

Summer influence of 1 and 2 yr old mussel cultures on benthic fluxes in Grande-Entrée lagoon, Îles-de-la-Madeleine (Québec, Canada)

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ABSTRACT: The summer influence of 1 and 2 yr old suspended mussel lines on benthic fluxes (oxygen, silicates, ammonium, phosphates, nitrates and nitrites) was studied in Grande-Entrée lagoon (GEL), Îles-de-la-Madeleine, Québec, Canada. This influence and its temporal variation were examined in relation to bottom water, sediment and macrofauna characteristics. *In situ* mensurative experiments using benthic chambers and sediment cores were carried out at 2 mussel sites (M1 and M2) and 2 control sites (C1 and C2) in July, August and September 2003. In contrast to 1 yr old mussel lines (M1), 2 yr old lines (M2) enriched the sediment in organic matter and increased silicate, ammonium, phosphate and nitrite fluxes at the water–sediment interface. Silicate, ammonium and phosphate fluxes were highest in August, when temperature was highest. The main nutrient releases observed at the water–sediment interface in M2 could reduce nitrogen and silica limitation in the water column. Mussel lines did not influence benthic macrofauna biomass, but favoured the recruitment of many small-sized organisms. No influence of mussel lines was observed on oxygen consumption at the water–sediment interface. Macrofauna biomass and oxygen consumption increased in parallel during the summer, but the respiration of the low biomass alone cannot explain the greater overall benthic oxygen demand. The latter was probably also driven by the oxidation of reduced compounds such as sulfides. The reduced nature of the sediment could be natural in GEL, but the continuous accumulation of mussel biodeposits since 1985 has probably contributed to the degradation of the benthic environment in the mussel farm.

KEY WORDS: Mussel line · Biogeochemical fluxes · Water–sediment interface · Organic enrichment · Benthic macrofauna

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INTRODUCTION

Mussels are suspension feeders which remove suspended particles from the water column before producing pseudofaeces and faeces (Navarro & Thompson 1997, Cranford et al. 2003, Hartstein & Rowden 2004). The latter rapidly settle to the seabed, especially under conditions of slow or poor water flushing and exchange (Cranford et al. 2003). In addition to the settlement of

relatively large volumes of biodeposits, mussel fall-off and shell debris accumulate beneath mussel longlines (Grant et al. 1995, Christensen et al. 2003).

Biodeposition could enhance sedimentation rate which has been shown to be 2 to 4 times higher inside than outside shellfish farms (Dahlbäck & Gunnarsson 1981, Hatcher et al. 1994, Callier et al. 2006). It could also induce organic matter enrichment of sediments (Deslous-Paoli et al. 1998, Stenton-Dozey et al. 2001,

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Miron et al. 2005) and affect the quality of the particulate organic matter (POM) available for benthic organisms (Grenz et al. 1990, La Rosa et al. 2001). Organic enrichment is known to stimulate biological activity, but also to change the benthic community structure (biomass, abundance and species; Pearson & Rosenberg 1978, Gray et al. 2002). Since metabolism of the whole benthic community depends partly on macrofauna biomass (Mazouni et al. 1996, Welsh 2003) and abundance (Nickell et al. 2003, Welsh 2003), changes in the macrofaunal community structure will affect the oxygen and nutrient fluxes at the water–sediment interface (Welsh 2003). Indeed, biodeposition has been shown to increase benthic fluxes (Baudinet et al. 1990, Grenz et al. 1992, Mazouni et al. 1996). Therefore aquaculture practices could induce changes in the relative concentrations of silica, nitrogen and phosphorus (Hatcher et al. 1994), thus modifying nutrient ratios (Redfield et al. 1963) and phytoplankton species composition (Smayda 1990). In particular, nitrogen turnover would be accelerated (Christensen et al. 2003).

Bivalve biodeposition (Lerat et al. 1985, Navarro & Thompson 1997) and mussel drop-offs (Myrand & Gaudreault 1995) are known to be higher in summer. The higher water temperature and food supply in summer stimulate the metabolic activities of benthic macrofauna (Pearson & Rosenberg 1978) and bacteria (La Rosa et al. 2001). Consequently, benthic fluxes would be greater during warm periods (Lerat et al. 1985, Mazouni et al. 1996). In summer, intensive bivalve production can induce excessive organic matter loading and critical nutrient releases and oxygen demand in the surrounding water. As a result, eutrophication can favour blooms of harmful phytoplankton (Smayda 1990, Cranford et al. 2003) while anoxia and poisoning of the bottom water (by excessive release and build up of ammonium and sulfide) can cause mass mortality of the whole macrofauna community (Deslous-Paoli et al. 1998, Gray et al. 2002). Excessive bivalve production could induce serious ecological and economical consequences. Assessing the potential impact of mussel farming is thus important for developing an ecologically sustainable management of aquaculture (Danovaro et al. 2004).

Shellfish production by aquaculture is increasing significantly throughout the world (Danovaro et al. 2004). In Canada, the bivalve aquaculture industry has expanded rapidly over the last 2 decades (Cranford et al. 2003). Since the 1980s, the mussel industry has developed in an oligotrophic lagoon (Souchu et al. 1991), called Grande-Entrée, in the Îles-de-la-Madeleine (47° 35' N, 61° 31' W, Québec, Canada).

Mussels *Mytilus edulis* L. are cultured suspended from long-lines for a 2 yr grow-out cycle in the Îles-de-la-Madeleine. Since Callier et al. (2006) showed that

sedimentation rates recorded beneath 2 yr old mussel lines were greater than those beneath 1 yr old lines, a greater influence of 2 yr old mussel lines on the benthic system was expected in this study.

The principal objective of this study was to test and compare the summer influence of the 2 age classes of suspended mussel lines on the oxygen demand, nutrient fluxes (ammonium, phosphates, nitrates, nitrites and silicates) and nutrient ratios at the water–sediment interface. The second objective was to examine the variability of these influences throughout the summer. More specifically, 2 hypotheses were tested: (1) benthic fluxes are greater at the 2 yr old mussel site than at the 1 yr old site, and both mussel sites have greater fluxes than control sites (these fluxes drive changes in nutrient ratios at the water–sediment interface); (2) benthic fluxes are significantly different among experimental dates. These 2 hypotheses were studied in relation to bottom water, sediments and macrofauna characteristics (abundance and biomass).

Although several cohorts of bivalves are usually present in worldwide culture areas, this study is the first to dissociate the influence of different ages of aquaculture structures on benthic fluxes in a coastal ecosystem. The results of this study are expected to be relevant for modelling the carrying capacity of marine ecosystems sustaining bivalve cultures comprising several different age classes.

