

Primary Research Paper

Seasonal patterns of pore-water nutrients, benthic chlorophyll *a* and sedimentary AVS in a macrobenthos-rich tidal flat

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Abstract

Monthly field investigations were carried out at controlled low-tide in an estuarine intertidal sandflat of the Seto Inland Sea (Japan) between January 1995 and April 1996. We assessed the spatial and temporal distribution of pore-water nutrient [NH_4^+ -N, $(\text{NO}_3^- + \text{NO}_2^-)$ -N, PO_4^{3-} -P and $\text{Si}(\text{OH})_4$ -Si], chlorophyll *a* (chl *a*) and acid-volatile sulphide (AVS) concentrations in the uppermost 0–10 cm sediment horizon, and evaluated their relationships with macrobenthic assemblages. Monthly hydrological data, nutrient and chl *a* concentrations in low-tide creek water adjacent to the flat were used as a complementary environmental characterisation of the study area. All different pore-water nutrients showed a 10 to >30-fold variability between different layers and periods. NH_4^+ -N, PO_4^{3-} -P and $\text{Si}(\text{OH})_4$ -Si concentrations were lowest in winter, progressively increased throughout spring and summer, and were highest between September and October, with a major increase at intermediate (4–8 cm) layers. In contrast, $(\text{NO}_3^- + \text{NO}_2^-)$ -N concentrations, correlated positively with chl *a*, peaked in winter and sharply decreased with depth in all different seasons and in most occasions. Depth-integrated NH_4^+ -N, PO_4^{3-} -P and $\text{Si}(\text{OH})_4$ -Si pools were correlated positively with biogenic nutrient flux calculated from the nutrient excretion rates of dominant bivalves *Ruditapes philippinarum* and *Musculista senhousia*. These relationships indicated rapid removal pathways of P, Si and N (i.e., every 0.1, 0.24 and 0.34 day, respectively), implying highly dynamic sediments. Based on the mass balance $P = F + I$, biogenic production (*P*) vs. diffusive flux (*F*) estimates suggested a predominant contribution of animal bioirrigation (*I*) to the upward flux of nutrients. AVS concentrations, correlated negatively with both $(\text{NO}_3^- + \text{NO}_2^-)$ -N and chl *a*, showed a progressive increase from late summer throughout winter, subsequent to that of NH_4^+ -N, PO_4^{3-} -P and $\text{Si}(\text{OH})_4$ -Si. The results indicate that in our study area the spatial and temporal distribution of pore-water nutrients, chl *a* and AVS in sediments are strongly interlinked and suggest that the metabolic processes (e.g., excretion, bio-deposition) and behavioural activities (e.g., particle mixing, bioirrigation) of abundant macrobenthos play an important role in the year-round biogeochemical processes occurring on this flat.

Introduction

An evaluation of the spatial and temporal distribution of nutrients, such as ammonium (NH_4^+ -N), nitrate + nitrite ($\text{NO}_3^- + \text{NO}_2^-$ -N), phosphate

(PO_4^{3-} -P) and silicate [$\text{Si}(\text{OH})_4$ -Si], represents a fundamental step in assessing the cycling of biophilic elements (e.g., nitrogen, phosphorous and silicon) and the system processes of production and respiration. It is known that in estuaries and tidal

flats numerous processes influence the behaviour of nutrients, whether they show conservative mixing or reflect removal or addition along an estuary (Montani et al., 1998; Magni et al., 2002). This variability is related to the close interaction between water chemistry, tidal hydrology and sedimentary processes (Nedwell et al., 1999; Magni et al., 2002; Viaroli et al., 2004). In these systems, abundant macrobenthos play a major role in the processes of nutrient regeneration and material cycling both at the sediment-water interface (Dame et al., 1984; Prins & Smaal, 1990) and within the sediment column (Kristensen, 1984; Kristensen et al., 1985; Mortimer et al., 1999).

In recent years, there is increasing evidence of a close relationship between nutrient concentrations in sediments and macrobenthos-influenced upward flux of nutrients, which in turn enhance primary production (see review by Herman et al., 1999 and therein references). This coupling has been recently shown, to varying degree, for a variety of benthic communities dominated by both suspension and deposit-feeders. The former, including semi-infaunal mussel species, such as *Musculista senhousia* or *Modiolus americanus* (Reush & Williams, 1998; Peterson & Heck, 2001), filtering particulate matter from the water column or algal detritus at the sediment-water interface (Magni et al., 2006); the latter, such as holothurians, consuming high amounts of sediment bacteria, microalgae and dead organic matter (Uthicke, 2001). Accordingly, these works highlight the need for parallel field investigations on solute distribution in the sediments and the biology, activity and behaviour of benthic animals (Christensen et al., 2000). However, relatively little work has been conducted in the field to evaluate the relationships among pore-water nutrients, sediment chemistry and macrobenthic assemblages (Lomstein et al., 1989; Reush & Williams, 1998; Mortimer et al., 1999), especially in estuarine intertidal sandflats on a year-round basis (Rysgaard et al., 1995; Peterson & Heck, 2001; Magni et al., 2006).

This work is a follow-up of a multidisciplinary study on the nutrient cycling and macrobenthic assemblages conducted in a tidal estuary of the Seto Inland Sea, Japan (e.g., Magni, 1998; Magni & Montani, 1997, 1998, 2000; Magni et al., 2002; Montani et al., 1998, 2003). In a previous paper, we showed that the excretory activity of dominant

bivalves, *Ruditapes philippinarum* and *Musculista senhousia*, scaled up to their temporal changes in terms of biomass, strongly influence the magnitude and variability of upward flux of nutrients within the intertidal zone (Magni et al., 2000). In this study, we aimed to assess the distribution of pore-water nutrients, chlorophyll *a* and acid-volatile sulphide (AVS) concentrations in the uppermost sediment horizon over a period of 1.5 years, and to evaluate how these variables are related to the composition, distribution and activity of macrobenthos which was followed in parallel.

Materials and methods

Study area and field surveys

The study area was located in an estuarine intertidal flat of the Seto Inland Sea, SW Japan (34° 21' N, 134° 05' E). The sampling site was set between the low water level (LWL) and the extreme low water level (ELWL); sediment emersion occurs twice a month during a spring low-tide (Magni & Montani, 1998). The sediments are sandy with a mud fraction (<0.063 mm) comprising <3% of the total weight (Magni & Montani, 1997). Total organic carbon concentrations in surface sediments (0–0.5 cm) range between 6.2 ± 1.0 and 11.7 ± 2.8 mg g⁻¹, with the tendency to be relatively higher in summer and autumn than in spring and winter (Magni et al., 2006). Detailed information on the sediment characteristics and microphyto-benthic assemblages (Magni & Montani, 1997; Montani et al., 2003; Magni et al., 2006), water chemistry and environmental variability (Magni & Montani, 2000; Montani et al., 1998), as well as the composition and distribution of macrobenthos in our study area (Magni & Montani, 1998; Magni et al., 2000, 2006) are reported in our associated pieces of work.

