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Spatial and temporal variability of benthic biogeochemical fluxes associated with macrophytic and macrofaunal distributions in the Thau lagoon (France)

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Abstract

The aim of the present study in the Thau lagoon was to determine spatial and temporal variations of biogeochemical fluxes at the sediment water interface (oxygen, nutrients and DIC) associated with macrophytic and/or macrofaunal distributions during spring time, which is a period of major vegetal growth. The pattern of benthic fluxes was studied in April 2002 and May 2003 for four main benthic biota of the lagoon, with one site subject to biodeposition by oysters cultured in suspension, one site representative of the central part of the lagoon that was only under general sedimentation, one site densely covered by macroalgae and one site located within a seagrass meadow. The results emphasize the role of oyster cultures on benthic fluxes and the impact of spatial heterogeneity of the benthos (macrophytes and macrofauna) distribution at various spatial scales. Hypoxic conditions were shown to develop at the sediment—water interface in May 2003 in the central part of the lagoon. Oxygen and DIC fluxes emphasized benthic respiration overall, and spatio-temporal variability mainly due to the presence/absence of the macroalgal cover on the sediment. The absence of benthic macroinfaunal organisms in the stations under the influence of oyster biodeposition and facing a dense macroalgal cover highlighted anoxic conditions in the sediment organic matter enrichment. The analysis of benthic fluxes over a productive period of the annual cycle provided a basis for describing spatial and temporal variations of the dynamics of sediment—water exchanges in the lagoon.

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1. Introduction

The Thau lagoon $(43^{\circ}24' \text{ N}-03^{\circ}36' \text{ E})$ is a shallow marine lagoon of 7500 ha (15 km long \times 5 km wide) located on the French Mediterranean coast. Besides its ecological interest as a recruitment area for a few marine fish species, the lagoon

* Corresponding author. *E-mail address:* gerard.thouzeau@univ-brest.fr (G. Thouzeau). is of noticeable importance due to shellfish cultivation. Semiintensive shellfish farming has developed in the lagoon since the beginning of the 20th century (Doumenge, 1959). Oyster (*Crassostrea gigas*) and to a lesser extent mussel (*Mytilus galloprovincialis*) farming extend on ca. 1500 ha, but suspended oyster tables are restricted to 150 ha (Mazouni et al., 1998a,b). Oyster and mussel productions reach 12,000 – 15,000 t annually (10% of the French seashell production; Gangnery et al., 2001), representing around 18 M \in and providing work for approximately 2000 people. Oyster

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production suffers major losses from time to time (1975, 1982, 1987, 1997 and 2003), however, with dystrophic crises generating anoxia and mass mortalities in summer (Mazouni et al., 1996; Plante-Cuny et al., 1998; Souchu et al., 1998; Chapelle et al., 2001; Hamon et al., 2003). At the end of summer, benthic fluxes and inorganic nitrogen and phosphate concentrations in the overlying water reach extreme values; the oxygen under-saturation (<50%) illustrates the spread of anoxic bottom conditions to the overlying water (see Mazouni et al., 1996; Mazouni, 2004). This phenomenon is known locally as the Malaïgue ('bad waters' in Occitan) and is triggered off by the coincidence of high water temperatures, absence of wind and the accumulation of organic matter in quantities that exceed the capacity for remineralization of the sediment (Caumette and Baleux, 1980). Benthic eutrophication (macrophytes) and likely sediment organic matter enrichment due to biodeposition by oysters and mussels lead to sediment oxygen consumption, a largely deficient O₂ balance at the sediment-water interface (SWI) and the proliferation of sulfide-oxidising bacteria (Mazouni et al., 1996; Plante-Cuny et al., 1998; Souchu et al., 1998). The Malaïgue only occurs when bottom anoxia is prolonged, the threshold being crossed when anaerobic heterotrophic populations take-over from aerobic populations (May, 1973; Caumette and Baleux, 1980). The resulting oyster mortalities lead to important economic losses: nearly one-third (3500 t) of the annual oyster production was lost in August 1997 (Hamon et al., 2003). Production losses were even greater in 1987 and 2003 (4000 t), 1982 (10,000 t) and 1975 (18,000 t).

During the last 15 years, the Thau lagoon has been extensively studied, with investigations on nutrient cycles and pelagic and benthic primary production (Jarry et al., 1990; Picot et al., 1990; Chapelle, 1995; Vaquer et al., 1996; Chapelle et al., 2000, 2001; Plus et al., 2003), benthic microphytic activity (Barranguet et al., 1994), macrophytobenthos distribution (Gerbal and Verlaque, 1995), the impact of the watershed and interactions with the Mediterranean sea (Amanieu et al., 1989; Picot et al., 1990; Souchu et al., 1997), sediment-water exchanges and the impacts of shellfish farming activities (Grenz et al., 1991; Barranguet and Alliot, 1995; Chapelle, 1995; Mazouni et al., 1996, 1998a,b; Deslous-Paoli et al., 1998; Dupuy et al., 2000; Souchu et al., 2001; Mazouni, 2004), the composition of biofouling communities on suspended oyster ropes (Mazouni et al., 2001), bottom anoxia and the disappearance of benthic macrofauna (see Mazouni et al., 1996 for review), etc. Various numerical models have been developed, focusing on hydrodynamics (Lazure, 1992), nitrogen and oxygen cycles (Chapelle, 1995; Chapelle et al., 2001; Mazouni, 2004), plankton ecosystem (Chapelle et al., 2000), macrophytes (Plus et al., 2003) and the impact of shellfish farming (Bacher et al., 1997; Mazouni, 2004). A coupled biological-hydrodynamical three-dimensional model integrating all lagoon compartments has allowed relevant simulations (Plus et al., 2003). These studies have contributed to a general understanding of biogeochemical cycles in the Thau lagoon. Estimations of algal productions at the lagoon scale have been proposed and allowed comparisons between primary producers and with other temperate lagoons (Plus et al., 2003). These comparisons have underlined the high productivity of the Thau lagoon and the importance of internal remineralization processes in nutrient cycling. In shallow-water environments, nutrient regeneration in the water column is usually ensured by sediments through benthic mineralization (e.g. Hammond et al., 1985; Kaspar et al., 1985; Hopkinson, 1987; Baudinet et al., 1990). Sediments regulate the production (fluxes) and standing stocks (concentrations) of nutrients in the water column. In the Thau lagoon, however, nutrient regeneration is strongly influenced by shellfish farming activities (Mazouni et al., 1996, 1998b; Souchu et al., 2001; Mazouni, 2004). Biodeposition resulting from aquaculture has been shown to increase sedimentation by a factor of 2-4 depending on the area (Grenz, 1989; Smaal, 1991; Gontier et al., 1992). As nutrient and oxygen fluxes are linked both to the temperature and to the amount of organic matter in the sediments (Boynton et al., 1980; Grenz et al., 1992), this input of organic matter on top of the sediments results in a large enhancement of the benthic fluxes (Boucher and Boucher-Rodoni, 1988; Dame and Dankers, 1988; Sornin et al., 1990; Grenz et al., 1991; Smaal, 1991; Hargrave et al., 1993; Prins and Smaal, 1994; Wu et al., 1994; Mazouni et al., 1996, 1998a,b). In particular, Mazouni et al. (1998b) showed that oyster culturing (oysters and epibiota) in the Thau lagoon plays a central role in nitrogen renewal in the water column by producing 2×10^7 mol N y⁻¹. At the lagoon scale, the annual biomass of the epibiota associated with suspended ovster devices (9000 t) would account for 50% of the total DIN flux produced by the reared filter-feeder assemblage (Mazouni et al., 2001).