MATERIALS AND METHODS

Study area. Grande-Entrée lagoon (GEL) is located on the NE of the Îles-de-la-Madeleine, Québec, Canada (Fig. 1A). The surface area of the lagoon is 58 km² and the mean depth is 3 m (Koutitonsky et al. 2002). A navigation channel separates the lagoon into a shallow (1 to 3 m) sandy area to the west and a relatively deep (5 to 7 m) muddy basin to the east (Koutitonsky et al. 2002; Fig. 1B). An amphidromic point close to the Îles-de-la-Madeleine decreases the influence of the tide, which has a mean amplitude of 0.58 m (Koutitonsky et al. 2002). In the Îles-de-la-Madeleine, it is frequently windy and wind speeds can reach 15 m s⁻¹ (Souchu et al. 1991). As a result, the water column tends to be well mixed (Souchu et al. 1991). West of the channel, current speeds up to 20 cm s⁻¹ have been recorded vs. 5 cm s⁻¹ in the deeper eastern zone (Koutitonsky et al. 2002). Water residence time in the deeper areas of the lagoon ranges between 20 and 35 d when tidal- and wind-driven currents are considered (Koutitonsky & Tita 2006). However, it significantly decreases in winter (>40 d) when ice-cover (December to April or May) prevents any wind influence on the lagoon hydrology (Koutitonsky & Tita 2006). In the

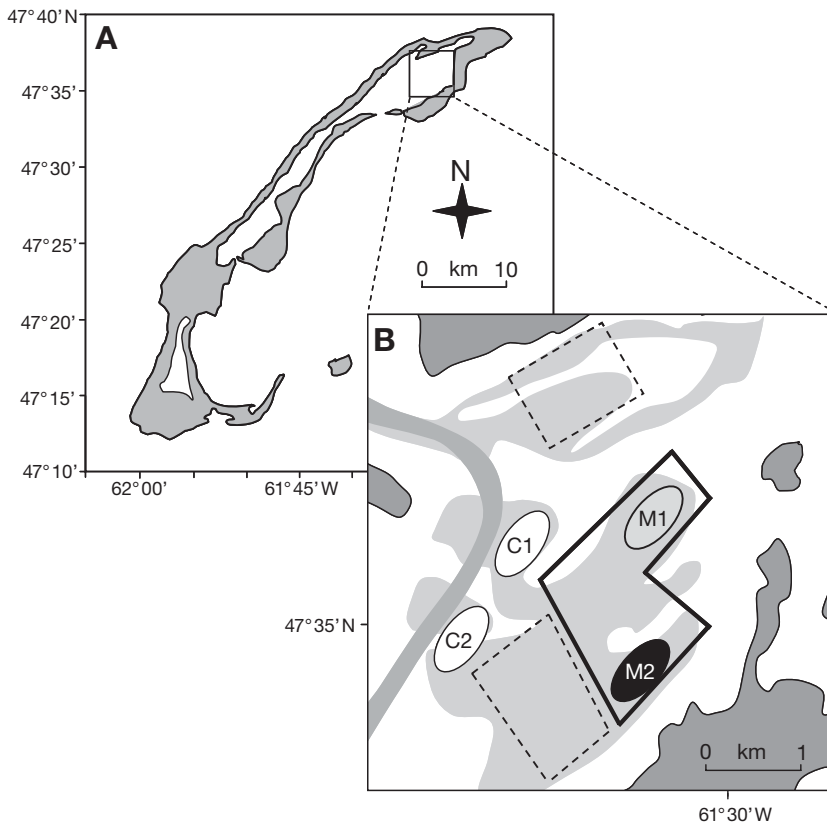


Fig. 1. (A) Îles-de-la-Madeleine. (B) Location of aquaculture farms and experimental sites in Grande-Entrée lagoon; black-contoured polygon: mussel farm location; dash-contoured quadrants: scallop farms (southern scallop farm was unproductive whereas northern farm was productive between 1999 and 2004); ellipses: the 4 sites (C1, Control 1; C2, Control 2; M1, 1 yr old mussel site; M2, 2 yr old mussel site); mid-grey area: channel; light grey areas: deeper zones (mean 6 m)

lagoon, water temperatures rise on average from 8°C in June to 20°C in the third week of August before decreasing to ca. 9°C by October (Koutitonsky et al. 2002). Salinity is about 30 to 31 from May to August (Souchu et al. 1991). Chlorophyll *a* concentration ranges between 0.5 and 2 $\mu\text{g l}^{-1}$ (Roy et al. 1991). Because of the absence of rivers, rainfalls are the only freshwater inputs (Souchu & Mayzaud 1991). Atmospheric input has been shown to contribute significantly to the inorganic nitrogen cycle (Souchu & Mayzaud 1991). The lagoon system exhibits oligotrophic characteristics: nutrient inputs could originate mainly from recycling resulting from bacterial remineralisation and excretion by heterotrophic organisms (Souchu et al. 1991).

Since 1985, the mussel industry has exploited GEL (Souchu et al. 1991). Before 2001, suspended mussel lines were deployed in the majority of the deepest zones of the lagoon (Fig. 1B). A few deep zones have never been exploited for aquaculture (e.g. the east zone of the navigation channel; Fig. 1B). In 2001, the

mussel farm was separated into 2 distinct zones sustaining 1 yr old (M1: 12 to 14 mo) or 2 yr old (M2: 24 to 26 mo) mussel lines (Fig. 1B). The latter are replaced by juveniles (0+) each autumn following harvesting. The mean mussel size was about 4 cm for M1 vs. 6 cm for M2 between 5 and 11 August 2003. At this time, mussel dry weight (DW, with shells; \pm SE) m^{-1} line was $1293.08 \pm 212.07 \text{ g DW m}^{-1}$ for M1 vs. $1657.28 \pm 373.87 \text{ g DW m}^{-1}$ for M2. In 2003, a total of 318 suspended mussel lines representing 114 km cumulative length were present in the lagoon over a 250 ha surface area (G. Tita pers. comm.). The lines were separated from each other by 20 m. Annual mussel production reached 180 metric tons in 2003. At the end of the 1990s, 2 scallop (*Placopecten magellanicus*) farming zones were set up in Grande-Entrée lagoon. However, the southern site (130 ha) has never been used for aquaculture, whereas the northern site (100 ha) was productive between 1999 and 2004 (Fig. 1B; G. Tita pers. comm.). During these years, the northern site contained suspended long-lines bearing scallops ranging in total numbers from 1.5 to 3 million individuals (3 age classes; G. Tita pers. comm.).

Experimental design. *In situ* mensurative experiments (*sensu* Hulbert 1984), called hereafter 'experiments', were performed in the GEL during the warmest months of the year. In 2003, experiments

were carried out between 20 and 26 July, 18 and 23 August, and 7 and 15 September (hereafter 'July, August and September'). Experiments were performed at 4 different sites: 1 yr old mussel lines (M1), 2 yr old mussel lines (M2), and 2 control sites that have never been exploited for aquaculture (C1 and C2; Fig. 1B). In contrast to many studies (Baudinet et al. 1990, Grenz et al. 1992, Hatcher et al. 1994, Grant et al. 1995, Mazouni et al. 1996), 2 control sites were selected rather than one to test the influence of aquaculture with no confounding factor (Underwood 1996). According to several authors (Dahlbäck & Gunnarson 1981, Mattsson & Lindén 1983), the influence of bivalve biodeposition would be restricted to a radius of 20 to 40 m around the farms. In GEL, the mean estimated dispersal of faecal pellets ranges from 0–7.4 m (2 yr old mussel) to 7–24.4 m (1 yr old mussel; Callier et al. 2006). During strong wind events, when current velocity can reach 18 cm s^{-1} , the estimated dispersion may be up to 19.4 m (M2) and 24.1 m (M1) (Callier et al. 2006). The control sites were located more than 500 m from the aqua-

culture sites (Fig. 1B) to avoid the influence of mussel biodeposition on the benthic environment. Control sites were separated from each other by more than 500 m. Mean (\pm SE) depth of the experimental sites was 6.14 ± 0.08 m. Experiments were carried out randomly within sites and among sites to integrate the spatial and temporal variability of our measurements in the whole data set. Three replicates were carried out per site and per date. The total number of *in situ* experiments was 36 (4 treatments, 3 dates, 3 replicates).