In the present work, we conducted parallel field investigations on pore-water nutrient [NH_4^+ -N, ($\text{NO}_3^- + \text{NO}_2^-$)-N, PO_4^{3-} -P and $\text{Si}(\text{OH})_4$ -Si], chlorophyll *a* (chl *a*) and AVS concentrations of sediments, and macrobenthic assemblages. On a monthly basis, sediment samples for geochemical analysis were collected at 7–8 locations using acrylic core tubes (3 cm i.d.) gently pushed by hand into undisturbed sediments within the same area sampled for the

macrobenthos. The surface (0–0.5 cm), sub-surface (0.5–2 cm) and deeper layers (1 cm interval each to a depth of 10 cm) of the sediments were carefully extruded and sliced. Sediment samples from the same layer were pooled together and brought to the laboratory within 2 h for further treatment and chemical analysis. Macrobenthic samples were collected in duplicate using a 100 cm² stainless steel core (10 cm in depth) and sieved on a mesh size of 1 mm. The residue of each replicate was separately fixed in 10%-buffered formalin with rose Bengal, for later determination of macrobenthos in the laboratory.

Sediment samples were always taken at low-tide soon after sediment exposure, to ensure protocol uniformity and to minimize within-day variability of pore-water nutrient profiles related to the tidal cycle. Samplings for chemical analysis and macrobenthos collection occurred simultaneously in all occasions, but 5 times (i.e., January to April and October 1995), when they elapsed with each other a few days up to 2 weeks (March 1995). Totally, 17 samplings for geochemical analysis and 18 samplings for macrobenthos were conducted between January 1995 and April 1996.

In a parallel work, low-tide ebbing water of a creek located near the flat was monitored at two stations monthly between 1994 and 1996, as extensively reported in Magni & Montani (2000). We present here the mean values of temperature, salinity, and dissolved oxygen, nutrient and chlorophyll *a* concentrations relative to the period of this study, and redirect for details on water sample treatment and analysis to our companion paper (Magni & Montani, 2000).

Laboratory procedure and analysis

From the small core samples, chlorophyll *a* (chl *a*) was extracted from duplicate subsamples of wet sediment (about 1 g) using 90% acetone. After 24 h of darkness at 4 °C, the samples were sonicated for 5 min, centrifuged at 1000 × *g* for 10 min, and extracts were spectrophotometrically analyzed (Jasco, Uvidec-320). Chl *a* concentrations were obtained according to Lorenzen's (1967) method, as described by Parsons et al. (1984), where the volume of water is substituted by the dry weight (DW) of the sediment expressed in grams. From the same pool of fresh sediment, the AVS-S

concentrations, as a measure of reducing conditions of sediments, were determined in duplicate subsamples (about 1 g) using a H₂S-absorbent column (GASTEC, Kanagawa, Japan) and expressed as μmol g⁻¹ of the DW. Part of each sediment layer was simultaneously centrifuged at 1000 × *g* and the extracted pore-water was filtered immediately, to minimize exposure to the atmosphere and sample oxidation, on disposable filters (0.45 μm) fitted to a 10 ml sterile syringe and transferred into polystyrene test tubes. The filtrate was stored at -20 °C for nutrient analysis, carried out within 2–3 weeks with a Technicon autoanalyzer II, according to Strickland & Parsons (1972). The macrobenthos was separated from the residue and transferred into a 75% ethanol and 2.5% ethylene-glycol solution. The animals were sorted and counted under a stereo-microscope (Olympus, Wild M3Z). They were weighed as a total wet weight (WW), including the shell for bivalves. The DW biomass of the soft tissues of dominant bivalves *Ruditapes philippinarum* and *Musculista senhousia* was calculated as 3.6% and 4.7% of the total (live) weight, respectively (Magni et al., 2000). The DW biomass of polychaetes and that of other minor and/or uncommon *taxa* was calculated as 20% of their WW biomass (Ricciardi & Bourget, 1998).

Calculation of depth-integrated nutrient pools in the pore-water

For each month, the pore-water nutrient concentrations measured in each layer were summed as to be representative of an all-layer nutrient pool and expressed on a square meter basis. This was obtained by calculating the sediment porosity of each layer from the water content (weight loss on drying at 105 °C for 20 h), assuming the bulk density of sediment particles as 2.5 g cm⁻³. The pore-water volume of each layer (not corrected for salinity) was then multiplied by the relevant nutrient concentrations which were finally expressed as areal depth-integrated values (mmol m⁻²). Throughout the study period, the pore-water content at individual layers varied from 17.4% (8–9 cm, February 1995) to 36.9% (2–3 cm, January 1995), for a total volume of pore-water per square meter in the uppermost 10 cm of sediments varying between 42.3 l in August 1995 and 49.2 l in May 1995.

Calculation of biogenic upward flux of nutrients

Ammonium and phosphate excretion rates of dominant bivalves *R. philippinarum* and *M. senhousia* were investigated in our associated piece of work conducted on the same sandflat (Magni et al., 2000). We applied and scaled-up these excretion rates to the bivalve biomass found in each month at the sampling location of the present study and expressed them as biogenic upward flux of nutrients ($\text{mmol m}^{-2} \text{day}^{-1}$). We extended this scaling to silicate, whose excretion rates by *R. philippinarum* and *M. senhousia*, measured during the same laboratory experiments, were found to be in average $6.6 \mu\text{mol g}^{-1} \text{DW h}^{-1}$ and $7.3 \mu\text{mol g}^{-1} \text{DW h}^{-1}$, respectively (Magni & Montani, 2005a). In order to evaluate the relationships between excretion-related upward flux of nutrients and pore-water nutrient pools, coefficients of determination, R^2 , were calculated for the whole study period. Coefficients of determination were also used to evaluate the relationships between individual nutrient species, chl *a*, AVS and the abundances and biomass of macrobenthos.

Results

Hydrological features, nutrients and chlorophyll *a* in low-tide water creek and surface sediments

The temperature in low-tide creek water ranged between 3.6 (December) and 29.0 °C (July), salinity ranged between 6.4 (May) and 31.4 (November) (Fig. 1a), and DO concentrations ranged between 5.7 and 15.1 $\text{mg O}_2 \text{l}^{-1}$, with a major increase in the spring of both years (Fig. 1b).

Ammonium concentrations tended to be much higher in the pore-water than in creek water in late-spring and autumn, while they were rather similar in the colder months for two consecutive years (Fig. 1c). Phosphate concentrations showed a temporal pattern to some extent similar to that of ammonium, with a major decrease in the pore-water in January 1995 and December 1995 (Fig. 1d). Major spatial differences in silicate concentrations were restricted to fewer months, i.e. between July and October, while they were rather comparable in most other occasions (Fig. 1e). In

contrast to the spatial and temporal distribution of ammonium, phosphate and silicate, nitrate + nitrite concentrations (Fig. 1f) were higher in creek water than in the pore-water, except in March and April of both years, with major peaks in coincidence of rainfall (Magni & Montani 2000) and a salinity decrease (Fig. 1a). The distribution of chl *a* showed a rather contrasting temporal pattern between the two compartments, being concentrations higher in creek water in summer, and higher in surface sediments in winter and early spring (Fig. 1g).