The aim of the present study was to determine spatial and temporal variations of biogeochemical fluxes (oxygen, total dissolved inorganic carbon (DIC) and nutrients) at the water-sediment interface associated with macrophytic and/ or macrofaunal distributions during spring time, that is a period of major phytoplankton and macroalgae growth. This study was associated with simultaneous measurements of metal and organometal fluxes at the SWI using the same benthic chambers (Point et al., 2007). The methodology (benthic chambers) and sampling scheme used to measure benthic fluxes are described in this paper. In particular, four main benthic biota of the lagoon were targeted, with one site subject to biodeposition by oysters cultured on suspended long-lines (C5; in Fig. 1), one site (C4) that was only subject to general sedimentation (and supposed to be colonised only by microphytes), one site densely covered by macroalgae (C7) and one site (C6) located within a Zostera meadow. Surprisingly, there are a number of studies dealing with biogeochemical fluxes at the SWI underneath oyster ropes, but little is known on the influence of other benthic biota such as areas covered by macrophytes. In this study, the analysis of the benthic fluxes over a productive period of the annual cycle provides a basis for describing spatial and temporal variations of the dynamics of the sediment-water exchanges in the Thau lagoon. The results clearly show the influence of the different types of benthic interface and that of oyster culture on these exchanges.



Fig. 1. Thau lagoon – study sites (C4, C5, C6 and C7) for in situ measurements of biogeochemical fluxes at the sediment—water interface using benthic chambers. Stations C5 and C7 were inside the shellfish farming area A, in contrast to C4 (central part of the *Grand Etang*) and C6 (southern fringe of the *Grand Etang*; *Zostera* meadow).

2. Materials and methods

2.1. Study area and study sites

Average depth in the Thau lagoon is 4 m (locally up to 10 m). Total water volume is about $30 \times 10^8 \text{ m}^3$ (Mazouni et al., 1998a,b); water residence time in this semi-enclosed coastal ecosystem ranges between 3 and 4 months (Millet, 1989). The water exchanges with the Mediterranean Sea occur through two narrow seawater inlets located in the south-western and south-eastern (Canal of Sète; 90% of the exchanges) parts of the lagoon. The catchment area (280 km²) is drained by numerous small streams with intermittent flows. Two rivers, La Vène (sub-watershed surface = 70 km²) and Le Pallas (SWS = 50 km²) account for about 50% of total freshwater inputs (Plus et al., 2003). The climate forcing imposes a wide annual range of water temperature (3-29 °C) and salinity (27-40; Mazouni et al., 1998a,b), while precipitations show large inter-annual variations (from 200 to 1000 mm y^{-1} ; Plus et al., 2003). Wind is often strong with a mean of 118.5 days y^{-1} above Beaufort force 5 (source: Météo-France), particularly when it is blowing from the Northwest (the so called "Tramontane"). Both meteorological factors play an important role in the lagoon hydrodynamics (Lazure, 1992). Chlorophyll biomass in surface water is in the range $0.5-5 \ \mu g \ l^{-1}$ (Mazouni et al., 1998a,b); primary production is nitrogen-limited (Picot et al., 1990).

The in situ study of biogeochemical fluxes at the SWI was carried out in four sites representative of the main benthic biota of the lagoon (see Mazouni et al., 1996; Plante-Cuny et al., 1998). Station C4 (7.5 m deep), located in – and quite representative of - the central part of the Grand Etang (ca. 31% of the total area; Plante-Cuny et al., 1998) outside the shellfish farm area (Fig. 1), was supposed to be macrophyte free and dominated by phytoplankton (plant biomass = 0 - 25 g DW m^{-2} ; Gerbal and Verlaque, 1995). Station C5 (7.4 m deep), located in a shellfish-farm corridor (at the bottom of oyster ropes), was representative of the "east part" (31% of the total area; plant biomass = $25-225 \text{ g DW m}^{-2}$) defined by Gerbal and Verlaque (1995). Station C7 (2.6 m deep), located on the northern fringe of the shellfish farming area, was representative of the shallow part of the corridors between oyster devices, with a dense macrophyte cover (Ulva spp., Gracilaria spp.). By comparison, plant biomass in the western part of the lagoon (where a dense macrophyte cover also occurs) was shown to vary between 225 and 700 g DW m⁻² (Gerbal and Verlaque, 1995). C7 benthic biota was characterised by a dense epibiontic community on macrophytes, especially grazing gastropods. Station C6 (3.3 m deep), located in the southern part of the central zone, was representative of the extensive seagrass beds developing in shallow waters of the southern fringe of the Grand Etang. Sediments of this area (fine sand) were much less silty than the sediments of the other stations (mean grain size between 10 and 20 um in C4 and C5: Schmidt et al., 2007). The central part of the lagoon is the preferential zone for sedimentation (Millet, 1989), with sedimentation rates in the range 0.19- 0.26 cm y^{-1} at C4 vs. $0.13-0.16 \text{ cm y}^{-1}$ at C5 (Schmidt et al., 2007).

2.2. Field measurements

Daily variations of surface-water temperature, salinity and chlorophyll *a* were provided by IFREMER Sète (http://www. ifremer.fr/envlit/surveillance/). At the lagoon scale, there is no significant difference (5% level) for surface-water temperature and salinity daily values between Marseillan ($43^{\circ}22.72'$ N $-3^{\circ}34.08'$ E; close to C4) and Bouzigues ($43^{\circ}26.17'$ N $-3^{\circ}39.94'$ E; close to C5), when considering the 1996–2003 period. Hydrological parameter values at Bouzigues will thus be considered hereafter. Additional surface-water samples were collected in this study for pigment analysis. Pigment concentrations were determined using a calibrated Turner 111 fluorometer according to Lorenzen (1967).

Measurements of biogeochemical fluxes at the SWI were performed using benthic chambers during two surveys in spring 2002 (9–14 April) and 2003 (12–15 May). Three replicate acrylic tubes (0.196 m²) were gently pushed by SCUBA divers into the sediment, separated from each other by a distance of ca. 2 m. Acrylic hemispheres (Boucher and Clavier, 1990; Boucher et al., 1994, 1998; Clavier et al., 1994; Clavier and Garrigue, 1999) were secured to each base to trap a known volume of bottom water, varying from 55.7 to 74.6 l according to base insertion into the substrate. Clear chambers were used

to assess net community production in daylight and opaque chambers to estimate respiration in dark conditions. A series of incubations were carried out for 1 h 40 min to 4 h 20 min, depending on associated metal and organometal flux measurements (Point et al., 2007), and replicated up to two times daily. The enclosures were opened for 60 min between successive incubations to restore ambient conditions. Homogenisation of water inside the enclosure was provided by adjustable submersible pumps connected to waterproof batteries. As metabolic responses depend on hydrodynamics (Patterson et al., 1991; Forja and Gomez-Parra, 1998), water flow in each enclosure was adjusted to the minimum value ($2 \ 1 \ min^{-1}$) allowing stable measurements to be recorded by the probes.

 O_2 concentrations (mg l⁻¹), salinity, temperature and depth were recorded every minute inside the chambers with YSI 6920 probes. Water samples were collected in the enclosures for nutrients, pH, total alkalinity (TA) and metallic contaminants (Point et al., 2007) using 500 ml polyethylene syringes at the beginning and end of the incubations. Outside water was admitted through a tap during sampling to avoid interstitial water release from the sediment. Water samples were also collected in the overlying water at the beginning of the incubations for nutrients. A LI-COR quantum sensor (LI-192SA) was deployed inside one of the clear hemispheres to record the amount of actual photosynthetically active radiation (PAR, 400–700 nm) available for the enclosed photosynthetic organisms. Irradiance (µmol m⁻² s⁻¹) was averaged every minute.

At the end of the experiments, the macrophytes enclosed in the chambers were collected manually by divers and the benthic fauna was sampled by cores (380 cm^2 surface area) placed randomly in each chamber (five replicates per enclosure).