Field measurements. Benthic chambers (Boucher & Clavier 1990, Thouzeau et al. 2007) were used to measure biogeochemical fluxes at the water–sediment interface, rather than peeper and core techniques which are less appropriate (Balzer et al. 1983, Grenz et al. 1991). We used dark instead of transparent chambers to avoid recording photosynthetic activity (Lerat et al. 1990), since this study focused on the comparison of benthic respiration and nutrient regeneration rates between mussel sites and control sites. Benthic chambers were composed of an acrylic tube and a removable acrylic hemisphere. Large enclosures (50 cm diameter) were selected to limit perturbation of the biogeochemical processes by insertion of the base into the sediment, which could damage fauna, funnels and burrows (Glud & Blackburn 2002). Moreover, the use of large benthic chambers minimises their effect on the spatial heterogeneity of the benthic fauna (Balzer et al. 1983). In addition, the large water volume of the chambers (66 to 78 l, depending on how deeply the base was inserted into the sediment) avoids or limits increases in biogeochemical fluxes caused by confinement or water warming.

Each benthic chamber was gently pressed into the sediment by SCUBA divers. The incubation time was set at 3 h, the period determined by a pilot study as the ideal incubation time for measurement of ammonium fluxes and for final oxygen concentrations to have attained levels not lower than 80% of the initial concentrations (Richard et al. 2006). Each benthic chamber was linked to a submersible pump and to a YSI 6600 probe. The adjustable submersible pumps connected to waterproof batteries provided homogenisation of the water inside the enclosures without noticeable particle resuspension. Water flow in each chamber was adjusted to 2 l min^{-1} , allowing stable measurements to be recorded by the YSI probe (Richard et al. 2006, Thouzeau et al. 2007). The latter recorded oxygen concentration ($\text{mg l}^{-1} \pm 0.01$), temperature ($^{\circ}\text{C} \pm 0.01$) and salinity (± 0.01) in the chamber at 1 min intervals. This monitoring allowed us to verify if there were any changes in the experimental conditions that could modify the biogeochemical processes in the chamber (e.g. an increase in water temperature).

Water samples were collected with 60 ml syringes at 90 min intervals (start, middle and end of incubation)

for nutrient analyses (ammonium, silicates, phosphates, nitrates and nitrites). Three syringes were filled at each sampling to minimise variability in nutrient concentrations. At the end of the incubation, the hemisphere was gently removed from its base. Using 60 ml disposable syringes whose ends had been cut off SCUBA divers collected 6 sediment samples for analysis of the organic matter contained in the top 2 cm. A large sediment core (surface area 262.5 cm^2 ; Wildish et al. 2003) was also collected by SCUBA divers to identify the macrofaunal community.

Sample processing. Sediment organic matter characteristics: Three samples of the top 2 cm of sediment were dried separately at 60°C for 48 to 72 h, weighed, and burned for 4 h at 450°C to calculate ash-free dry weight (AFDW) of the sediment (Byers et al. 1978). Sediment AFDW was measured to the nearest 10^{-5} g with an AG285 Mettler Toledo balance. Sediment organic matter content is expressed as percent of total sediment weight. Three further samples of the top 2 cm of sediment were analysed for particulate organic carbon (POC) and particulate organic nitrogen (PON) contents with a Carlo Erba NC 2500 elementary analyser. Finally, POC:PON ratios were calculated.

Macrofauna community: In the field, macrofauna samples were washed over a 0.5 mm sieve and frozen at -18°C . In the laboratory, samples were thawed and organisms were counted to calculate total macrofaunal abundance. Samples were then dried at 60°C for 48 to 72 h and weighed to obtain total macrofauna biomass (dry weight; mg). Dry mass was measured to the nearest 10^{-5} g with an AG285 Mettler Toledo balance. Abundance and biomass were standardised to 1 m^2 .

Nutrient analyses: Ten ml per syringe were immediately sampled in the field to measure ammonium concentration according to the OPA (*o*-phthalaldialdehyde) method (Holmes et al. 1999) with an Aquaflo handheld Turner Designs fluorometer. Because of technical problems in July, ammonium measurement was performed only in August and September. The remaining water samples were stored in 3 cryovials and frozen (-80°C) after filtering through $0.2 \mu\text{m}$ cellulose acetate Target syringe filters. Analyses of dissolved nitrates, nitrites, phosphates and silicates were performed on a II PAA II Brann + Luebbe auto-analyser according to Tréguer & Le Corre (1975).

Flux and ratio calculations. Oxygen consumption was determined from the slopes of the linear regressions established between concentration and incubation time. Nutrient fluxes were estimated from the change in nutrient concentration over incubation time. Nutrient fluxes were expressed as $\mu\text{mol m}^{-2} \text{ h}^{-1}$. Ammonium, nitrate and nitrite concentrations were summed to calculate total nitrogen concentration for each treatment and date at the beginning (t_0) and at

Table 1. Results of analyses of variance (ANOVAs) testing effect of: treatment, Tr (Control 1, Control 2, 1 yr old mussel and 2 yr old mussel sites); date, Da (July, August, September) and their interaction (Tr \times Da) on bottom water (temperature, salinity, oxygen concentration); sediment (organic matter content, OM, and POC:PON ratios) and macrofauna (biomass, abundance) characteristics. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Variation source	df	Water						Sediment				Macrofauna			
		Temperature		Salinity		Oxygen		OM		POC:PON		Biomass		Abundance, ln(x)	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Tr	3	0.40	0.82	0.02	0.71	2.16	1.61	16.74	6.23*	0.36	1.44	2.39	0.11	2.1	4.84**
Da	2	54.14	109.71***	0.22	7.37**	10.18	7.60**	6.14	2.29	1.56	6.30*	92.31	4.36*	16.02	36.94***
Tr \times Da	6	0.91	1.70	0.01	0.32	1.45	1.08	1.06	0.39	0.21	0.83	7.29	0.34	0.35	0.81
Error	24	0.49		0.03		1.34		2.69		0.25		21.19		0.43	

the end (t_{3h}) of each incubation. Initial and final N:P and Si:N ratios were calculated in atomic equivalents in August and September whereas Si:P ratios were calculated for all dates.