Pore-water nutrients, chlorophyll *a* and AVS in the 0–10 cm sediment horizon

Concentrations of all different nutrient species varied 10 to >30-fold between layers and months (Fig. 2a–d). Ammonium ranged between 75.1 (0–0.5 cm, January 1995) and 908 μM (0–0.5 cm, 30 October 1995), phosphate between 0.9 (0–0.5 cm, January 1995) and 36.9 μM (4–5 cm, September 1995), silicate between 17.1 (0–0.5 cm, February 1996) and 379 μM (5–6 cm, 30 September 1995), and nitrate + nitrite between 0.2 (7–8 cm, May and September 1995) and 21.1 μM (2–3 cm, April 1996). Ammonium, phosphate and silicate showed rather similar spatial and temporal patterns (Fig. 2a–c). They were lowest in winter in the uppermost layers, progressively increased throughout spring and summer, and were highest between September and October 1995, with a major increase at intermediate layers (i.e., between 4 and 8 cm). In contrast, nitrate + nitrite concentrations were highest at the surface (0–0.5 cm), peaked in winter to early-spring both in 1995 and 1996, and sharply decreased with depth in most occasions, with a noticeable exception in April 1995 (Fig. 2d).

Similarly to the pattern of nitrate + nitrite, chl *a* concentrations were highest at the surface, with major peaks in March–April and November 1995, up to a maximum of 20.0 $\mu\text{g g}^{-1}$ in February 1996. Yet, the vertical profiles of chl *a* concentration showed a progressive decrease with depth in all different periods, with a minimum value of 1.3 $\mu\text{g g}^{-1}$ at the 8–9 cm layer in August 1995 (Fig. 2e). As a whole period, chl *a* concentrations in surface sediments accounted only for $22.8 \pm 5.7\%$ of the total standing stock in the uppermost 10 cm

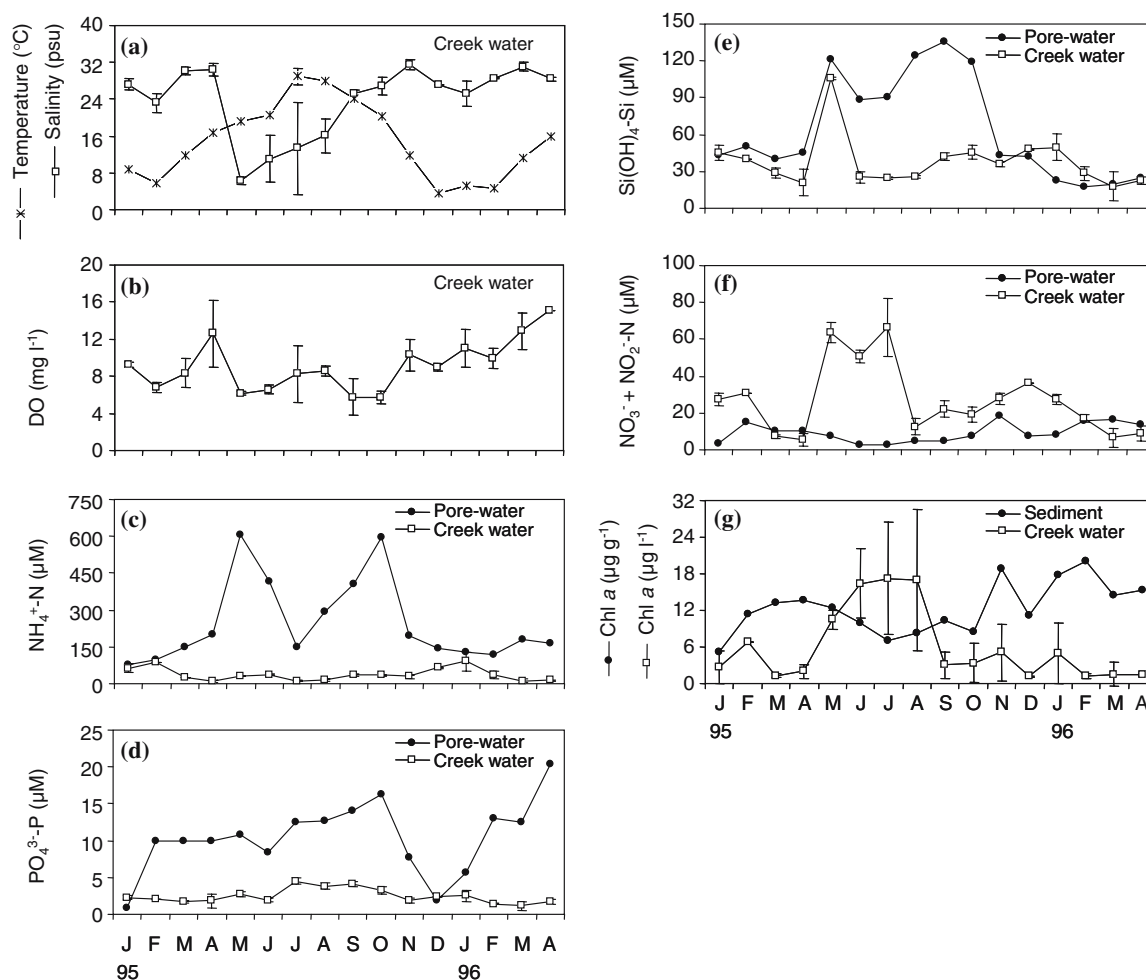
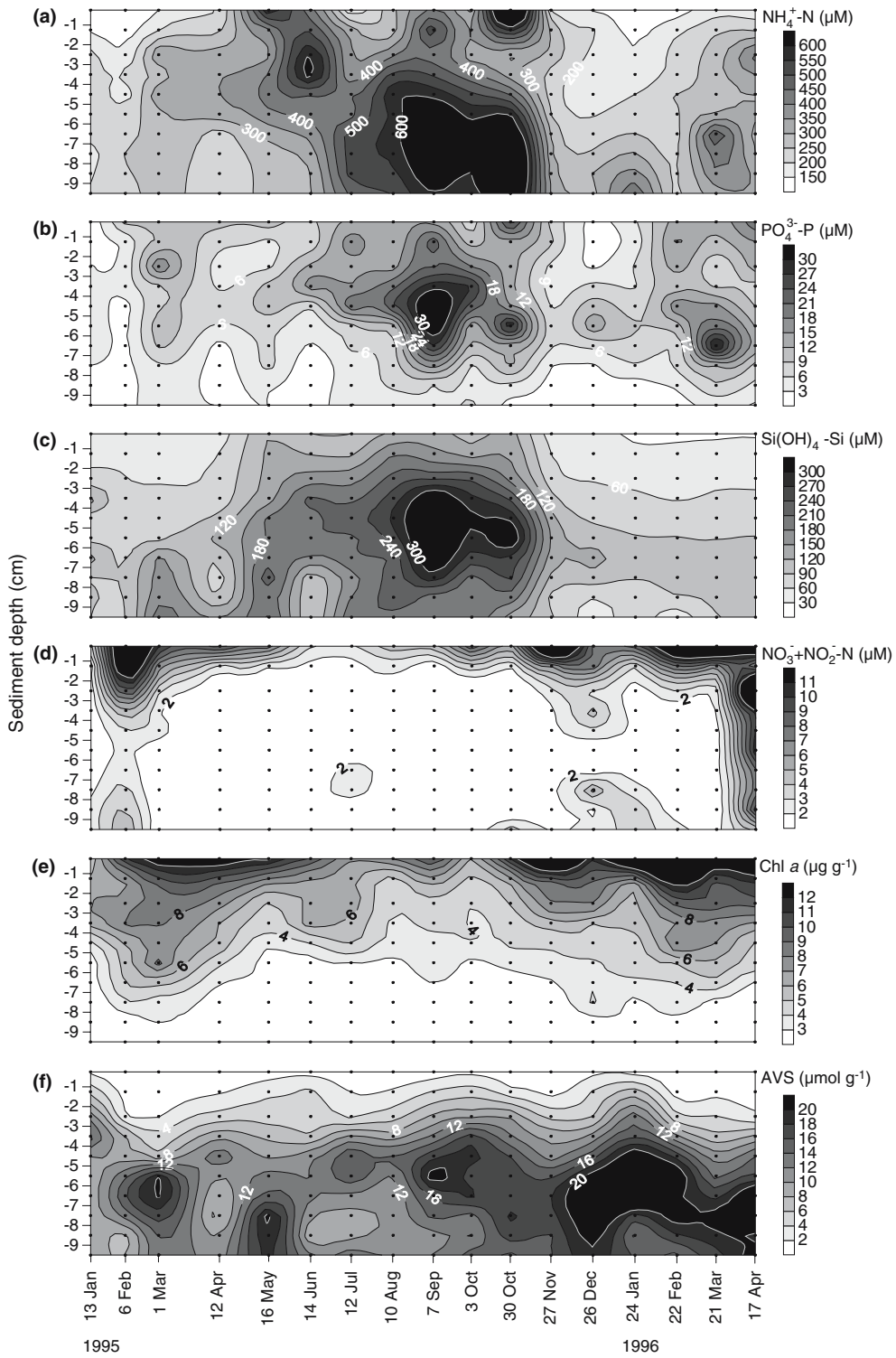