2.3. Sample processing

Nutrient samples were immediately frozen after filtering on 0.8- μ m filters, except silicate and ammonium samples which were treated according to Strickland and Parson (1972) and Koroleff (1976), respectively. Analyses for dissolved nitratenitrites, phosphates and silicates were performed on a Technicon Autoanalyser II according to Tréguer and Le Corre (1975). All values are expressed in μ M.

Water samples for pH and total alkalinity (TA) were filtered on GF/F filters before the poison mercuric chloride was added (DOE, 1994). The pH in the total scale was measured less than 6 h after the incubation using a pH meter (PHM 240 Radiometer) previously standardised with the aid of buffer solutions TRIS/HCl and 2-amminopyridine/HCl (DOE, 1994). TA was measured for 50 ml sub-samples by the automatic potentiometric method using HCl 0.1 M on an automatic titrator (Titrilab TIM 865 Radiometer). The concentrations of total dissolved inorganic carbon (DIC) in seawater were calculated from pH, total alkalinity, salinity and temperature data (Lewis and Wallace, 1998).

In the field, macrofaunal samples were gently washed on a 1-mm sieve, sorted and kept fresh in seawater before counting and identification to the species level under a dissecting or a compound microscope. Individuals were then frozen in liquid nitrogen before metal and organometal contaminant analyses and biomass determination in the laboratory. For macrophyte and macrofauna biomass determination, samples were dried at 60 °C for 48 h and the ash-free dry weight (AFDW) was calculated after 4 h ignition at 450 °C.

2.4. Calculation of metabolic fluxes

The net primary production and respiration were calculated by the difference between the initial and final concentrations in the enclosures (Eqs. (1) and (2)):

$$P_{\rm net}(O_2) = \frac{\Delta(O_2) \times v}{s \times \Delta t} \tag{1}$$

$$P_{\rm net}(\rm CO_2) = \frac{\Delta \rm DIC \times v}{s \times \Delta t}$$
(2)

where $P_{\text{net}} = \text{community}$ net primary production (mmol m⁻² h⁻¹), $\Delta(O_2) = \text{change}$ in the concentration of dissolved O_2 during the incubation (mM1⁻¹), $\nu = \text{chamber volume}$ (l), s = enclosed surface area (m²), $\Delta t = \text{incubation time}$ (h) and $\Delta \text{DIC} = \text{change}$ in total inorganic carbon (mM1⁻¹). Gross primary production corresponds to the sum of absolute values of net production and respiration. As TA can be modified by anaerobic processes such as sulfate-reduction, only incubations with slight TA changes ($\Delta \text{TA} < 5 \,\mu\text{eq} \,1^{-1} \,h^{-1}$) were considered for DIC calculation (see Forja et al., 2004).

2.5. Statistical treatment and modelling

Community respiratory (CRQ = $|\Delta DIC/\Delta O_2|$) and photosynthetic (CPQ = $|\Delta O_2/\Delta DIC|$) quotients were established for the whole data set. As O₂ (or DIC) production and DIC (or O₂) consumption are both affected by natural variability and measurement errors, the community metabolic quotients were calculated by means of functional regressions (Ricker, 1973; Clavier et al., 1994).

Analytical and synthetic methods (Clarke and Warwick, 2001) were used to assess spatial and temporal variations of the macrofaunal assemblages at C4, C6 and C7. Results interpretation is based on data expressed as species richness, density, dominance and biomass. A similarity matrix using square-root transformed data and the Bray-Curtis (1957) coefficient were used to build up a hierarchical, agglomerative classification (CLUSTER), applying group-average linking. Ordination used non-metric multidimensional scaling (MDS) based on the Bray-Curtis similarity matrix (Kruskal and Wish, 1978; Clarke and Green, 1988). The trophic guilds of the macrofaunal species sampled in this study were determined from Fauchald and Jumars (1979) and Gros and Hamon (1988).

3. Results

3.1. Hydrological conditions during the surveys

Surface-water temperature in the study area ranged from 13.9 to 14.2 °C during the early spring 2002 sampling, vs. 19.9 to 20.2 °C in mid May 2003 (data source: IFREMER Sète). Surface-water salinity was in the range 36.3-37.2 in April 2002, vs. 32.2-32.7 in May 2003. Both surface-water temperature and salinity values in this study were in the ranges of monthly values recorded in the lagoon between 1996 and 2003 (Fig. 2), though meteorological conditions led to particular trends (discussed later on). Bottom-water temperature ranged from 13.5 °C (Station C7) to 14.3 °C (Station C6) in April 2002 and from 17.3 °C (Station C4) to 19.8 °C (Station C7) in May 2003 (data from the YSI temperature probes in the benthic chambers; Table 1). Bottom-water salinity exhibited low variations in April 2002 (from 36.2 at C4 to 36.5 at C7) and May 2003 (from 32.9 at C7 to 33.6 at C4).

Concentrations of NH_4^+ , $NO_2^- + NO_3^-$ and PO_4^{2-} in the overlying water showed little spatial variations in April



Fig. 2. Temporal variations of surface-water temperature (°C), salinity and chlorophyll *a* concentration (mg m⁻³) at Bouzigues during the 1995–2003 periods (data source: IFREMER Sète). Sampling periods of this study are indicated by dotted lines.

2002. The bottom-water concentrations in nitrate-nitrites (0.29 μ M), ammonium (1.09 μ M) and phosphates (0.38–0.57 μ M) were typical of the early spring minimum values recorded in the shellfish farming area of the lagoon (Mazouni et al., 1996). In May 2003, higher spatial heterogeneity was observed, with minimum nutrient concentrations being consistently recorded at C7 over the macroalgae. The ammonium (0.96–2 μ M), nitrate-nitrite (0–1.16 μ M) and phosphate (0.31–0.52 μ M) concentrations were in the ranges of the values measured by Mazouni et al. (1996) in May 1992. Bottom-water silicate concentrations were in the range 6–10 μ M in April 2002 (C7: 9.91 ± 0.76 μ M; C4: 9.17 ± 0.08 μ M; C6: 8.32 ± 0.40 μ M; C5: 6.47 ± 0.25 μ M), vs. 8.2–10.4 μ M in May 2003.

The chlorophyll *a* concentration in surface water at Bouzigues was $2.3 \ \mu g \ l^{-1}$ on 17 April 2002 (data source: IFREMER Sète) and $1.6 \ \mu g \ l^{-1}$ on 12 May 2003. By comparison, Chl *a* and pheophytin *a* concentrations at C4 on 12 May 2003 were 1.44 and 0.09 $\ \mu g \ l^{-1}$, respectively (this study). The surface-water chlorophyll *a* concentration at Bouzigues was consistently higher during spring 2002 (5–6 $\ \mu g \ l^{-1}$ in May– June), compared to spring 2003 ($\leq 1.6 \ \mu g \ l^{-1}$ in May–June; Fig. 2).

Oxygen concentrations at the SWI ranged from $7.85 \pm 0.38 \text{ mg l}^{-1}$ (Station C4) to $8.22 \pm 0.45 \text{ mg l}^{-1}$ (C7) in April 2002, and from $4.29 \pm 0.26 \text{ mg l}^{-1}$ (C4) to $12.64 \pm$ 1.56 mg l^{-1} (C7) in May 2003 (C5: 7.41 ± 0.32 mg l^{-1}), at the beginning of the incubation experiments (chamber closure). Except for C4 on 12 May 2003 (56.6%), oxygen saturation at the SWI was in the range 93-177% at the beginning of the experiments, highlighting oxic conditions in the water overlying the sediment during the daytime sampling periods. Water was oversaturated with oxygen at C7 during daytime, due to macroalgal photosynthesis. Oxygen saturation in the chambers at the end of the incubations remained higher than 77% in all cases except for C4 (49.5-52.9%) and C5 (59.9-67.4%) in May 2003. The deficient O₂ balance at the SWI in the latter two stations is likely to have influenced benthic respiration rates during the incubations.