Statistical treatment. Analyses of variance (ANOVAs) were performed to compare: (1) the characteristics of bottom water (temperature, salinity and oxygen concentration), sediment (organic matter content, POC:PON ratios) and macrofauna (biomass and abundance) (see Table 1); and (2) biogeochemical fluxes (oxygen consumption and nutrient fluxes) (see Table 2) among the 4 treatments, Tr (C1, C2, M1 and M2) and 3 dates, Da (July, August and September with the exception of ammonium fluxes: August and September only). A final series of ANOVAs were also performed to compare nutrient ratios among the 4 treatments (C1, C2, M1, M2), different dates (July, August and September for Si:P; August and September for N:P and Si:N) and 2 incubation times, Ti (t_0 and t_{3h}) (see Table 3). Cochran's C-test was used to verify homogeneity of the variances (Underwood 1997); when required, data were transformed (see Tables 1 to 3). When a source of variation was significant, Student-Newman-Keuls (SNK) pair-wise multiple comparison tests were carried out to identify the differences.

RESULTS

Bottom water

Date was a significant source of variation for bottom-water temperature, salinity and oxygen concentration (Table 1). The mean bottom-water temperature showed a significant decrease ($>3^\circ\text{C}$) from July and August to September (Fig. 2A). The mean water salinity measured in July and August was significantly lower than in September (30.75 vs. 30.98). Finally, the mean oxygen concentration at the water-sediment interface increased significantly from July and August to September (Fig. 2B).

Sediment organic matter

Treatment was a significant source of variation for the total amount of organic matter contained in the top 2 cm of sediment (Table 1). The results of the SNK tests showed that the mean organic matter content was significantly higher at the 2 yr old mussel site than at the control and 1 yr old mussel sites (1.5 times higher; Fig. 3A). According to the ANOVAs (Table 1), POC:PON varied significantly among dates. Mean POC:PON was significantly higher in July and August than in September (Fig. 3B).

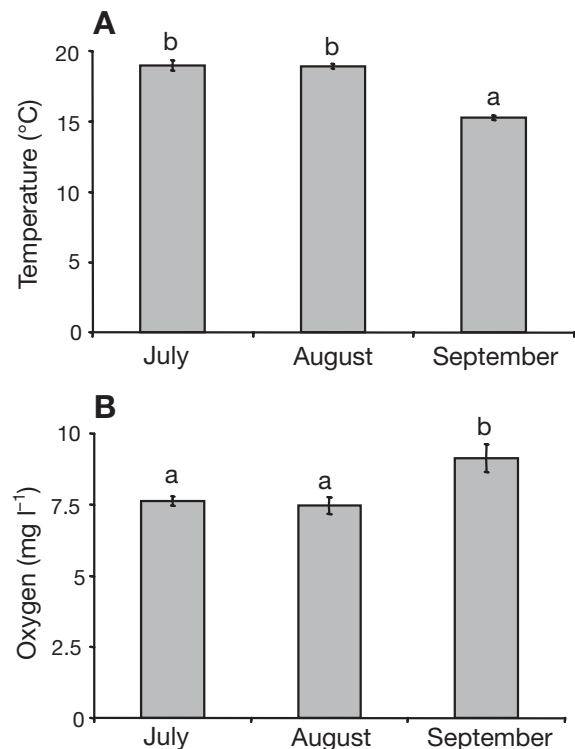


Fig. 2. (A) Bottom water temperature and (B) oxygen concentration at the 3 experimental sites. Different letters indicate statistically significant difference between dates. Data are means \pm SE

Macrofauna community

For total macrofauna biomass, there was no difference among treatments, but date was a significant source of variation (Table 1). The mean total macrofauna biomass was almost 5 times higher in September than in July and August (Fig. 4A). In contrast, treatment and date were significant sources of variation for total macrofaunal abundance (Table 1): abundance was 2 times higher at the mussel sites (M1 and M2) than at the control sites (C1 and C2; Fig. 4B). Mean total macrofaunal abundance increased between July and August at each site (Fig. 4B).

Biogeochemical fluxes

Oxygen flux was always negative during this study, highlighting oxygen consumption at the water–sediment interface. There were no significant differences among treatments, but date was a significant source of variation for oxygen consumption (Table 2). Mean oxygen consumption was about 3 times higher in September than in July and August (SNK; Fig. 5).

Silicate flux was the highest nutrient flux recorded in this study, reaching $867.58 \mu\text{mol} (\text{SiOH})_4 \text{m}^{-2} \text{h}^{-1}$. The interaction of treatment and date was a significant source of variation for silicate flux (ANOVA; Table 2).

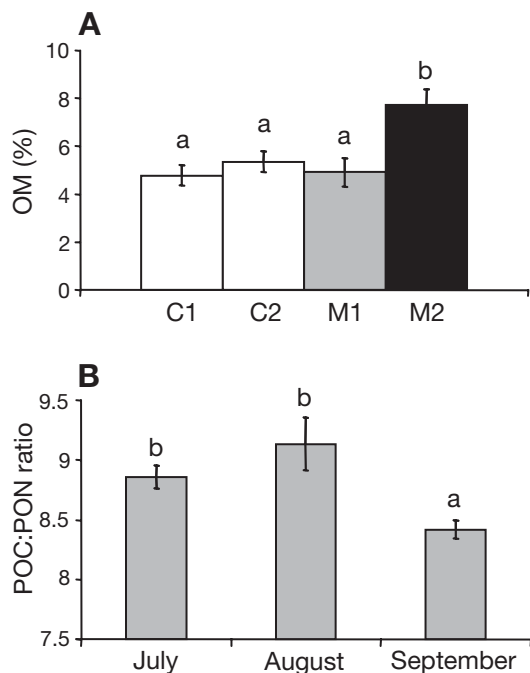


Fig. 3. (A) Organic matter content (OM) of sediment at the 4 sites; (B) POC:PON ratio calculated for the 3 experimental dates: Different letters indicate statistically significant difference between treatments (A) or dates (B). Data are means \pm SE; site abbreviations as in Fig. 1

Silicate flux measured at the water–sediment interface of M2 was significantly greater than that measured at control sites (C1 and C2) and at M1 for all dates (Fig. 6). The maximum mean silicate flux observed at M2 was in August and was almost 8 times greater than the maximum mean silicate flux observed in C1, C2 and M1. No significant temporal variation was observed at M1, C1 and C2, whereas silicate flux in M2 increased significantly from July to August and decreased from August to September (SNK; Fig. 6).