Figure 1. Temporal distribution of (a) temperature and salinity, and (b) dissolved oxygen (DO) concentrations in low-tide creek water, (c–f) nutrient and (g) chlorophyll *a* (Chl *a*) concentrations in low-tide creek water (open squares; data source: Magni & Montani (2000), with kind permission of Springer Science and Business Media) and surface (0–0.5 cm) sediments (closed circles; October 1995: monthly mean of 2 sampling dates, see Fig. 2).

of sediment, while the 9–10 cm layer accounted for $3.2 \pm 1.4\%$ (Montani et al., 2003).

The temporal change and vertical distribution of AVS concentrations (Fig. 2f) were rather opposite to those of nitrate + nitrite and chl *a*, with values constantly lowest at the surface, reaching $<1 \mu\text{mol g}^{-1}$ down to the subsurface layer between February and April, both in 1995 and in 1996. At deeper layers, AVS showed a major increase between early autumn and winter, subsequent to that of ammonium, phosphate and silicate, up to the highest values of $27 \mu\text{mol g}^{-1}$ at 6–7 cm in December 1995 and January 1996.

Consistent with the above patterns, depth-integrated ammonium, phosphate and silicate pools were correlated positively among each others, most strongly ammonium *vs.* phosphate and silicate (Fig. 3a). The ratios between each nutrient pair were rather consistent with the Redfield et al. (1963) ratios, as indicated by the regression slope of ammonium *vs.* phosphate which maintained the Redfield stoichiometry, and by the silicate *vs.* phosphate ratio which averaged 16.1 (Fig. 3a). Moreover, ammonium, phosphate and silicate pools were correlated negatively with the nitrate + nitrite pool (Fig. 3b). Finally, chlorophyll