3.2. Benthic fluxes at the sediment-water interface

A total of 18 benthic incubations (with 2–6 replicates per incubation) were realised in April 2002 and May 2003 in the Thau lagoon, among which 43 chambers were in daylight conditions and 11 in dark conditions.

Oxygen: in daylight conditions, net oxygen fluxes at the SWI were negative in all cases except for C7, emphasizing the dominance of benthic respiration overall. Mean net oxygen fluxes in daylight conditions were similar at C6, C5 and C4 ($-1.6 \text{ to} -1.7 \text{ mmol m}^{-2} \text{ h}^{-1}$) in April 2002, while net oxygen production by the macroalgae reached 1.32 mmol O₂ m⁻² h⁻¹ at C7 (Table 1; Fig. 3). Mean oxygen fluxes in dark conditions were -4.03 mmol m⁻² h⁻¹ at C5 and -3.14 mmol m⁻² h⁻¹ at C6, in April 2002. A higher magnitude was recorded for mean oxygen fluxes in May 2003, from -3.87 mmol m⁻² h⁻¹ (C5) to 23.88 mmol m⁻² h⁻¹ (C7) in daylight conditions

Bottom-water temperature (°C), s O_2 and DIC (mmol m ⁻² h ⁻¹). E,	alinity and mean b in situ irradiance	iogeochemical flux« (μmol quanta m ⁻² s	es at the sediment $(^{-1})$; values were	 water interface a averaged for each 	is measured by the r experiment in da	benthic chambe tylight condition	rs in daylight or s; *, no data	dark conditions. A	All fluxes in µmol m ⁻	$^{-2}$ h $^{-1}$ except for
	C4		C5			C6		C7		
	2002	2003	2002		2003	2002		2002	2003	
	Day light	Day light	Day light	Dark	Day light	Day light	Dark	Day light	Day light	Dark
Date	9 - 10/4	12/5	13/4	13/4	15/5	12/4	12/4	14/4	14/5	14/5
Bottom-water temperature (°C)	14.23	17.30	13.88	13.88	18.60	14.25	14.25	13.50	19.80	19.80
Bottom-water salinity	36.21	33.60	36.49	36.49	33.00	36.27	36.27	36.51	32.90	32.90
In situ irradiance, E	22.5 - 33.0	29.7	20.0 - 41.8	0	39.1	299.9-65.3	0	333.1	590.6	0
Number of replicates	6	3	4	2	3	4	2	2	3	3
Oxygen saturation (%), SD	99.05, 5.57	56.57, 0.38	95.00, 3.95	93.45, 4.03	96.47, 4.03	96.05, 8.55	96.45, 8.27	99.03, 5.62	177 40, 26.26	154.13, 8.95
O ₂ flux, SD	-1.58, 0.43	-0.73, 0.32	-1.68, 0.39	-4.03, 0.06	-3.87, 0.20	-1.74, 0.55	-3.14, 0.17	1.32, 0.87	23.88, 2.57	-10.98, 0.70
DIC flux, SD	1.09, 0.11	0.54, 0.18	1.99, *	3.36, 0.76	3.09, 0.40	1.87, 1.83	3.52, *	-1.22, 0.95	-24.78, 3.62	7.20, 2.75
NH ₄ flux, SD	*	63.41, 29.75	*	*	342.75, 22.11	*	*	*	-12.72, 2.74	21.86, 94.03
$NO_3 + NO_2$ flux, SD	*	34.39, 50.59	*	*	-11.56, 57.26	*	*	*	-215.32, 362.69	9.36, 77.95
PO ₄ flux, SD	-15.29, 11.00	-58.84, 163.86	7.86, 6.69	17.03, 0.11	56.66, 10.62	13.62, 14.42	7.52, 12.49	5.51, 2.04	20.69, 31.63	-13.82, 48.40
Si(OH) ₄ flux, SD	69.41, 31.19	144.67, 23.24	370.13, 98.73	380.27, 120.63	629.31, 41.29	9.92, 11.08	23.58, 18.91	140.45, 22.92	176.66, 44.10	570.20, 195.91

Table 1

(C4: $-0.73 \text{ mmol m}^{-2} \text{ h}^{-1}$). Benthic respiration on the macroalgae-dominated community (C7) was $-10.98 \text{ mmol m}^{-2} \text{ h}^{-1}$ on 14 May 2003.

DIC: the average DIC fluxes for each set of incubations highlighted net DIC release from the sediments in all cases (from 0.5 to 7.2 mmol m⁻² h⁻¹), except for the incubations conducted in daylight conditions at C7 (both years; Table 1, Fig. 3). The DIC uptake at C7 was much higher in May 2003 compared to April 2002 (-24.8 vs. $-1.2 \text{ mmol m}^{-2} \text{ h}^{-1}$). In addition to DIC uptake with clear domes, the macroalgae-dominated community also exhibited the highest DIC release in dark conditions.

Nitrate-nitrites: nitrogen (both NH_4^+ and $NO_3^- + NO_2^-$) fluxes are not presented for April 2002, due to water contamination by nitric acid in the benthic chambers (for metal and organometal analyses, chambers were soaked with 10% nitric acid after decontamination by a biocide detergent). Nitratenitrite fluxes in daylight conditions exhibited strong spatial patterns of variation in May 2003, with a major nitrogen uptake $(-215.3 \,\mu\text{mol}\,\text{m}^{-2}\,\text{h}^{-1})$ by the macroalgae-dominated community at C7, a small uptake at C5, but nitrate-nitrite release at the SWI at C4 (Table 1). High standard deviations in most cases highlighted spatial heterogeneity at small scale (a few meters that is the distance between the chamber replicates). Indeed, one of the three incubation chambers always showed an opposite trend for nitrate-nitrite fluxes to the two other chambers in May 2003, whatever the station and lighting conditions during the incubations.

Ammonium: except for C7 in daylight conditions, ammonium release by the sediments was measured in all stations in May 2003 (Table 1), with the highest fluxes (342.8 µmol $m^{-2} h^{-1}$) recorded at the station under the influence of oyster culture devices (C5). Ammonium release at the SWI was six times lower at C4, compared with C5. By contrast, a small ammonium uptake by the macroalgal-dominated community was measured at C7 in daylight conditions (-12.7 µmol m⁻² h⁻¹).

Phosphates: phosphate release by the sediments was observed overall in April 2002 $(5.5-17.0 \,\mu\text{mol}\,\text{m}^{-2}\,\text{h}^{-1})$ and May 2003 (20.7-56.7 μ mol m⁻² h⁻¹; Table 1), except for C4. Station C7 also showed phosphate uptake in one chamber (dark conditions) on 14 May 2003; this uptake was associated with ammonium uptake (but nitrate-nitrite release), while the two other chambers in dark conditions exhibited opposite trends. Phosphate uptake was measured for both years in C4, with a fourfold difference in mean fluxes between the two years (Table 1). Once again, the high standard deviations associated with the mean fluxes emphasized small-scale spatial heterogeneity. In particular, phosphate fluxes measured at C4 (daylight) and C7 (dark) in May 2003 (-58.84 ± 163.86 and $-13.82 \pm 48.4 \ \mu mol \ m^{-2} \ h^{-1}$, respectively) were highly variable from one chamber to the other, with opposite trends even between two adjacent chambers.