Ammonium flux was the second highest nutrient flux measured in this study (up to $448.83 \mu\text{mol} \text{NH}_4 \text{m}^{-2} \text{h}^{-1}$). As for silicate flux, the interaction of treatment and date was a significant source of variation for ammonium flux (Table 2). According to *a posteriori* test results, ammonium flux measured at the water–sediment interface at M2 was significantly greater than that measured at C1, C2 and M1 in August and in Septem-

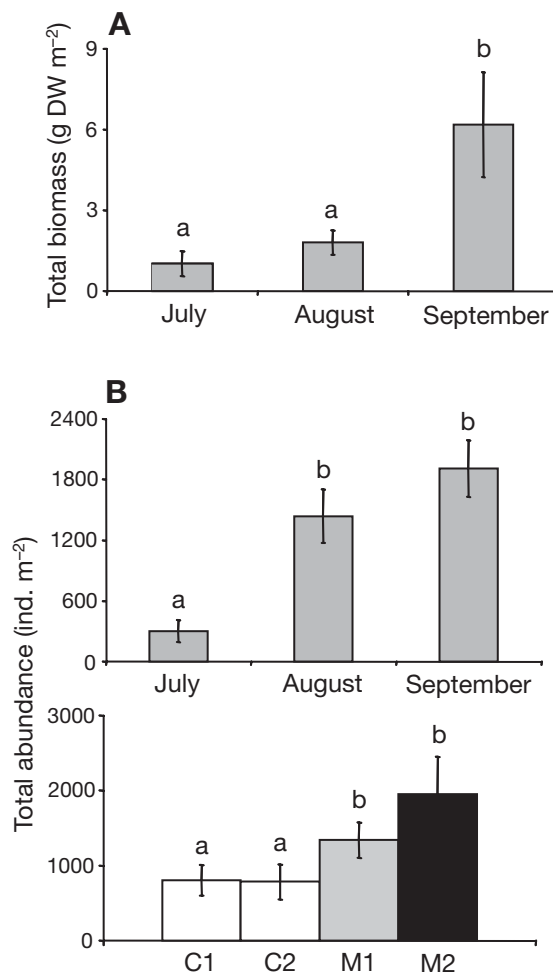


Fig. 4. (A) Total macrofauna biomass and (B) abundance on the 3 experimental dates and at the 4 sites. Different letters indicate statistically significant difference between dates (A and B) or treatments (B). Data are means \pm SE; site abbreviations as in Fig. 1

Table 2. Results of analyses of variance (ANOVAs) testing effect of treatment, date and their interaction on oxygen and nutrient fluxes (ammonium fluxes were not measured in July). Abbreviations and significance levels as in Table 1

Flux	Variation source	df	MS	F
O ₂	Tr	3	301.41	0.01
	Da	2	329768.05	12.93 ***
	Tr × Da	6	4872.11	0.19
	Error	24	25495.57	
Si(OH) ₄	Tr	3	314099.35	35.82 ***
	Da	2	35386.16	4.04 *
	Tr × Da	6	39377.52	4.49 **
	Error	24	8768.4	
NH ₄	Tr	3	60844.11	43.29 ***
	Da	1	23557.43	16.76 ***
	Tr × Da	3	9794.15	6.97 **
	Error	16	1405.46	
PO ₄ ^a	Tr	3	3.12	6.20 **
	Da	2	2.98	5.90 **
	Tr × Da	6	1.01	2.01
	Error	24	0.50	
NO ₃	Tr	3	1.44	0.69
	Da	2	5.01	2.41
	Tr × Da	6	3.33	1.60
	Error	24	2.08	
NO ₂	Tr	3	4.91	14.36 ***
	Da	2	0.43	1.25
	Tr × Da	6	0.11	0.34
	Error	24	0.34	

^aln(x+1)

ber (Fig. 7). Ammonium flux measured at M2 was highest in August and was more than 5 times greater than that measured at C1, C2 and M1 on the same date. Ammonium flux did not vary temporally in C1, C2 and M1, whereas it decreased from August to September in M2 (Fig. 7).

Phosphate flux ranged from 0.42 to 128.48 $\mu\text{mol PO}_4 \text{ m}^{-2} \text{ h}^{-1}$. Date was a significant source of variation (Table 2). The mean phosphate flux measured in July

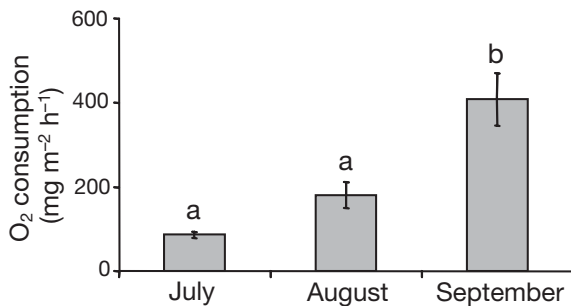


Fig. 5. Mean (\pm SE) oxygen consumption on the 3 experimental dates. Different letters indicate statistically significant difference between dates

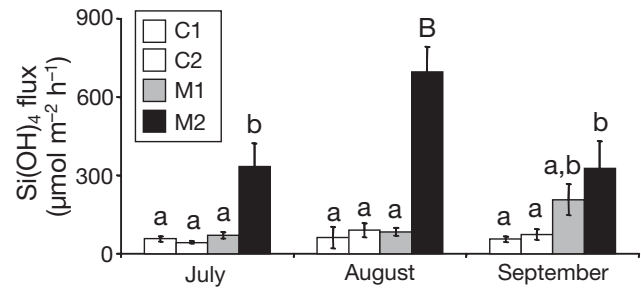


Fig. 6. Mean (\pm SE) silicate flux at the 4 sites on the 3 experimental dates. Different letters indicate statistically significant difference between treatments on a given date; capital letter indicates significant difference between dates for given treatment; site abbreviations as in Fig. 1

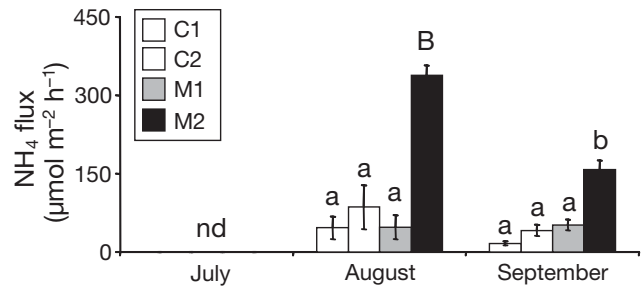


Fig. 7. Mean (\pm SE) ammonium flux at the 4 sites on the 3 experimental dates. Different letters indicate statistically significant difference between treatments on a given date; capital letter indicates significant difference between dates for given treatment; nd: no data; site abbreviations as in Fig. 1

and August was almost 3 times greater than in September (Fig. 8). Treatment was also a source of variation (Table 2): mean phosphate flux was significantly higher at M2, with values 4 times greater than at the other sites for all dates (Fig. 8).

Nitrate flux was low during this study, ranging from -8.25 to $4.52 \mu\text{mol NO}_3 \text{ m}^{-2} \text{ h}^{-1}$. No pattern was observed for nitrate flux (no significant source of variation; Table 2). Nitrite flux was also low (-0.43 to $2.44 \mu\text{mol NO}_2 \text{ m}^{-2} \text{ h}^{-1}$), but, in contrast to nitrate flux, a significant difference was observed among treatments (Table 2). Indeed, the mean nitrite flux was on average 6 times greater in M2 than in C1, C2 and M1 (Fig. 9).