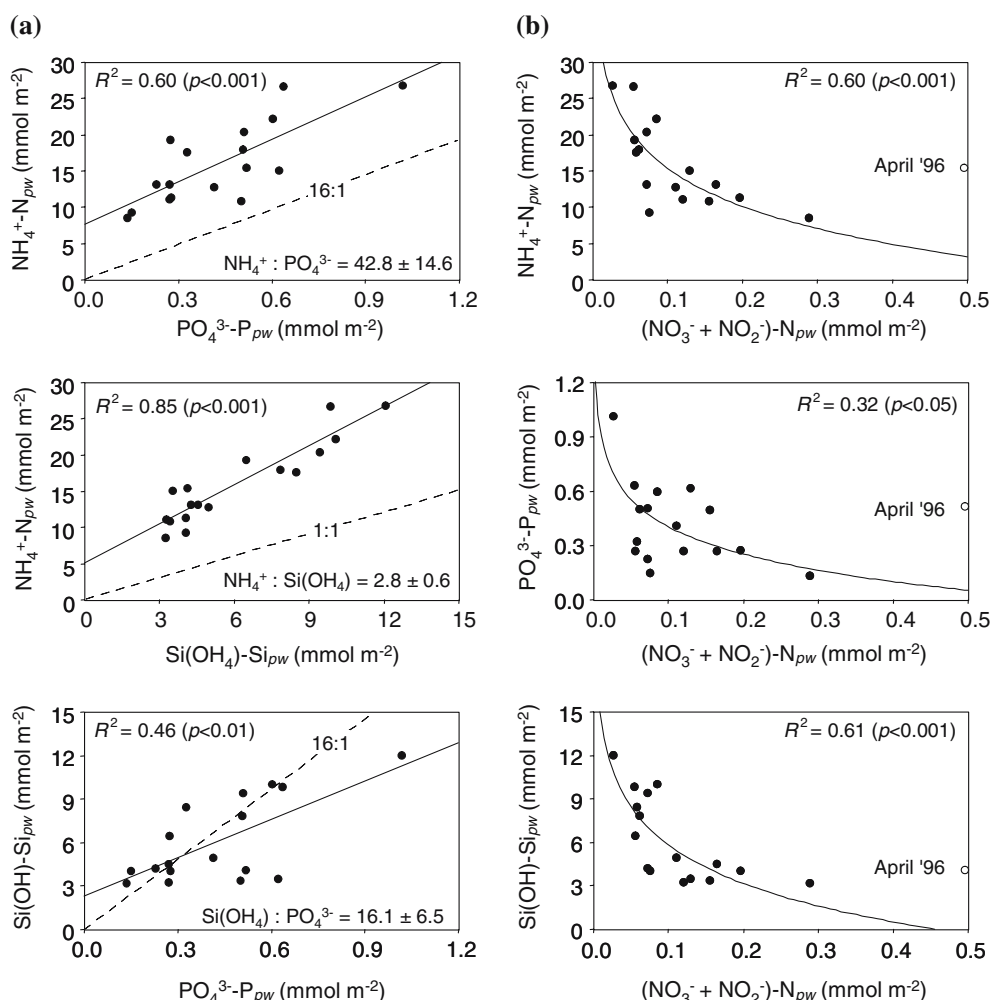


Figure 3. Relationships between depth-integrated pools of pore-water (*pw*) nutrients: (a) pair-plots for ammonium (NH₄⁺-N), phosphate (PO₄³⁻-P) and silicate [Si(OH)₄-Si]; (b) plots of nitrate + nitrite [(NO₃⁻ + NO₂⁻)-N] vs. ammonium (NH₄⁺-N), phosphate (PO₄³⁻-P) and silicate [Si(OH)₄-Si], (open circle: April 1996, not included in the regression). In (a) the mean ± standard deviation of the ratio of each pair nutrient species is also indicated; dashed lines: Redfield et al. (1963) N:P:Si ratios (N:P:Si = 16:1:16).

a was correlated positively with nitrate + nitrite and negatively with AVS (Fig. 4a and b, respectively), and nitrate + nitrite and AVS were correlated negatively with each other (Fig. 4c).

Macrobenthos

The total abundance and biomass of macrobenthos ranged between 7400 (July 1995) and

22050 ind m⁻² (October 1995), and between 59.4 (March 1995) and 244 g DW m⁻² (September 1995), respectively (Fig. 5a and b). The bivalves *Ruditapes philippinarum* and *Musculista senhousia* and the polychaetes *Ceratonereis erithraeensis* and *Cirriformia tentaculata* were dominant, accounting for 60.5% and 94.7% of the total abundance and biomass, respectively. Most remarkably, *R. philippinarum* and *M. senhousia* alone accounted for

Figure 2. Temporal distribution of pore-water ammonium (NH₄⁺-N, a), phosphate (PO₄³⁻-P, b), silicate [Si(OH)₄-Si, c] and nitrate + nitrite [(NO₃⁻ + NO₂⁻)-N, d], and chlorophyll *a* (chl *a*, e) and acid-volatile sulphide (AVS, f) concentrations in the uppermost 0–10 cm sediment horizon. Figure 2e based on Figure 4a of Montani et al. (2003) (with kind permission of Inter-Research). Data are interpolated according to Kriging using the program Surfer.

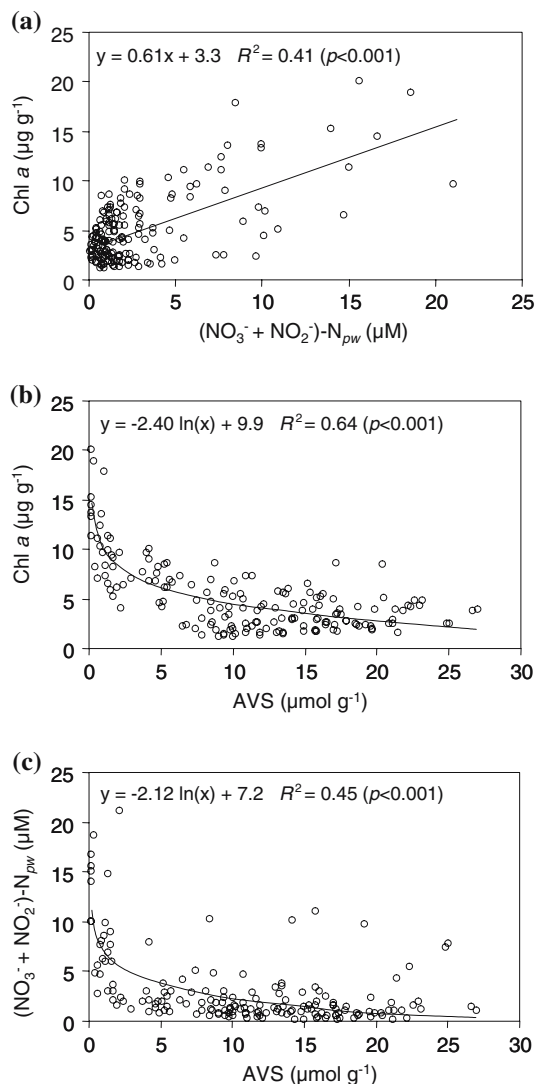


Figure 4. Relationships between (a) chlorophyll *a* (Chl *a*) vs. $(\text{NO}_3^- + \text{NO}_2^-)\text{-N}_{pw}$, (b) Chl *a* vs. acid-volatile sulphide (AVS), and $(\text{NO}_3^- + \text{NO}_2^-)\text{-N}$ vs. AVS concentrations (all dataset: $n = 170$).

up to 83% of the total biomass, when this exceeded 120 g DW m^{-2} (i.e., between August 1995 and April 1996, Fig. 5b).

Relationships between macrobenthos and pore-water nutrients

The total abundance of macrobenthos was not significantly correlated ($p > 0.05$) with ammonium, phosphate and silicate pools (Fig. 6a), while the total biomass showed a positive correlation

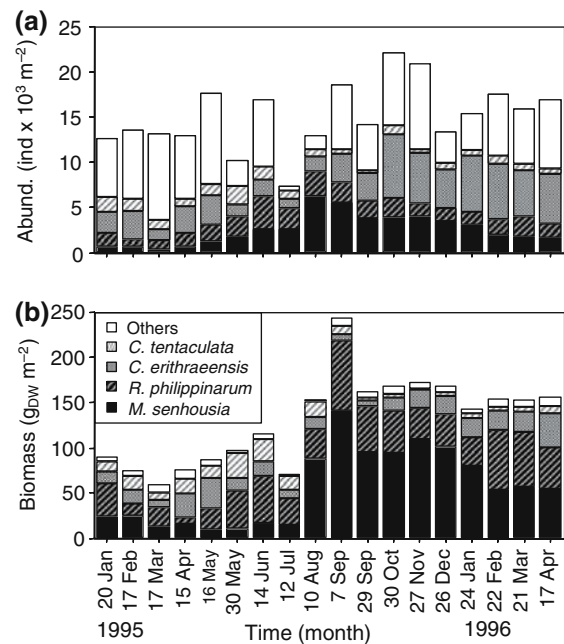


Figure 5. Temporal distribution of the abundance (a) and biomass (b) of macrobenthos (DW: dry weight). Note that in May 1995 and September 1995 sampling of macrobenthos was carried fortnightly (based on Magni & Montani, 2005b).

with ammonium and phosphate (Fig. 6b). Slight improvement of these correlations was obtained using the combined abundance and biomass of *R. philippinarum* and *M. senhousia* (plots not shown). By contrast, a strong relationship was found between nutrient pools and biogenic upward flux of nutrients calculated from the nutrient excretion rates of the two dominant bivalves. These relationships were positive and linear for all three nutrient species (i.e., ammonium, phosphate and silicate), with coefficients of determination explaining a large portion of the total variance, up to $R^2 = 0.72$ ($p < 0.001$) that of phosphate (Fig. 7).