Silicates: silicate release by the sediments was measured in all incubation experiments (Table 1), with higher benthic fluxes in May 2003 compared to April 2002 (C4, C5, C7 in daylight conditions: $69-370 \mu mol m^{-2} h^{-1}$ in April 2002 vs. $145-629 \mu mol m^{-2} h^{-1}$ in May 2003). The lowest silicate



Fig. 3. Mean (\pm SD) oxygen and DIC fluxes (mmol m⁻² h⁻¹) measured in the benthic chambers in April 2002 and May 2003. L, daylight conditions; D, dark conditions.

fluxes were measured on the *Zostera* meadow (C6) in April 2002 and the highest at the station under the influence of oyster culturing (C5). Highest silicate release in C5 was a consistent pattern in the 2-year survey. Silicate release was 2.36 times higher in dark conditions at C6 (2002) and C7 (2003), the two stations exhibiting dense macrophytic populations on top of the sediments, compared to daylight conditions. By comparison, silicate fluxes were similar in both light conditions at C5 in April 2002 (Table 1).

3.3. Community respiration and oxygen production

The overall CRQ, estimated each year from the whole data set (functional regressions; Ricker, 1973), was 1.00 in April 2002 ($R^2 = 0.89$) and May 2003 ($R^2 = 0.99$; Fig. 4). Gross benthic primary production can be estimated from the net production/consumption fluxes of oxygen and DIC measured at C5 and C6 in April 2002 and at C7 in May 2003. The mean gross primary production was 2.35 mmol O₂ m⁻² h⁻¹ at C5 on 13 April 2002 (mean bottom irradiance: 20–42 µmol quanta m⁻² s⁻¹) and 1.40 mmol O₂ m⁻² h⁻¹ at C6 on 12 April 2002 (irradiance: 65–300 µmol quanta m⁻² s⁻¹). By comparison, the mean gross oxygen production at C7 was 34.86 mmol O₂ m⁻² h⁻¹ on 14 May 2003 (irradiance: 591 µmol quanta m⁻² s⁻¹). The mean gross DIC uptake fluxes at the same times were 1.37 (C5), 1.65 (C6) and 31.98 mmol DIC m⁻² h⁻¹ (C7).

3.4. Benthic macrophytes and macrofauna

Species richness: a total of 50 macrofaunal (size > 1 mm) and 23 macrophytic species or taxa were identified from the chamber samples during this study. In addition to the macro-algal cover (including epibionts) collected by hand by the scuba divers, a total of 105 core samples collected within the benthic chambers were analysed, among which 60 cores in April 2002 and 45 in May 2003. The different macroalgal

species collected in the chambers included chlorophycae (Ulva spp., Cladophora liniformis, Enteromorpha compressa), phaeophycae (Cutleria multifida Gf, Colpomenia peregrina, Cystoseira barbata, Sargassum muticum, Ectocarpales) and rhodophyceae (Gracilaria bursa-pastoris, Gracilaria sp., Gracilariopsis longissima, Chylocladia verticillata, Ceramium diaphanum, Heterosiphonia plumosa, Nitophyllum punctatum, Pterosiphonia pennata, Spermothamnion repens, Alsidium



Fig. 4. Relationships between oxygen and DIC fluxes (mmol m⁻² h⁻¹) measured in the benthic chambers in April 2002 and May 2003. The community respiratory quotient (CRQ = DIC production/O₂ consumption) was estimated from the whole data set using functional regression (Ricker, 1973).

corallinum, *Audouinella daviesii*, Gelidiales). *Zostera noltii* and *Zostera marina* were the two seagrass species sampled at C6; they would account for 80% and 20% of the total macrophytic biomass in this area of the lagoon, respectively (Plus

et al., 2003). The highest macroalgal species diversity (21 species) was recorded within the shellfish-farm area (C5 and C7). Macrofaunal species richness (Table 2) ranged from 0 (C5) to 23 (C4) in April 2002 and from 0 (C5) to 20 (C7) in May

Table 2

Mean abundance A (ind m⁻²) and mean biomass B (g AFDW m⁻²) of the benthic macrofauna (size >1 mm) collected from core samples or by hand (macroalgae) in the incubation chambers in April 2002 and May 2003. Species trophic group is also mentioned (S, suspension feeder; SD, surface deposit feeder; SSD, subsurface deposit feeder; H, herbivore; C, carnivore; Com, commensal), as well as mean total abundance and biomass (±SD). There was no macrofauna in the cores collected at C5 in April 2002 and May 2003

Genus	Species	Trophic group	C4			C6		C7		
			2002 (<i>n</i> = 18)		2003 (<i>n</i> = 9)		2002 (n=9)		2003 (<i>n</i> = 9)	
			A	В	A	В	A	В	A	В
Abra	ovata	SD	153.45	0.63						
Aeginia	longicornis	SD	5.85	0.00						
Ampelisca	brevicornis	S	230.92	0.05	23.38	0.01				
Ampharete	grubei	SD	23.38	0.04	128.61	1.14				
Anapagurus	sp.	SD							1.70	0.06
Asterina	cf. gibbosa	С							10.19	0.04
Bittium	simplex	SD	53.34	0.00	11.69	0.001				
Bittium	scabrum	SD							33.95	0.26
Capitella	capitata	SSD			771.66	4.38				
Cerianthus	llovdii	S	6.58	0.08	93.53	1.40				
Cirriformia	sp.	SD							1.70	0.00
Clymene	modesta	SSD	5 85	0.01	11.69	0.07	759.97	1.08		
Corbula	gibba	S	29.23	0.70	35.08	0.41	107171	1100		
Coronhium	sn	SD	76.00	0.01	22100	0111				
Crenidula	sp. fornicata	S	70.00	0.01					1 70	0.00
Funice	vittata	C	18 27	0.15	35.08	0.29			1.70	0.00
Gammarolla	sn	SD	10.27	0.15	55.00	0.2)			144 30	0.13
Gantrana	sp. fragilis	S	68 60	0.62					144.50	0.15
Gibbula	yaria	5 Ц	00.07	0.02					57 72	0.81
Gluouna	alba	II C	76.00	4.05			16 77	2 40	51.12	0.81
Uguera	halitis	C	70.00	4.05			40.77	2.49	27.16	0.22
Haminoea	natitis	C CD	11.60	0.01					27.10	0.22
Heieromysis	sp.	3D	11.09	0.01					2 40	6.04
Hexaplex	trunculus	C					11.60	0.07	5.40	0.94
Hinia	sp.	C					11.69	0.07	0.40	0.00
Idotea	balthica	SD	20.22	0.00					8.49	0.00
Jassa	sp.	SD	29.23	0.00					(1(01	50 40
Jujubinus	striatus	H							646.81	52.48
Lineus	sp.	SD			175.00		23.38	0.02		
Lucinoma	lactea	Com	357.33	2.87	175.38	1.44	1192.57	9.56		
Lumbrineris	impatiens	C					11.69	0.06		
Lysidice	ninetta	C	35.08	0.07						
Mediomastus	sp.	SSD	132.27	0.11	81.84	0.08				
Mytilus	galloprovincialis	S							3.40	0.07
Nassarius	comiculum	С							117.14	1.00
Nematods		SD	380.72	0.19	35.08	0.02				
Notomastus	latericeus	SSD					432.6	1.64		
Paracentrotus	lividus	Н	19.73	3.00						
Parvicardium	exiguum	S							5.09	0.03
Pectinaria	auricoma	SSD	5.85	0.01			198.76	0.41		
Phoronis	psammophilla	S					46.77	0.14		
Phyllochaetopterus	costarum	S	11.69	0.00	35.08	0.08				
Phyllodoce	lamelligera	С	11.69	0.04						
Platynereis	dumerilii	SD							8.49	0.00
Rissoa	lineolata	SD							22.07	0.01
Rissoa	sp.	SD							10.19	0.00
Sipunculus	nudus	SSD					46.77	0.36		
Sphaeroma	sp.	SD							1.70	0.00
Venerupis	aurea	S	1073.46	2.31	70.15	0.16	2127.91	4.59	10.19	0.02
Thracia	phaseolina	S					46.77	0.05		
Tricolia	speciosa	SD							79.79	0.49
Total	-		2016 27	14.07	1509.05	0.47	4045 (4	20.49	1105 15	() =7
Total			2816.27	14.97	1508.25	9.47	4945.64	20.48	1195.15	02.57
20			8/8.82	13.02	556.84	2.79	9/1.5/	4.88	169.25	10.75