Nutrient ratios

The interaction between treatment and time was significant for Si:P and N:P ratios (Table 3). For both ratios, no significant difference was observed between the initial ratio (t_0) measured at the different sites, whereas the final ratio ($t_3 \text{ h}$) measured at M2 was greater than that at C1, C2 and M1 (Fig. 10). The final

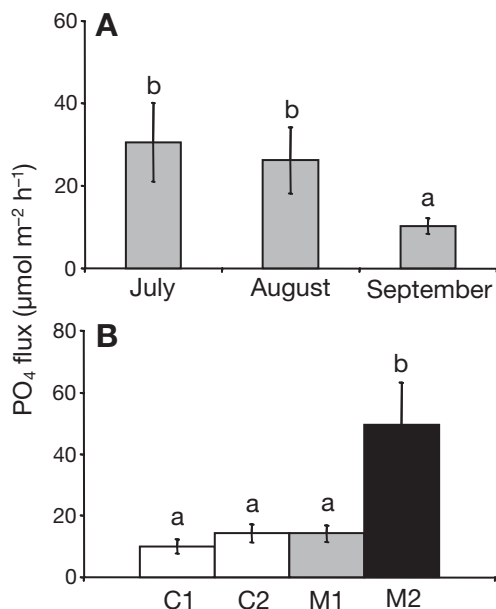


Fig. 8. Mean (\pm SE) phosphate flux at the 4 sites on the 3 experimental dates. Different letters indicate statistically significant difference between dates (A) or treatments (B); site abbreviations as in Fig. 1

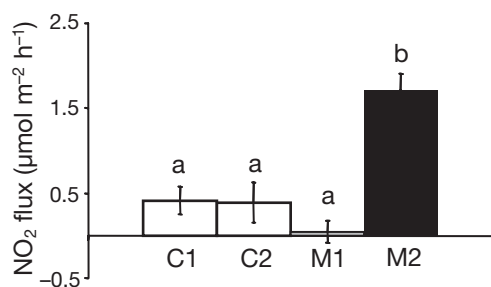


Fig. 9. Mean (\pm SE) nitrite flux at the 4 sites. Different letters indicate statistically significant difference between treatments; site abbreviations as in Fig. 1

Si:P ratio at M2 was about 1.7 times greater than the initial ratio (Fig. 10A), whereas the final N:P ratio was 3 times greater than the initial value (Fig. 10B). Time was a significant source of variation for the Si:N ratio (Table 3). The mean of the initial Si:N ratio was significantly greater than that of the final ratio.

DISCUSSION

Influence of suspended mussel long-lines

Bottom water temperature, salinity and oxygen concentration were similar in all experimental sites. The mean oxygen concentration measured at the water-sediment interface (7.6 to 9.1 mg l⁻¹) during the chamber experiments indicated normoxic conditions, since

Table 3. Results of analyses of variance (ANOVAs) testing effect of treatment, date, incubation time, Ti (t_0 , t_{3h}) and their interactions on Si:P, Si:N and N:P ratios (Si:N and N:P ratios were not calculated in July). Other abbreviations and significance values as in Table 1

Ratio	Variation source	df	MS	F
Si:P	Tr	3	4.8791	5.35 **
	Da	2	47.6704	52.30 ***
	Ti	1	22.4821	24.66 ***
	Tr × Da	6	4.5118	4.95 ***
	Tr × Ti	3	6.8044	7.46 ***
	Da × Ti	2	5.3111	5.83 **
	Tr × Da × Ti	6	0.9368	1.03
	Error	48	0.9116	
N:P	Tr	3	1.3858	2.80
	Da	1	0.4218	0.85
	Ti	1	12.7486	25.79 ***
	Tr × Da	3	1.7232	3.49 *
	Tr × Ti	3	2.7212	5.51 **
	Da × Ti	1	0.0009	<0.01
	Tr × Da × Ti	3	0.1844	0.37
	Error	32	0.4943	
Si:N ^a	Tr	3	0.3927	2.20
	Da	1	0.0591	0.33
	Ti	1	1.2162	6.81 *
	Tr × Da	3	0.1775	0.99
	Tr × Ti	3	0.2762	1.55
	Da × Ti	1	0.1858	1.04
	Tr × Da × Ti	3	0.0281	0.16
	Error	32	0.1786	

^a(x + 1)²

hypoxia occurs at ca. 6 mg l⁻¹ (Gray et al. 2002). The mussel farms in Grande-Entrée lagoon did not induce oxygen depletion in bottom waters leading to anoxia—as has been observed in oyster farms in France (Deslous-Paoli et al. 1998, Thouzeau et al. 2007). However, organic matter content in surface and subsurface sediments was greater at M2 than at the other sites. As in many shellfish farms (Dahlbäck & Gunnarsson 1981, Mattsson & Lindén 1983, Stenton-Dozey et al. 2001), mussel lines in GEL (M2) induced enrichment of sediment organic matter through biodeposition that enhanced sedimentation rates (Hatcher et al. 1994, Cranford et al. 2003). Indeed, the sedimentation rates observed under 2 yr old mussel lines were almost twice as high as those observed in control sites in GEL (mean = 34.8 g DW m⁻² d⁻¹ at M2 vs. 16.8 g DW m⁻² d⁻¹ at control sites in July 2003; Callier et al. 2006). In contrast, no significant enrichment of sediment organic matter was observed at M1 compared to control sites during the summer period. It is possible that the lower biomass of 1 yr old mussels compared to that of 2 yr old mussels was insufficient to induce organic enrichment, as suggested by some authors (Miron et al. 2005).

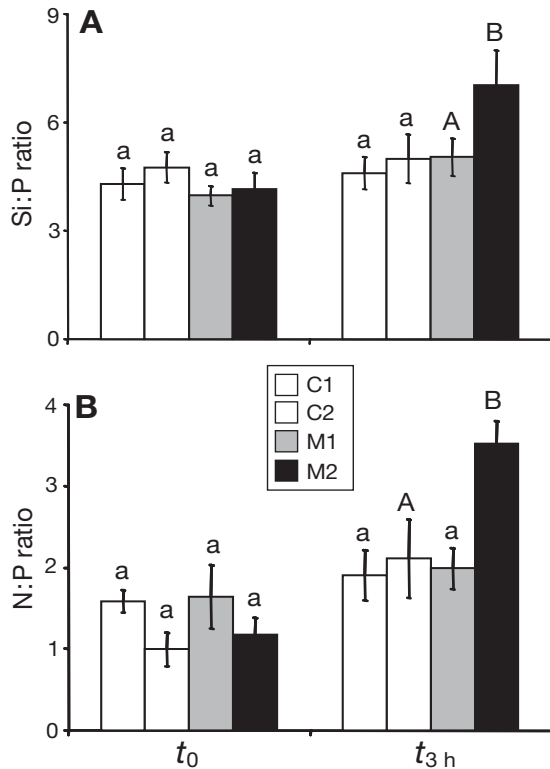


Fig. 10. Mean (\pm SE) of (A) Si:P and (B) N:P calculated for the 4 sites at beginning (t_0) and at end (t_{3h}) of incubation. Different letters indicate statistically significant difference between treatments; site abbreviations as in Fig. 1

Shellfish biodeposits could affect the quality of particulate organic matter available for benthic organisms (Grenz et al. 1990, La Rosa et al. 2001). The ratio of particulate organic carbon to particulate organic nitrogen (POC:PON) has been used as a proxy for organic matter quality (Nickell et al. 2003). Since nitrogen is degraded more rapidly than carbon, low ratios indicate labile organic matter whereas high values signify refractory organic matter (Nickell et al. 2003). POC:PON ratios between 4 and 8 correspond to phytoplankton, faecal pellets and other easily degraded material of high nutritional value, whereas ratios larger than 10 characterise detritus, sediment or other mineralised material of low nutritional value (Kautsky & Evans 1987). In GEL, the POC:PON ratios between 8.4 and 9.1 observed during this study indicate fresh or slightly degraded material. In agreement with the findings of Hatcher et al. (1994) at a suspended mussel farm in Upper South Cove, Nova Scotia, Canada, we observed no significant difference between the POC:PON ratios measured in the upper 2 cm of sediment at mussel sites and those at control sites. The measurement of POC:PON ratios in the superficial (e.g. 0.5 cm) layer of the sediment could be a better indicator of mussel farm influence than measurements in the top 2 cm, since

most of the particulate carbon and nitrogen that sink to the bottom may not be incorporated into the sediment (Hatcher et al. 1994) and could be rapidly degraded by the benthic community.