Discussion

The variability of pore-water nutrients in estuaries and tidal flats has been investigated at various spatial and temporal scales by several authors (Matsukawa et al., 1987; Langner-van Voorst & Höpner, 1996; Trimmer et al., 1998; Usui et al., 1998; Takayanagi & Yamada, 1999; Caffrey et al., 2002; Kuwae et al., 2003). In these systems,

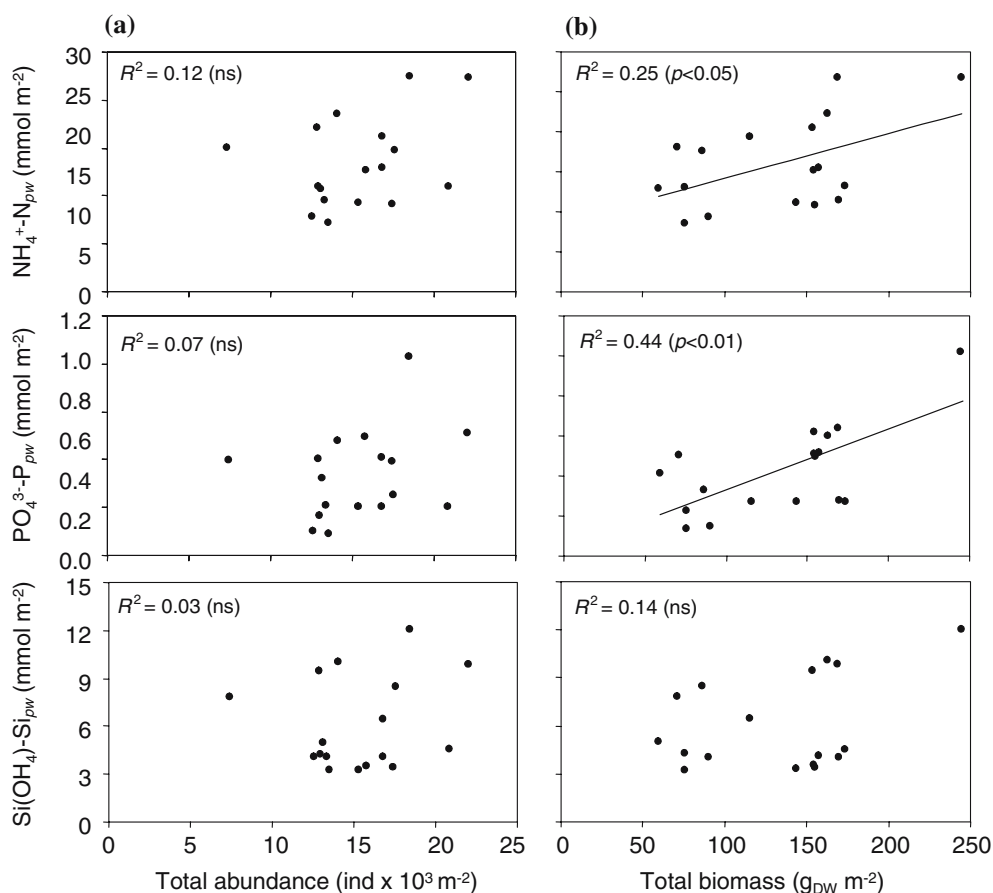


Figure 6. Plots of macrobenthos total abundance (a) and biomass (b) vs. depth-integrated pore-water (pw) ammonium ($\text{NH}_4^+\text{-N}$) phosphate ($\text{PO}_4^{3-}\text{-P}$) and silicate [$\text{Si}(\text{OH})_4\text{-Si}$] pools.

however, relatively few studies have followed in parallel the temporal distribution of macrobenthos and evaluated their influence on the seasonal variability of nutrient flux (Prins & Smaal, 1994; Rysgaard et al., 1995; Mortimer et al., 1999). To our knowledge, the present study is one of the few investigations conducted in an estuarine intertidal flat which describes in parallel the year-round distribution of pore-water nutrients, benthic chl *a* and sedimentary AVS through the uppermost 0–10 cm sediment horizon, and relates these variables to the abundance, biomass and activity of *in situ* macrobenthos. The comparison between nutrient and chl *a* concentrations in surface sediments and low-tide creek water presented in this study further provides a general framework for evaluating the extent of environmental variability,

at controlled low-tide, of a small-sized temperate, estuarine sandflat of Japan. This integrates our previous work conducted within the same estuary on the temporal changes in hydrological features, nutrients and particulate compounds over a complete tidal cycle (Montani et al., 1998; Magni et al., 2002)

Typical solute profiles in the pore-water indicate the tendency of ammonium, phosphate and silicate concentrations to increase progressively with sediment depth, with a major depletion in the uppermost few cm (e.g., Barbanti et al., 1992; Marinelli et al., 1998). Conversely, nitrate and nitrite concentrations tend to rapidly decrease through the sediment column due to nitrate ammonification and/or denitrification processes (Rysgaard et al., 1995; Sundbäck et al., 2000).