2003. Sediment samples from C5 (underneath the macroalgal cover) were devoid of macrofauna in both surveys.

Macrofaunal density and biomass: the highest macrofaunal density was recorded at C6 in April 2002 and the lowest (except C5) at C7 in May 2003 (Table 2). Total density in April 2002 was dominated by infaunal bivalves at C4 and C6; a major change in dominance was observed at C4 in May 2003, with Capitella capitata (opportunistic species characteristic of sediment organic matter enrichment; Grall and Glémarec, 1997) accounting for 51% of total density. Epibiontic gastropods (located on top of the macroalgae) were dominant in density at C7 in May 2003 (Table 2). The highest macrofaunal biomass was recorded at C7 and the lowest at C4, both in May 2003 (Table 2). Glycera alba, infaunal bivalves (Venerupis aurea, Lucinoma lactea and Corbula gibba) and Paracentrotus lividus were dominant taxa in biomass at C4 in April 2002, vs. C. capitata in May 2003. Infaunal bivalves were also dominant in biomass at C6 in April 2002, while the herbivorous gastropod Jujubinus striatus accounted for 83.9% of total biomass at C7 in May 2003. With respect to the macroalgae, only the biomasses of Ulva sp., Cutleria multifida Gf and Gracilaria spp. were determined. Biomass of the other macroalgae was negligible. Total macroalgal biomass was only 9.0 ± 7.8 g AFDW m⁻² at the bottom of the oyster culture devices (C5) in April 2002, but it reached 463.55 ± 224.73 g AFDW m⁻² in the shallow-water corridor between the culture units (C7) in May 2003.

Macrofaunal trophic groups: suspension feeders (mainly *Venerupis aurea*) accounted for 50.4% of total abundance at C4 in April 2002 (Fig. 5); surface deposit feeders (mainly nematods) were sub-dominant (26.1%), in front of the commensal bivalve *Lucinoma lactea* (12.7%) and carnivorous polychaetes (5%). Total biomass (Fig. 5) was more equally distributed between carnivores (28.8%), suspension feeders (25.2%), herbivores (20%; *Paracentrotus lividus*) and *L. lactea* (19.1%). Deposit feeders were less represented in biomass (6.9%). A different pattern was observed in May 2003, with sub-surface deposit feeders (mainly *Capitella capitata*) leading in abundance (57.4%) and biomass (47.8%). Suspension feeders, surface deposit feeders, and *L. lactea* were subdominant groups, while herbivores were absent and carnivores only accounted for 3.1% of total biomass.

Suspension feeders (mainly *Venerupis aurea*) were the dominant taxa in density (44.9% of total density) within the *Zostera* meadow (C6) in April 2002 (Fig. 5). Sub-surface deposit feeders (29.1%; mainly *Clymene modesta*, *Notomastus latericeus* and *Pectinaria auricoma*) and *Lucinoma lactea* (24.1%) were sub-dominant, while surface deposit feeders were scarce. *L. lactea* was the leading species in biomass (46.7% of total biomass; Fig. 5), in front of suspension feeders (23.4%), sub-surface deposit feeders (17%) and carnivores (12.8%; mainly *Glycera alba*).

The benthic macrofauna associated with the dense macroalgal cover at C7 was mainly constituted of herbivorous epibiontic gastropods (59% of total density and 85.2% of total biomass). Carnivores (mainly *Asterina* cf. *gibbosa* and drilling snails) were sub-dominant (19.9% of total density and 13.9%



Fig. 5. Mean total abundance $(ind m^{-2})$ and mean total biomass (g AFDW m⁻²) of the macrofaunal trophic groups sampled in the benthic chambers in April 2002 and May 2003. H, herbivores; S, suspension feeders; SSD, sub-surface deposit feeders; SD, surface deposit feeders; Com, commensal; C, carnivores.

of total biomass), as well as surface deposit feeders in density (19.5%; mainly amphipods and gastropods). There was no macrofauna found in the cores underneath the macroalgae in May 2003, thus emphasizing sediment anoxia.

Macrofaunal assemblages: on the basis of numerical classification of samples (Fig. 6), four major groups of stations were distinguished, reflecting bottom type- or sampling year-related differences in macrofaunal species composition. Groups I (04/ 02) and II (05/03; two distinct subgroups on the dendrogram), consisted of samples from station C4. Groups III and IV were macrophyte-dominated groups as group III included all samples from C6 and group IV included samples from C7. These groups reflect distinct environmental conditions, both spatially and temporally, since maximum variability in the diagram appears at station C4 between samples from April 2002 and May 2003.

4. Discussion

4.1. Comparison of the different sampling techniques used to estimate oxygen fluxes

Oxygen exchanges at the SWI represent an integrated measure of diffusive, advective and fauna- or plant-mediated O_2 consumption or production (Archer and Devol, 1992; Glud et al., 1994; Grenz et al., 2003). The large-sized benthic chambers used in this study provided data integrating spatial



Fig. 6. (a) Hierarchical, agglomerative clustering of square-root transformed macrobenthos data using group-average linking on Bray–Curtis similarities (%). (b) Multidimensional scaling ordination for square-root transformed macrobenthos data based on Bray–Curtis similarities (stress = 0.05). Groups of samples appearing on the clustering were reported on the MDS. Samples 03-C44, 03-C45 and 03-C46 were combined to group II, although they formed a single group by themselves (dashed line), because they were clearly associated to group II on the MDS plot. Sample code identification: year-station number-sample number (e.g. sample 03-C44 refers to sample No. 4 at C4 in May 2003).

heterogeneity of the organism distribution at the enclosure size scale, in contrast to the electrochemical microsensors (Dedieu et al., 2007) which provided punctual measurements (tip outer diameter of the O_2 microsensor: 100 µm). The latter are well-suited to perform high resolution measurements of O_2 profiles, to determine the oxic penetration depth (Revsbech et al., 1980) and to calculate the diffusive O_2 fluxes and consumption rates within the oxic zone when unaffected by irrigation (Rasmussen and Jørgensen, 1992; Berg et al., 1998). Despite these major differences, the two techniques provided results in good agreement at C5 (both years) and C4 (May 2003; see Dedieu et al., 2007). Indeed, the diffusive oxygen uptakes (DOU) calculated from the O_2 microprofiles and the net O_2 fluxes (NOF) measured by the YSI probes in the clear-dome chambers were similar at C5 that is the station devoid of infaunal organisms >1 mm. This result would indicate that the process governing oxygen transport at the SWI is mainly diffusion in the shellfish farming area, while the potential for sediment irrigation is limited (only small-sized *Capitella capitata* were found by Duport et al. at C5). A different pattern was observed at C4, with similar DOU and NOF in May 2003, but a threefold difference in oxygen exchanges in April 2002 (with DOU representing 36% of NOF). This result emphasizes different composition of the infauna between the two years. A diversified macrofauna was sampled at C4 in April 2002, with large-sized infaunal species feeding in the bottom water or on top of the sediment, thus favouring bioirrigation of the sediment. About two-thirds of the oxygen uptake would have been fauna-mediated at C4 in April 2002. By contrast, the benthic macrofauna was less abundant in May 2003 and mainly composed of small-sized surface deposit feeders (C. capitata). Decreased bioirrigation of the sediment by the latter and the absence of macrophytes would explain why the NOF in the chambers were similar to the DOU measured by the microelectrodes. The role of macroalgae in oxygen exchanges at the SWI is emphasized by the April 2002 data at C5. The lower (if any) net oxygen consumption measured in the two chambers containing macroalgae, compared with the microelectrodes, was due to net fluxes integrating oxygen production by the macrophytes in daylight conditions (the net oxygen uptake measured in the third enclosure without macrophyte was not statistically different (t test; $\alpha = 0.05$) from the mean DOU recorded at C5 by Dedieu et al.). The microelectrodes characterise small-scale DOU at the SWI only when the interface is free of macrophytes (otherwise the interface is displaced on top of the macrophytes), while the benthic chambers provide integrated values of biogeochemical fluxes at larger scale and whatever the substrate. When considering the macrophyte distribution at the lagoon scale, more information is provided by the enclosure method for biogeochemical flux budgets.

