relative availability of inorganic nutrients in the water column could influence the composition of the primary producer community (see Cloern, 2001 for review). Therefore at first glance, it would appear that mussel farming in the Sacca di Goro could influence primary production processes not only quantitatively by stimulating overall inorganic nutrient regeneration rates, but also qualitatively by inducing a shift in the N:P ratio of the inorganic nutrients in the water column, due to the preferential recycling of organic N compared to P. However, at our control station, although there was a significant regeneration of inorganic N from the sediment, there was no regeneration of P and the sediment was in fact a net sink for phosphate from the water column during the study period. Consequently, although mussel farming favours inorganic N regeneration compared to that of P, the net effect of mussel farming is to increase the relatively availability of inorganic P compared to N.

In order to assess the impacts of mussel farming and the relative contributions of the sediment and mussel ropes to overall rates of oxygen consumption and nutrient recycling, we calculated these parameters for a hypothetical 1 m^2 area below five mussel ropes, which is the mean cultivated density in the Sacca di Goro. The results of these calculations (Fig. 5), clearly demonstrate the enormous differences in oxygen consumption and nutrient regeneration rates in the mussel-farmed area compared to the control station and the dominant role of the mussel ropes in source/sink relationships at the farmed site. For example, the overall oxygen demand of -47.8 ± 4.3 mmol m^{-2} h^{-1} was more than six times that at the control station and more than 75% of this oxygen was directly consumed by the mussel rope community. Similarly, the overall

ammonium regeneration rate of 10.3 ± 0.3 mmol m^{-2} h^{-1} was approx. 25 times higher than at the control station and 84% of this ammonium was regenerated by the mussel ropes and 70% of the phosphate release of 0.3 mmol m^{-2} h^{-1} was via mussel rope community. However, to gain a true appreciation of the impacts of the mussel farming and the direct contribution of the mussel ropes, two further factors must be taken into consideration. First, in the mussel-farmed area, for every square metre covered by mussel ropes, there are 15–20 m^2 of open water. The sediments in these areas would be expected to exhibit rates of SOD and nutrient regeneration rates intermediate between those measured directly below the mussels and those at the control station, depending upon their distance from the mussel ropes. Therefore above, we overestimate the impacts of mussel farming and the contribution of the mussel ropes to these large scale impacts. Secondly, our study was conducted in early September, shortly after the mussel ropes had been seeded and the ropes had an average total weight of only 3 kg, whereas, in spring or early summer when the mussels are harvested, individual ropes yield 9–12 kg fresh weight of mussels and can have total weight of over 20 kg. Therefore, one would expect that at other times of the year the impacts of mussel farming and the contribution of the mussel ropes to the overall impacts would be greater than at the time of our study.

Taking these two factors into account it was estimated that mussel farming increases local oxygen consumption and ammonium regeneration rates by 2–4 and 5–10 times respectively compared to the control area, and that the mussel ropes are directly responsible for 20–50% of the total oxygen consumption, and ammonium and phosphate regeneration in the farmed area. These estimates are in line with a previous study of intensive oyster (*Crassostrea gigas*) farming (Boucher et al., 1988), where the contribution of the cultivated organisms to oxygen consumption and ammonium production rates was calculated to be between 5–7% and 10–60% respectively.

Conclusions

Our data demonstrate the importance of taking into account the activity of the cultivated organisms and their epiphytic community when assessing the impacts of intensive, suspended cultivation of filter-feeding shellfish. Since, at least in intensive shellfish farming systems, such as the studied mussel farm, the suspended biological community is directly responsible for a large and in some cases the major part of the overall oxygen demand and inorganic N and P regeneration.

The results of this study also question two commonly held beliefs about shellfish farming and/or natural dense shellfish populations, such mussel beds or oyster reefs. Namely, dense populations of filter feeders act as a buffer against eutrophication processes by exerting a top-down control on phytoplankton growth, and that farming of filter-feeding bivalves has intrinsically lower impacts than finfish farming as it requires no external feed inputs. Since, firstly whilst it is true that the mussel ropes in this study exerted an intense grazing pressure on the phytoplankton, the ingested organic nutrients were rapidly recycled back to the water column by the mussel ropes and the underlying sediments, where they would fuel further phytoplankton growth. Thus, the net effect of the filter feeders may be to increase phytoplankton turnover and productivity, rather than to decrease phytoplankton biomass. And secondly, in the Sacca di Goro the combination of high mussel densities and weak hydrodynamics which favour localised accumulation of biodeposits, result in the sediments underlying the mussel ropes having oxygen demands and nutrient regeneration rates equivalent to or higher than those recorded for intensive finfish farms. If the activity of the mussel rope were also included, these oxygen demands and nutrient regeneration rates would be very much greater than any recorded for finfish farming. Unfortunately, comparable data sets for finfish farming, which include oxygen consumption and nutrient excretion data for the fish do not exist to allow direct comparison of the global impacts of the two types of aquaculture.

Finally, at a local scale, given the recent vulnerability of the Sacca di Goro to dystrophic crises, mussel farming at the current intensity is a high-risk activity, which is inherently vulnerable to major economic losses due to mass mussel mortalities. Since, the high oxygen demands of the mussel ropes and underlying sediments favour the local occurrence of anoxia in the water column and the sustained high organic matter loads have depleted

the iron-manganese buffering capacity against sulphide mobility of the underlying sediments and consequently, toxic free sulphides rapidly efflux to the water column once it becomes anoxic.

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