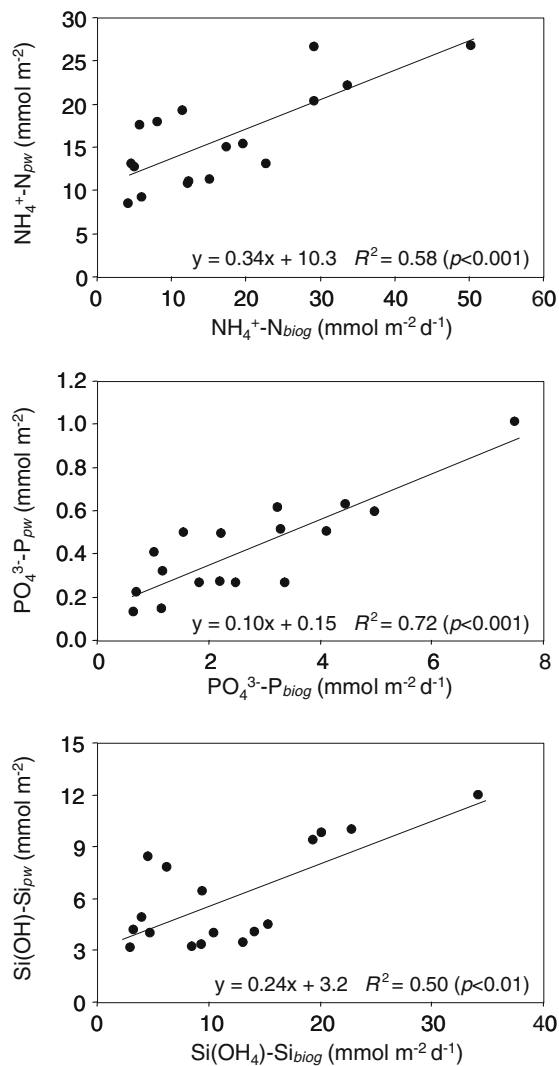


Figure 7. Plots of depth-integrated pore-water (*pw*) ammonium ($\text{NH}_4^+\text{-N}$), phosphate ($\text{PO}_4^{3-}\text{-P}$) and silicate [$\text{Si}(\text{OH})_4\text{-Si}$] pools vs. biogenic (*biog*) upward flux of the same nutrient species calculated from the nutrient excretion rates of *Ruditapes philippinarum* and *Musculista senhousia* (based on Magni & Montani, 2005c).

Similar profiles are also found in intertidal sediments (Höpner & Wonneberger, 1985; Ruardj & Van Raaphorst, 1995; Kuwae et al., 1998), besides the short-term change in nutrient concentrations related to the tidal cycle and exposure time (Trimmer et al., 1998; Usui et al., 1998; Kuwae et al., 2003). Especially in sandflat systems, however, major peaks can also be found at the sub-surface (e.g. nitrate, Kuwae et al., 1998; Trimmer

et al., 1998) or intermediate layers within the upper 10 to 30 cm of sediments (Matsukawa et al., 1987; Langner-van Voorst & Höpner, 1996), consistently with a more pronounced small-scale heterogeneity of nutrient profiles in sandy than in muddy sediments (Black et al., 2002).

As to seasonal trends, several studies demonstrated that the distribution and production rate of nutrients, such as ammonium, are strongly dependent on temperature (e.g., Klump & Martens, 1989; Landén & Hall, 1998). Consistently, Marinelli et al. (1998) found in the South Atlantic Bight continental shelf a marked increase of pore-water ammonium, phosphate and silicate profiles from spring to summer. By contrast, Lerat et al. (1990) showed a temporal and spatial mismatch in silicate and ammonium distribution within an oyster bed sediment, the former having the highest peak in July and concentrations progressively increasing down to 10 cm depth, the latter showing a major increase in November and December at intermediate layers (3–6 cm). The authors indicated that silicate was regenerated by dissolution of biogenic compounds and was highly correlated with temperature. Whereas, late pore-water ammonium accumulation within the sediment column was suggested to be the result of oxidation of sedimentary organic nitrogen. In that case, nutrient regeneration would occur at different periods of the year. In our study area, pore-water ammonium, phosphate and silicate concentrations, positively correlated with temperature (Magni & Montani, 2005c), followed similar temporal and spatial patterns. This suggests that in our study area major events of nutrient production and regeneration within the sediments are governed by concurrent processes.

It is well known that solute and particle distribution and behaviour in sediments are greatly influenced by a variety of physical (Huettel & Gust, 1992; Rusch & Huettel, 2000) and biological (microbial and animal) processes and structures (Herman et al., 1999; D'Andrea et al., 2002; Marinelli et al., 2002). Animals, in particular, have multiple effects on nutrient fluxes, namely (1) via excretion and bio-deposition, a direct positive effect; (2) via their associated bacteria, an indirect effect; and (3) via their influence on sediment transport properties through particle mixing (i.e., bioturbation) and in particular bioirrigation.

In our companion paper we have shown that the dominant bivalves *Ruditapes philippinarum* and *Musculista senhousia* excrete high amounts of ammonium and phosphate to the overlying water (on average, 7.1 and 11.8 $\mu\text{mol NH}_4^+\text{-N g}^{-1}\text{ DW h}^{-1}$, and 1.9 and 1.4 $\mu\text{mol PO}_4^{3-}\text{-P g}^{-1}\text{ DW h}^{-1}$ at 21 °C, respectively) and that the temporal changes in animal biomass strongly influence the magnitude of this flux (Magni et al., 2000). Those results are consistent with the positive correlation found in this study between macrobenthic biomass and pore-water ammonium and phosphate pools (Fig. 6). Similarly, Lomstein et al. (1989) found that a high macrobenthic biomass was correlated with high rates of urea gross production, high concentrations of urea and ammonium, and high sediment-water exchange rates of urea and ammonium. Bartoli et al. (2001) further showed that the flux of ammonium and silicate, linearly correlated with the biomass of *R. philippinarum*, was stimulated about 10-fold by the presence and excretion of the clams. By contrast, the flux of phosphate did not correlate with the biomass of clams, although a high amount of remineralised phosphate was released to the water column (Bartoli et al., 2001). Our laboratory experiments on bivalve nutrient excretion have provided evidence that both *R. philippinarum* and *M. senhousia* are also able to recycle silicate efficiently [on average, 6.6 and 7.3 $\mu\text{mol Si(OH}_4\text{)-Si g}^{-1}\text{ DW h}^{-1}$, respectively] (Magni & Montani, 2005a). On the other hand, in the present study silicate pool did not correlate with animal abundances, nor with biomass (Fig. 6).

As a consequence of the multiple effect of macrobenthos on nutrient fluxes, however, we would not necessarily expect a linear relationship between macrobenthic abundance or biomass and nutrient pools and/or flux. Production of bio-deposits by macrobenthos, for instance, may greatly enhance the input of N, P and Si. This in turn will stimulate microbial mineralization, reportedly higher in sandy than muddy sediments irrespective of organic enrichment (Hansen & Kristensen, 1998). Hiwatari et al. (2002) showed that in an intertidal sandflat in Tokyo Bay the bivalve *Macra veneriformis*, a dominant species in terms of biomass, excreted 8.6% of the filtered nitrogen as ammonia and egested 22.2% of the filtered nitrogen as faeces and pseudofaeces. Also in this case the biomass of

M. veneriformis did not correlate with the excretion rates of ammonium, whereas the total ammonium released from the sediments was reportedly several fold higher than that due to clams' excretory activity. Modeling and experimental studies have consistently shown that animal activities are closely linked to mineralization processes in the sediments, and that macrobenthos directly influence microbial communities in burrows (Branch & Pringle, 1987; François et al., 2002; Marinelli et al., 2002) and have a positive feed back through gardening on bacterial growth stimulated by an increased supply of nutrients (Grossmann & Reichardt, 1991 and therein references). Welsh & Castaldelli (2004) further pointed out that the macrofaunal stimulation of nutrient fluxes may not be solely due to the animals' burrow walls serving as sites for nitrification, but also to the fact that internal and external surfaces of the animals, such as *R. philippinarum*, themselves are also colonized by nitrifying bacteria.