4.2. Temporal variations of biogeochemical fluxes at the sediment-water interface

Net oxygen uptakes measured in Thau lagoon (75–264 mmol $O_2 m^{-2} d^{-1}$ in dark chambers) were among the highest ever recorded in coastal marine ecosystems (see Forja et al., 2004 for review). Only shallow coastal ecosystems of the Iberian Peninsula exhibited similar fluxes (98-199 mmol $O_2 m^{-2} d^{-1}$). By comparison, the mean DIC releases in the dark chambers $(81-173 \text{ mmol } \text{CO}_2 \text{ m}^{-2} \text{ d}^{-1})$ were similar or lower than those recorded elsewhere (63-732 mmol $CO_2 m^{-2} d^{-1}$; see Forja et al., 2004). In this study, except for C4, the oxygen, DIC and nutrient fluxes measured at the SWI were higher in May 2003 compared to April 2002. The sampling periods exhibited particular meteorological and hydrological trends compared to the spring-time conditions usually observed in the lagoon. Temperature and salinity values were in the ranges of monthly values recorded between 1996 and 2003 (Fig. 2), but the April 2002 survey occurred during a cloudy but dry period with stable surfacewater temperature (13.8–13.9 °C during 3 weeks) and salinity among the highest (after 1999) ever recorded at that time of year. In particular, the irradiance values measured at C4 and C5 were extremely low (<42 μ mol m⁻² s⁻¹). Low light and low water temperature are likely to explain the low oxygen production at C5 in the enclosures containing macroalgae. On the other hand, the water column exhibited high surface temperature (highest value after the year 2000), but low salinity (minimum value after the year 1996) in mid-May 2003. These particular environmental conditions led to oxygen fluxes being characteristic of late winter-early spring conditions in April 2002, while May 2003 was close to summer conditions. Mean oxygen uptake at C5 in May 2003 (daylight

conditions) was higher than the mean value recorded in August 1992 ($-2.21 \text{ mmol m}^{-2} \text{h}^{-1}$) during bottom anoxia, while the hypoxic conditions recorded outside the culture area (C4) agreed with the 1992 data at Station OC (Mazouni et al., 1996). Nutrient (N and P) fluxes were in the same orders of magnitude as those previously reported for April-May in the lagoon (Mazouni et al., 1996, 1998a,b; Mazouni, 2004). In particular, the phosphates net outflux measured at C5 in May 2003 was close to the maximum value recorded in 1992 in the shellfish farm area (Station UC: 53.2 μ mol m⁻² h⁻¹). The nitrate-nitrite uptake and the ammonium release at C5 in May 2003 were also similar to the values found at Station UC in May 1992 (ca. -5 and 360 μ mol m⁻² h⁻¹, respectively). On the other hand, the nitrate-nitrite uptake measured in the shellfish farm corridor (C7) in May 2003 was typical of June values at Sation UC $(-158 \ \mu mol \ m^{-2} \ h^{-1})$. With respect to the water column, the estimate, from bottle incubations (³²Si), of surface-water biogenic silica (BSi) production at C4 on 10 April 2002 and 14 May 2003 was 1.3 and 1.8 μ mol l⁻¹ d⁻¹, respectively (Monperrus et al., 2007); the associated carbon primary production was 6.9 and 14.1 μ mol C l⁻¹ d⁻¹. The latter are consistent with the values found by Souchu et al. (2001) in April 1992 (6.54 μ mol C l⁻¹ d⁻¹; water temperature: 12 °C) and July 1991 (38.2 μ mol C l⁻¹ d⁻¹ at 25 °C). By comparison, a maximum BSi production of 2.8 μ mol l⁻¹ d⁻¹ (50 μ mol C l⁻¹ d⁻¹) has been measured during spring time in the eutrophic Bay of Brest (Leynaert, pers. comm.), with values of ca. 1 μ mol l⁻¹ d⁻¹ during secondary blooms. The high Si:C ratios obtained in the Thau lagoon (0.19 in April 2002 and 0.13 in May 2003), as compared to the mean elemental diatom composition (0.13; Brzezinski, 1985), would indicate that diatom populations dominated the pelagic production during the surveys. However, diatoms (mainly small-sized Nitzschia seriata) only accounted for 19.5% of total cell counts in May 2003, after cryptophycae (35.2%), dinoflagellates (22%) and chlorophycae (20.3%). Nanoplanktonic diatoms would mainly contribute to the lagoon phytoplankton biomass on a yearly basis (Chrétiennot-Dinet et al., 1995), but the shift induced by filter feeders (oysters plus epibionts) in phytoplankton composition would favour picophytoplankton (higher growth rates; Vaguer et al., 1996; Souchu et al., 2001).

The well-marked inter-annual patterns observed between the two years of study allow scrutiny of the role of parameters (bottom-water oxygenation, water temperature, irradiance and organic matter supply to the sea-bed) influencing both abiotic and biologically catalysed processes (Jørgensen, 1977, 1996; Froelich et al., 1979; Candfield et al., 1993; Epping and Helder, 1997; Thamdrup et al., 1998). The unusually warm conditions in May 2003 were associated with mean O₂ concentration in bottom water at C4 and C5 as low as the summer minimum of August 2002 (160–194 µmol 1⁻¹; Dedieu et al., 2007). Higher oxygen depletion may occur in summer in the eastern part of the lagoon, however, with oxygen concentration falling to 7% of the saturation (42 µmol 1⁻¹; Plus et al., 2003). Such large bottom-water oxygen decreases lead to major DOU drops in summer (up to 60% at C4 and C5; Dedieu et al., 2007). About half of the DOU seasonal variations would be driven by water temperature in the lagoon. Labile organic matter (OM) delivery to the sediment and its temporal changes in quality would also influence the seasonal dynamics of oxygen demand at C4, while oyster biodeposition would provide high inputs of OM to the underlying sediments at C5 whatever the season. Finally, temporal (and spatial) variations of the oxygen and DIC fluxes at the SWI in the shallower part of the shellfish farm corridors (C7) and at the bottom of oyster ropes (C5) appeared strongly driven by the presence/absence of macroalgae on the sediment and by water depth- or turbidity-regulated lighting conditions.