Following the Pearson & Rosenberg (1978) model, or more recently derived models (Nilsson & Rosenberg 2000, Gray et al. 2002), high enrichment of organic matter through biodeposition could result in the disappearance of large-sized animals (e.g. echinoderms; Mattsson & Lindén 1983), in biomass decreases (Mazouni et al. 1996, Stenton-Dozey et al. 2001), and in the proliferation of small-sized opportunistic species (Mattsson & Lindén 1983, Christensen et al. 2003, Hartstein & Rowden 2004). While 2 yr old mussel lines induced enrichment of sediment organic matter in GEL, no significant difference was observed in the macrofauna biomass between M2 and the control sites. However, macrofaunal abundances in mussel sites (M1 and M2) were greater than in control sites, indicating that individual mass was lower in mussel sites than in control sites and suggesting an increase in organisms of smaller size at the mussel sites. Callier et al. (2006) observed that benthic communities were dominated by small-sized opportunistic species in mussel sites in GEL. These results indicate benthic habitat degradation during mussel culture.

The measurement of oxygen consumption in the water overlying undisturbed sediments is a rapid and sensitive index of benthic community metabolism (Hargrave 1969). Enrichment of sediment organic matter is known to stimulate biological activity, thus increasing oxygen demand at the water-sediment interface (Pearson & Rosenberg 1978). Indeed, oxygen consumption rates measured under aquaculture structures are often greater than those measured outside the farms (Hargrave et al. 1993, Mazouni et al. 1996, Christensen et al. 2003). Even though organic enrichment and increased macrofaunal abundance were observed in M2, no significant difference was observed for oxygen consumption between mussel and control sites in GEL. According to Grant et al. (1995) and Stenton-Dozey et al. (2001) and contrary to the statement by Hargrave (1969), oxygen consumption is not a sensitive indicator of the impact of mussel culture on the benthic system since it is affected by many factors. Sediment oxygen demand is driven by the respiration of benthic organisms and by the microbial-mediated oxidation of organic matter and reduced inorganic metabolites (Nickell et al. 2003). The relative proportions of each of these processes could be different between mussel and control sites. Further characterisation of aerobic and anaerobic metabolisms using asphyxiation techniques (Van der Loeff et al. 1984) could help to better understand the processes driving oxygen consumption at the water-sediment interface in GEL.

In GEL, as in other shellfish farms (Hatcher et al. 1994, Stenton-Dozey et al. 2001, Christensen et al. 2003), increased sedimentation rates and organic enrichment observed at the culture sites induced increased nutrient fluxes compared to the other sites. Indeed, silicate, ammonium, phosphate and nitrite releases were 4 to 8 times greater in M2. In our study, silicate releases in GEL were the largest, followed by ammonium, phosphate, nitrate and nitrite releases, as already observed in mussel and oyster farms by Baudinet et al. (1990) and Grenz et al. (1992), respectively. The large silicate fluxes observed at M2 could originate from the dissolution of biogenic silica trapped in mussel biodeposits accumulated at the water–sediment interface (Lerat et al. 1990). Mussel biodeposits are composed of large-sized diatom cells and chain forms (pseudofaeces) or frustules of small-sized diatom cells and chains forms (faeces; Navarro & Thompson 1997). Diatom tests are made of biogenic silica (Balzer et al. 1983), which could explain the pattern observed in our study. The large ammonium and phosphate fluxes observed at M2 could originate from the decomposition of faeces, pseudofaeces and animal tissues accumulated in sediment, since bivalve biodeposits are usually considered to be an important source of nitrogen (Kautsky & Evans 1987) and phosphorus (Sornin et al. 1986). Organic matter decomposition with nitrification–denitrification processes induces nitrate–nitrite releases at the water–sediment interface. Nitrification occurs in the upper aerated sediments and denitrification in the deeper anoxic zone (Jenkins & Kemp 1984). Increased reductive processes (denitrification and dissimilative reduction of nitrate into ammonium) have often been noted in shellfish farms (Christensen et al. 2003). In GEL, the high nitrite fluxes at M2 could be due to these reductive processes. Overall, the high nutrient fluxes observed at M2 highlight the direct influence of mussel biodeposition on the benthic environment. In contrast, biodeposition at M1 may not have been high enough to increase benthic nutrient releases.

Under oyster lines in Thau lagoon (France), Thouzeau et al. (2007) showed that bivalve biodeposition could favour biogenic silica, organic nitrogen and phosphorus retention at the water–sediment interface. High mineralisation rates of biodeposits do accelerate nutrient turnover by massive releases of nutrients at the water–sediment interface, which in turn can modify the nutrient budgets around farms (Baudinet et al. 1990, Thouzeau et al. 2007). The ecological importance of nutrient regeneration is the lessening of nutrient limitation for phytoplankton, which could result in increased primary production and turnover (Smaal 1991). However, disequilibria in nutrient release kinetics can change the original nutrient ratios and the

specific composition of phytoplankton communities (Baudinet et al. 1990). According to Redfield et al.'s (1963) theories, normal nutrient ratios for phytoplankton growth are 16:16:1 for Si:N:P, respectively. Any variation in these ratios results in nutrient limitation. In Grande-Entrée lagoon, initial N:P ratios were <16, indicating potential nitrogen limitation for phytoplankton production as previously mentioned by Souchu et al. (1991). In the same way, low Si:P ratios (<16) would mean that silicate was limiting in GEL. However, these potential limitations could originate from greater phosphate releases compared to nitrogen and silicate releases at the experimental sites. Phosphate release would be enhanced by the dissolution of ferric oxides and hydroxides in reduced conditions (Balzer et al. 1983, Mazouni et al. 1996). Indeed, low redox values were recorded in the first centimetre of sediment in August 2003 (–67 to –141 Eh [mV], depending on site; M. D. Callier unpubl. data), which indicates hypoxic conditions (Wildish et al. 1999). By increasing N and Si releases, mussel-biodeposit remineralisation in the 2 yr old mussel sites induced an increase in the Si:N and N:P ratios, which could reduce the potential nitrogen and silica limitation in the overlying water of this oligotrophic lagoon.