In addition to animal excretion and bio-deposition, and the related effects of microbial mineralization, infaunal bioturbation and bioirrigation has been shown to strongly influence solute distribution in sediments and the sediment-water flux of nutrients (Herman et al., 1999 and therein references). An early mathematical study by Aller (1980) demonstrated that the effect of bioirrigation on pore-water ammonium gradients and fluxes greatly depend on the sizes and spacing of animal burrows. The author pointed out that the behaviour of ammonium (and phosphate) differs from that of silicate for continuous irrigation, being their distribution produced by zero-order and first-order reactions, respectively. A subsequent study by Boudreau and Marinelli (1994) highlighted the additional dependence of solute fluxes on discontinuous irrigation, for which ammonium is quite sensitive, but silicate is little. More recent work using a three-dimensional finite element model (Meysman et al., 2005) and a novel two-dimensional pocket-injection model (Meysman et al., 2006) demonstrated that the permeability of the bulk sediment exerts an important control on ventilation activity of macrobenthos, such as the polychaete *Arenicola marina*, and that pore-water bioirrigation in sandy sediments is pervasive.

In our study, we showed that pore-water nutrient pools were strongly correlated with the biogenic nutrient flux calculated from bivalve

excretion rates (Fig. 7). Based on the relevant regression slopes, this implies that P, Si and N are renewed every 0.1, 0.24 and 0.34 day, respectively, indicating highly dynamic sediments. In order for these sediments not be loaded with N, P and Si, it is therefore necessary that there are rapid removal pathways. As an attempt to provide an indirect estimate of the influence of pore-water irrigation due to animals on the upward flux of nutrients, we considered the following mass balance: $P = F + I$, where P is the production (i.e., biogenic regeneration) of nutrients, F is the diffusive flux of nutrients and I is the irrigation rate. Our previous calculations of nutrient flux due to molecular diffusion in all different seasons were on average $0.26 \text{ mmol NH}_4^+ \text{-N m}^{-2} \text{ day}^{-1}$ and $0.01 \text{ mmol PO}_4^{3-} \text{-P m}^{-2} \text{ day}^{-1}$ (Magni et al., 2000), and $0.06 \text{ mmol Si(OH)}_4 \text{-Si m}^{-2} \text{ day}^{-1}$ (Magni, unpublished). We acknowledge that *in situ* diffusive flux can be augmented by advective flows induced by boundary layer current-bottom topography interactions (Huettel & Gust, 1992; Marinelli et al., 1998) and other physical events occurring at various temporal and spatial scales (Asmus et al., 1998; Jahnke et al., 2000). On the other hand, we found that our diffusive flux estimates are within the same range as those reported for other intertidal and coastal areas of Japan where *in situ* benthic chambers have been used (Kuwae et al., 1998) and the effect of tidal exchange taken into account (Matsukawa et al., 1987). By contrast, nutrient production calculated from the bivalve excretion rates was more than 1 order of magnitude higher than the diffusive flux of nutrients based on density gradients, i.e. on average $16.8 \text{ mmol NH}_4^+ \text{-N m}^{-2} \text{ day}^{-1}$, $2.7 \text{ mmol PO}_4^{3-} \text{-P m}^{-2} \text{ day}^{-1}$ and $11.8 \text{ mmol Si(OH)}_4 \text{-Si m}^{-2} \text{ day}^{-1}$ (Fig. 7). According to the above mass balance, bioirrigation accounted for >90% of the total upward flux of all three nutrient species, suggesting a significant role of macrobenthos on the distribution of pore-water nutrients on this flat. Direct measurements of bioirrigation would certainly provide a major evidence of the relevance of macrobenthos on the nutrient flux in our study area. Yet, direct flux measurements should also be conducted on a year-round basis to take into account the strong temporal changes in animal abundances, biomass and composition, as described in this study.

We infer that polychaetes and tube-dwelling organisms, dominant on this flat in terms of abundances (Magni et al., 2006), may have a major influence in our study area in favouring fast removal pathways of pore-water nutrients through bioirrigation and sediment reworking (Kristensen, 1984; Huettel, 1990; Bartoli et al., 2000). The dominant burrowing polychaete *Ceratonereis erithraeensis*, for instance, showed a marked increase in autumn (Fig. 5) and was able to cope with a parallel increase in AVS concentrations observed in the lower layers of sediments (Fig. 2f). Resistance of nereidid polychaetes to exposure to anaerobic sediments has been shown in field experiments for *Nereis diversicolor* (Saiz-Salinas & Francés-Zubillaga, 1997). Bartoli et al. (2000) conducted microcosm experiments on sediment recolonisation by the burrowing *N. succinea* and suggested a significant role of this nereidid in the reoxidation and detoxification of highly reduced sediments. Consistently in our study area, *C. erithraeensis* may have promoted, through gallery formation and particle reworking, oxygenation of the sediment column and a progressive AVS reduction between winter and the subsequent spring. Particle mixing of abundant macrobenthos will also favour downward particle transport. This may have facilitated to some extent microphytobenthos penetration through the (sandy) sediment layers (Fig. 2e). Besides relatively high chl *a* concentrations found below the surface, chl *a* correlated significantly with nitrate + nitrite concentrations, sharply decreasing with depth in most occasions, which appeared to be an important factor triggering microphytobenthos development in the uppermost layer of sediments during the colder months. Extended observations on the seasonal and interannual variability of microphytobenthos biomass and the production rates of a dominant diatom, *Navicula* sp., can be found in our associate piece of work (Montani et al., 2003). Along this line, it is interesting to note the contrasting temporal pattern of chl *a* concentrations in surface sediments and low-tide water, with a lower availability of phytoplankton and suspended material in the cold months and higher amounts of algal material from both water and sediments in spring-summer (Fig. 1g). These patterns are much consistent with the results of our companion paper in which we investigated the

seasonal dynamics of macrobenthic assemblages and showed that dominant species rely on multiple food sources, varying with seasons and including fresh (i.e., living) and detrital algal material from both the overlying water and the sediments (Magni et al., 2006). Finally, it is worthwhile to highlight the negative correlation of both chl *a* and nitrate + nitrite with AVS (Fig. 4 b, c). This was an evidence of the contrasting spatial and temporal patterns between production-related vs. decomposition-related sediment variables, which nevertheless have been poorly studied in combination on a year-round basis in an estuarine intertidal sandflat.

Our investigations on the distribution of pore-water nutrients, sediment chemistry and associated macrobenthic assemblages over a period of about 1.5 years provide an important and comprehensive insight on the structure and functioning of a typical small-size, temperate estuarine sandflat of Japan. The results indicate that in our study area the spatial and temporal distribution of pore-water nutrients, chl *a* and AVS in the uppermost 0–10 cm sediment horizon are strongly interlinked and suggest that the metabolic processes (e.g., excretion, bio-deposition) and behavioural activities (e.g., particle mixing, bioirrigation) of abundant macrobenthos play an important role in the year-round biogeochemical processes occurring on this tidal flat.

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