4.3. Spatial variations of biogeochemical fluxes at the sediment—water interface

Except for May 2003 where the oxygen concentration in bottom water was higher in the station under the influence of oyster culture (C5), mean oxygen content was equivalent outside and under the culture areas between December 2001 and May 2003 (Dedieu et al., 2007). This result is in agreement with the previous study of Souchu et al. (2001) showing a decrease of only a few percents of oxygen concentration in the vicinity of shellfish farms. The annual averages of seasonal DOU values were, however, about three times greater at C5 $(37-88 \text{ mmol m}^{-2} \text{ d}^{-1})$ compared to C4 (9-1)31 mmol $m^{-2} d^{-1}$), highlighting a biogeochemical gradient at the lagoon scale. The impact of oyster cultures on oxygen and DIC fluxes at the SWI was also clear in the warm conditions of May 2003, with fivefold increases of the mean net oxygen uptake and DIC production in the enclosures at C5 compared with C4 (Table 1). The oyster-driven biodeposition of higher OM quantities at C5 compared to C4 was shown by Mesnage et al. (pers. com.) through higher values of particulate and dissolved organic carbon at the SWI and the presence of more labile OM. This OM pool was associated with a 70% increase in sulfate-reduction rates measured in surface sediments at C5 compared with C4 (0-1 cm: 16.9 vs. 9.9 mmol SO_4^{2-} m⁻² d⁻¹; Monperrus et al., 2007). The strengthening of the anaerobic oxidation routes in proportion to the increase of the organic carbon content of the sediment has also been found by Forja et al. (2004). Sulfate-reduction rates in the Thau lagoon were typical of organic carbon enriched sediments (see Welsh et al., 1996). Biodeposit remineralization by the microbial loop does explain the larger oxygen demand and DIC release in the shellfish farming area, especially in May 2003. In addition, this study shows a significant excess of nutrients $(NH_4^+, PO_4^{2-} \text{ and } Si(OH)_4;$ both in concentrations and fluxes) at the SWI at C5, compared with C4 (Table 1). The influence of oyster culture on nutrient concentrations in overlying water was also all the more significant in the study of Souchu et al. (2001), with increases (on a yearly basis) of 73%, 36% and 19% for ammonia, phosphates and silicates, respectively. At the lagoon scale, the main impact of the suspended oyster cultures on the nitrogen cycle is through DIN renewal in the water column, not PON enrichment of the sediment (Mazouni, 2004). Increased nutrient fluxes at the SWI underneath oyster ropes emphasize the impact of oyster filter-feeding and biodeposition activities on particulate matter trapping, and subsequent remineralization by the bacteria. This process may be all the more important in ecosystem functioning when, for example, it contributes to maintain diatom-dominated phytoplankton populations in summer despite low Si:N ratios in freshwater inputs (Chauvaud et al., 2000; Ragueneau et al., 2002). The four- to fivefold increase of silicate release at the SWI in the shellfish farming area, compared with the central part of the lagoon (Table 1), emphasizes biogenic silica retention and recycling in the sediments under the oyster ropes.

The other main spatial variations observed for biogeochemical fluxes at the SWI were related to the presence/absence of macrophytes on the sediments. Eutrophication has generated macrophytic biomass in the Thau lagoon reaching 10,073 t dry weight in autumn 1986 (Gerbal and Verlague, 1995) and 12,039 t DW in May-June 1998 (Plus et al., 2003). Spatial variations of the biomass distribution are highlighted by the shellfish farming area A (including C5 and C7) exhibiting 2222 t DW in 1998, vs. 1505 t DW in the mixed seagrass meadow of the southern fringe (including C6) and no macrophyte in the central zone (including C4; Plus et al., 2003). In this study, the nitrophilous opportunistic seaweed Ulva spp. (Picot et al., 1990) exhibited a more widespread distribution than in previous ones, being all the more abundant in the shallow parts of the corridors between ovster ropes (shellfish farming area A). Macroalgae were less abundant at C5, likely due to greater water depth and light limitation (only detritus material was observed in the deeper central part of the corridors). Station C7, characterised by a dense macroalgal cover (including Ulva), consistently exhibited the highest oxygen, DIC and nitrogen fluxes at the SWI. In particular, significant net uptakes of CO₂, ammonium and nitrate-nitrites were measured in the enclosures in daylight conditions in May 2003, while opposite trends were observed at C4 and C5 in the enclosures without macroalgae (Table 1). Macrophytes would account for a decrease of ca. 33% of the ammonium concentrations in the water column during the spring productive period, in the northern part of the lagoon (Plus et al., 2003). Yet the macrophyte uptake does not match the remineralization process in summer, when macrophytes mainly enhance the detritus pool. The influence of macroalgal photosynthesis on benthic fluxes of trace elements, mercury species and organotin compounds is shown in Point et al. (2007).

The fact that the seagrass bed was not sampled in May 2003 does not allow comparing the benthic fluxes measured on macroalgae with those recorded on the seagrass meadow in "warm" conditions. In contrast to the macroalgae bottom, photosynthesis during daylight was not sufficient in the meadow in April 2002 to compensate respiration of the seagrass and its associated benthic fauna. Plus et al. (2003) showed that the rhizophytes have a smaller influence on nutrient concentrations in the water column in the southern part of the lagoon, compared with the macroalgae in the northern area. This pattern can be explained by the ecophysiology of seagrasses, which preferentially take up sedimentary nitrogen. On the other hand, more oligotrophic conditions were simulated by Plus et al. (2003) in the southern part of the lagoon, compared with the north border. Now seagrasses are well adapted to nutrient-poor environments, having internal processes of nitrogen redistribution, from belowground components to leaves and vice versa, and reclamation from old to young tissues (see Plus et al., 2003 for review).

4.4. Sediment oxygenation and macrofaunal changes

The oxygen penetration depth in the sediment was shallowest during the warm periods of August 2002 and May 2003 (Dedieu et al., 2007). Oxic penetration depth was similar at the two stations in May 2003 $(0.9 \pm 0.2 \text{ mm} \text{ at } \text{C4} \text{ vs.})$ 0.7 ± 0.3 mm at C5), but the oxic zone thickness was two to three times larger during the cold periods outside the shellfish farm, compared to inside (April 2002: 3.9 ± 1.0 mm at C4 vs. 1.4 ± 0.5 mm at C5). This result explains the differences observed for macrofaunal distribution in this study. First, anoxic conditions in the sediments precluded the presence of infaunal organisms at C5. Second, the development of hypoxic conditions in bottom water at C4 in May 2003 (Table 1) and reduced oxic penetration depth in the sediment were associated with major benthic community shifts, from a welldiversified assemblage including numerous individuals of infaunal mollusc species in April 2002 to a community mainly reduced to opportunistic Capitellidae in May 2003. Major changes in benthic macrofauna community structure were observed between December 2001 and May 2003 at C4 and C5 overall; all of them were related to sediment organic matter enrichment during the survey (Duport et al., 2007). On the other hand, the dominance in biomass of the symbiotic chemoautotrophic bivalve Lucinoma lactea within the seagrass meadow (Table 2) emphasizes a sulfide-rich habitat. Indeed, this species hosts sulfide-oxidizing symbiotic bacteria in its gills (Southward and Southward, 1986). Lucinoma also accounted for 15-20% of the total macrofauna biomass at C4, thus highlighting the importance of anaerobic oxidation of the organic matter in the lagoon.

5. Conclusions

The in situ measure of biogeochemical fluxes at the sediment—water interface over a productive period of the annual cycle provided a basis for describing spatial and temporal variations of the dynamics of the sediment—water exchanges in the Thau lagoon. The results emphasize the role of oyster cultures on benthic fluxes and the impact of spatial heterogeneity of the benthos (macrophytes and macrofauna) distribution and community structure at various spatial scales (from the study zones to the meter scale). They also highlight that this eutrophicated ecosystem, colonised by dense macrophyte populations, is facing severe hypoxic conditions in bottom water as soon as mid-spring during warm years. Eutrophication is mainly benthic in the lagoon, the reared bivalves controlling phytoplankton biomass. As a result, the amount of primary production which is not consumed by macrofaunal herbivores does accumulate on the bottom and becomes detritus (one may note that, in this case, the magnitude of carbon and nutrient export drops compared with pelagic-oriented primary production). The first impact of this shift is a severe decrease of oxygen concentration at the SWI and in overlying water during the night. On the other hand, the absence of oxygen in the sediments under the influence of oyster culture precludes the installation or survival of infaunal macro-organisms (>1 mm). The unusually warm conditions observed in May 2003 lasted all summer, with water temperature reaching 29.5 °C on 14 August. High water temperature and the absence of strong winds in August led to bottom anoxia and another episode of oyster mass mortality in the Thau lagoon. The multiplication of these dystrophic events in the lagoon is likely, with on-going and future climate changes (global warming).

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