Summer variability

Sediment organic matter content is partly linked to temporal variations in sedimentation rates (decay of phytoplankton blooms, faeces and pseudofaeces sedimentation) and mussel drop-off. During the summer, the succession of phytoplankton blooms (Roy et al. 1991) and mass mortality events (Myrand & Gaudreault 1995) are well known in GEL; both phenomena can induce summer variations in organic matter inputs to the sediment. Nevertheless, no variation in organic matter content was observed in the first 2 cm of sediment in July, August and September 2003. This indicates that either organic matter accumulations in the surface layer (small-sized particles) were high enough to be measurable, or organic matter degradation was fast. In addition, the spatial variability (aggregated distribution) of mussel drop-offs could have induced variability in organic matter within treatments that led to non-significant temporal variations in sediment organic content at M2.

The POC:PON ratios measured in the first 2 cm of sediment decreased slightly from July and August to September. Organic matter would be more degraded in July and August than in September; this could be partly explained by variations in temperature. Indeed, in parallel, silica, ammonium and phosphate fluxes varied over the 3 mo at the 2 yr old mussel site. Maxi-

ammonium and phosphate releases in July and August would be linked to the high water temperatures in early summer. Indeed, high water temperature and organic matter enrichment from M2 could have stimulated bacterial proliferation (La Rosa et al. 2001, Lomstein et al. 2006) and favour organic matter mineralisation that induced greater nutrient releases. The decreasing water temperature in September would be responsible for decreasing metabolic activities and lower ammonium and phosphate releases. The highest ammonium fluxes (observed in August) could also result from the decomposition of large numbers of decaying mussels (Balzer et al. 1983, Lomstein et al. 2006) resulting from mass mortality events. In addition, lower oxygen concentration in the overlying water in August compared to September would have favoured ammonium and phosphate releases (Balzer et al. 1983, Mazouni et al. 1996, Lomstein et al. 2006). Dissolution of biogenic silica is also positively related to temperature (Lerat et al. 1990), which could explain the high silica releases observed in August. However, biogenic silica (BSi) dissolution is a long-term process (Baudinet et al. 1990), while ammonium and phosphate fluxes originate mainly from the rapid degradation of fresh organic material by macrofauna and bacteria. The slow dissolution of BSi accumulating in the sediment could explain the lower releases observed in July (although water temperature was high) compared with August. In contrast to silicate, ammonium and phosphate fluxes, no temporal variation was observed for nitrite and nitrate fluxes in the lagoon. Nitrite and nitrate regenerations were not correlated with temperature, in agreement with observations by Mazouni et al. (1996).

Oxygen consumption increased from July and August to September. Although water temperature and oxygen consumption are often positively correlated (Hargrave 1969, Pearson & Rosenberg 1978, Hatcher et al. 1994), oxygen consumption in this study increased whereas temperature decreased. Since oxygen consumption depends on the benthic community biomass (Mazouni et al. 1996) and abundance (Nickell et al. 2003), a parallel could be drawn between the increases in oxygen consumption and benthos biomass/abundance which originated from recruited organisms. Nevertheless, oxygen consumptions in GEL (from 133 mg O₂ m⁻² h⁻¹ in July and August to 408 mg O₂ m⁻² h⁻¹ in September) are high in comparison with previously reported values under mussel cultures in Canada (e.g. 48 mg m⁻² h⁻¹: Hatcher et al. 1994) and in France (e.g. 64 mg m⁻² h⁻¹: Baudinet et al. 1990). The GEL values correspond to oxygen demands measured under salmon cages in the Bay of Fundy (132 mg m⁻² h⁻¹: Hargrave et al. 1993) and in Loch Creran (579 mg m⁻² h⁻¹: Nickell et al. 2003). In contrast, the mean macrofauna

biomasses observed in GEL (1.56 in July, 1.75 in August, 4.75 g DW m⁻² in September) were very low and corresponded to values observed under oyster lines in the Thau lagoon during an anoxic event (Mazouni et al. 1996) or in areas impacted by mussel lines in South Africa (<5 g DW m⁻² in mussel site vs. 20 to 60 g DW m⁻² in control sites: Stenton-Dozey et al. 2001). Respiration by the low macrofaunal biomass in GEL cannot explain the high oxygen consumption rates recorded. Hargrave et al. (1993) related the high oxygen uptake under salmon cages with sediment sulfide accumulation and not with water temperature. In GEL, reduced sediment could promote sulfate reduction (Cranford et al. 2003) and lead to sulfide accumulation in surface sediments (Dahlbäck & Gunnarsson 1981). Indeed, high sulfide concentrations were observed in the first 1 cm of sediment in August 2003 (mean 1747 to 2407 μM l⁻¹, depending on site; M. D. Callier unpubl. data) and characterised hypoxic sediment (Wildish et al. 1999). Oxygen uptake should be driven by oxidation of these reduced metabolites. The production of hydrogen sulfide and the hypoxic conditions, which are toxic for macrofauna (Hargrave et al. 1993, Gray et al. 2002, Miron et al. 2005), would explain the low macrobenthic biomass and the occurrence of small-sized individuals. The increased oxygen demand would originate partly from the respiration of newly recruited organisms, and mainly from the oxidation of sulfides accumulated during the summer. Sulfide oxidation would be favoured by irrigation activities of small-sized organisms (Nickell et al. 2003).

CONCLUSIONS AND PERSPECTIVES

As expected, the 2 yr old suspended mussel lines had a greater influence on the benthic environment than the 1 yr old mussel lines in Grande-Entrée lagoon. The 2 yr old mussel lines induced local organic enrichment and increased benthic nutrient fluxes whereas the 1 yr old mussel lines did not. In the oligotrophic GEL, the benthic area beneath the 2 yr old mussel lines acts as source of nutrients (particularly of nitrogen and silica) in the summer, whose magnitude varies according to bottom-water and sediment characteristics. This source could induce summer variations in the nutrient standing stocks and ratios of overlying waters. In contrast, the 1 yr old mussel lines seemed not to influence nutrient cycling. The results of this study highlight the importance of dissociating the influence of differences in age of the culture organisms when modelling the carrying capacity of marine ecosystems comprised of bivalve cultures of various age classes.

Considering their low macrofaunal biomass, high oxygen demand (this study), low redox, high sulfide

concentration and the presence of opportunistic species (M. D. Callier unpubl. data) in their sediment, it is likely that the control sites were affected by organic load. Benthic metabolism in GEL could be mainly driven by microbial-mediated oxidation of organic matter and reduced inorganic metabolites. Reduced conditions in the sediment could be natural in GEL, since the sediment of some deep zones has already been described as 'black, soft, and stinking' in 1982, i.e. before aquaculture development (Poirier & Myrand 1982). In 1982, the maximum depth of GEL was 10 m (Poirier & Myrand 1982) compared to 7.2 m in 2003 (YSI probe data, this study). Mussel biodeposits could have accumulated in sediment of the deeper zones since 1985 and partly explain this silting. Continuous biodeposit accumulation could have progressively brought about degradation of the benthic environment in the deeper zones of the lagoon.

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